









Diet and bathymetric distribution of juvenile Lake Trout *Salvelinus namaycush* in Lake Huron

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Rehabilitation efforts for Lake Trout *Salvelinus namaycush* in Lake Huron have resulted in increased capture of young wild Lake Trout in annual bottom trawl surveys conducted by the U.S. Geological Survey. To better understand the ecology of juvenile (<400 mm) Lake Trout, we summarized the spatial distribution of their capture in bottom trawls at six ports in Lake Huron during October/November 2008–2017 and analyzed diets of wild ($n = 306$ of 337 total) and hatchery-origin ($n = 18$ of 30 total) fish captured. Lake Trout ranged in size from 27 to 399 mm, representing at least three age-classes, and 92% were wild origin. Most wild juvenile Lake Trout (83%) were captured at 46–64 m depths at the two northernmost ports, typically below the thermocline. *Mysis diluviana* was the most prevalent prey type, found in 75% of wild fish with non-empty stomachs, followed by two non-native species: Spiny Water Flea *Bythotrephes longimanus* (31%) and Round Goby *Neogobius melanostomus* (12%). Small Lake Trout (<185 mm) consumed invertebrates but transitioned to mostly fish-based diets by >185 mm (~age 2). The variety of taxa consumed by young Lake Trout increased with length. Further declines in *Mysis* populations due to increased predation pressure after the loss of *Diporeia* from the system may hinder the recovery of wild Lake Trout, and although they have been able to utilize invasive species as prey, impacts to Lake Trout growth remain unknown. Additional research on the habitat use and diets of wild juvenile Lake Trout may provide insight into the reasons behind the recent successful natural reproduction and recruitment of Lake Trout in Lake Huron.

Keywords: rearing habitat, restoration, *Mysis*

Introduction

Lake Trout, *Salvelinus namaycush*, were the top native predator in the Laurentian Great Lakes, but most populations severely declined by the 1950s due to overfishing and sea lamprey *Petromyzon marinus* parasitization. Despite widespread restoration and stocking efforts (Krueger et al., 2004),

there was little evidence of natural recruitment of Lake Trout outside of Lake Superior and limited areas in Lake Huron (Eshenroder et al., 1995; Reid et al., 2001). However, since about 2004, natural reproduction and survival of Lake Trout has been observed throughout Lake Huron (Riley et al., 2007; He et al., 2012). More than 40% of Lake Trout aged 4–7 years captured in gillnet surveys in

the main basin of Lake Huron from 2011–2013 were wild fish, compared to rates at/near zero for fish aged 12–18 (Johnson et al., 2015). The resurgence of wild-origin Lake Trout provides an opportunity to understand their early life history and identify possible impediments to recruitment.

Compared to adults, the ecology of juvenile Lake Trout is understudied (Martin and Olver, 1980), and less is known about their ecology during this period of increased wild Lake Trout recruitment and widespread ecosystem change in Lake Huron. Lake Huron has undergone drastic ecosystem-wide perturbations roughly coinciding with the resurgence of wild Lake Trout, including collapse of the demersal fish community (Riley et al., 2008) and the invasion of Ponto-Caspian species (dreissenid mussels and Round Goby *Neogobius melanostomus*) which shifted productivity from offshore waters and altered food webs across the lower Great Lakes (Hecky et al., 2004; Campbell et al., 2009; Higgins and Vander Zanden, 2010). Early observations of juvenile Lake Trout in the Great Lakes and elsewhere suggested that they may move to deeper water relatively soon after leaving spawning reefs (Royce, 1951; Martin, 1957; Rupp and DeRoche, 1960; Eschmeyer, 1964; DeRoche, 1969; Martin and Olver, 1980). More recent studies suggest that many juvenile Lake Trout in the Great Lakes and Lake Champlain tend to occupy waters between approximately 10–80 m deep (Elrod and Schneider 1987; Bronte et al., 1995; Marsden et al., 2018), but little work has been directed at characterizing juvenile Lake Trout habitat use. Wild juvenile Lake Trout diets have been reported to consist of invertebrates such as *Mysis diluviana* (formerly *Mysis relicta*; Audzijonytė and Väinölä, 2005), Chironomidae [Diptera], and zooplankton in the first year, with fish becoming important diet components as Lake Trout age, but recent studies of early-life stage Lake Trout diets are limited (Eschmeyer, 1956; Anderson and Smith, 1971; Hudson et al., 1995; Roseman et al., 2009; Ladago et al., 2016).

The U.S. Geological Survey (USGS) Great Lakes Science Center (GLSC) has conducted an autumn bottom trawl survey at six ports in the main basin of Lake Huron since the 1970s, and this survey has sampled wild juvenile Lake Trout in most years since widespread natural reproduction reoccurred. These data provide an

opportunity to conduct a large-scale (basin-wide), long-term (10-year) analysis of juvenile Lake Trout distribution and diet in the main basin of Lake Huron during a period of ecosystem change. Wild age-0 Lake Trout diet data from 2004–2006 were reported previously (Roseman et al., 2009), and our objective here is to describe the diets and geographic and bathymetric distribution of wild and hatchery-origin juvenile (age 0 to age 2+) Lake Trout captured in the USGS bottom trawl survey since 2008, post-fishery collapse.

Methodology

Field collection

Juvenile Lake Trout were captured by bottom trawls during annual demersal fish community surveys in October/November 2008–2017 (e.g. Riley et al., 2007, 2008). This survey monitors fish abundance using a 21-m headrope bottom trawl (4.76-mm mesh cod end) at fixed transects at up to twelve station depths (9–110 m) at five ports in Michigan (DeTour, Hammond Bay, Thunder Bay, Au Sable Point, and Harbor Beach) and one in Ontario (Goderich; Fig. 1). The depth range of transects varied among ports, but all ports had transects 27–73 m deep. Depths or ports sampled varied each year (Appendix Fig. 1). Single 10-min trawl tows were conducted at each transect during daylight. Further details of trawl sampling are provided by Riley et al. (2008, 2017). Only Lake Trout <400 mm were considered juveniles (Sitar and He, 2006) for the purposes of this study and we report the number collected per 10-minute trawl. Fish were designated as hatchery-origin based on the presence of fin clips. An electronic bathythermograph (SeaCAT Profiler CTD, SeaBird Scientific, Bellevue, WA) was used to measure lake bottom water temperatures after each trawl was completed. If temperature profile data (lake surface to lake bottom) were retained, we used the R package 'rLakeAnalyzer' (Winslow et al., 2019) to estimate the thermocline depth for each station and calculated the mean thermocline depth at each port/year.

Diet analysis

All juvenile Lake Trout were euthanized and stored in ethanol or frozen immediately upon capture. In the lab, we measured total length to

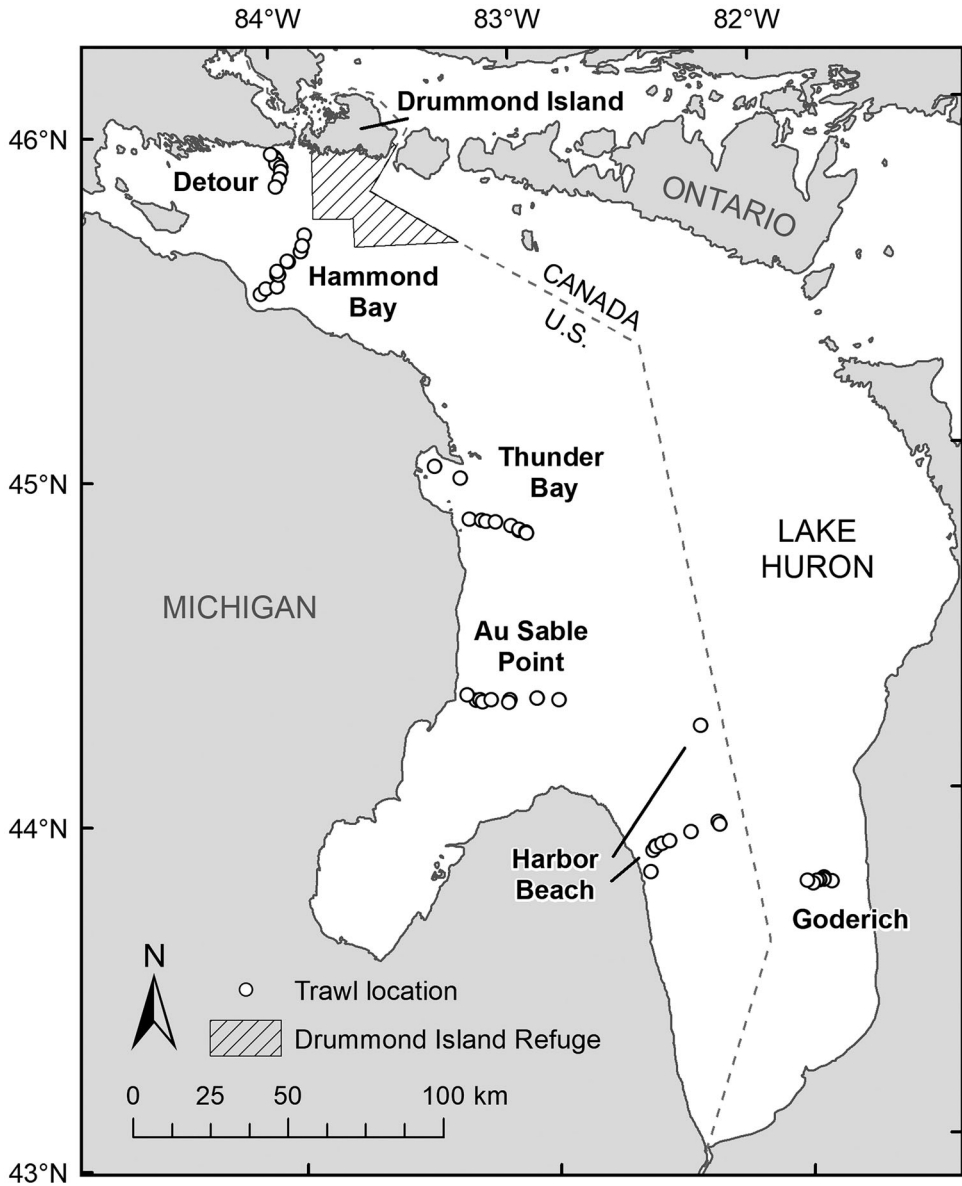


Figure 1. Locations of transects sampled by the USGS fall bottom trawl survey in Lake Huron, 2008–2017.

the nearest mm, stomachs were dissected under a stereoscopic microscope, and contents were stored in 95% ethanol. All prey items anterior to the pyloric caecum were identified to the lowest possible taxonomic unit and enumerated. We considered pairs of eye stalks for *Mysis diluviana* (hereafter *Mysis*), head capsules of Chironomidae pupae, and spines of Spiny Water Flea *Bythotrephes longimanus* (hereafter *Bythotrephes*) as evidence that one prey item was consumed.

Bythotrephes spines may be retained longer than other diet items in fish stomachs (resulting in inflated counts; Parker et al., 2001) but this effect is not always observed (Coulas et al., 1998). We elected to count spines in this study because few whole *Bythotrephes* were observed and removing them from analysis would have resulted in an underestimate of their consumption.

Fish prey were identified to species if possible. Depending on the state of digestion, we

measured the total length, standard length, or length of the vertebral column for each prey fish. We converted measurements of *Mysis* antennal scales to total body length and measured the caudal spine of *Bythotrephes* (Appendix Table 1). When many similarly sized prey were present (e.g. *Daphnia*) we measured a subset of the total. We created generalized additive models (GAMs) with the R package ‘mgcv’ (Wood, 2019) using lengths of measured prey and the total lengths of Lake Trout as a predictor to estimate lengths of unmeasured prey (either due to advanced digestion or due to large numbers present; Appendix Table 2). Dry mass of prey was then estimated using length-weight regressions and fish-species-specific estimates of dry weight:wet weight (Appendix Table 1). Seven unidentifiable diet items were removed from analysis (0.14% of items found).

Diet results are reported separately for three size-classes of Lake Trout: ‘Size 0’ (<100 mm, ~age 0), ‘Size 1’ (100–185 mm, ~age 1 year), and ‘Size 2’ (>185 mm, ~age 2 years and older). Size classes were determined by natural breaks in the length-frequency distributions of wild fish captured (Fig. 2) and reflect approximate ages. We calculated the following diet indices for each diet item type: mean number of prey items per gut (excluding zero values where prey items were not observed), percent frequency of occurrence (%FO), percent contribution by number (%N) and dry weight (%W; equations ‘NM1’ and ‘MM1’ in Ahlbeck et al., 2012), prey-specific contribution by number (%SN) and dry weight (%SW; Amundsen et al., 1996), and the Prey-Specific Index of Relative Importance (%PSIRI; Brown et al., 2012). Prey-specific metrics differ from the typical %N and %W calculations in that they exclude zero values/absences and are used to calculate the compound metric %PSIRI, which improves upon the traditional IRI metric by reducing bias toward diet items with higher %FO. We calculated these metrics per 1) Lake Trout size class, 2) size class by port, 3) size class by station depth, 4) size class by year, 5) per size class by origin (wild vs. hatchery, including only ports and years where both were present), and 6) all wild Lake Trout combined. Due to low sample sizes we did not identify statistical differences in diet compositions between any groupings. We identified percent diet overlap

between the three Lake Trout size classes using Schoener’s index of %N and %W (combining all fish and all cladocerans as single categories; Linton et al., 1981). Lastly, we calculated the 5th, 50th (median), and 95th percentile regressions between lengths of diet items and Lake Trout with quantile regression in the R package ‘quantreg’ (Koenker, 2019) sensu Gaeta et al. (2019) to identify predator/prey size trends using only log-transformed actual (non-predicted) measurements.

Results

Spatial distribution

We collected 367 juvenile Lake Trout during 2008–2017, including 337 wild-caught fish and 30 of hatchery-origin. Most (58%) wild juveniles were captured at DeTour, 32% at Hammond Bay, and 10% at the remaining sites (Fig. 2; Appendix Table 3). The majority (92%) of wild juvenile Lake Trout captured at all sites were taken from trawls conducted at 46–64 m with 83% of the wild juvenile Lake Trout captured from DeTour and Hammond Bay. Of 30 hatchery-origin juvenile Lake Trout, 21 were from DeTour, but at least one was captured per port. Most (63%) hatchery-origin Lake Trout were also captured at 46 and 55 m. The median wild fish catch was 22/year, but more than one-third of wild juveniles were captured in 2012 alone (Appendix Table 3). Length-frequencies (Fig. 2) indicated that we captured at least three distinguishable size/age classes of Lake Trout. Most wild fish captured were Size 0 (<100 mm; $n = 124$, 37% of the total) and Size 1 (100–185 mm; $n = 130$, 39%), while the majority of the few hatchery-origin fish captured were Size 2 (>185 mm; $n = 16$, 53%). All size classes of wild Lake Trout were most commonly captured at 46–64 m depths (Size 0 = 94%, Size 1 = 97%, Size 2 = 81%), but only Size 2 fish were found both at the shallowest (27 m; $N = 1$) and deepest depths (82–91 m, $N = 4$) occupied by Lake Trout. Size 2 wild Lake Trout were also the only size class found at Goderich.

Lake bottom temperatures varied by port, depth, and date, ranging from 4–16.5°C (Appendix Fig. 3). The mean bottom temperature at the depths where wild juvenile Lake Trout were

Table 1. Diets of wild juvenile Lake Trout of three size classes from six ports in the main basin of Lake Huron, 2008–2017. N = number of stomachs included for analysis per size class, %FO = percent frequency of occurrence, Count = the total number of diet items counted, %N = percent by number, %SN = species-specific percent by number, %W = percent by dry weight, %SW = species-specific percent by dry weight, PSIRI = Prey-Specific Index of Relative Importance (Brown et al., 2012), and MNG = mean number per gut (withholding stomachs where prey item was not consumed). Fish with empty stomachs (N = 12) or unidentifiable food remains (N = 5) were not included in this analysis.

Diet item	Size 0: <100 mm; N = 111						Size 1: 100-185 mm; N = 122						Size 2: >185 mm; N = 56							
	%FO (Count)	%N (%SN)	%W (%SW)	PSIRI	MNG	%FO (Count)	%N (%SN)	%W (%SW)	PSIRI	MNG	%FO (Count)	%N (%SN)	%W (%SW)	PSIRI	MNG	%FO (Count)	%N (%SN)	%W (%SW)	PSIRI	MNG
Invertebrates																				
Arachnida	0.9 (1)	0.9 (100.0)	0.9 (100.0)	0.9	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bosmina</i>	0.9 (1)	0.0 (0.8)	0.0 (0.1)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bythotrephes</i>	9.9 (13)	5.7 (57.8)	5.5 (55.5)	5.6	1.2	45.9 (791)	33.0 (71.8)	17.2 (37.6)	25.1	14.1	41.1 (668)	31.8 (77.5)	11.8 (28.6)	21.8	29					
Chironomidae	5.4 (10)	2.9 (54.2)	0.2 (3.0)	1.6	1.7	13.1 (46)	4.0 (30.8)	0.4 (3.3)	2.2	2.9	3.6 (2)	0.4 (11.0)	0.0 (0.0)	0.2	1					
pupae																				
<i>Daphnia</i>	6.3 (1 617)	6.2 (98.8)	2.7 (42.4)	4.4	231	0.8 (942)	0.8 (97.6)	0.7 (83.1)	0.7	942	1.8 (9)	1.8 (100.0)	1.8 (100.0)	1.8	9					
<i>Mysis</i>	91.9 (214)	84.2 (91.6)	90.8 (98.8)	87.5	2.1	77.0 (402)	55.4 (71.9)	70.1 (91.0)	62.8	4.3	37.5 (140)	15.6 (41.7)	17.8 (47.5)	16.7	6.7					
Fish																				
Alewife	0	0	0	0	0	0	0	0	0	0	5.4 (5)	3.6 (66.7)	2.9 (55.0)	3.3	1.7					
Bloater	0	0	0	0	0	0.8 (1)	0.1 (9.1)	0.5 (61.6)	0.3	1	3.6 (2)	1.0 (29.2)	2.1 (58.0)	1.6	1					
Deepwater	0	0	0	0	0	0	0	0	0	0	7.1 (7)	3.6 (50.0)	5.8 (80.7)	4.7	1.8					
Sculpin																				
Round Goby	0	0	0	0	0	4.9 (11)	3.3 (67.2)	3.4 (69.4)	3.4	1.8	51.8 (58)	30.6 (59.2)	43.9 (84.9)	37.3	2					
Rainbow Smelt	0	0	0	0	0	5.7 (9)	1.2 (21.6)	4.2 (72.7)	2.7	1.3	5.4 (3)	0.3 (6.0)	2.5 (46.9)	1.4	1					
Slimy Sculpin	0	0	0	0	0	0	0	0	0	0	1.8 (1)	0.6 (33.3)	0.6 (36.0)	0.6	1					
Unidentified	0	0	0	0	0	4.1 (9)	2.2 (53.0)	3.4 (84.1)	2.8	1.8	25.0 (21)	10.6 (42.5)	10.8 (43.1)	10.7	1.5					

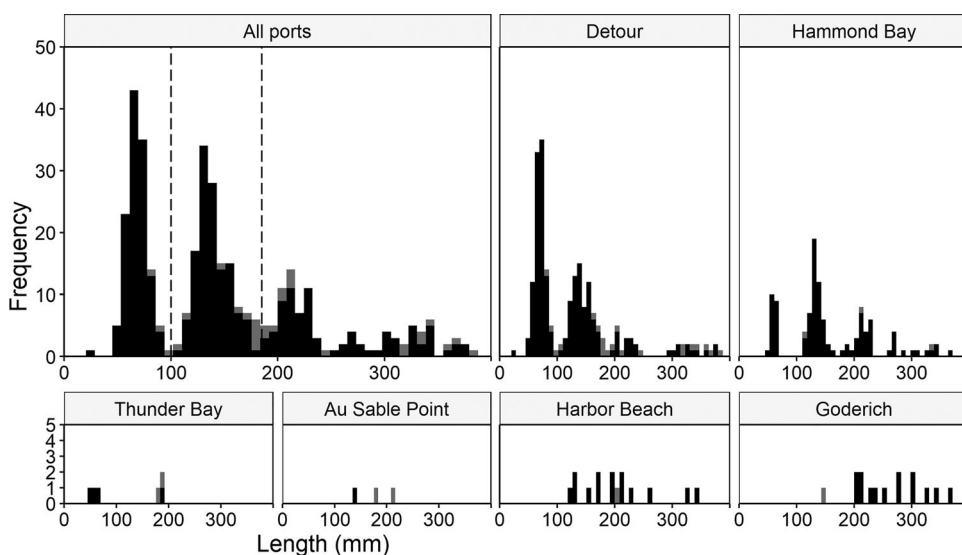


Figure 2. Length-frequency distributions of juvenile Lake Trout captured by the USGS fall bottom trawl survey at all ports combined and each individual port (from north to south) during 2008–2017. Dashed lines indicate cutoffs for each size class of Trout used in analysis: ‘Size 0’ (<100 mm; ~age 0), ‘Size 1’ (100–185 mm; ~age 1 year), and ‘Size 2’ (>185 mm; ~age 2 years and older). Black bars = wild fish, gray = hatchery-reared. Note the difference in scale on the y-axis for the southern ports.

most frequently captured (46–64 m) was 7.2 °C (± 2.1 s.d.). Shallower (<46 m) sites averaged 9.7 °C (± 2.5 s.d.), and deeper sites (>64 m) averaged 5.5 °C (± 1.2 s.d.). The mean lake bottom temperature across all ports weighted by the number of wild Lake Trout was 6.5 °C. Wild Lake Trout were only found at their shallowest depths (27 m) when bottom temperatures there were <8 °C (Appendix Fig. 4). Temperature profile data were available for 35 of 57 port/year combinations surveyed, representing port/years with 72% of the total wild Lake Trout. A thermocline was detected for 94% of port/years available. On average, the thermocline was 36.4 m deep (range: 18.5–71 m). Of wild Lake Trout available for comparison, 71% were found below the thermocline when one was present/detectable. Only 5% of wild Lake Trout available for comparison were captured when no thermocline was detected.

Diet analysis

We used 324 Lake Trout for diet analysis (306 wild fish and 18 hatchery-origin fish; Appendix Table 4). Of the 306 wild juvenile Lake Trout stomachs analyzed, 294 (96%) contained food remains, and 289 (94%) had identifiable food remains representing 13 prey types (including

‘unidentified fish’ as a category) that were retained for analysis. The most prevalent diet item across all size classes of wild juvenile Lake Trout was *Mysis* (75.1% FO, 63.3% PSIRI), followed by *Bythotrephes* (31.1% FO, 17% PSIRI), and Round Goby (12.1% FO, 8.6% PSIRI). Schoener’s indices (SI) showed a high degree of dietary overlap between Size 0 and 1 fish by %N (SI = 0.65) and %W (SI = 0.77). There were intermediate levels of overlap between Size 1 and 2 fish (%N SI = 0.56, %W SI = 0.42), and low levels of overlap between Size 0 and 2 fish (%N SI = 0.24, %W SI = 0.25). The number of prey types consumed increased with size class (from 6 types for Size 0 to 11 types for Size 2; Table 1). Median relative diet item length decreased with Lake Trout length for most taxa except for Round Goby, which remained at 25–29% of Lake Trout length (Appendix Fig. 5). While Lake Trout sometimes consumed prey up to 42% of their length, the median relative prey length was <10% after Lake Trout reached 80 mm.

Mysis was the most frequently consumed food item for Size 0 and Size 1 wild Lake Trout and had the highest %PSIRI (Table 1; Fig. 3). *Daphnia* had the highest count of any diet item in these two size classes, but they had low %FO. Size 1 wild Lake Trout frequently consumed *Bythotrephes* and Chironomidae pupae, but also

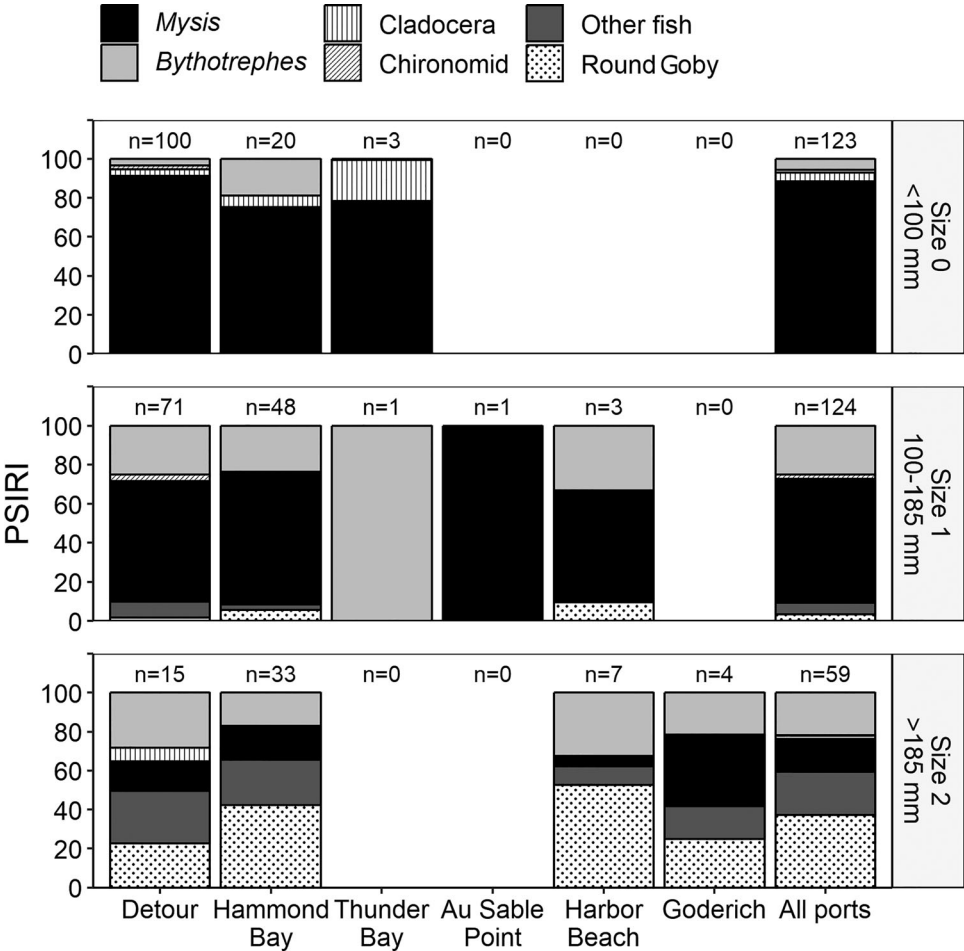


Figure 3. Prey-specific Index of Relative Importance (PSIRI) values of wild juvenile Lake Trout prey at each port and all ports combined for each Lake Trout size class. n = total number of diets.

several fish species including Round Goby, Rainbow Smelt *Osmerus mordax*, and Bloater *Coregonus hoyi* (each <6% FO). Prey fish consumed by Size 1 wild Lake Trout ranged from 17.0–59.0 mm (median: 35.9 mm). By Size 2, Round Goby was the most important food item consumed by wild Lake Trout by PSIRI (Table 1), followed by *Bythotrephes* and *Mysis*. Size 2 wild Lake Trout also consumed several other fish (each <8% FO), including Alewife *Alosa pseudoharengus*, Rainbow Smelt, Deepwater and Slimy Sculpins *Myoxocephalus thompsonii* and *Cottus cognatus*, and Bloater. Despite the large numbers of *Bythotrephes* and *Mysis* consumed by Size 2 Lake Trout, prey fish represented 98.5% of total biomass. Prey fish in Size 2 Lake Trout

diets were larger than those in Size 1, ranging from 29.7–119.8 mm (median: 63 mm).

PSIRIs per wild Lake Trout size class did not differ greatly between ports, although the variance in the sample sizes complicates comparison (Fig. 3). *Bythotrephes* and *Mysis* were consumed at most ports by most Lake Trout size classes, and Round Gobies were consumed by Size 2 fish at each port sampled. Low numbers of Chironomidae pupae, Alewife, Deepwater Sculpin, and Slimy Sculpin were only found in diets from DeTour and Hammond Bay, but the appearance of these prey may represent the large sample size at these locations rather than a spatial effect. Bloater were found in diets from DeTour and Goderich, and Rainbow Smelt were found in

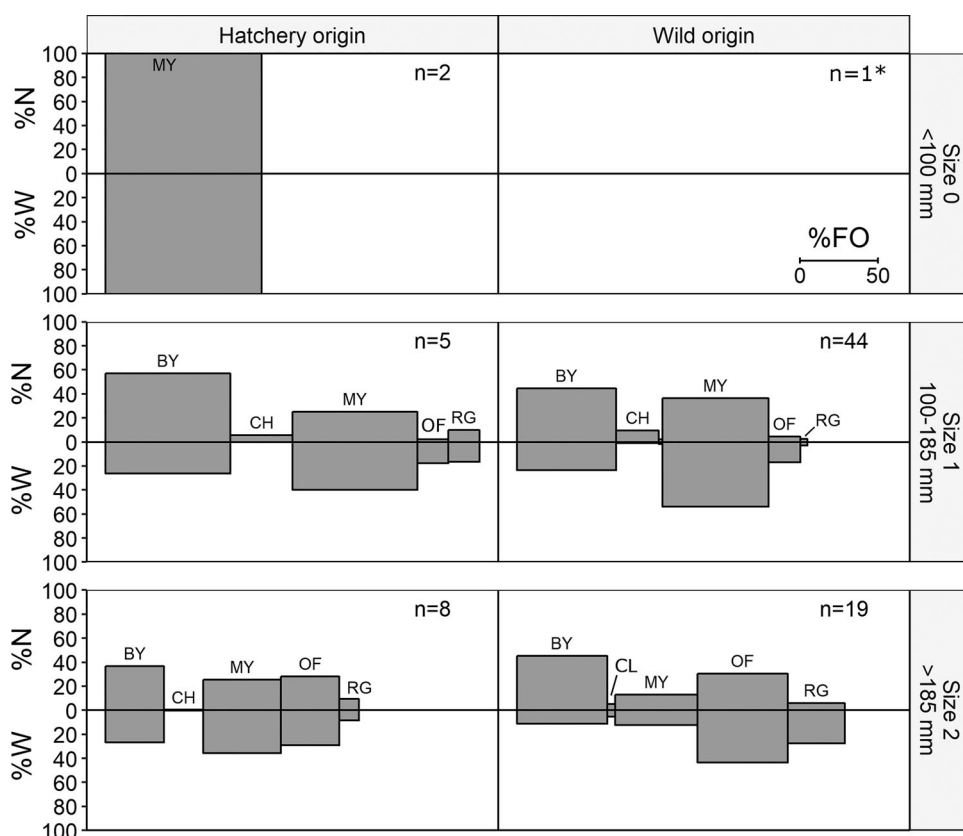


Figure 4. Diet metrics (%N = percent by number, %W = percent by weight, and %FO = frequency of occurrence) for prey of each size class of hatchery-origin and wild-caught juvenile Lake Trout from the same ports and years. The width of each box indicates the %FO (see scale in top right plot; sensu Brown et al., 2012). n = total number of diets, * = only one unidentifiable, unmeasurable diet item was found and could not be plotted. BY = *Bythotrephes*, CH = Chironomidae pupae, CL = Cladocera, MY = *Mysis*, RG = Round Goby, OF = Other fish.

diets from DeTour, Hammond Bay, and Harbor Beach. There were few quantifiable differences in diet composition between years or station depths for each size class (Appendix Figs. 6–7) except that cladocerans were found primarily (90%) in 2017 diets. As with differences between ports, identifying differences in diets between years and depths is complicated by highly disproportionate sample sizes.

The assessment of diet differences between hatchery (N = 18) and wild-origin fish (N = 60) yielded few fish for comparison and all fish were from DeTour, Hammond Bay, or Thunder Bay (Appendix Table 4). Three hatchery fish and one wild-origin fish had empty stomachs and were not included in the analysis. Overall, diets of hatchery-origin Lake Trout were similar to those of wild-caught Lake Trout (Fig. 4): *Mysis* the only prey type consumed

by Size 0 hatchery fish (100% PSIRI) and *Mysis* and *Bythotrephes* were the most important prey for Size 1 hatchery fish (41.6% and 32.4% PSIRI, respectively). Size 2 hatchery fish had a greater reliance on *Mysis* (30.6% PSIRI) than wild-caught fish from the same ports/years (12.7% PSIRI), which instead consumed more Round Goby (Wild PSIRI: 16.7% vs. Hatchery PSIRI: 9%) and other fish (Wild PSIRI: 37.1% vs. Hatchery PSIRI: 28.6%).

Discussion

Wild Lake Trout

Our results support previous observations that wild juvenile Lake Trout occupy habitats in relatively deep water in the Great Lakes and other lakes near the southern limit of their range. Lake

Trout fry abundance near spawning sites declines quickly post-emergence, suggesting that they move away to deeper areas where they have been observed at 15 m to >80 m (Royce, 1951; Eschmeyer, 1956; DeRoche, 1969; Martin and Olver, 1980; Bronte et al., 1995; Marsden et al., 2018). These deepwater sites likely provide thermal refugia; optimal temperatures for Lake Trout growth are 8–12 °C (Stewart et al., 1983; Christie and Regier, 1988) and most juvenile Lake Trout are found at <13 °C (Martin, 1957; Galligan, 1962; Elrod and Schneider, 1987; Bronte et al., 1995). There is evidence that Lake Trout in Canadian lakes congregate in areas with even cooler temperatures (<8 °C) if they are available (Mackenzie-Grieve and Post, 2006). Lake Trout in Lakes Superior and Great Bear Lake occupy nearshore habitats (Miller and Kennedy, 1948; Peck, 1982) where colder water temperatures do not necessitate movement to avoid unfavorable temperatures. We captured juvenile Lake Trout in bottom trawls, suggesting that they were occupying habitats near or at the lake bottom during the day at depths below the thermocline. The depth of the Lake Huron thermocline is usually 20–30 m, but changes over the season and may deepen in the fall (Bartone and Schelske, 1982; Gorham and Boyce, 1989). Our survey is conducted in late fall when the thermocline is becoming unstable and breaking down (e.g. Sundaram and Rehm, 1973), but bottom temperatures in the summer would have probably been in the lower range of observed temperatures (4.4–13.6 °C), providing thermal refugia.

The depths at which we observed most juvenile Lake Trout may also be related to the density of *Mysis*, their most important prey item (Eschmeyer, 1956; Anderson and Smith, 1971; Martin and Olver, 1980; Hudson et al., 1995; Roseman et al., 2009). *Mysis* remain along the lake bottom during the day, making them vulnerable to predation by benthic juvenile Lake Trout. *Mysis* exhibit diel vertical migrations (DVM) up to >100 m at night (Beeton, 1960; Ahrenstorff et al., 2011), but some larger mysids may forgo DVM (O'Malley et al., 2017). *Mysis* densities increase with depths >25 m (Carpenter et al., 1974; Jude et al., 2018). In Lake Huron, summer *Mysis* densities are highly variable at the depths at which Lake Trout were common, but some of the highest densities found (>100/m²) have

occurred at ~60 m (Jude et al., 2018). Juvenile Lake Trout may undergo seasonal movements, moving deeper in fall (Eschmeyer, 1956; Elrod and Schneider, 1987; Bronte et al., 1995), possibly to access greater concentrations of *Mysis* or benthic prey such as Round Goby which can move offshore down to 100 m depth (Charlebois et al., 2001; Johnson et al., 2005; Walsh et al., 2007; Pennuto et al., 2010, 2012). Seasonal sampling of our Lake Huron sites would be necessary to determine how the depth distribution of juvenile Lake Trout changes seasonally.

Over 90% of wild juvenile Lake Trout were captured at DeTour and Hammond Bay, suggesting that they originated from spawning habitats located in the northern main basin of Lake Huron. There are several historic Lake Trout spawning locations in this area (Goodyear et al., 1982), and recent research has identified current spawning areas near Drummond Island (Fig. 1) that are associated with specific glacial features (Riley et al., 2014, 2017a; Binder et al., 2016, 2017). It is surprising that so few juvenile Lake Trout were captured near Thunder Bay, as there is an active Lake Trout spawning population there (Marsden et al., 2016; Binder et al., 2017) and naturally produced juvenile Lake Trout have been occasionally captured near there since the 1980s (Nester and Poe, 1984; Johnson and VanAmberg, 1995). Spawning aggregations of adult Lake Trout and Lake Trout fry are common on or near artificial spawning reefs constructed in Thunder Bay (Marsden et al., 2016), and it is possible that juvenile Lake Trout remain near these habitats and outside the range of our transects.

We confirmed the continued importance of *Mysis* to juvenile Lake Trout in Lake Huron (Roseman et al., 2009). *Mysis* even remained important to Size 2 fish despite their ability to capture prey fish. The frequencies of *Mysis* with estimated lengths >10 mm consumed by wild juvenile Lake Trout in our study were often greater than those observed in Lake Huron *Mysis* surveys (Carpenter et al., 1974; Jude et al., 2018; Appendix Fig. 8), which may indicate selection for larger individuals. *Mysis* > 20 mm, which are usually rare or absent in the Great Lakes (Sell, 1982), composed more than 10% of the *Mysis* measured in our diets. However, size-frequency relationships of *Mysis* vary widely by season,

habitat, and behavior, and comparisons between studies are complicated by varying measures of body length (Grossnickle and Beeton, 1979; Sell, 1982; O'Malley et al., 2017; Jude et al., 2018). Invasive Round Gobies were the most important prey fish we observed and have been a major component of adult Lake Trout diets in Lake Huron (Roseman et al., 2014) and elsewhere (Rush et al., 2012; Luo et al., 2019) since at least 2009, but their prevalence in the diets of juvenile Lake Trout is less well-established. The current abundance of Round Gobies in the Great Lakes is unknown, as they are cryptic and poorly sampled by bottom trawls, but they are widespread throughout the benthic habitats of Lake Huron (Riley et al., 2017b). Round Goby appear to provide a valuable fall food source and were most common at the same depth strata as juvenile Lake Trout.

We observed ontogenetic dietary changes in juvenile Lake Trout and little dietary overlap between Size 0 and 2 fish. However, Size 2 fish still consumed many prey with relative lengths <10%. While diet items with smaller relative lengths (10–20%) are most common in diets of other Great Lakes fishes (Gaeta et al., 2018), the importance of *Bythotrephes* in juvenile Lake Trout diets was somewhat surprising. *Bythotrephes* was not previously an important component of juvenile Lake Trout diets in Lake Huron (Roseman et al., 2009) or Lake Superior (Hudson et al., 1995), but more recent surveys of Lake Superior Lake Trout found that *Bythotrephes* dominated fall diets by number (Gamble et al., 2011). The predatory cladoceran *Bythotrephes* invaded Lake Huron in the 1980s and is responsible for declines in zooplankton densities (Barbiero and Tuchman, 2004; Bunnell et al., 2011) and may now be a potentially important component of food webs in Lake Huron. Consumption of non-predatory zooplankton by Lake Trout after the fry stage (Ladago et al., 2016) may be limited and opportunistic (Roseman et al., 2009; current study).

Prevalent observations of taxa that undertake DVM in stomachs (*Bythotrephes*, *Mysis*, and *Daphnia*; Beeton, 1960; Loose and Dawidowicz, 1994) suggest Lake Trout may also undertake DVM. However, we have no direct evidence of this other than the large numbers of these taxa consumed. Although *Bythotrephes* densities are

highest at offshore, deeper sites in Lake Huron, they are usually restricted to the top 30 m of the water column at depths where we sampled most juvenile Lake Trout (Bunnell et al., 2012; Keeler et al., 2015; Armenio et al., 2017). While Lake Trout fry are more benthic (Stauffer, 1978), adult Siscowet Lake Trout in Lake Superior regularly exhibit DVM following pelagic prey (Hrabik et al., 2006; Jensen et al., 2006; Gorman et al., 2012). Adult Lake Trout can also abandon their thermal optima, making forays into the warmer epilimnion to feed (Sellers et al., 1998). However, Lake Trout in Lake Huron are rarely found in GLSC midwater trawls (O'Brien et al., 2017), and only three juveniles (<400 m) have been observed in these surveys since they began in 2004 (U.S. Geological Survey, Great Lakes Science Center, 2019). In addition, only one terrestrial invertebrate (a spider) was found in our diet study, in contrast to higher rates observed in larger Lake Trout and other Lake Huron salmonids (Roseman et al., 2014). Therefore, it is also possible that the fish in our study remained near the bottom, consuming bottom-dwelling *Mysis* and dead, sinking *Bythotrephes* (Evans, 1988). *Bythotrephes* has a sinking rate of ~40 m/hour (Evans, 1988) and could explain why they are prevalent in the diets of benthic Round Gobies and Deepwater Sculpin, some found up to 97 m deep (Evans, 1988; O'Brien et al., 2009; Keeler et al., 2015). We are aware of no direct observations of the foraging behavior of juvenile Lake Trout at deep habitats, and we consider this an understudied aspect of juvenile Lake Trout ecology.

The juvenile Lake Trout sampled here had a low proportion of empty stomachs compared to the average rate for such studies (Arrington et al., 2002; Vinson and Angradi, 2011; Roseman et al., 2014; Luo et al., 2019). This could indicate that these fish occupy habitats that support prey densities that allow frequent foraging opportunities. However, the proportion of empty stomachs we observed may be biased by inclusion of *Bythotrephes* spines in our diet analysis, removing them increases the percent empty stomachs from 4 to 15%. It is tempting to suggest that perhaps juvenile Lake Trout only consumed *Bythotrephes*, a prey item that is energetically dense but difficult to handle and digest (Stetter et al., 2005), when other more desirable prey

items were not available, but 70% of wild Lake Trout diets with *Bythotrephes* contained at least one other type of prey. In laboratory experiments, Lake Trout <100 mm actively avoid *Bythotrephes* and find them distasteful (Barnhisel and Kerfoot, 2004), but larger size classes appear to consume them willingly (Gamble et al., 2011; current study). Whether spines are retained in juvenile Lake Trout (leading to an overestimate of consumption rates) is unknown, and spine retention rates in other fish vary (Coulas et al., 1998; Parker et al., 2001). We elected to include counts of *Bythotrephes* in our diet analysis because we did not want to discount their prevalence in the diets, and because other diet studies have shown that *Bythotrephes* has the potential to increase (Mills et al., 1992) or at least maintain (Coulas et al., 1998) fish condition. However, Stetter et al. (2005) found that if formed, spine boli represent ‘empty calories’ that limited fish growth. We did not assess rates of *Bythotrephes* spine retention in juvenile Lake Trout, but this information would improve and inform future diet assessments and bioenergetics studies.

Hatchery-origin Lake Trout

The transects sampled here have been trawled annually since the 1970s, but few hatchery-reared juvenile Lake Trout have been captured by the survey, suggesting low hatchery Lake Trout survival or that these fish do not use the same habitats as the wild fish we captured. Hatchery-reared fish are released at larger sizes than wild fry but would be similar in size to the Size 1 fish (>100 mm) sampled here. Little is known about the habitat use of hatchery-reared juvenile Lake Trout in Lake Huron, but we captured most near areas where wild juveniles were found (DeTour and Hammond Bay). Diet composition did not appear to differ between wild and hatchery origin juvenile Lake Trout, although our sample sizes for comparison were low. Interestingly, 20% of the hatchery fish we studied had empty stomachs vs. ~2% (N = 1) empty stomachs from the wild Lake Trout from the same ports and years. Hatchery-reared salmonids tend to exhibit lower survival and growth rates than their wild counterparts, and just-released fish may undergo an acclimation period (from a week to several months) during which they learn to recognize and

capture prey items (O’Grady, 1983; Johnsen and Ugedal, 1986; McDermid et al., 2010). There is also evidence that hatchery-origin Lake Trout in Lake Superior may not be as adept at capturing prey fish as wild-caught fish even at larger sizes (Gamble et al., 2011). Whether hatchery-reared Lake Trout differ significantly from wild-caught fish would require targeted surveys to acquire numbers of fish not represented by our opportunistic study.

Summary and conclusions

Our observations suggest that wild juvenile Lake Trout occupy relatively deep benthic habitats below the thermocline in the main basin of Lake Huron through at least age 2. Benthic habitats 40–70 m deep may be important for the restoration of Lake Trout populations in the Great Lakes, but the ecology of Lake Trout in these habitats has been poorly studied due to their depth and relative inaccessibility. The depths that wild Lake Trout frequent may point to recent food web alterations; in Lake Ontario, age 2 Lake Trout transitioned from 30–40 m depths to >50 m post-dreissenid mussel invasion (O’Gorman et al., 2000) and in Lake Huron adult Lake Trout moved to colder (and possibly deeper) areas post-food-web collapse (Bergstedt et al., 2012), and it was hypothesized in both cases that Lake Trout moved deeper to follow the increasing relative abundance of benthic prey offshore. Monitoring depth distributions of wild Lake Trout may elucidate changes in the available prey base.

Mysis still provide an important early food for Lake Trout, but densities of *Mysis* in Lake Huron are lower than the other Great Lakes (except Lake Erie) and have decreased five-fold since the 1960s–1990s (Jude et al., 2018). Despite this initial decline, populations in Lake Huron did not fluctuate significantly from 2006–2016 (Jude et al., 2018), and our results suggest that they remain common enough in Lake Huron to be major components of the diets of Lake Trout and other species such as Deepwater Sculpin (e.g. Thompson et al., 2017). Further declines in *Mysis* populations due to increased predation pressure after the loss of *Diporeia* from the system may hinder the recovery of wild Lake Trout. Juvenile Lake Trout in our study relied heavily on two

non-native species—*Bythotrephes* and Round Goby—which may have implications for growth, survival, or distribution of juvenile Lake Trout. Additional research on the habitat use and diets of wild juvenile Lake Trout in may provide insight into the reasons behind the recent successful natural reproduction and recruitment of Lake Trout in Lake Huron (e.g. Riley et al., 2007; He et al., 2012) and may aid in the restoration of Lake Trout populations throughout the Great Lakes and elsewhere.

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Author contributions

E. Roseman was responsible for study conception and design. E. Roseman and S. Riley supervised and participated in fieldwork, and S. Farha, T. Tucker, and D. Bowser participated in fieldwork. E. Roseman, S. Riley, and T. Tucker wrote the manuscript, T. Tucker performed statistical analyses and created figures and tables, S. Farha assisted with data preparation, and S. Jackson and D. Bowser performed stomach content analyses.

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Supplementary material

Supplementary material for this article can be viewed on-line at www.taylorandfrancis.com

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