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ARTICLE

Shifting Diets of Lake Trout in Northeastern Lake Michigan

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Abstract
Prey fish communities in Lake Michigan have been steadily changing, characterized by declines in both the quantity and quality of Alewife *Alosa pseudoharengus*. To evaluate concurrent changes in the diet of Lake Trout *Salvelinus namaycush* in northeastern Lake Michigan, we analyzed stomach contents of Lake Trout caught during gill-net surveys and fishing tournaments from May through October 2016. We then compared the composition, on a wet-weight basis, of 2016 diets with those previously described in a recent survey conducted in 2011. Overall, we found that Lake Trout diets in 2016 consisted mostly (94% by wet weight) of Alewives and Round Goby *Neogobius melanostomus*. Averaging across May through October, 61% of the Lake Trout diet consisted of Alewives. A clear seasonal shift was apparent: the diet was dominated by Round Goby (67%) during May–June, whereas Alewives dominated the diet (76%) during July–October. Seasonal dominance of Round Goby in spring Lake Trout diets has not been previously observed in northeastern Lake Michigan as Round Goby represented only 21% of the Lake Trout diet in spring of 2011. Diet composition of Lake Trout caught in gill nets did not significantly differ from diet composition of Lake Trout caught by anglers in either the May–June period or the July–October period. Although Lake Trout showed increased diet flexibility in 2016 compared with 2011, Alewives were still the predominant diet component during 2016, despite reduced Alewife biomass throughout Lake Michigan. Nonetheless, this further evidence of diet plasticity suggests that Lake Trout may be resilient to ongoing and future forage base changes.

Lake Trout *Salvelinus namaycush* was the native apex predator of the Lake Michigan food web and supported a large commercial fishery until populations were extirpated by the 1950s (Eschmeyer 1957; Wells and McLain 1973; Holey et al. 1995). These declines were attributed to overfishing and predation from invasive Sea Lamprey *Petromyzon marinus* (Eschmeyer 1957; Wells and McLain 1973; Hansen 1999). Extirpation of the piscivorous Lake Trout triggered a proliferation of invasive Alewife *Alosa pseudoharengus* that reached peak abundance in 1966

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(Brown 1972; Madenjian et al. 2005; Collingsworth et al. 2014). Rapid increases in Alewife biomass eventually led to massive die-offs of the Alewife population, creating a serious nuisance and health concern to people who used the lake as a water supply or for recreation (Brown 1972; Hatch et al. 1981). A large-scale salmonine stocking program was launched in 1965 to control the nuisance Alewife population, establish an economically valuable recreational fishery, and rehabilitate the Lake Trout population (Tody and Tanner 1966; Holey et al. 1995; Madenjian et al. 2002). In addition to Lake Trout, nonnative Chinook Salmon *Oncorhynchus tshawytscha*, Coho Salmon *O. kisutch*, Rainbow Trout *O. mykiss*, and Brown Trout *Salmo trutta* were also stocked into Lake Michigan (Tody and Tanner 1966; Eshenroder et al. 1995). This stocking program, in conjunction with concurrent Sea Lamprey and harvest control efforts (Smith and Tibbles 1980; Bronte et al. 2008), has largely succeeded in increasing Lake Trout populations throughout Lake Michigan—albeit not to pre-1950 levels—and establishing an important recreational fishery for both Lake Trout and nonnative salmonine predators (Madenjian et al. 2002; Tsehaye et al. 2014a, 2014b; Clark et al. 2017). Though the prey fish community in the lake has undergone drastic changes over the last 50 years (Madenjian et al. 2015, 2018), this stocking program remains an important component of lake management.

Alewife populations have been successfully controlled throughout Lake Michigan, but densities are now so low that managers are concerned about forage supply for the salmonine sport fishery. Alewives have long been the dominant prey for salmonine predators in Lake Michigan (Jude et al. 1987; Madenjian et al. 1998), but the biomass of adult Alewives was greatly reduced by 1983 and reached historic lows in the 2010s (Madenjian et al. 2002, 2018; Collingsworth et al. 2014). As a result, fishery managers were concerned that salmonine consumption of Alewives could not be sustained (Stewart and Ibarra 1991), especially after bacterial kidney disease caused mortality in the Chinook Salmon population from 1986 through the early 2000s (Holey et al. 1998; Benjamin and Bence 2003; Tsehaye et al. 2014b). Managers began to estimate the annual consumption of Alewives by salmonines in order to adjust salmonine stocking rates to avoid creating a predator–prey imbalance (Stewart et al. 1981; Stewart and Ibarra 1991; Tsehaye et al. 2014a). Chinook Salmon has been the primary consumer of Alewives in Lake Michigan since 1975 (Tsehaye et al. 2014a; Madenjian et al. 2015). Chinook Salmon stocking rates were first reduced in the 1980s (Hansen et al. 1993), and additional cuts were made during the 1990s, 2000s, and 2010s (Lake Michigan Committee 2014; Tsehaye et al. 2014b). As a result, the total consumption of Alewives in Lake Michigan has recently trended downward, but other predators now contribute a greater proportion to the total consumption. In light of record low densities of Alewives combined with increases in abundances of Lake Trout, Rainbow Trout, and Coho Salmon since 2010 (Madenjian et al. 2017, 2018; Kao et al. 2018), concern regarding the impact of predation on residual Alewives across Lake Michigan has increasingly focused on predators other than Chinook Salmon, as have discussions on further salmonine stocking reductions.

Effective management of the Lake Michigan ecosystem requires a balance between maintaining nonnative prey species at low levels, while sustaining the popular and economically important recreational fishery and the effort to rehabilitate native Lake Trout populations (Dettmers et al. 2012; Tsehaye et al. 2014b). Continued stocking of Lake Trout is needed in certain regions, such as the Northern Refuge in northeastern Lake Michigan, due to a lack of detectable natural reproduction (Bronte et al. 2008; Madenjian et al. 2017). Currently, stocking rates and salmonine fisheries management in Lake Michigan are guided by the multispecies predator–prey model developed by Tsehaye et al. (2014a) (Lake Michigan Committee 2014). This simulation model combines bioenergetics models with statistical catch-at-age models for salmonines to estimate their annual consumption of Alewives. The current simulation model does not include Round Goby *Neogobius melanostomus* as a potential diet item despite evidence of its increased importance as forage for some salmonines (e.g., Kornis et al. 2012; Roseman et al. 2014; Happel et al. 2018), prompting the need for updated diet information. Additionally, the Alewife population size is also tracked using a statistical age-structured population model, which assesses the trade-off between predatory demand and prey productivity. The model is updated every year using the latest data, and if the predator-to-prey biomass ratio is considered to be too high (>0.10 based on the value for Lake Huron immediately prior to the Alewife collapse in that lake), fishery managers would consider a stocking reduction of salmonines to maintain a balanced pelagic community.

Despite the importance of the Tsehaye et al. (2014a) predator–prey model to fishery management, the most recent published information on Lake Trout diet in Lake Michigan is from 2011 (Happel et al. 2018). Moreover, the seasonal diet schedule currently used as a model input has not been updated in over 20 years (Madenjian et al. 1998). Seasonal diet schedule refers to a table of diet composition across seasons. Although diet studies have been conducted on Lake Trout since 1994–1995, all have only focused on a specific time of year. An updated seasonal schedule is needed for managers to properly manage the salmonine fishery. With decreasing abundance of Alewives, there is growing uncertainty in the lakewide predatory demand on Alewives and other prey by the combined consumption of all predators. Rainbow Smelt *Osmerus mordax*, Bloater *Coregonus hoyi*, and Slimy Sculpin *Cottus cognatus* have also declined in abundance since the 1980s (Madenjian et al. 2018), while Round Goby biomass rapidly increased during 2000–2010 (Madenjian et al. 2018). Updated information on Lake Trout diets will allow for more realistic predator–prey model results and better-informed management of Lake Michigan fisheries.

Alewives have been the predominant prey of salmonines in Lake Michigan since the 1970s (Stewart and Ibarra 1991; Madenjian et al. 1998; Warner et al. 2008; Happel et al. 2018), representing over 80% of the diet, on a wet-weight basis, of Lake Trout ≥ 400 mm in total length (TL) during the 1970s (Stewart et al. 1983; Jude et al. 1987). The last published study of Lake Trout diet in Lake Michigan conducted throughout the growing season (April through November) was during 1994–1995 (Madenjian et al. 1998). Although seasonal consumption patterns varied widely between locations, Alewives represented between 55% and 60% of the diet of Lake Trout in the 400–599 mm TL size range and roughly 65% of the diet of Lake Trout ≥ 600 mm TL when averaged over all seasons and locations. More recent diet studies have been conducted in Lake Michigan but have only focused on spring (April–June) sampling (Jacobs et al. 2010; Happel et al. 2018). The most recent study in northeastern Lake Michigan showed Alewives to be the primary contributor to Lake Trout diets in 2011, with Round Goby comprising roughly one quarter of their diet (Happel et al. 2018). In Lake Huron, Lake Trout shifted their diet to the more abundant Rainbow Smelt and Round Goby after the Alewife population completely collapsed in 2003 (O'Gorman et al. 2012; Roseman et al. 2014). In Lake Michigan, adult Lake Trout have previously been shown to select large Alewives, even when other potential prey species are more abundant (Eck and Brown 1985; Eck and Wells 1986; Madenjian et al. 1998), although these studies were conducted prior to the Round Goby population becoming well established in the lake. It is unknown whether the continued decline in Alewife abundance in Lake Michigan has resulted in Lake Trout having a greater reliance on other forage since 2011.

The primary objective of our study was to develop an updated diet schedule for Lake Trout from northeastern Lake Michigan that could be used as a bellwether of lakewide diet changes since 2011. A secondary objective was to characterize diets seasonally. We analyzed stomach contents of Lake Trout caught in northeastern Lake Michigan from May through October 2016. In addition, we compared our findings for May 2016 with those of Happel et al. (2018) for Lake Trout caught in northeastern Lake Michigan during spring 2011. Considering results from previous studies, we hypothesized that Alewives would remain the dominant prey of Lake Trout from Lake Michigan in 2016 but that Round Goby would be consumed in greater quantities in 2016 compared with 2011.

METHODS

Field sampling.— Lake Trout were collected throughout northeastern Lake Michigan from May through October 2016 using two sampling methods (Table 1). Fish collections in May and October were part of annual bottom-set gill-net surveys conducted by the U.S. Geological Survey Great Lakes Science Center within and near the Northern Refuge. In May, fish were captured at Fisherman's Island, Boulder Reef, North Fox Island, and Irishman's Ground (Figure 1). At each site, six sets of two gill nets joined lengthwise were deployed. Each gill net consisted of eight 1.8- × 30.5-m panels, with mesh sizes ranging from 6.4 to 15.3 cm stretched measure in 1.3-cm increments, according to the Lake Michigan lakewide assessment plan protocol (Schneeberger et al. 1998). At each site, two gill-net sets were within each of the following three depth strata: 15–30 m, 31–45 m, and 46–60 m, based on the stratified random sampling protocol of the Lake Michigan lakewide assessment plan. The October survey, targeting spawning aggregations, was conducted at Boulder Reef, North Fox Island, and Gull Island Reef (Figure 1). At each site, two sets of two gill nets joined lengthwise were deployed, with each gill net consisting of four 30.5-m panels with mesh sizes of 11.4, 12.7, 14.0, and 15.2 cm stretched measure (Madenjian and Desorcie 2010). These gill nets were typically set in shallow areas on or near the top of each reef to target spawning fish, and depths ranged from 6.6 to 13.4 m. All set gill nets were deployed for approximately 24 h prior to retrieval. Captured fish were removed from the net, weighed to the nearest gram, and measured to the nearest millimeter for TL. The gastrointestinal tract from the esophagus to the anus was removed and frozen for later analysis. All Lake Trout used in this study were handled in accordance with guidelines of the American Fisheries Society (2004).

Fish collected during June–August were caught by anglers at fishing tournaments throughout northeastern Lake Michigan. June and August tournaments were located in both Charlevoix and Frankfort, while the July tournament took place in Manistique. At all tournaments, U.S. Fish and Wildlife Service technicians from the Great Lakes mass-marking program collected gastrointestinal tracts of Lake Trout from anglers returning from fishing trips, in addition to determining TL and weight for each Lake Trout (Bronte et al. 2012).

Stomach content analysis.— We followed the protocol by Elliott et al. (1996) in our analysis of Lake Trout stomach contents. In the laboratory, each stomach was thawed and dissected, then all prey items were visually identified to species when possible, using residual bony structures when necessary (Elliott et al. 1996; Traynor et al. 2010). All prey items, regardless of stage of digestion, were measured to the nearest millimeter (standard length [SL] and TL, when possible) and weighed to the nearest 0.1 g

TABLE 1. Sampling method used, number of Lake Trout sampled (N), mean ± SE Lake Trout total length, number of stomachs containing food, percent of nonempty stomachs, and average number of prey items in nonempty stomachs by month for Lake Trout caught in northeastern Lake Michigan during 2016. For the May–June, July–October, and May–October groupings, gill-net-caught and angler-caught Lake Trout were pooled.

Month	Sampling method	N	Mean ± SE total length (mm)	Nonempty stomachs	Percent nonempty	Average number of prey
May	Gill net	221	607 ± 60	210	95	11.8
Jun	Angler	59	632 ± 78	30	51	3.9
Jul	Angler	19	613 ± 36	16	84	2.4
Aug	Angler	66	627 ± 98	30	45	2.5
Oct	Gill net	131	667 ± 42	23	18	1.5
May–Jun		280	612 ± 65	240	86	10.8
Jul–Oct		216	650 ± 69	69	28	2.2
May–Oct		496	629 ± 69	309	62	8.9

(wet weight). Unidentifiable prey items were also weighed to the nearest 0.1 g. For Alewives and Round Goby, completely intact individuals were used to develop linear regressions to convert SL to TL. The calculated linear regressions were as follows:

$$\text{TL} = 1.23 \times \text{SL} - 2.4\,(N = 320; r^2 = 0.976) \text{ for Alewife;}$$

$$\text{TL} = 1.21 \times \text{SL} - 2.6\,(N = 356; r^2 = 0.980) \text{ for Round Goby.}$$

Not enough intact individuals were found during our study for all other prey fish, so published regressions (Van Oosten and Deason 1938; Elliott et al. 1996; Jacobs et al. 2010) were used to estimate TL from partially digested prey items. Total lengths were then used to reconstruct the original wet weight of each prey item using published length–weight regression equations (Piccolo et al. 1993; Elliott et al. 1996; Dietrich et al. 2006). Reconstructed prey weights were used for all statistical analyses involving prey biomass.

We generated TL frequency distributions for both Alewives and Round Goby found in the Lake Trout stomachs, using actual and reconstructed TLs of individual prey items. For each prey fish species, a TL frequency distribution was generated for both the May–June period and the July–October period. All TL frequency distributions were constructed using 10-mm TL bins.

Invertebrate prey were identified to taxonomic order, counted, and weighed en masse to the nearest 0.1 g. Adult dipterans and terrestrial adult lepidopterans comprised less than 0.1% of the total prey weight and were considered in trace amounts and removed from further analysis. Dreissenid mussels were occasionally found in stomachs but were likely either consumed incidentally or were assumed to be prey of other fish, particularly Round Goby (Barton et al. 2005), and omitted from further analysis. Only identifiable prey items were included in the statistical analyses of the diet data.

Statistical analyses.— To summarize Lake Trout stomach content data, total prey biomass and total number of prey in a stomach were summed across all stomachs pooled together within each sampling month. Then, for each month, per capita total prey biomass and per capita frequency of occurrence of prey were calculated by dividing the sum of total prey biomass and the sum of total number of prey, respectively, by the number of Lake Trout with a nonempty stomach sampled during the month. For each combination of prey species and month, we also calculated per capita prey biomass by dividing the total amount of biomass of the prey type consumed by all of the Lake Trout sampled during the month by the corresponding number of Lake Trout with a nonempty stomach. An analogous calculation was used to determine per capita frequency of occurrence for each prey species, by month. The percent contribution of each prey species to per capita total prey biomass and to per capita frequency of occurrence of prey were then computed for each month.

We used analysis of similarities (ANOSIM) to test for differences in the diet composition of Lake Trout between different Lake Trout size categories, sampling methods, and sampling months. An ANOSIM is a multivariate analog of analysis of variance and was originally used to assess differences in species abundances among biological communities. Here, we tested for differences in diet compositions between groupings of Lake Trout. This analysis involves a nonparametric permutation to a Bray–Curtis rank dissimilarity matrix (Clarke and Green 1988; Clarke and Warwick 2001). For each Lake Trout with a nonempty stomach, we calculated the percent contribution of each prey species to total prey biomass for that Lake Trout, thereby determining the diet composition for each Lake Trout. Then ANOSIM was applied to these diet

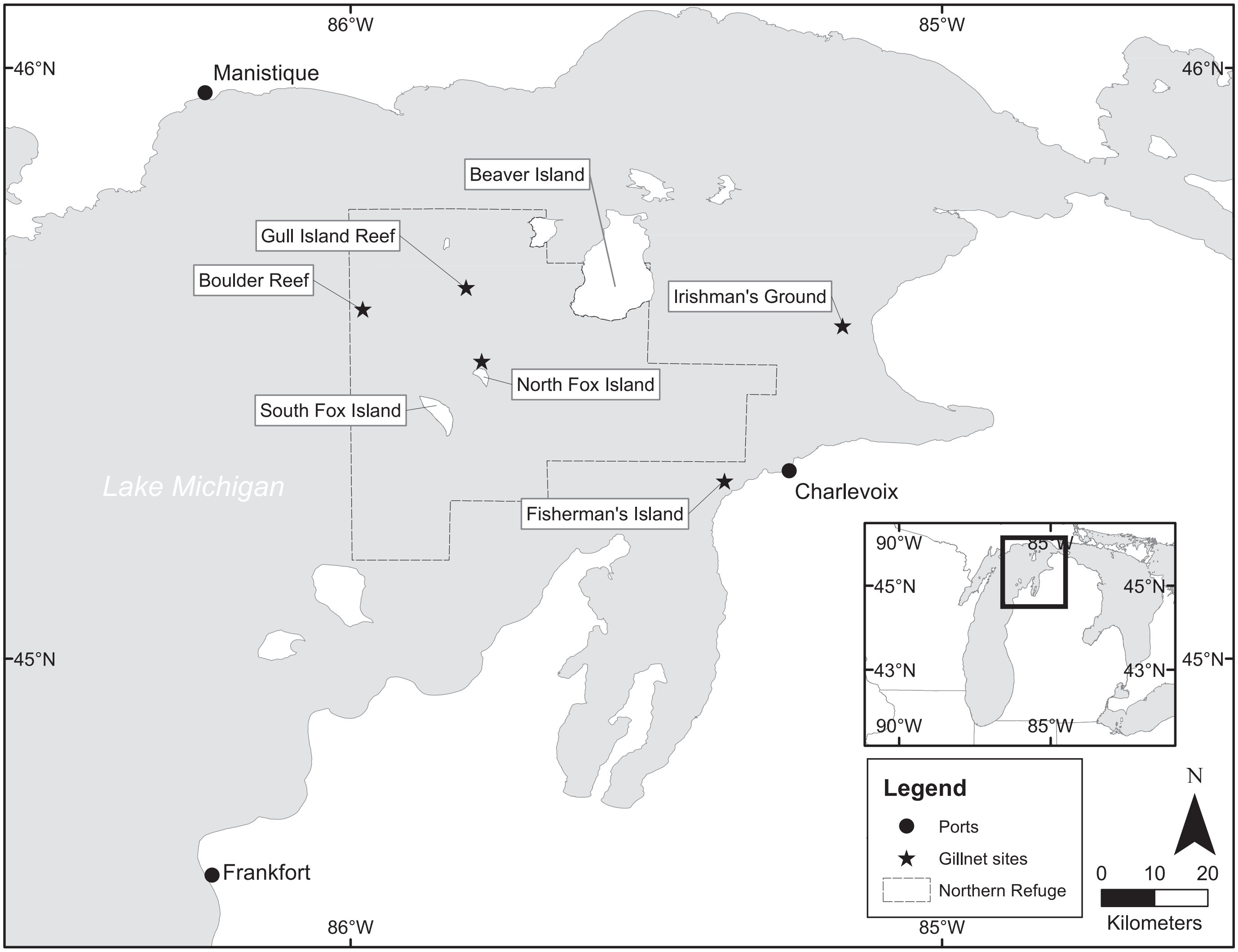

FIGURE 1. Map of the 2016 sampling locations throughout northeastern Lake Michigan. Lake Trout were caught by anglers at the ports of Manistique, Charlevoix, and Frankfort.

composition data for Lake Trout individuals. Dissimilarity matrices were constructed by quantifying the compositional dissimilarity index between the diet compositions of individual Lake Trout (BC_{ij}), which is expressed sensu Bray and Curtis (1957) as follows:

$$BC_{ij} = \frac{1 - 2C_{ij}}{S_i + S_j},$$

where C_{ij} is the sum of only the lesser counts for each of the species found in both stomach samples and S_i and S_j are the total number of specimens counted within each respective stomach, with i and j indicating different individual Lake Trout. Diet composition data for each Lake Trout was square-root transformed to reduce the importance of dominant prey species (Clarke and Warwick 2001). In addition to generating a P-value to indicate significant differences between tested groups, ANOSIM generates an R-value indicating the degree of separation between these groupings; R-values close to 0 indicate indistinguishable groups, R-values < 0.25 indicate little separation between groups and a high amount of overlap, R-values of 0.50 to 0.75 indicate some separation between groups and less overlap, and R-values > 0.75 indicate clear separation between groups with little overlap (Clarke and Gorley 2001). Lake Trout were grouped into the following size categories: 200–399 mm TL, 400–599 mm TL, 600–799 mm TL, and TL $\geq$ 800 mm, as recommended by Elliott et al. (1996), and then ANOSIM was used to determine whether diet composition varied significantly among size categories. If results from the ANOSIM application indicated that size category did not have a significant effect on diet composition, we pooled sizes in all other ANOSIM applications.

To detect a significant diet shift since 2011, we also used ANOSIM to compare diet composition of Lake Trout caught in May 2011 with that of those caught in May 2016. The May 2011 data were taken from Happel (2018). Lake Trout in both years were captured using gill nets, and procedures to determine diet composition were consistent across both sampling years.

We identified the prey species that were most important in defining observed differences between diet compositions among groupings of Lake Trout of different size categories, sampling methods, or months of collection by following ANOSIM procedures with a similarity percentage (SIMPER) analysis. A SIMPER analysis uses the Bray–Curtis dissimilarity index to compare differences among the proportional mass of each prey species consumed by each grouping of Lake Trout. Both ANOSIM and SIMPER were performed using the vegan package (Oksanen et al. 2017) in Program R version 3.3.2 (R Core Team 2014). All nonempty stomachs were included in these analyses.

A diet schedule for Lake Trout ≥ 400 mm TL was constructed by averaging diet composition across individual Lake Trout within each of two seasons: the May–June season and the July–October season. Seasons were defined based on our preliminary examination of the diet composition results. Prey categories included Alewife, Round Goby, Lake Trout, Rainbow Smelt, and other species, based on the importance of these species in this study and in previous diet studies (Stewart and Ibarra 1991; Happel et al. 2018). The "other species" category included Slimy Sculpin, Ninespine Stickleback *Pungitius pungitius*, and Bloater. Alewives were further divided into small (≤120 mm TL) and large (>120 mm TL) fish, based on the recommendation by Stewart et al. (1981, 1983). To calculate diet proportions over the entire May–October period, we computed the weighted average of the percentage for each of the diet categories between the two seasons, weighting each season by the number of months in that season.

RESULTS

A total of 496 Lake Trout stomachs were collected from northeastern Lake Michigan, with 342 collected using gill nets and 154 by anglers (Table 1). The mean TL of all collected Lake Trout was 629 ± 69 mm, while TLs ranged from 373 to 881 mm. The numbers of Lake Trout in the length categories of 200–399 mm TL, 400–599 mm TL, 600–799 mm TL, and TL ≥ 800 mm were 1, 158, 328, and 9, respectively. The only Lake Trout less than 400 mm TL was angler caught in August, and its stomach did not contain any food. Of the 158 Lake Trout in the 400–599-mm category, only 18 Lake Trout were less than 500 mm in TL. Thus, over 95% of the Lake Trout used in our study were ≥500 mm in TL. From the 309 stomachs containing food, 2,949 individual prey items were found, of which 2,737 (93%) were conclusively identified, accounting for 99% of the total raw prey weight. Stomachs collected earlier in the year were less likely to be empty as 86% of stomachs collected during May–June contained food items compared with only 28% of stomachs collected during July–October. An average of 5.5 prey items was found in each stomach, with nonempty stomachs containing an average of 8.9 prey items. A higher number of prey items were found in the nonempty stomachs collected earlier in the year than in stomachs collected later in the year (10.8 and 2.2 prey items, respectively). Numbers (and percentages) of Lake Trout with a nonempty stomach in the categories of 400–599 mm TL, 600–799 mm TL, and TL ≥ 800 mm were 122 (77%), 182 (55%), and 5 (56%), respectively.

The two most commonly found prey in the Lake Trout stomachs were Alewives and Round Goby (Table 2). Rainbow Smelt, Slimy Sculpin, Bloaters, and Ninespine Sticklebacks were also found in the Lake Trout stomachs, but the total number of individuals of these prey fish species recovered from the stomachs was only about 2% of that for Alewives and Round Goby. Several instances of cannibalism were observed, with a total of 15 Lake Trout ranging from 95 to 185 mm found in six stomachs. Invertebrate prey of the taxonomic orders Diptera and Lepidoptera were found in small quantities in three stomachs. All of these insects were adults, and the lepidopterans were terrestrial.

Alewives and Round Goby were the most important prey items in the May–June period, with Round Goby being the dominant prey species (Table 2). However, this dramatically changed in the July-October period, when Alewife became the dominant prey species and Round Goby occurrence declined; Round Goby were found in only 17% of the nonempty stomachs from the July–October period. Along with Alewife, Rainbow Smelt presence in Lake Trout diets increased from the early months to the later months, increasing from 1% to 4% of the total prey biomass. These temporal trends were consistent regardless of sampling method. All other species were far less abundant, with each occurring in only a small fraction of diet samples throughout the year. None of these other species accounted for more than 3% of the total prey biomass.

Over 99% of the Alewives found in Lake Trout stomachs during May–June were small (≤120 mm TL), whereas both small and large Alewives were commonly observed in Lake Trout stomachs during July–October (Figure 2). In contrast, most of the Round Goby eaten by Lake Trout were less than 100 mm in TL in both the May–June and July–October periods. Modal TL of Alewives found in Lake Trout stomachs increased from 65 mm in May–June to 155

TABLE 2. Total and per capita prey biomass and total and per capita frequency of occurrence of prey consumed by Lake Trout during each month of 2016. Lake Trout total lengths ranged from 408 to 881 mm ($N = 309$). Statistics are also provided for the May–June and July–October sampling periods.

		Prey biomass			Frequency of occurrence		
Month	Prey species	Total (g)	Per capita (g)	Percent	Total	Per capita	Percent
May	Alewife	2,948	14.0	21	1,168	5.6	47
	Round Goby	10,497	50.0	76	1,250	6.0	51
	Lake Trout	268	1.3	2	13	0.1	1
	Rainbow Smelt	116	0.6	1	31	0.1	1
	Other fish	26	0.1	0	10	0.0	0
Jun	Alewife	169	5.6	14	30	1.0	26
	Round Goby	1,002	33.4	86	86	2.9	74
	Lake Trout	0	0	0	0	0	0
	Rainbow Smelt	0	0	0	0	0	0
	Other fish	0	0	0	0	0	0
Jul	Alewife	905	56.6	95	34	2.1	89
	Round Goby	8	0.5	1	1	0.1	3
	Lake Trout	0	0	0	0	0	0
	Rainbow Smelt	37	2.3	4	2	0.1	5
	Other fish	4	0.3	0	1	0.1	3
Aug	Alewife	1,474	49.1	81	48	1.6	64
	Round Goby	219	7.3	12	16	0.5	21
	Lake Trout	48	1.6	3	1	0	1
	Rainbow Smelt	81	2.7	4	10	0.3	13
	Other fish	8	0.3	0	1	0	1
Oct	Alewife	305	13.3	83	29	1.3	83
	Round Goby	27	1.2	7	5	0.2	14
	Lake Trout	36	1.5	10	1	0	3
	Rainbow Smelt	0	0	0	0	0	0
	Other fish	0	0	0	0	0	0
May–Jun	Alewife	3,117	13.0	21	1,198	5.0	46
	Round Goby	11,499	47.9	76	1,336	5.6	52
	Lake Trout	268	1.1	2	13	0.1	1
	Rainbow Smelt	116	0.5	1	31	0.1	1
	Other fish	26	0.1	0	10	0.0	0
Jul–Oct	Alewife	2,684	38.9	85	111	1.6	75
	Round Goby	254	3.7	8	22	0.3	15
	Lake Trout	83	1.2	3	2	0.0	1
	Rainbow Smelt	118	1.7	4	12	0.2	8
	Other fish	12	0.2	0	2	0.0	1

mm in July–October, while modal TL of Round Goby increased just slightly from 75 mm in May–June to 85 mm in July–October (Figure 2).

We did not find a statistically significant difference in diet composition between smaller (400–599 mm TL) Lake Trout and larger (600–799 mm TL) Lake Trout (ANOSIM: $P = 0.430$). Thus, Lake Trout from the 400–599-mm-TL and 600–799-mm-TL categories were pooled in all other analyses. No nonempty stomachs were found in Lake Trout measuring under 400 mm in TL, while only five Lake Trout ≥ 800 mm in TL had nonempty stomachs. Due to the low sample sizes of fish from these two size categories, these fish were excluded from all ANOSIM and SIMPER applications. The ANOSIM results also showed that the diet composition of Lake Trout captured in May by gill nets did not significantly differ from that of Lake Trout captured in June by anglers ($P = 0.972$). Likewise, there was no significant difference between the diet composition of Lake Trout captured by anglers in July and August and that of Lake Trout captured by gill nets

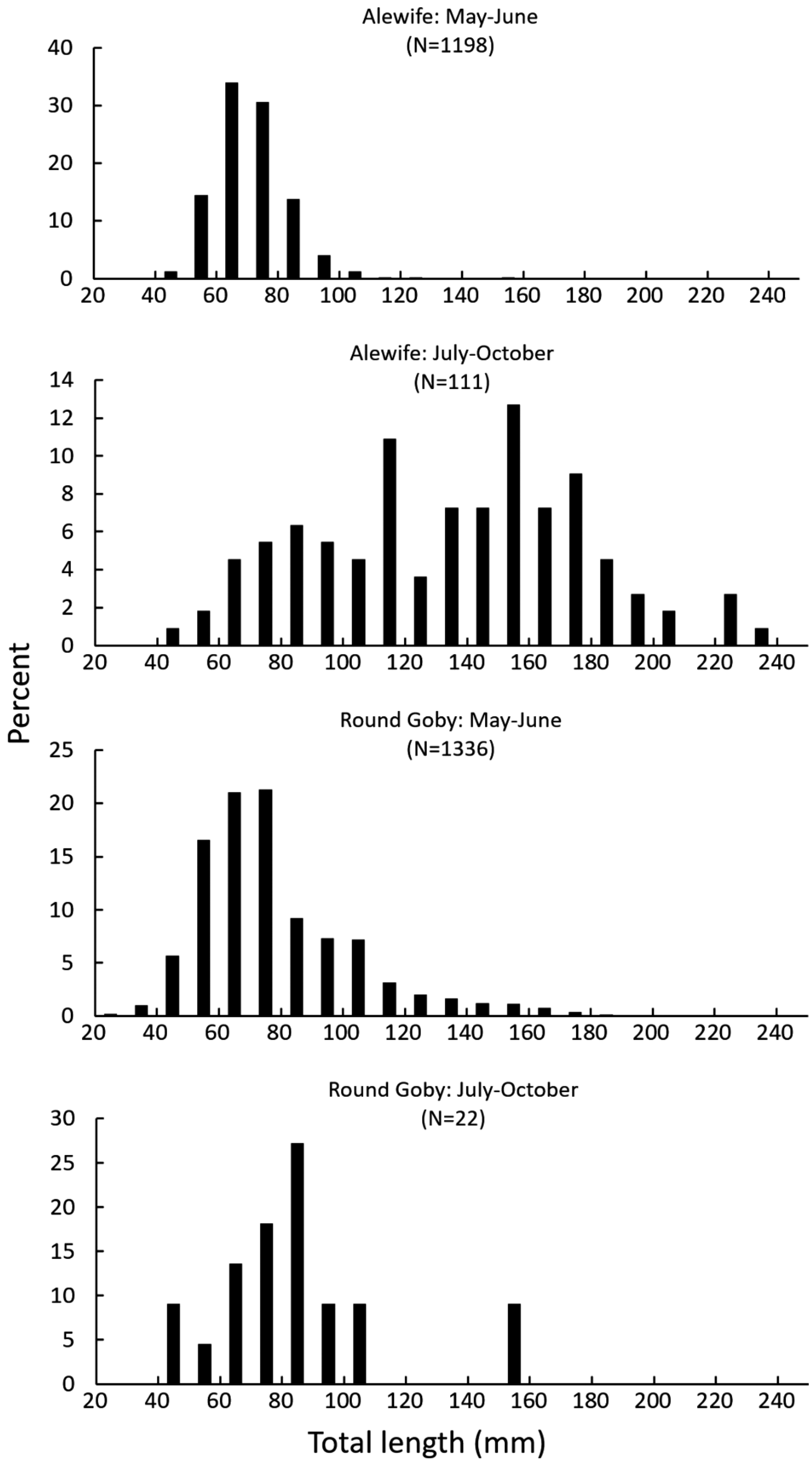

FIGURE 2. Length-frequency distributions of Alewives and Round Goby found in the stomachs of Lake Trout caught in Lake Michigan in 2016. Stomachs were pooled by period (May–June and July–October). Total lengths were measured directly, when possible, or calculated from linear regressions used to convert backbone lengths or standard lengths to total lengths.

in October ($P = 0.690$). Thus, our presentation of the diet composition results in two groupings, namely the May–June grouping and the July–October grouping, was justified by our ANOSIM results. Moreover, these results suggest that sampling-method effects were minimal.

The diet composition of Lake Trout significantly differed between the May–June period and the July–October period (ANOSIM: $P = 0.001$). In the May–June period, Alewives and Round Goby represented 31% and 67%, respectively, of Lake Trout diet, on a wet-weight basis (Table 3). In stark contrast, Alewives and Round Goby represented 76% and 14%, respectively, of Lake Trout diet during the July–October period (Table 3). The diet overlap index (generated from the ANOSIM run) between the May–June and July–October periods was moderately high (R-value = 0.30). As mentioned above, the diet composition of gill-net-caught Lake Trout did not significantly differ from the diet composition of angler-caught Lake Trout in either the May–June period or the July–October period. Diet overlap between the two gears was very high (R-value < 0.10) for both periods. The differences in diet compositions between groupings of Lake Trout were largely driven by differences in the percentages of Alewives and Round Goby, as these two species contributed more than 88% of the dissimilarity between diet compositions for all comparisons.

In May 2016, Lake Trout diet composition in northeastern Lake Michigan was dominated by Round Goby (65%). In contrast, Lake Trout consumed far more Alewives (62%) than Round Goby (21%) during the spring of 2011. Although there was a significant difference in diet composition between the 2 years (ANOSIM: $P = 0.001$), diet overlap was still substantial between years (R-value = 0.24).

Over the May–October period, Alewives were the dominant prey item and accounted for 61% of the identified prey biomass, while Round Goby accounted for 32% of the identified prey biomass (Table 3). Although Round Goby has become increasingly important in the spring diet, Alewife is still the most important prey species for Lake Trout in northeastern Lake Michigan over the May–October period (Table 3). Large Alewives were a minor component of Lake Trout diet during the May–June period but were the most important diet component during the July–October period. Over the May–October period, the contribution of large Alewives to Lake Trout diet (31%) was just slightly higher than the contribution of small Alewives to Lake Trout diet (30%) (Table 3). In our study, all five of the Lake Trout over 800 mm in TL with a nonempty stomach were caught by anglers in August. These fish fed exclusively on large (>120 mm TL) Alewives.

TABLE 3. Diet schedule of Lake Trout calculated by averaging the proportional diet composition, based on prey biomass, across all individual Lake Trout for both the May–June period and the July–October period of 2016. Proportions over the entire May–October period were calculated by the weighted average between the May–June and July–October periods, weighting by the number of months within each period. Entries in the table are expressed as percentages. Each column sums to 100%.

Diet item	May–Jun	Jul–Oct	May–Oct
Small Alewife (≤120 mm)	27.3	31.4	30.0
Large Alewife (>120 mm)	3.5	44.4	30.8
Lake Trout	1.3	3.1	2.5
Round Goby	66.8	14.3	31.8
Rainbow Smelt	1.0	5.6	4.1
Other	0.1	1.2	0.8

DISCUSSION

As we hypothesized, Alewife was the dominant prey species of Lake Trout ≥ 400 mm TL in northeastern Lake Michigan in 2016, while Round Goby has become more important in the Lake Trout diet since 2011. We estimated that Alewives represented 61% of the diet of Lake Trout over the course of our sampling period, which spanned from spring to fall. This suggests that the importance of Alewives in the diets of Lake Trout over this spring-to-fall period has not significantly changed in Lake Michigan since the last spring-to-fall study conducted in 1994–1995, when Alewives represented between 55% and 65% of prey consumed (Madenjian et al. 1998). However, the composition of the other ~40% of Lake Trout diets has changed substantially. Bloaters, Rainbow Smelt, and sculpin (family Cottidae) comprised much of the non-Alewife diet in 1994–1995, which was after the initial discovery of Round Goby in Lake Michigan but prior to its proliferation (Kornis et al. 2012). By contrast, Round Goby accounted for approximately 32% of the Lake Trout diet over the May–October period in 2016, while contributions of Rainbow Smelt, Bloaters, and sculpin combined for only 5% of the diet composition by weight over this same period. Contrary to 1994–1995, Lake Trout consumption in 2016 consisted almost exclusively of Alewives and Round Goby.

We found a strong seasonal effect whereby Round Goby was the dominant prey species in spring (67% of diet by weight), while Alewives contributed an overwhelming portion of the food consumed by Lake Trout in summer and fall (76% of diet by weight). Our study represented the first documentation ever of this drastic seasonal shift in Lake Trout diet composition in Lake Michigan. The most recent published diet study in northeastern Lake Michigan in spring of 2011 showed that Alewife was still the most important prey species (62% of the diet) and Round Goby was of relatively low importance (21% of diet; Happel et al. 2018).

The diet shift from Round Goby in spring to Alewives in summer and fall did not appear to be an artifact of the collection method. In other words, gear appeared to have little effect on Lake Trout diet composition. Similarly, Jacobs et al. (2013) concluded that there was little difference in diet composition between Chinook Salmon caught by anglers and those caught with suspended gill nets. However, even greater differences in the diet composition of gill-net-caught Lake Trout versus angler-caught Lake Trout were anticipated because bottom gill nets were thought to be more likely to catch fish feeding on the bottom, where Round Goby are prevalent, while anglers often troll through the water column where Alewives are prevalent. This lack of a sampling-method effect is an important finding for fisheries managers who have questioned whether observations of more Round Goby in the Lake Trout diet in the spring compared with summer was a result of a difference in prevailing sampling methods (gill nets in spring, angling in summer).

Gill nets used in May included smaller mesh sizes than those used in October spawner surveys, so May sampling was more likely to capture smaller Lake Trout. Predictably, May sampling captured Lake Trout with a wider length range than in October, with more fish caught in the 400–599-mm-TL range. While Lake Trout caught in May were, on the average, smaller than those caught in October, the difference was not statistically significant. Despite differences in size distribution of Lake Trout captured between these two sampling methods, we did not find Lake Trout TL to be a good predictor of diet composition, and we concluded that the use of different gill nets in May and October did not influence our results. Moreover, these findings further support our conclusion that changes in diet composition were the result of seasonality and not gear selectivity.

The seasonal shift from Round Goby to Alewives is likely a result of a difference in the seasonal depth distributions between these two prey fish species, as well as a seasonal shift in the vertical movements of Lake Trout. In the spring of some years, the bulk of the mature Alewife population inhabits waters deeper than 70 m (O'Gorman et al. 2000), which is considerably deeper than the waters where Lake Trout were captured for our study. Mature Alewives make spawning migrations towards shore during spring and spawn in shallow waters during the late spring and summer (Wells 1968; Brown 1972; O'Gorman et al. 2000). Peak spawning occurs during early summer, though some spawning continues through early August. Individual Alewives spawn just once each year and then move to deeper water soon after spawning. Lake Trout are generally found in colder and deeper water, especially during the summer, meaning they do not overlap with spawning Alewives (Eck and Wells 1986). However, since adult Alewives do not all spawn at the same time of year, there is always a portion of the adult Alewife population spatially overlapping with Lake Trout throughout summer and fall. Round Goby similarly move from deeper water to shallow habitats during their spawning season, which can start as early as April but largely occurs from June to September (Kornis et al. 2012). In contrast to Alewives, Round Goby spawn multiple times each year and largely remain in shallow water into early autumn before migrating back to deeper water to overwinter (Charlebois et al. 1997; Walsh et al. 2007). Round Goby spawning mostly occurs in relatively shallow nearshore areas less than 15 m deep, although some spawning at greater depths has been observed (Corkum et al. 1998; Johnson et al. 2005; Taraborelli et al. 2009; Kornis et al. 2012). With Lake Trout inhabiting deeper, colder water, they do not overlap with the bulk of the Round Goby population during summer and early fall (Dahlberg 1981; Eck and Wells 1986; Kornis et al. 2012). However, during the May–June period, Lake Trout spatially overlap with Round Goby as Round Goby migrate from deep to shallow water. During the summer and fall, a substantial portion of the adult Alewife population spatially overlaps with the Lake Trout population in Lake Michigan, while most Round Goby are in shallow nearshore waters, explaining the dominance of adult Alewives in Lake Trout diet during this time. In addition to species-specific differences in seasonal depth distributions of prey fish, a seasonal shift in the vertical movements of Lake Trout also likely contributed to the observed seasonal change in Lake Trout diet composition. Results from recent telemetry studies have indicated that Lake Trout tend to be primarily demersal in the spring but then become more pelagic, with increased vertical movements during the summer and fall (Guzzo et al. 2017; Gallagher et al. 2019). Because Alewives are a more pelagic prey than Round Goby, the availability of Alewives to Lake Trout would be expected to increase from spring to summer and fall.

Round Goby has become significantly more important in the spring diet of Lake Trout from northeastern Lake Michigan over the past 10 years. Round Goby accounted for <2% of spring diet by weight in Lake Trout during 2006–2008 (Jacobs et al. 2010). This percentage increased to 21% of prey biomass by 2011 (Happel et al. 2018) and then to 67% by 2016. In southeastern Lake Michigan, Round Goby had become important in the spring diet of Lake Trout by 2011, when this prey species represented 49% of the diet composition (Happel et al. 2018). Perhaps the availability of Alewives in the spring declined at a faster rate in southeastern Lake Michigan than in northeastern Lake Michigan, triggering Lake Trout to change their feeding behavior there first. Reduced abundance of all pelagic forage may make feeding more energetically efficient in benthic habitats, where Round Goby are more abundant, instead of pelagic habitats previously inhabited by higher densities of Alewives, Bloaters, and Rainbow Smelt (Wells 1968; Charlebois et al. 1997; Tsehaye et al. 2014a). This diet shift from Alewives to Round Goby in spring resembles findings in Lake Ontario and Lake Huron, where Round Goby became a more important component of Lake Trout diets as the abundances of Alewives and Rainbow Smelt declined (Rush et al. 2012; Roseman et al. 2014; He et al. 2015). Continued declines in Alewife biomass may cause further shifts to consumption of Round Goby.

We considered the possibility that the increased importance of Round Goby in Lake Trout diets during May and June could be explained by an expanding range or an increasing Round Goby population abundance since 2011. However, this is unlikely, as Round Goby was found in the Northern Refuge as early as 2007 (Jacobs et al. 2010), and recent prey fish surveys indicate that their biomass has leveled off or even decreased since the early 2010s (Madenjian et al. 2018), suggesting that increased consumption of Round Goby was not linked to increases in Round Goby abundance. Instead, it appears that Round Goby spatially overlapped with Lake Trout prior to 2016 but may not have immediately become important forage due to the time lag generally observed in predators exposed to novel prey (Pothoven and Madenjian 2013). In addition, Lake Trout have been shown to forage on Alewives at a disproportionately high level relative to Alewife ambient abundance, even when alternative prey species are also abundant (Eck and Wells 1986; He et al. 2015). For example, Round Goby did not become an important diet component of Lake Trout in Lake Huron until the Alewife population completely collapsed in the early 2000s (Riley et al. 2008; He et al. 2015). The significant change in feeding behavior further suggests that Lake Trout in Lake Michigan could be more responsive to declines of preferred prey than to increases in abundance of alternative prey species.

The size of Alewives consumed by Lake Trout in Lake Michigan during 2016 was less than that during 1994–1995. In 1994–1995, the modal TLs of small and large Alewives consumed by Lake Trout were 75 mm and 175 mm, respectively (Madenjian et al. 1998). In 2016, modal TLs of small and large Alewives consumed by Lake Trout were 65 mm and 155 mm, respectively. This shift to the consumption of smaller Alewives was expected as annual bottom trawl surveys indicated that Alewives have decreased in both abundance and size (Madenjian et al. 2006, 2015, 2018). Jacobs et al. (2013) documented a similar decline in the size of Alewives consumed by Chinook Salmon in Lake Michigan between 1994 and 2010.

A comparison of Lake Trout diet composition in Lake Superior with that in Lakes Michigan, Huron, and Ontario suggests that Alewives form the mainstay of the adult Lake Trout diet when they are readily available for consumption by Lake Trout. Alewives successfully invaded Lakes Ontario, Huron, and Michigan to become well established in these three lakes, but Alewives never became well established in Lake Superior (O'Gorman et al. 2012). Alewives have dominated the diet of adult Lake Trout in Lake Ontario during the 1980s, 1990s, and 2000s (Madenjian et al. 1995; Rush et al. 2012), and Alewives have been the predominant prey of adult Lake Trout in Lake Michigan since the 1970s. Alewives represented the single most important prey for Lake Trout in Lake Huron during the 1980s and 1990s (He et al. 2015). However, following the complete collapse of the Alewife population in Lake Huron during 2002–2004, the importance of Alewives in the adult Lake Trout diet was greatly reduced, and the contribution of Alewives to adult Lake Trout diet in recent years has been practically negligible. Alewives in the diet of adult Lake Trout in Lake Huron were mainly replaced by Rainbow Smelt and Round Goby beginning in 2005 (He et al. 2015). Since the 1980s, adult Lake Trout in Lake Superior have fed on a variety of fish, including coregonines (mainly Cisco *Coregonus artedi*), Rainbow Smelt, sculpin (mainly Deepwater Sculpin *Myoxocephalus thompsonii*), Ninespine Stickleback, and Burbot *Lota lota* (Ray et al. 2007; Gamble et al. 2011a, 2011b).

Management Implications

Our results will be useful in updating the predator–prey model by Tsehaye et al. (2014a) used to guide salmonine-stocking decisions in Lake Michigan. Round Goby consumption has not been considered previously when running this simulation model. Thus, our results could be used to better advise the future management of salmonines in Lake Michigan. We observed a substantial increase in the importance of Round Goby in the spring diet of Lake Trout from 2011 to 2016, and it is possible that Round Goby has also become increasingly important for other piscivores over this period. A lakewide analysis of Lake Trout and other salmonine diets is ongoing for updating the predator–prey model, but our regional analysis does provide important insights into the shifting diet composition of Lake Trout, as well as into gear effects (or lack thereof) on diet composition of Lake Trout. We were the first to show that the diet of adult Lake Trout in Lake Michigan undergoes a dramatic shift between the spring and summer, whereby Round Goby dominates the spring diet while Alewives dominates the diet during summer and fall months. In addition, our findings indicated that gill-net-caught Lake Trout and angler-caught Lake Trout were similar in their diet composition. Overall, our findings will aid in the sound management of the salmonine communities in Lake Michigan, thereby achieving the goals set out by the Lake Michigan Committee, which operates under the auspices of the Great Lakes Fishery Commission (Eshenroder et al. 1995; Bronte et al. 2008; Dexter et al. 2011).

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