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Diet complexity of Lake Michigan salmonines: 2015–2016

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ABSTRACT

In Lake Michigan, the unintended introduction of invasive species (e.g., zebra mussel, *Dreissena polymorpha*; quagga mussel, *D. rostriformis bugensis*; round goby, *Neogobius melanostomus*) and reduced nutrient loading has altered nutrient dynamics, system productivity, and community composition over the past two decades. These factors, together with sustained predation pressure, have contributed to declines of several forage fish species, including alewife (*Alosa pseudoharengus*), which has dominated diets of the five primary salmonine species of Lake Michigan for the last 50 years. Salmonines that have inflexible, less complex diets may struggle if alewife declines continue. We analyzed stomach contents of salmonines collected throughout the main basin of Lake Michigan in 2015 and 2016 to investigate diet composition, diet diversity, and individual variation of alewife lengths consumed. Chinook salmon (*Oncorhynchus tshawytscha*) almost exclusively consumed alewife and had lower diet diversities compared to the other four species, which consumed relatively high frequencies of round goby (brown trout, *Salmo trutta*; lake trout, *Salvelinus namaycush*), aquatic invertebrates (coho salmon, *Oncorhynchus kisutch*) and terrestrial invertebrates (rainbow trout, *Oncorhynchus mykiss*) along with alewife. Although clear spatio-temporal feeding patterns existed, much of the variation in diet composition and diet diversity was expressed at the individual level. Salmonine populations consumed the entire size range of alewife that were available, whereas individual stomachs tended to contain a narrow range of alewife sizes. Due to their reliance on alewife, it is likely that Chinook salmon will be more negatively impacted than other salmonine species if alewife abundance continues to decline in Lake Michigan.

Introduction

Food web studies often describe trophic connections within a population based on measures of central tendency (e.g., mean diet composition), which assumes consistent behavior and trophic roles among individuals. However, intraspecific diet variation can play a vital role in the trophic stability of an ecosystem (Faulks et al., 2015). Niche partitioning among individuals within a population can lead individuals to specialize on a small subset of resources compared to a population's overall resource use (Bolnick et al., 2003). A population of specialists may function similarly to a population of generalists, in that the cumulative resource use of each population will be the same, but the two populations can have different impacts on the connectivity of food webs (Quevedo et al., 2009), flexibility in responding to environmental disturbances (Layman et al., 2007), and potential responses to management actions. Not only can individual variation affect diet complexity, but variable environmental factors and behavior, such as seasonal and spatial variation in availability of resources and ontogenetic diet shifts, can influence the use of resources (e.g., Foley et al., 2017; Happel et al., 2018, 2015a, 2015b; Jude et al., 1987;

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Svanbäck et al., 2015). Given that intraspecific and spatio-temporal variability in resource use can comprise a key component of food web complexity, it may act to promote species and ecosystem resilience in response to ecological change.

Over the past two decades, the Lake Michigan food web has undergone dramatic changes due to the establishment of invasive species, such as dreissenid mussels (zebra mussel, *Dreissena polymorpha*; quagga mussel, *D. rostriformis bugensis*), predatory cladocerans (spiny waterflea, *Bythotrephes longimanus*; fishhook waterflea, *Cercopagis pengoi*) and round goby (*Neogobius melanostomus*). Decreased offshore production has been attributed to reduced nutrient loading (Dolan and Chapra, 2012) and intense filtering by dreissenid mussels has shifted production from offshore pelagic to nearshore benthic pathways (Hecky et al., 2004; Fahnenstiel et al., 2010; Stadig et al., 2020; Vanderploeg et al., 2010). Additionally, invasive predatory cladocerans have had a dramatic effect on zooplankton communities in the Great Lakes with zooplankton communities now being dominated by smaller species (Barbiero and Tuchman, 2004; Barbiero and Warren, 2011). Coincidently, there has been a near extirpation of the amphipod, *Diporeia* (Nalepa et al., 2009), a historically important prey for many invertivorous fish in the lake. In the absence of such energy-rich prey, invertivorous fishes have used alternative, lower energy prey items, resulting in declines in condition for species like alewife (*Alosa pseudoharengus*; Madenjian et al., 2003; Pothoven and Madenjian, 2008). Offshore prey fish biomass has declined since the early 2000′s, including alewife, bloater (*Coregonus hoyi*), rainbow smelt (*Osmerus mordax*), slimy sculpin (*Cottus cognatus*), and deepwater sculpin (*Myoxocephalus thompsonii*; Madenjian et al., 2018). In contrast to offshore areas, sequestration of nutrients and increased water clarity (both attributed to dreissenid mussels) have led to increased chlorophyll concentrations (Stadig et al., 2020), the resurgence of benthic algae (i.e., *Cladophora*; Auer et al., 2010), and high densities of benthic invertebrates (Pothoven et al., 2000) in nearshore areas. Moreover, high densities of round goby in many nearshore areas (Foley et al., 2017; Vanderploeg et al., 2002), have potentially limited the availability of food and cover for other nearshore, benthic fishes (French and Jude, 2001; Houghton and Janssen, 2015; Janssen and Jude, 2001; Lederer et al., 2008). While round goby are seemingly abundant, due to their affinity to rocky substrates, densities have been difficult to measure (Bunnell et al., 2017). Collectively, these changes have contributed to the observed increased importance of nearshore trophic pathways, relative to offshore pathways in Lake Michigan (Turschak et al., 2014) and potentially reduced pelagic prey available to upper food webs.

Lake Michigan supports a valuable recreational salmonine fishery composed of one native (lake trout, *Salvelinus namaycush*) and four non-native species (brown trout, *Salmo trutta*; Chinook salmon, *Oncorhynchus tshawytscha*; coho salmon, *Oncorhynchus kisutch*; rainbow trout, *Oncorhynchus mykiss*), that may vary in their diet plasticity and ability to respond to food web changes. In the past, invasive alewife has constituted the dominant prey for these salmonines (Jude et al., 1987), but recent substantial declines in alewife abundance and other forage fish (e.g., bloater, sculpin species; Madenjian et al., 2018) may prompt changes to salmonine diets. For example, brown trout, lake trout, and rainbow trout, have displayed diverse diets in the Great Lakes and are known to consume round goby (Colborne et al., 2016; Dietrich et al., 2006; Happel et al., 2018, 2017; Jacobs et al., 2010; Roseman et al., 2014; Tsehaye et al., 2014). In contrast, Chinook salmon and coho salmon appear to be less plastic in their diet composition, primarily consuming alewife (Happel et al., 2017; Jacobs et al., 2013; Savitz, 2009; Yuille et al., 2015). Although several studies have examined salmonine diets in Lake Michigan, the most recent studies have focused primarily on Chinook salmon (Jacobs et al., 2013) and lake trout (Happel et al., 2018; Jacobs et al., 2010) and have either lacked spatial variation across all of Lake Michigan or seasonal variation in diet composition. Few studies have examined the diet composition of brown trout, coho salmon, and rainbow trout in Lake Michigan (Jude et al., 1987), and with Lake Michigan's rapidly changing forage base, there is need to update salmonine consumption models used by managers to inform stocking decisions (Tsehaye et al., 2014). In 2016, over 50% of the prey fish biomass was apportioned to bloater and only 3% apportioned to alewife (Bunnell et al., 2017), and thus it is of interest if pelagic predators will shift from alewife to bloater or to other prey. In summary, Lake Michigan salmonine species appear to differ in diversity of prey items consumed, which may have important implications for their flexibility to adjust to changes in relative availability of different prey and how these species are managed.

Bottom substrate (Janssen et al., 2005), local watershed size (Larson et al., 2013), and land-use (Cloutier et al., 2015) varies considerably across Lake Michigan, which can influence dominant energy pathways and diet patterns across distinct areas of the lake (Foley et al., 2017; Happel et al., 2018, 2015a, 2015b). For example, spottail shiner (*Notropis hudsonius*), round goby, and yellow perch (*Perca flavescens*) collected from southeast Lake Michigan during 2010 relied more on pelagic energy pathways, whereas those from the southwest relied more on benthic energy pathways (Foley et al., 2017; Happel et al., 2015a, 2015b). These patterns may be partially attributed to the rocky habitat, clear water, and high frequencies of upwellings on Lake Michigan's western coast (Foley et al., 2017; Happel et al., 2015a, 2015b; Turschak et al., 2019). Previous work has shown that lake trout diets can vary greatly across different regions of Lake Michigan, with alewife being the dominant prey on the western side of the lake and round gobies comprising greater proportions of diets on the eastern side (Happel et al., 2018). Additionally, the consumption of alewife by salmonines has been shown to change seasonally with greater proportions of alewife in the diet in the spring, while consumption of other fish, like rainbow smelt and bloater, increases in the summer and fall (Jude et al., 1987; Rybicki and Clapp, 1996). However, this seasonal pattern was documented prior to substantial decline in the abundances of these forage fish, and it is not known whether this historical pattern persists.

The diets of fishes can be characterized not only by prey taxa consumed, but also by the diversity of sizes of prey consumed. Lake Michigan salmonines are known to consume a broad length range of alewife (Jacobs et al., 2013; Jude et al., 1987; Rybicki and Clapp, 1996), which could be beneficial because alewife are known to have highly variable recruitment (Madenjian et al., 2005). A poor recruitment year could result in a limited range of alewife sizes available (e.g., lack of small alewife), which may lead salmonines to depend on alewife sizes that are most abundant rather than their preferred sizes. Warner et al. (2008) found that when the abundance of small alewives was high, age-1 Chinook salmon would switch to consuming small alewives over large alewives. In addition, consuming a broad length range of alewife could allow individuals to specialize on alewife lengths or consume a small subset of alewife lengths compared to the overall population, which has the potential to reduce competition among salmonines for alewife (Bolnick et al., 2010, 2003; McCann et al., 1998).

Examining how diet composition, diet diversity, and sizes of alewife consumed by salmonine species varies across seasons and areas of Lake Michigan may provide insights to potential future success of salmonines in a changing Lake Michigan ecosystem. To evaluate the diet complexity of Lake Michigan salmonines, we explored: 1) the diet patterns of Lake Michigan salmonines in 2015 and 2016, 2) variation of diet diversity within and among salmonine species and 3) the sizes of alewife consumed by salmonines. Based on results of previous studies, we hypothesized that Chinook salmon and coho salmon would primarily consume alewife and have less diverse diets compared to brown trout, lake trout, and rainbow trout which we expected to consume a wider range of prey, including round goby. Lastly, we expected salmonines, particularly Chinook salmon and coho salmon, to consume similar sizes of alewife across space and time and for the sizes of alewife consumed to roughly match the available sizes of alewife and for the range of alewife consumed to be similar at individual and population levels.

Methods

Field collections

Stomachs of brown trout, Chinook salmon, coho salmon, lake trout, and rainbow trout were collected from April-November of 2015 and 2016. The majority of stomachs were collected from angler-caught fish via the US Fish and Wildlife Service's Great Lakes Mass Marking Program, which is a coordinated tagging and field recovery program that involves all state, federal, and tribal agencies that stock salmon and trout in the Great Lakes and its tributaries (Bronte et al., 2012). To supplement these samples, stomachs were also collected in annual fishery-independent surveys conducted by Michigan Department of Natural Resources, Indiana Department of Natural Resources, Wisconsin Department of Natural Resources, and Little Traverse Bay Band of Odawa Indians. Once stomachs were collected, they were immediately frozen (-20^{0}C) until processing. In addition to the collection of stomachs, salmonines were measured for total length (to 1 mm).

To examine spatial variation in salmonine diets, Lake Michigan was divided into four regions: Northeast, Northwest, Southeast, and Southwest (Fig. 1). These regions are based on regional trophic patterns established in previous Lake Michigan diet studies (Foley et al., 2017; Happel et al., 2018, 2015a, 2015b). Because prey availability is likely to vary across the year, stomachs were grouped into two seasons: Early (April-July) and Late (August-November). Salmonines were split into two size classes (<600 mm and $\geq$600 mm) to account for potential size effects on diets. Due to minimum size limits and angler preferences, it was difficult to collect large numbers of salmonines <400 mm in length. Regions, seasons, and size classes were chosen *a priori* to the collection to allow for consideration of variation while maintaining sufficient sample sizes among groups. Specifically, we sought to collect 20 stomachs for each salmonine species for each region, season, size-class, and year combination although this was not always achieved. Additionally, lengths of alewife collected during lake-wide 2015 and 2016 USGS annual September bottom trawl surveys were obtained for context and to compare with sizes of alewife consumed by salmonines (D.B. Bunnell, USGS, pers. comm.).

Stomach processing

Individual fish prey from thawed stomachs were identified to species (except for sculpins, which were identified to family), weighed to the nearest 0.01 g wet weight, and measured to the nearest 1 mm standard or vertebral length depending on stage of digestion. Highly digested fish prey were identified using cleithras (Traynor et al., 2010) and vertebrae (Elliott et al., 1996). Total lengths of alewife were estimated from standard or vertebral length using published conversion formulae (Elliott et al., 1996), and from measures of cleithra attached to partial vertebrae (Dub and Czesny, 2016). Invertebrate prey were identified to the lowest possible taxonomic level and wet-weighed in aggregate to the nearest 0.01 g by prey category.

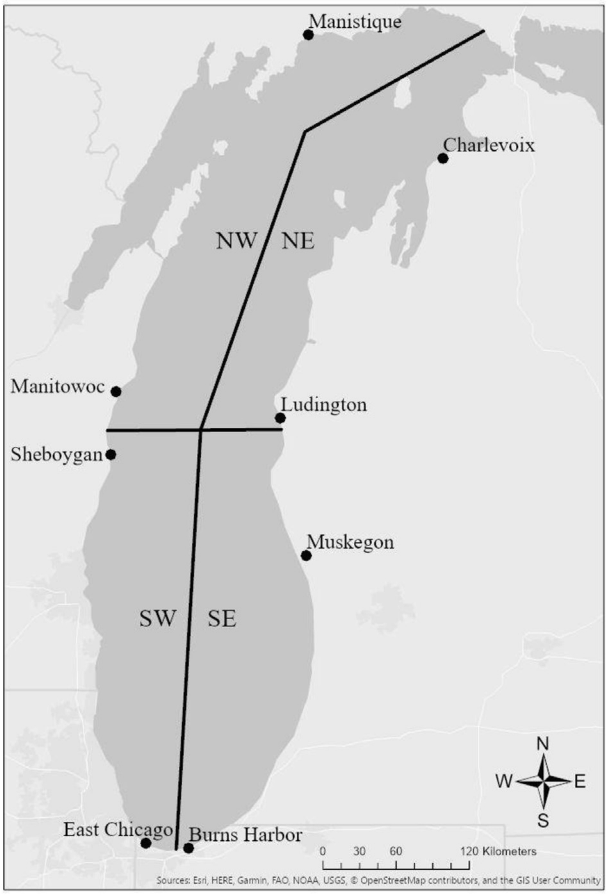

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Fig. 1. Map of Lake Michigan showing the different regions (Northeast = NE; Northwest = NW; Southeast = SE; Southwest = SW) where salmonines were collected. Northeast was defined as fish collected at or between the ports of Ludington and Charlevoix. Northwest was defined as fish collected at or between the ports of Manitowoc and Manistique. Southeast was defined as fish collected at or between the ports of Sheboygan and East Chicago. Southeast was defined as fish collected at or between the ports of Muskegon and Burns Harbor.

Stomach contents were summarized into 11 categories with relatively rare prey grouped together: alewife, bloater, predatory cladocarens (spiny waterflea and fishhook waterflea), *Mysis diluvania* (hereafter *Mysis*), round goby, terrestrial invertebrates, yellow perch, other fish, other, unknown fish, and unidentifiable stomach contents. Other fish included fish prey that rarely appeared in salmonine stomachs, which included rainbow smelt, sculpin spp., juvenile lake trout, green sunfish (*Lepomis cyanellus*), creek chub (*Semotilus atromaculatus*), larval fish, and threespine stickleback (*Gasterosteus aculeatus*). The other category included additional diet items that showed up in relatively few salmonines, namely dreissenid mussels, amphipods, chironomids, and fish eggs. Unknown fish were fish parts (bones, tissue, etc.) that could not be identified to species, whereas unidentifiable stomach contents were stomach contents that were too digested to be identified to any diet category. Diet items that were not included in diet composition estimations included plastic particles, rocks, vegetation, and fishing bait (i.e., earthworms and cocktail shrimp). We summarized diet compositions using two calculation methods. First, mean individual percent diet composition of stomach contents was estimated by a) including only non-empty stomachs, b) calculating percent diet compositions for each individual stomach, and c) taking the mean of individual percent diet compositions across individuals. Second, we estimated a population-level index of ration, using stomachs with food and empty stomachs and averaging prey category weights across all individual salmonines, which were then expressed as proportions (Elliott et al., 1996). Note that the first method will undervalue relatively heavy diet categories that only show up in a few diets, while the second method will overvalue such diet categories.

Statistical analyses

Variation in diet composition

We conducted a permutational multivariate analysis of variance (PerMANOVA) to investigate the variance partitioning of diet composition of Lake Michigan salmonines. A PerMANOVA is analogous to the parametric MANOVA and compares an observed test statistic value (pseudo-F ratio) against recalculated test statistic values from permutations of the data (Anderson, 2001). The benefit of PerMANOVA is that results are not constrained by parametric statistic assumptions or effects of unbalanced sample sizes. To identify the effect of species on variance partitioning of diet composition, we conducted a PerMANOVA across all individuals (excluding individuals with empty stomachs) with species, region, season, size class, and year as independent variables and proportional diet composition by weight (unknown fish, unidentifiable stomach contents categories were excluded) as the response variable. We assessed temporal, spatial, and size-related variation in diet composition within species by performing species-specific PerMANOVA with region, season, size class, and year as independent variables and proportional diet composition by weight as the response variable. We quantified explanatory power (R^2) and P-values for each independent variable for each PerMANOVA analysis. Each PerMANOVA analysis was conducted using Bray-Curtis distances as the dissimilarity measure and 999 permutations using the ADONIS function from the R package vegan (Oksanen et al., 2018; R Core Team, 2018).

Diversity of prey consumed

We used the complexity-as-diversity method described by Marion et al. (2015b) and as used by Feiner et al. (2019) to quantify salmonine diet diversity. This method uses Shannon's effective diversity ${}^{q}D$:

$$ {}^{q}D_{q} = \left(\sum_{i=1}^{K} p_i^{q} \right)^{1/(1-q)} \quad (1) $$

where p_i is the proportion of diet item i across all K diet items and ${}^{q}D$ signifies diet diversity. The parameter q allows the index of diversity to be weighted by the relative abundances of each prey category within stomach contents. When $q = 0$ the relative abundances are ignored and ${}^{q}D$ signifies diet richness, but as the value for q increases, the relative abundance of diet items has greater influence on diet diversity. General diversity was represented by $q = 1$. Although there is no solution for $q = 1$, the limit is the exponentiated Shannon's diversity index (Marion et al., 2015b). Additionally, we quantified diversity at $q = 3$, which gives more weight to the more abundant prey categories. This analysis was conducted separately for each salmonine species and across all salmonines at five (i.e., region, season, size-class, year, and global) and six (i.e., species, region, season, size-class, year, and global) nested-hierarchical levels, respectively. We used the group-wise partitioning method of Marion et al. (2015b), which averages the diversity for each level across the components of that level (e.g., regional diversity represents the mean diversity across individuals at that region). Bootstrap uncertainties (1000 iterations) were estimated for components at each hierarchical level and the diversity of each component was considered significantly different if they did not have overlapping 95% confidence intervals.

Next, we determined how excess salmonine diet diversity was partitioned across individuals, species, regions, seasons, size class, and years, again using the group-wise partitioning approach of Marion et al. (2015b) and as applied by Feiner et al. (2019). We estimated beta diversity, which is the difference between alpha diversity, the effective number of prey items that could be expected within an average component (e.g., region, season, etc.) of a hierarchical level and total diversity at a hierarchical level. In other words, beta diversity represents the effective number of prey items that were not observed across an average component of a hierarchical level (Marion et al., 2015b). From these estimates, we calculated the proportion of the total diversity at each level that was attributed to beta diversity (e.g., the proportion of diet diversity observed across regions that would not be observed on average within a region would represent the regional-level contribution). With this, we were able to determine which hierarchical level contributed the most to diet diversity. To assess the effects of species on diet diversity partitioning, we conducted these analyses across all individuals with individuals, species, regions, seasons, size-classes, within-years, and between-years as our hierarchical levels. Then to assess temporal, spatial, and size-related variation in diet diversity within species, we performed species-specific diversity partitioning analyses. We implemented partitioning at $q = 0$ through $q = 6$ to elucidate how increasing the influence of relative abundances affects diversity partitioning. All diversity analyses were conducted in R (R Core Team, 2018) using the R package hierDiversity (Marion et al., 2015a).

Due to the nature of stomach content analysis (e.g., varying digestion rates of prey items), not all contents could be identified to the same taxonomic level. For example, dreissenid mussels were identified to genus and fish were identified to species. Such different taxonomic resolution can confound interpretations of diet diversity. To evaluate such effects, we conducted our analyses of diet diversity and the partitioning of diversity by grouping stomach contents in three different ways: 1) using abundance-based groupings (i.e., categories described above), 2) using only fish prey by species, and 3) groupings based on coarse trophic pathways. For the second grouping method, we included: alewife, bloater, creek chub, green sunfish, larval fish, juvenile lake trout, rainbow smelt, round goby, sculpin (deepwater sculpin and slimy sculpin grouped together), threespine stickleback, and yellow perch. For the third grouping method, we divided diet items into five groups: pelagic fish, benthic fish, pelagic invertebrates, benthic invertebrates, and terrestrial invertebrates. The pelagic fish group included alewife, bloater, larval fish, three-spine stickleback, and rainbow smelt, whereas the benthic fish category included creek chub, green sunfish, juvenile lake trout, round goby, sculpin, yellow perch, and fish eggs (Turschak et al., 2014). Invertebrates that reflect pelagic carbon sources included predatory cladocerans, *Mysis*, and dreissenid mussels, whereas benthic invertebrates included amphipods and chironomids (Turschak et al., 2014). Due to the qualitative consistency of results between the three groupings only the abundance-based groupings will be described in the results. The results of using only fish prey and coarse trophic groupings can be found in the Electronic Supplementary Material (ESM) Figs. S1–S5.

Individual variation of alewife lengths consumed

To describe patterns of alewife lengths consumed by individual salmonines, we used the total niche width (TNW) method developed by Roughgarden (1974). TNW can be defined as all the dietary resources that a population exploits (in this instance, the length range of all alewives consumed) and consists of within individual components (WIC; variation in alewife lengths within one individual salmonine diet) and between individual components (BIC; variation in alewife lengths among individual salmonines; Roughgarden, 1974). The extent of individual variation can be measured as the proportion of TNW explained by WIC (i.e., WIC/TNW; Bolnick et al., 2002). Values of individual variation fall between 0 and 1, with smaller values signifying more variation among individuals. To test the null hypothesis that all individuals are sampling equally from the overall distribution of alewife lengths consumed, a Monte Carlo (999 iterations) resampling technique was used to calculate a P-value. Individual variation was measured for each species lake-wide and by region, season, and size-class for each year. For these analyses, only individuals that consumed more than one alewife were included. To balance statistical power and the potential of Type I errors due to multiple comparisons, we set the significance level at $\alpha = 0.01$. These analyses were conducted using the R package RInSp (Zaccarelli et al., 2013).

Results

Within-species diet patterns

Brown trout

In 2015 and 2016, a total of 114 and 96 (respectively) brown trout were collected and analyzed (Table 1). Of the identifiable prey, alewife and round goby represented the majority of diet items by both mean individual percent diet composition (alewife: 51% in 2015 and 38% in 2016; round goby: 11% in 2015 and 21% in 2016) and by the index of ration (alewife: 0.87 in 2015 and 0.34 in 2016; round goby: 0.06 in 2015 and 0.50 in 2016; Fig. 2). In the spring of 2016, round goby was more important in stomachs on the eastern side of Lake Michigan than elsewhere (Fig. 4). When partitioning variance in diet composition, region ($F_{3,\ 94} = 2.67$, $R^2 = 0.07$, $P = 0.013$) had the largest explanatory power followed by year ($F_{1,\ 94} = 4.62$, $R^2 = 0.04$, $P = 0.008$) with 87% of the variation being left unexplained. For brown trout, the bulk of diversity variation was partitioned to the individual (9–37% across the range of q), region (32–51%), and between years (11–20%; Fig. 5). Lake-wide individual variation of alewife lengths consumed was not significant for brown trout in either year potentially due in part to relatively small sample sizes (Table 2).

Chinook salmon

In 2015 and 2016, a total of 524 and 315 (respectively) Chinook salmon stomachs were collected and analyzed (Table 1). In both years, alewife was the primary prey consumed by Chinook salmon (mean individual percent diet composition in 2015: 69%, 2016: 73%; index of ration in 2015: 0.90, 2016: 0.94; Fig. 2). Much of the diet composition variance was left unexplained (93%) with only region ($F_{3,\ 375} = 5.90$, $R^2 = 0.04$, $P = 0.001$) and season ($F_{1,\ 375} = 10.06$, $R^2 = 0.02$, $P = 0.001$) having a significant, albeit minor, effect. Almost the entirety of diet diversity variation was observed at the individual (9–69%) and regional levels (29–50%; Fig. 5). Significant lake-wide individual variation of alewife lengths consumed by Chinook salmon was evident during both years, meaning individual Chinook salmon consumed a narrower range of alewife lengths than expected (2015: WIC/TNW = 0.35, P = 0.001; 2016: WIC/TNW = 0.21, P = 0.001; Table 2).

Coho salmon

In 2015 and 2016, a total of 227 and 232 (respectively) Coho salmon were collected and analyzed (Table 1). Overall, coho salmon fed primarily on alewife (mean individual diet composition 2015: 51%, 2016: 54%), but terrestrial invertebrates (2015: 12%; 2016: 3%), *Mysis* (2015: <1%; 2016: 13%), and predatory cladocerans (2015: 6%; 2016: 17%) made up considerable proportions of coho salmon stomach contents (Fig. 2). Despite terrestrial invertebrates, *Mysis*, and predatory cladocerans contributing a large proportion to the mean individual diet composition of coho salmon, the index of ration for all invertebrates expressed as proportions (<0.05 in 2015 and 2016) found in coho salmon stomachs was minimal compared to alewife (2015: 0.78; 2016: 0.88; Fig. 2). The diet composition of coho salmon was explained most by region ($F_{3,\ 304} = 10.72$, $R^2 = 0.10$, $P = 0.001$) followed by year ($F_{1,\ 304} = 9.49$, $R^2 = 0.03$, $P = 0.001$), season ($F_{1,\ 304} = 8.26$, $R^2 = 0.02$, $P = 0.001$), and size-class ($F_{1,\ 304} = 6.04$, $R^2 = 0.02$, $P = 0.001$), but 83% of the variance was unexplained. Variation of coho salmon diet diversity was partitioned primarily to the individual (10–50%) and regional levels (45–56%; Fig. 5). Significant lake-wide individual variation of alewife lengths consumed was evident during both years (2015: WIC/TNW = 0.16, P = 0.001; 2016: WIC/TNW = 0.20, P = 0.001; Table 2).

Lake trout

In 2015 and 2016, a total of 469 and 484 (respectively) lake trout were collected and analyzed (Table 1). Alewife and round goby represented the majority of diet items by both percent diet composition (alewife: 51% in 2015 and 56% in 2016; round goby: 32% in 2015 and 30% in 2016) and the index of ration (alewife: 0.66 in 2015 and 0.68 in 2016; round goby: 0.27 in 2015 and 0.24 in 2016; Fig. 2). Similar to brown trout, the bulk of round goby consumption occurred in the eastern regions in the spring, whereas alewife was the dominant prey in the western regions in the same season (Figs. 3 and 4). For lake trout, only region ($F_{3,\ 474} = 34.40$, $R^2 = 0.17$, $P = 0.001$) and season ($F_{1,\ 474} = 29.66$, $R^2 = 0.04$, $P = 0.001$) had significant influence on diet composition with 78% of the variance being left unexplained. Much of the variation in diet diversity was attributed to individual (8–50%), regional (32–42%), and seasonal levels (12–22%; Fig. 5). Significant lake-wide individual variation in the alewife lengths consumed by lake trout only occurred in 2016 (WIC/TNW = 0.23, P = 0.001; Table 2).

Rainbow trout

A total of 291 and 253 rainbow trout were collected and analyzed in 2015 and 2016 (respectively; Table 1). Terrestrial insects and alewife represented the majority of diet items by both percent diet composition (terrestrial insects: 66% in 2015 and 33% in 2016; alewife: 20% in 2015 and 37% in 2016) and by the index of ration

Table 1
Total number of stomachs, number of stomachs with food, percent of stomachs that were empty, mean length, and range of lengths for each salmonine species in 2015 and 2016.

Species	Year	Total stomachs	# with food	Percent empty	Mean length (mm)	Range of lengths (mm)
Brown trout	2015	114	63	45.6%	554	311–810
	2016	96	63	34.3%	577	299–855
Chinook salmon	2015	524	262	50.0%	684	305–970
	2016	315	180	42.9%	639	262–1000
Coho salmon	2015	227	147	35.2%	556	306–881
	2016	232	187	19.4%	581	289–826
Lake trout	2015	469	228	51.3%	648	305–987
	2016	484	280	42.1%	652	330–921
Rainbow trout	2015	291	198	32.0%	608	373–912
	2016	253	206	18.6%	642	359–850

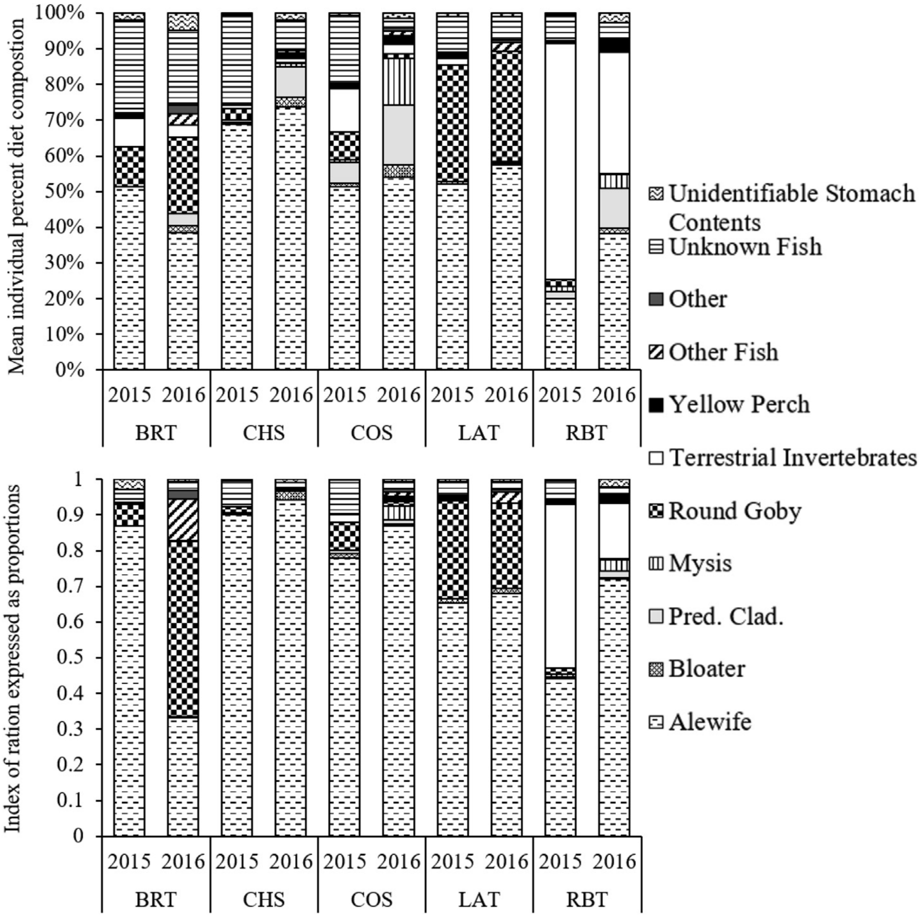

Fig. 2. Mean individual percent diet composition (top) and index of ration expressed as proportions (bottom) for each salmonine species in 2015 and 2016. Mean individual percent diet composition was estimated by taking the mean of individual percent stomach compositions across each species in a given year using only stomachs with food. The index of ration was estimated by averaging weights of each prey category across individual salmonines for each species and then expressed as proportions in a given year using both stomachs with food and empty stomachs. BRT = brown trout; CHS = Chinook salmon; COS = coho salmon; LAT = lake trout; RBT = rainbow trout.

(terrestrial insects: 0.46 in 2015 and 0.16 in 2016; alewife: 0.44 in 2015 and 0.72 in 2016; Fig. 2) Variance of rainbow trout diet composition was significant and roughly equally explainable across all variables (year: $F_{1,\ 381}$ = 27.55, R^2 = 0.06, P = 0.001; season: $F_{1,\ 381}$ = 26.14, R^2 = 0.05, P = 0.001; size-class: $F_{1,\ 381}$ = 21.70, R^2 = 0.05, P = 0.001; region: $F_{3,\ 381}$ = 6.74, R^2 = 0.04, P = 0.001), but 80% of the variance was unexplained. Most of the diversity was partitioned to the individual (10–36%), regional (31–47%), and seasonal levels (9–18%; Fig. 5). Significant individual variation of alewife lengths consumed by rainbow trout was evident during both 2015 (WIC/TNW = 0.07, P = 0.001) and 2016 (WIC/TNW = 0.48, P = 0.001; Table 2).

Across-species diet patterns

Diet composition

When partitioning variation in diet composition across all species, the largest contributor to diet composition variation was species ($F_{4,\ 1652}$ = 94.69, R^2 = 0.17, P = 0.001) followed by region ($F_{3,\ 1652}$ = 40.32, R^2 = 0.05, P = 0.001), with 74% of the variation being unexplained. Season ($F_{1,\ 1652}$ = 42.54, R^2 = 0.02, P = 0.001), size-class ($F_{1,\ 1652}$ = 27.72, R^2 = 0.01, P = 0.001), and year ($F_{1,\ 1652}$ = 21.88, R^2 = 0.01, P = 0.001) had roughly equal and minimal explanatory power. Though there were distinct intraspecific diet patterns, there were some consistent regional and seasonal patterns in the consumption of prey items across the five species. In the spring of 2016, alewife made up larger proportions of the diet in the western region compared to the eastern region for all salmonines, but this trend was not observed in the fall (Fig. 4). *Mysis* and juvenile yellow perch were consumed most in the southern regions in the spring and fall, respectively (Figs. 3 and 4). The consumption of predatory cladocerans and bloater was most common in the late season. Generally, smaller salmonines (<600 mm) consumed more aquatic and terrestrial invertebrates compared to large salmonines (≥600 mm; ESM Fig. S1).

Diet diversity

Chinook salmon had lower diet diversity than other species, especially when compared to lake trout and rainbow trout (Fig. 6). Across all the hierarchical levels, diet diversity declined from $q = 1$ to $q = 3$ (Fig. 6), supporting the general trend of salmonine species consuming primarily a single or few prey types. When all species were considered, the majority of the diversity was partitioned to the individual (9–47%) and species levels (20–59%; Fig. 5).

Alewife lengths consumed and individual variation

The length distribution of alewives consumed by salmonines varied considerably by year (Figs. 7 and 8). Length frequencies of consumed alewives were similar to length frequencies of alewives collected in USGS fall bottom trawls in both years (Fig. 7). In 2015, the length frequency of consumed alewife was unimodal and dominated by large alewife. The few small alewives that were consumed were found in salmonines collected in the southern

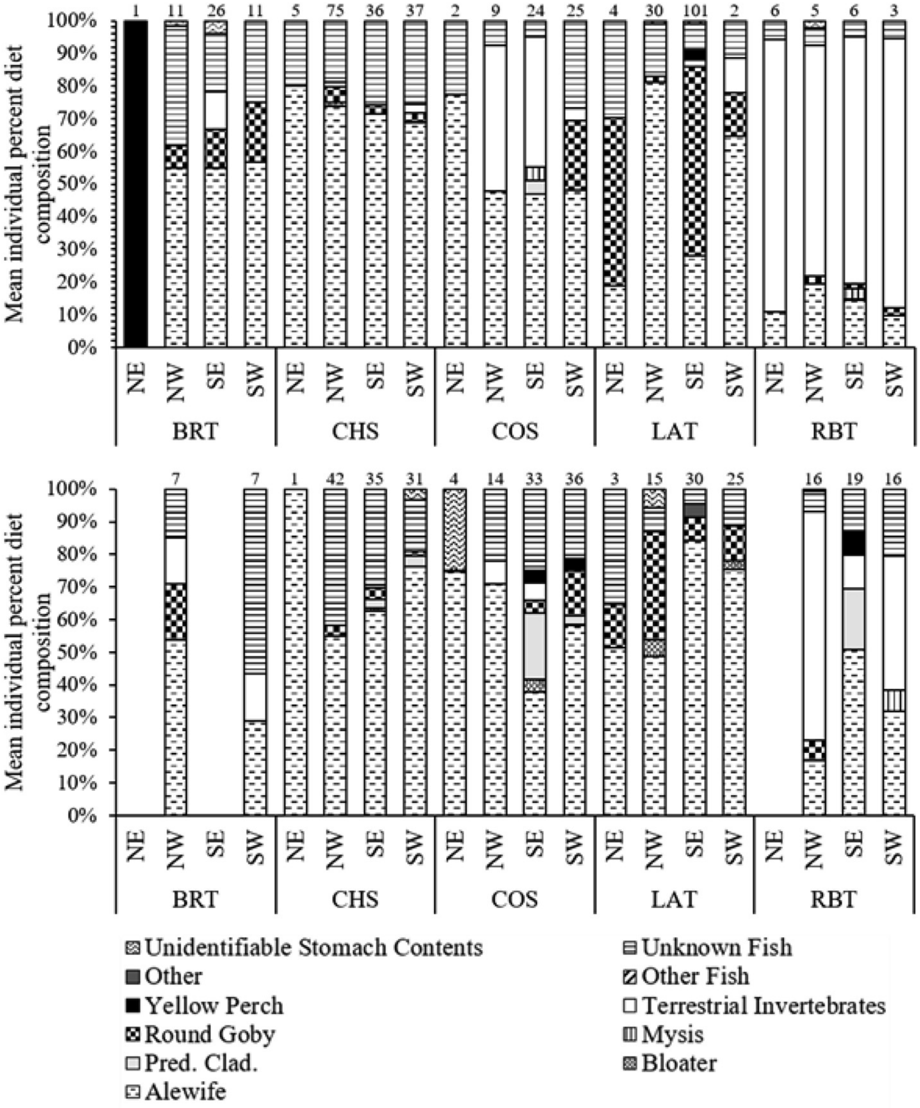

Fig. 3. Regional patterns of mean individual percent diet composition for Lake Michigan salmonines collected in the early (top) and late (bottom) seasons in 2015. Numbers above bar represent the total number of stomachs with food examined.

portions of the lake in the fall (Fig. 8). In 2016, the length frequency of consumed alewife was bimodal with the majority of consumed alewife being alewife <120 mm (Figs. 7 and 8). Most small alewives consumed in 2016 were found in salmonines collected in the western regions of the lake; whereas, salmonines were more likely to consume large alewife in the southeastern region of the lake (Fig. 8). For each salmonine species, the mean alewife length consumed was larger in 2015 (126–140 mm) compared to 2016 (95–131 mm; Table 2). On average, rainbow trout consumed the smallest alewife in both years (2015: 126 mm; 2016: 95 mm) compared to other salmonine species (Table 3; Fig. 7). In 2015, individual variation in alewife lengths consumed was most apparent in southern regions, in the fall, and by small salmonines (ESM Tables S1–S5). In 2016, individual variation in alewife lengths consumed was most common in western regions and was common across all seasons and size-classes (ESM Tables S1–S5).

Discussion

Alewife was clearly the dominant prey for salmonine species in Lake Michigan despite differences in consumption patterns among salmonines. Chinook salmon almost exclusively consumed alewife, with small contributions from other prey, like round goby, yellow perch, bloater, and invertebrates. These observations are consistent with previous studies in lakes Michigan (Jacobs et al., 2013) and Huron (Roseman et al., 2014), in that Chinook salmon have fed almost exclusively on alewife even when alewife abundances were low. In the early 1990′s, there was evidence that Chinook salmon would feed on bloater in times of low alewife abundance and high bloater abundance and even selected bloater over alewife in some cases (Rybicki and Clapp, 1996), but this does not seem to be the case in the recent time period despite bloater abundance again being much higher than alewife (Bunnell et al., 2017). Coho salmon consumed primarily alewife and aquatic (*Mysis* and predatory cladocerans) and terrestrial invertebrates with little contribution from round goby, yellow perch, and bloater. Although the mean individual percent diet composition suggests alewife and invertebrates have equal importance in coho salmon diets, the index of ration suggests coho salmon rely on alewife almost as much as Chinook salmon. That is, stomachs primarily composed of aquatic invertebrates generally weighed much less than stomachs that contained only alewife. Nonetheless, due to alewife scarcity, some

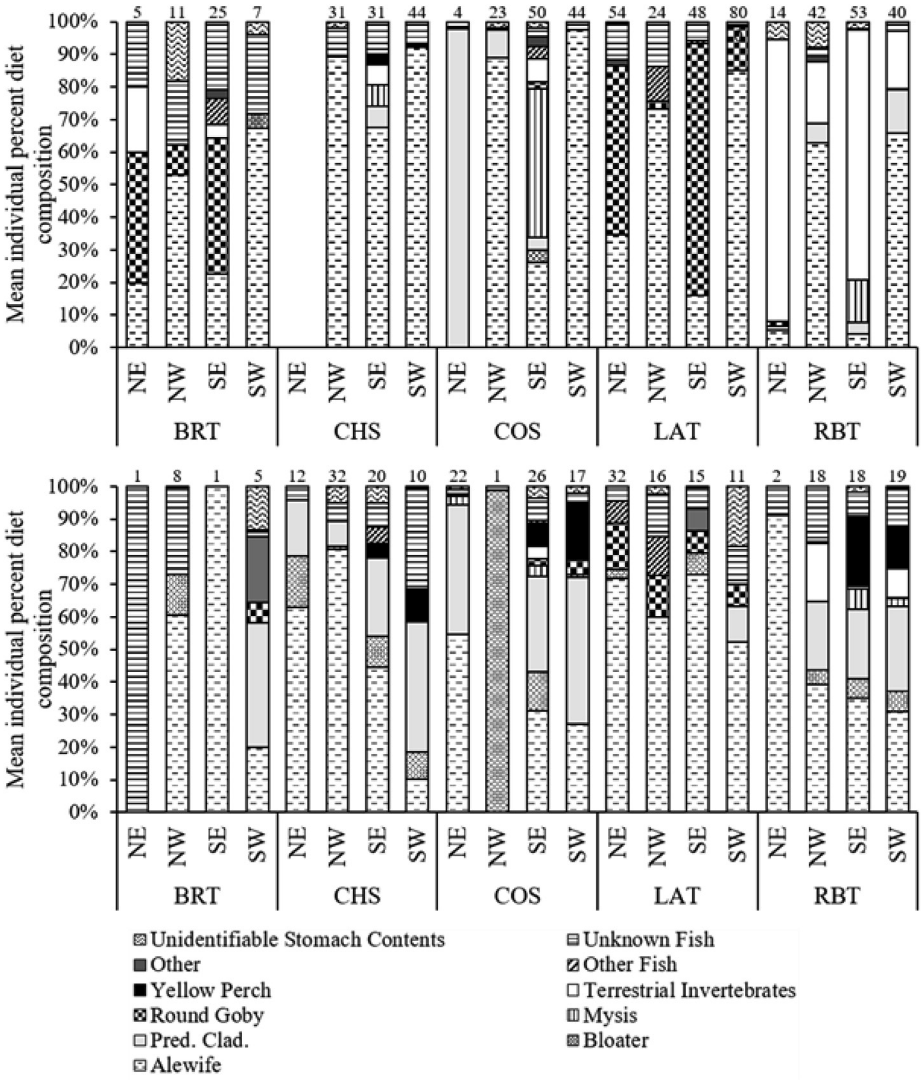

Fig. 4. Regional patterns of mean individual percent diet composition for Lake Michigan salmonines collected in the early (top) and late (bottom) seasons in 2016. Numbers above bar represent the total number of stomachs with food examined.

individual coho salmon have switched to rely on aquatic invertebrates. In contrast, following alewife decline in Lake Huron, coho salmon switched to feeding on shiners (29% by weight), round goby (14.9%), and terrestrial invertebrates (25.9%; Roseman et al., 2014). Rainbow trout were the only predator in this study for which terrestrial invertebrates contributed a substantial proportion to the overall diet, which is consistent with past diet studies completed in lakes Michigan (Rand et al., 1993), Huron (Roseman et al., 2014), and Superior (Conner et al., 1993). Unlike coho salmon, the contribution of invertebrates to rainbow trout diets did translate into a significant portion of total mass consumed and thus likely represents a substantial source of energy. Nevertheless, this seemingly high proportion of terrestrial prey could reflect potential study biases: 1) longer digestion rates for terrestrial insects compared to soft-bodied prey (e.g., fish; Kionka and Windell, 1972) and 2) reliance on angler-caught rainbow trout which may be targeted near features such as thermal bars and scum lines, where terrestrial invertebrates can accumulate (Aultman and Haynes, 1993; Höök et al., 2004; Roseman et al., 2014).

Brown trout and lake trout were the primary consumers of round goby. The diets of lake trout are consistent with previous Lake Michigan studies (Happel et al., 2018; Jacobs et al., 2010), showing that lake trout have increased their reliance on round goby with the decline of alewife. In addition, previous work in Lake Ontario has suggested that round goby is contributing substantially more to the diets of lake trout and brown trout compared to the other three salmonine species (Happel et al., 2017; Yuille et al., 2015). Lake trout does not appear to be switching to its historical native prey, like bloater and sculpins, despite estimated native prey abundance being higher than alewife and round goby (Bunnell et al., 2017). Chinook salmon, coho salmon, and rainbow trout did consume round goby in our study, but their presence in stomachs was comparatively minimal. In Lake Huron during 2009–2011, round goby constituted roughly 10–15% of coho salmon and rainbow trout diet by weight (Roseman et al., 2014), which is higher than was observed in this study. This may suggest that alewife abundance is sufficiently high in Lake Michigan to allow coho salmon and rainbow trout to continue to rely on alewife as their main fish prey. Consistent with the study reported herein, there is little evidence that Chinook salmon consume round goby in lakes Huron (Roseman et al., 2014) and Ontario (Happel et al., 2017; Yuille et al., 2015), which points to the apparent diet inflexibility of Chinook salmon and reliance on pelagic food sources. Because round goby are primary consumers of dreissenid mussels, this indicates that brown trout and lake trout appear to be the pri-

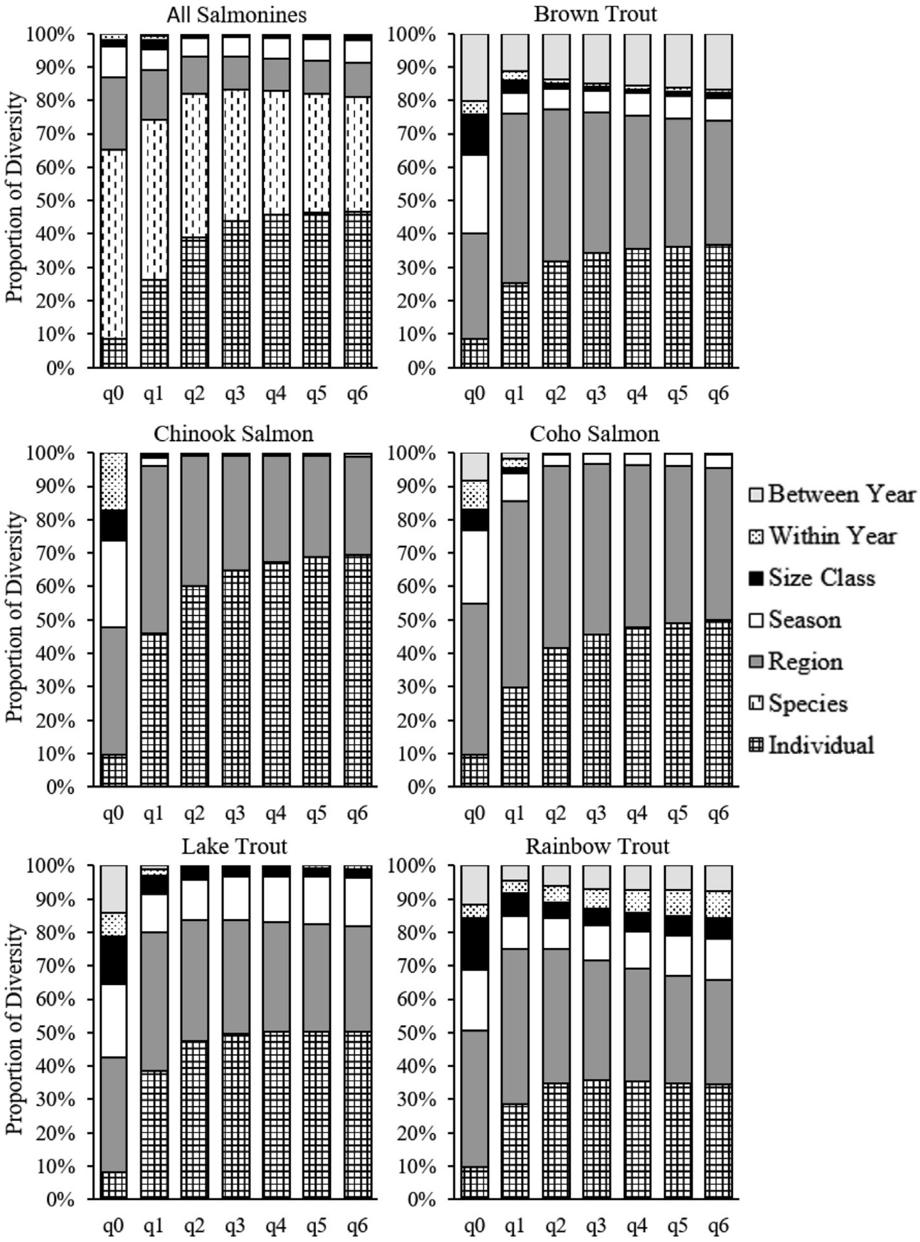

Fig. 5. Diversity partitioning by proportion of diet items found by weight using the abundance categorizations for salmonine species as a whole and each salmonine species individually at q = 0 to q = 6. The species level was only considered for All Salmonines.

Table 2
Results of tests for lake-wide individual variation of alewife lengths consumed by Lake Michigan salmonines in 2015 and 2016. Individual variation was calculated as within individual component divided by total niche width (WIC/TNW) for each species and on individuals that consumed more than one measurable alewife. Values close to 0 indicate individual variation of alewife lengths consumed whereas values close to 1 indicate alewife length generalization. * indicates significant individual variation.

	2015				
	Brown trout	Chinook salmon	Coho salmon	Lake trout	Rainbow trout
WIC	183.74	216.80	187.50	180.22	99.54
TNW	369.15	618.58	1188.63	361.38	1339.97
WIC/TNW	0.50	0.35	0.16	0.50	0.07
P-value	0.096	<0.001*	<0.001*	0.012	<0.001*
Sample Size	15	85	33	70	18
	2016				
	Brown trout	Chinook salmon	Coho salmon	Lake trout	Rainbow trout
WIC	69.34	246.58	250.05	350.24	303.39
TNW	1341.63	1171.39	1271.33	1553.11	628.07
WIC/TNW	0.05	0.21	0.20	0.23	0.48
P-value	0.013	<0.001*	<0.001*	<0.001*	<0.001*
Sample Size	6	70	63	109	53

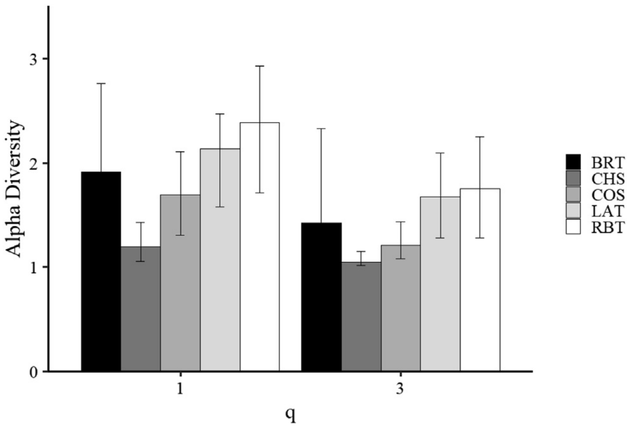

Fig. 6. Overall diet diversity of salmonines at q = 1 and q = 3 using abundance based categorizations. Error bars represent 95% confidence intervals, where non-overlapping intervals represent significant differences. BRT = brown trout; CHS = Chinook salmon; COS = coho salmon; LAT = lake trout; RBT = rainbow trout.

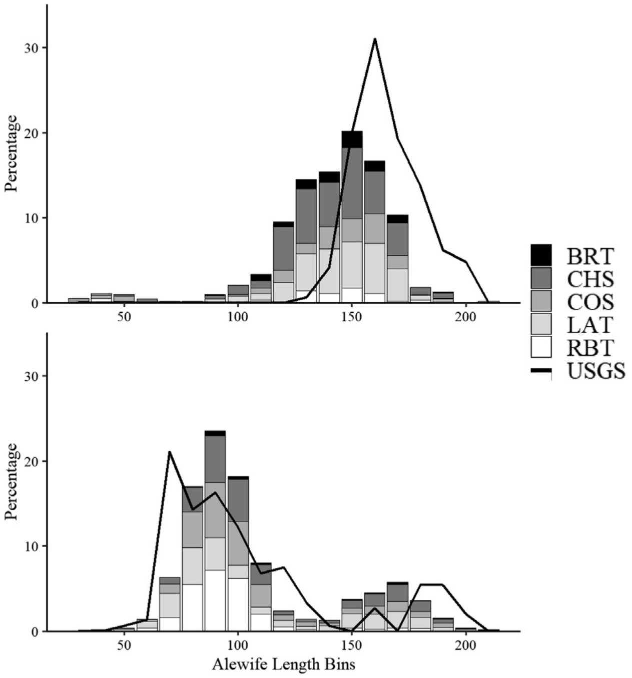

Fig. 7. Length-frequency distributions (percent of total number) for alewives consumed separated by species in 2015 (top) and 2016 (bottom). Additionally, length (mm) frequencies of alewife collected in annual USGS September bottom trawl surveys in 2015 and 2016 are included (black line; B. Bunnell, USGS, pers. comm). BRT = brown trout; CHS = Chinook salmon; COS = coho salmon; LAT = lake trout; RBT = rainbow trout.

mary salmonines taking advantage of the potentially more abundant nearshore, benthic energy pathway in Lake Michigan.

While we observed relatively low diet variation across regions, some spatio-temporal feeding patterns were evident. For brown trout in the spring of 2016 and lake trout in the spring of both years, round gobies were more abundant in diets in eastern regions. Happel et al. (2018) documented similar patterns in lake trout collected from Lake Michigan in the spring of 2011. The eastern shoreline has much less complex (i.e. sandy) habitat compared to the more rocky western shoreline (Janssen et al., 2005), and so benthic fishes such as round goby may be more susceptible to predation along the eastern shore. Additionally, salmonines and round gobies likely have some spatial overlap in spring, when salmonines occupy nearshore areas (Olson et al., 1988) and round gobies are migrating from offshore overwintering habitats to nearshore spawning grounds (Kornis et al., 2012; Walsh et al., 2007). By contrast, alewife typically spawn in spring in Lake Michigan and move back offshore in summer and fall (Brown, 1972), where they may overlap more with salmonines. As a result, salmonines may consume round gobies at a relatively higher rate in the spring and alewife at a higher rate in summer and fall. Other spatial patterns included yellow perch and *Mysis* being consumed more in the southern regions, which is consistent with previous work showing higher catches of these species in southern regions of Lake Michigan (Happel et al., 2015a; Pothoven et al., 2004). Additionally, increased consumption of predatory cladocerans in the late season is consistent with relatively higher *Bythotrephes* abundance in late summer and fall in Lake Michigan (Pothoven et al., 2012; Stadig, 2016).

In 2016 (but not 2015), there were strong spatial and seasonal patterns in the consumption of alewife, which likely arose due to spatial and seasonal differences in their availability as prey. In spring of 2016, alewife consumption was highest in the western regions for all five salmonine species. This is consistent with prior studies finding that particularly high densities of alewife may occur along the western shoreline during spring (Brandt et al., 1991), but this cannot be confirmed for 2016 since annual USGS lake-wide bottom trawl, midwater trawl, and acoustic surveys are conducted in the late summer and early fall (Bunnell et al., 2017; Warner et al., 2017). Nonetheless, it may have been more energetically efficient for salmonines in western Lake Michigan to forage on alewife as opposed to other prey species, like round goby, which prefer rocky substrate and have small home ranges (Janssen et al., 2005; Ray and Corkum, 2001), potentially limiting their encounter rates with salmonines. In the late season, this trend may not have been observed due to offshore movements of alewife during the summer (after spawning has occurred) and are no longer congregated in nearshore areas (Brandt et al., 1991). Alewife distributions across Lake Michigan have been shown to be highly variable from year to year (Warner et al., 2017), which may be why we did not see similar feeding patterns in 2015 and 2016.

Invertebrates are typically an important prey item for smaller salmonines (Jacobs et al., 2013; Jude et al., 1987), and we found this to be especially true for small coho salmon and rainbow trout. This is somewhat consistent with Jude et al. (1987), who documented that brown trout, Chinook salmon, and lake trout appear to switch to a primarily piscivorous diet at a smaller size than rainbow trout and coho salmon. The threshold we used for small salmonines was <600 mm, which is larger than previous studies (<300 mm, Jude et al., 1987; <500 mm, Jacobs et al., 2013). Moreover, since we relied primarily on angler-caught fish and minimum size-limits in Lake Michigan range from 254 (Michigan, Illinois, and Wisconsin waters; MDNR, 2015, 2016; ILDNR, 2016; WDNR, 2016) to 356 mm (Indiana waters; INDNR, 2016), the sizes of salmonines examined may have been too large to observe any distinct size-related effects on relative consumption of invertebrates versus fish prey for brown trout, Chinook salmon, and lake trout. In addition, the prevalence of small alewife and reduced growth rates of alewife (Madenjian et al., 2003) may increase the availability of small alewives to smaller salmonines and allow them to switch from invertebrates to alewife at a smaller size. Further, there has been a significant decline in the abundance of *Diporeia* (Nalepa et al., 2009), which have previously been shown to be important diet items for small Chinook salmon and lake trout (Jacobs et al., 2013; Madenjian et al., 1998). Small salmonines may have shifted toward increased consumption of fish prey as a consequence of the reduced availability of this once important energy-rich, benthic invertebrate.

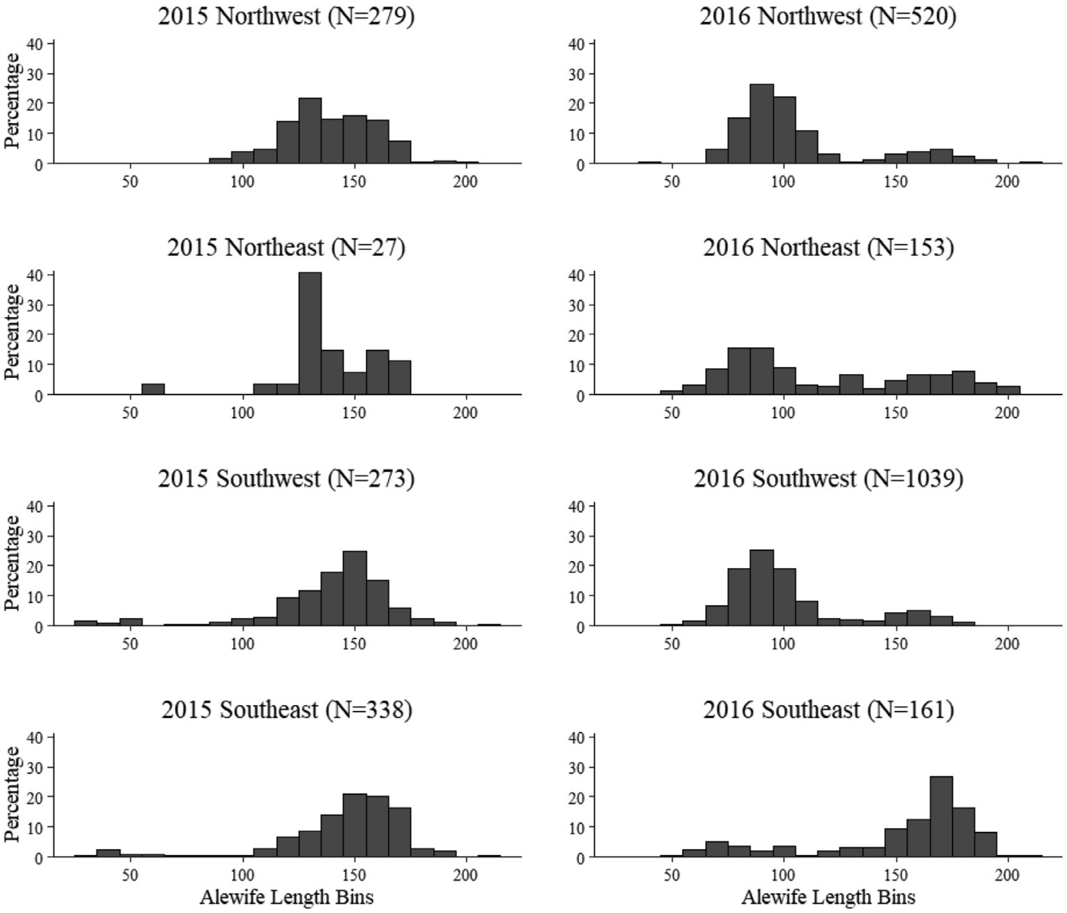
2015 Northwest (N=279)
2016 Northwest (N=520)
2015 Northeast (N=27)
2016 Northeast (N=153)
2015 Southwest (N=273)
2016 Southwest (N=1039)
2015 Southeast (N=338)
2016 Southeast (N=161)

Fig. 8. Regional length (mm)-frequency distributions (percent of total number) for alewives consumed by the five salmonine species in 2015 and 2016. N represents the total number of measurable alewife consumed by salmonines in that region.

Table 3
Mean length (mm) and standard deviation of alewives consumed by each salmonine species in 2015 and 2016.

	Brown trout	Chinook salmon	Coho salmon	Lake trout	Rainbow trout
2015	139 ± 14	134 ± 20	133 ± 32	140 ± 14	126 ± 36
2016	131 ± 43	121 ± 36	115 ± 36	118 ± 35	95 ± 25

At the population level, diet diversity of Chinook salmon and coho salmon hovered around one prey category, whereas the other species generally consumed 2–3 prey categories, depending on *q* values. Chinook salmon and coho salmon are continuing to rely primarily on alewife over other prey items, likely leading to their consistent, relatively low diet diversity. This could be problematic for Chinook salmon and coho salmon if alewife populations were to further decline to similar levels as observed in Lake Huron; although coho salmon displayed some diet plasticity in Lake Huron after the collapse of alewife (Roseman et al., 2014). Differences in diet diversity and observed feeding patterns could also be associated with different foraging behavior of the five species. Previous work has shown that brown trout are associated with nearshore areas with structure (Olson et al., 1988), which could provide better opportunities for feeding on a wider variety of prey, including round goby. The charter boat harvest of lake trout and rainbow trout has shifted closer to shore in recent years (Simpson et al., 2016), which could be reflective of decreased dependence on alewife and greater reliance on nearshore prey items, like round goby or terrestrial invertebrates. In contrast, Chinook salmon and coho salmon harvest has not shifted closer to shore (Simpson et al., 2016), and Chinook salmon feeding at the thermocline (Olson et al., 1988) may limit the diversity of prey items available to these piscivores.

While salmonines expressed variable diet compositions at the population level, much of the variation in the diet composition and diversity was attributed to the individual, especially for Chinook salmon. Although there were clear regional patterns in diet compositions, the overwhelming importance of alewife through space and time reduced the amount of explained variation in diet composition. The high mobility of salmonines, particularly Chinook salmon (Adlerstein et al., 2008), likely allows them to follow and search for schools of alewife, which likely reduces detectable spatial and temporal effects on diet patterns. When compared to Chinook salmon and coho salmon, Kornis et al. (in press) observed greater regional differences in isotopic signatures of brown trout, lake trout, and rainbow trout relative to Chinook salmon and coho salmon. This could suggest that brown trout, lake trout, and rainbow trout are less mobile and consume what is available in their area. Additionally, diet diversity variation observed at the individual level may indicate that individuals have a preference for a specific prey item, which has been documented in some inland trout species (Bridcut and Giller, 1995; Jirka and Kraft, 2017). The lack of diet diversity within an individual could also be associated with the patchiness of prey items in the environment, especially if captured salmonines recently foraged pelagically near the thermocline where alewife tend to inhabit (Brandt, 1980; Riha et al., 2017). Finally, abundances of many forage fish species in 2015 and 2016 were relatively low (Bunnell et al., 2017; Warner et al., 2017), which could make it difficult for individual salmonines to come across multiple types of prey items in a single foraging event.

Clearly, the five species of salmonines in Lake Michigan have the potential to consume a broad range of alewife lengths (this study; Jude et al., 1987; Jacobs et al., 2013). Our study was novel in that the length distributions of alewife varied pronouncedly between the two study years, which allowed the investigation of how salmonines respond to change in alewife length distributions. In 2015, USGS bottom trawl catches (Madenjian et al., 2016) and salmonine stomachs were dominated by large alewife (>110 mm), whereas in 2016, USGS bottom trawls (Bunnell et al., 2017) and salmonine stomachs had a bimodal distribution dominated by small alewife (80–110 mm) with fewer large alewife (150–190 mm; Fig. 7). The substantial number of small alewives consumed in 2016 are likely yearlings that represent a relatively strong 2015 year-class (Madenjian et al., 2016). In 2016, alewife consumed by rainbow trout were almost exclusively small alewives (Fig. 7). On average, rainbow trout consumed the smallest alewife (95 ± 25 mm) compared to the other salmonines, which likely reflects both small alewife and rainbow trout occupying shallower areas of the water column (Aultman and Haynes, 1993; Brandt, 1980). Unlike rainbow trout, the other four species fed on similar sized alewife to one another and roughly in proportion to sizes available in the environment. The 2016 length distribution of consumed alewife showed substantial spatial variation with most small alewives consumed on the western side of Lake Michigan compared to the eastern side where stomachs were dominated by large alewife. It appears that salmonines can be quite flexible in response to annual and spatial variations in alewife length distributions, which may prove beneficial since high variability in alewife recruitment success can cause pronounced year-to-year (Madenjian et al., 2005) and potentially spatial changes in alewife length distributions.

To our knowledge, elucidating consumption patterns of salmonines on different sizes of alewife has only been conducted at the population level (e.g., Jude et al., 1987; Jacobs et al., 2013) rather than investigating individual-level feeding patterns on alewife. Our results show that individual variation of alewife lengths consumed was common for Lake Michigan salmonines in both years; though there was a much broader size range available in 2016 compared to 2015. Individual variation may help limit competition through reduced niche overlap (Bolnick et al., 2010, 2003) and help reduce the intensity of predation (McCann et al., 1998) on a specific size range of alewife. Although individual variation is commonly associated with competition, it can also be due to individuals feeding in patchy environments. When foraging in a patchy environment, individual stomach contents can represent the localized prey abundance rather than an individual's preferred prey or the prey abundance over a broad area. For example in 2016, salmonines foraging on the eastern side of Lake Michigan may have had limited opportunities to feed on both small and large alewife compared to the western side. Young-of-year and adult alewives occupy distinct parts of the water column and do not typically school together (Brandt, 1980), which likely further increases the patchiness of the environment. When a salmonine encounters a school of alewife it may simply consume the alewife available in the school regardless of size. Brown trout, Chinook salmon, and lake trout of Lake Ontario have been shown to forage above, within, and below the thermocline, which overlaps with the different thermal distributions of young-of-year and adult alewife (Olson et al., 1988). This could result in some individuals feeding on young-of-year and others on adult alewife, making it appear that individuals have a preference. Due to the limitations of stomach content analyses (representing diet over past 12–48 h; Hyslop, 1980), it is impossible to confirm that individual variation is due to an individual's long-term preference or to patchy environments unless the same individual's stomach contents are collected multiple times.

Lake Michigan salmonines have altered their foraging patterns in response to lake-wide shifts in food web energy flow and community structure. Alewife continues to be the dominant prey item for Lake Michigan salmonines, especially for Chinook salmon, which appear less flexible than the other salmonine species. Coho salmon did have similar reliance as Chinook salmon on alewife; but, if alewife populations continue to decline evidence in Lake Huron suggests that coho salmon could rely more on other prey, like shiners, round goby and terrestrial invertebrates (Roseman et al., 2014). Brown trout, lake trout, and rainbow trout, exhibited greater diet diversity and took advantage of other prey like round goby and terrestrial invertebrates. The continued success of Lake Michigan's salmonine fishery and the stability of the upper food web may depend on the ability of salmonines to rely less on alewife and potentially more on abundant invasive round goby and other prey items. In addition, most variance in diet composition and diversity was expressed at the individual level, suggesting individual variability in foraging behavior or preference may represent an important aspect of the offshore Lake Michigan food web. The Lake Michigan food web is likely not near steady state, as the abundance and distribution of various invasive species continues to change. During this transitional period, salmonine management plans will need to be informed by ongoing measurements of trophic structure to determine the ability of each species to adjust to changes in the availability and quality of invertebrates and forage fish. Specifically, the diet data included in this study could help update diet inputs used by fisheries managers to model salmonine consumption in Lake Michigan. These consumption models feed directly into the predator/prey ratio model (Tsehaye et al., 2014) that managers rely on to inform stocking decisions. In addition, our study underscores spatio-temporal and individual feeding patterns that go beyond lake-wide summaries in providing insight to managers.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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cle are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2020.05.010.

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