



ORIGINAL ARTICLE

The influence of ontogeny and prey abundance on feeding ecology of age-0 Lake Whitefish (*Coregonus clupeaformis*) in southeastern Lake Michigan

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Abstract

A shift towards oligotrophic conditions in Lake Michigan has led to concern that altered trophic pathways are leading to lower early life survival and recruitment for Lake Whitefish (*Coregonus clupeaformis*). This study evaluated ontogenetic shifts in age-0 Lake Whitefish diets and evaluated how feeding ecology and the amount of food eaten varied with prey abundance and composition at a site in southeastern Lake Michigan during 2014–2017. Although prey densities varied among years, cyclopoid copepods were overall the most abundant prey available. In turn, cyclopoids were the predominant prey item in diets each year, particularly for the smallest larval Lake Whitefish. However, there was a tendency for the importance of cyclopoids to decline somewhat in each diet index as fish grew and other prey such as calanoid copepods, Bosminidae, Daphniidae and/or chironomids increased in importance. High zooplankton abundance, especially high cyclopoid abundance, available to the small size groups of Lake Whitefish (<21 mm) in 2014 was associated with high food mass/fish, high number of zooplankton eaten/fish, and low incidence of empty stomachs compared with 2015–2017. As fish grew, the impact of food abundance on prey consumption diminished somewhat, indicating that the relationship between fish feeding ecology and the prey environment can change quickly with fish size during the early life period.

KEYWORDS

coregonid, Cyclopoida, early life history, Great Lakes, larval fish, prey selection

1 | INTRODUCTION

The Laurentian Great Lake, Lake Michigan, has undergone a dramatic transformation over the last two decades. Zebra mussels *Dreissena polymorpha* were found in the lake in the late 1980s, and were soon replaced by quagga mussels *Dreissena rostriformis bugensis*, which were found in northern Lake Michigan in 1997 (Nalepa, Fanslow, & Lang, 2009). Quagga mussels rapidly spread throughout the lake leading to declines in pelagic primary production and

a shift towards a more oligotrophic state (Fahnenstiel et al., 2010). The benthic amphipod *Diporeia* spp., which had accounted for over 70% of the benthic biomass in offshore regions, underwent dramatic declines throughout Lake Michigan in the late 1990s (Nalepa et al., 2009). Finally, the biomass of crustacean zooplankton also declined as the community composition shifted towards more oligotrophic tolerant species (Pothoven & Fahnenstiel, 2015).

As Lake Michigan and other Great Lakes have shifted towards oligotrophy, concern has risen about sustainability for one of the

most economically valuable and culturally important fisheries in the Laurentian Great Lakes, the Lake Whitefish *Coregonus clupeaformis* fishery (Brenden et al., 2010; Ebener et al., 2008; Gobin, Lester, Cottrill, Fox, & Dunlop, 2015; Gobin, Lester, Fox, & Dunlop, 2016; Hoyle, Johannsson, & Bowen, 2011). Changes in adult Lake Whitefish diets and declines in their condition and growth have been attributed to the changing food web in the Great Lakes (Lumb, Johnson, Cook, & Hoyle, 2007; Pothoven, Nalepa, Schneeberger, & Brandt, 2001; Rennie, Sprules, & Johnson, 2009). Low recruitment to the fishery has recently led to concern about the impact that food web changes have had on the early life stages of Lake Whitefish because environmental changes can have a disproportionate effect on the early life stages of fish (Claramunt, Muir, Johnson, & Sutton, 2010; Claramunt, Muir, Sutton, et al., 2010; Muir et al., 2010; Ryan & Crawford, 2014). Declines in zooplankton following re-oligotrophication of some European lakes led to reduced survival, growth rates and year class strength for larval coregonids (Eckmann, 2013; Rellstab, Bürgi, & Müller, 2004).

Knowledge about the early life period is critical for understanding Lake Whitefish recruitment because their year class strength is likely determined during the embryonic and larval stages (Freeberg, Taylor, & Brown, 1990; Muir et al., 2010; Taylor, Smale, & Freeberg, 1987). Adult Lake Whitefish spawn in late fall and the eggs overwinter in rocky areas and hatch soon after ice-out. Larval Lake Whitefish move into nearshore beach areas or embayments where exogenous feeding begins soon after hatching. It is generally assumed that adequate food quality and quantity are required for larval fish growth, which in turn, is critical for survival (Miller, Crowder, Rice, & Marschall, 1988). Food shortage, whether due to low prey numbers or high larval densities, is considered a source of elevated mortality for coregonid larvae (Karjalainen, 1992; Naesje, Sandlund, & Jonsson, 1986; Rellstab et al., 2004), including Lake Whitefish (Claramunt, Muir, Sutton, et al., 2010; Freeberg et al., 1990; Taylor & Freeberg, 1984; Taylor et al., 1987).

Understanding early life feeding ecology is critical to understand the bottlenecks for recruitment of Lake Whitefish. The first objective of this study was to describe the feeding ecology of Lake Whitefish through their early life history. The second objective was to determine the relationship between prey abundance and the amount of food eaten by age-0 Lake Whitefish. To achieve these objectives, diet composition and prey selectivity of age-0 Lake Whitefish and zooplankton abundance and composition were determined during four years at a site in southeastern Lake Michigan. The results will provide insight into what trophic pathways support Lake Whitefish recruitment and whether these pathways change during early life ontogeny and across years.

2 | METHODS

Sampling took place in southeastern Lake Michigan at a site in Muskegon, Michigan, USA, along Pere Marquette Beach, just south of the South Breakwater, at about 43°13.41'N, 086°20.19'W.

Sampling took place within the March–June period during 2014–2017, with sampling beginning just after ice-out. Initial sampling was done using a 1 m (depth) × 2 m (width) × 3 m (length), 500- μ m mesh neuston net, that was towed by hand by two people using bridles on each side of the net. Two 61-m long tows were made with the net in about 0.5 m water, with sampling occurring once each week. Once Lake Whitefish were about 20 mm long, neuston net sampling ended and collections were made with a beach seine. The seine was 45.7 m (length) × 1.8 m (height) with a 1.8 m × 1.8 m × 1.8 m bag and 3.2-mm delta mesh. One end of the seine was pulled perpendicular from shore until the seine was fully extended into the lake (45.7 m) and then the offshore end was pulled back to shore in a loop-like fashion. During each sampling date, a total of three seine hauls were conducted with a distance of at least 50 m between tows. Seining was done at least twice each year, with at least one week between sampling events. Lake Whitefish were preserved in 95% ethanol upon collection.

Once Lake Whitefish were observed in neuston nets, zooplankton collections began. A single zooplankton tow was done at each site immediately after fish sampling using a 0.3 m (diameter) × 0.9 m (length), 64- μ m mesh zooplankton net. The zooplankton net was attached to a pole and towed by hand off to the side of the individual in water about 0.5 m deep for a distance of 15.2 m. Zooplankton were narcotized and preserved using 10% buffered sugar formaldehyde. Water temperature was determined using a YSI Pro Plus probe.

In the laboratory, total length (not corrected for shrinkage) of Lake Whitefish was measured and the entire digestive tract was removed and the contents were identified and enumerated. A subsample of fish was weighed to determine preserved weight and a weight–length regression was created to determine the preserved weight for all fish. The first branchial arch on a subsample of fish was also removed, and gill raker spacing (GRS) was determined following Palkovacs and Post (2008).

All fish, or a subsample of about 30 fish/haul if large numbers were caught, were used for diet analysis. Whole prey organisms and partial organisms with heads attached were counted as individuals. Zooplankton were classified as Cyclopoida, Calanoida, Harpacticoida, Daphniidae, Bosminidae, Chydoridae, Sididae and copepod nauplii. No dreissenid veligers were eaten and they were excluded from further analyses. Benthic macroinvertebrates were classified to varying levels and included Chironomidae (larvae and pupae), Amphipoda, Ostracoda and Ephemeroptera. Lengths of whole organisms were measured using Image-Pro (V. 9.1). Weight–length regressions were used to estimate the mean dry mass for each prey type from stomachs (Benke, Huryn, Smock, & Wallace, 1999; Culver, Boucherle, Bean, & Fletcher, 1985; Malley, Lawrence, MacIver, & Findlay, 1989; Nalepa & Quigley, 1980), which was then multiplied by the total number of that respective prey to determine its dry mass contribution to the diet for each fish. Fish were binned into 5 mm size groups (i.e., ≤ 16 mm, 16.1–21 mm, 21.1–26 mm, 26.1–31 mm and ≥ 31 mm) for analysis of diet patterns. For zooplankton analysis, a subsample was taken with a Hensen–Stemple pipette so that at least 600 organisms were counted and identified.

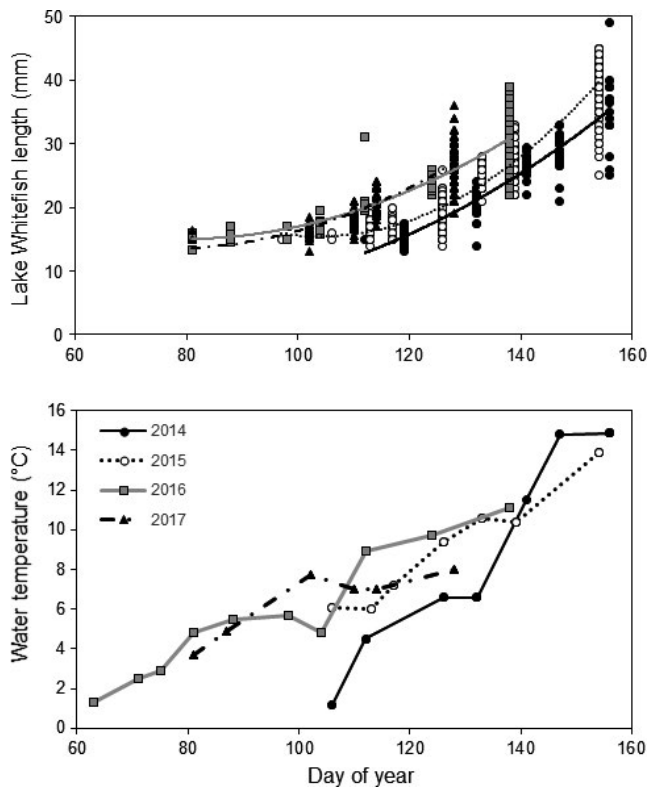


FIGURE 1 Lake Whitefish total length (top) and water temperature (bottom) as a function of day of year for 2014–2017

Analysis of similarities (ANOSIM) was used to test for differences in diet assemblages (based on dry mass) among size groups within each year and within each size group across years. This approach is analogous to ANOVA, with a nonparametric permutation applied to a rank similarity matrix of samples (Clarke & Warwick, 2001). Diet mass was square root transformed to down-weight highly abundant species (Clarke & Warwick, 2001) and was used to create a Bray–Curtis similarity matrix for ANOSIM. R -values from ANOSIM range from -1 to $+1$, and generally lie between 0 , where groups are indistinguishable and $+1$, where all similarities within groups are less than any similarity between groups (Clarke & Gorley, 2001). R -values provide a measure of how separated groups are, with R -values < 0.25 indicating almost no separation between groups, R -values of 0.25 – 0.5 indicating different groups but with considerable overlap, R -values of 0.5 – 0.75 indicating clearly different group with some overlap, and R -values > 0.75 indicating clear separation between groups (Clarke & Gorley, 2001, 2006). R -values were used rather than P -values from ANOSIM tests because this is the most useful measure of how separated the groups are (Clarke & Gorley, 2001, 2006). ANOSIM was performed using Primer v 5.2.9.

To calculate the amount of prey available for a given size group of fish, prey abundances from each sample date were weighted by the number of fish with nonempty stomachs in a particular size group of interest for each corresponding date. Selectivity of various zooplankton groups was determined using the selectivity coefficient W' (Vanderploeg & Scavia, 1979) using prey numbers for both diets

and the availability in the environment. Only zooplankton prey were considered for selectivity because prey availability was not known for other prey types. However, this analysis should provide accurate insight into selectivity patterns for the size of Lake Whitefish that were collected because 99% of prey eaten (by number) were zooplankton. The selectivity coefficient W' varies between 0 for no ingestion of a prey type to 1 , the value for the most preferred prey type(s). Selectivity was calculated for each individual fish and the percentage of fish that preferred a particular prey item above all other prey, that is the number of times $W' = 1$ for that prey type, was determined.

The dry mass of food/fish (ln transformed), was compared across years with ANCOVA after first checking for interactions between the covariate (fish length or fish weight) and factor (year). The number of prey eaten/fish was compared across years for each size group of fish using ANOVA. The analyses of food amounts were restricted to a similar size range of fish across years (i.e., ≤ 32 mm). To evaluate the role of prey abundance on feeding, the mean number of zooplankton eaten/fish was evaluated as a function of cyclopoid copepod abundance (ln transformed) for each size group.

3 | RESULTS

Overall, 768 of the 800 age-0 Lake Whitefish examined had identifiable food in their digestive tract. The length range of Lake Whitefish examined was 13–49 mm. Fish preserved weight as a function of length was described by the equation: $\text{Weight (g)} = 0.00000188 \times \text{TL (mm)}^{3.296}$ ($R^2 = 0.99$, $n = 121$). Nearly, all individuals with yolk sacs were ≤ 16 mm, and 38% of the Lake Whitefish ≤ 16 mm still had yolk sacs. The timing of Lake Whitefish hatching appeared to vary each year, with initial appearance ranging from late March (2016 and 2017) to late April (2014) (Figure 1). Catch rates were highly variable within each year, with highest overall CPUE for the neuston net in 2015 and for the seine in 2017 (Table 1). Water temperatures were considerably cooler in 2014 compared with other years, but rose rapidly once warming began (Figure 1).

There was strong separation in diet assemblages (by weight) among size groups each year, particularly between the two smallest size classes and the largest size class, although the differences among size groups were less strong in 2017 compared with the other years (Table 2). Although there were differences in diet assemblages among years for each size group, there was still substantial overlap across years (Table 3). In general, cyclopoid copepods were the most important prey for all size classes, but as fish grew, other prey including Bosminidae, calanoid copepods, Daphniidae and chironomids made higher contributions to the diets, except during 2017, when prey other than cyclopoids were relatively minor for all size classes (Figure 2). Prey other than cyclopoids contributed more to the diets of the smallest Lake Whitefish in 2015 and 2016 than in 2014 and 2017.

The highest abundance of zooplankton prey available to age-0 Lake Whitefish was in 2014, especially for the 16.1–26 mm size

TABLE 1 Mean CPUE (SD) for age-0 Lake Whitefish collected in neuston nets and seines during 2014–2017

Year	Gear	CPUE (SD)
2014	Neuston	0.37 (0.81)
2015		0.94 (1.39)
2016		0.04 (0.06)
2017		0.15 (0.20)
2014	Seine	21 (26)
2015		86 (109)
2016		84 (133)
2017		200 (249)

Note: Units for CPUE are number/m³ for the neuston net, and number/haul for the seine and is based on the mean of each daily mean catch.

TABLE 2 Diet overlap (*R*-values) from ANOSIM between pairs of Lake Whitefish size groups for each year

Size groups (mm)	Year			
	2014	2015	2016	2017
≤16, 16.1–21	0.11	0.12	–0.06	0.37
≤16, 21.1–26	0.42	0.58	0.92	0.64
≤16, 26.1–31	0.57	0.69	0.99	0.92
≤16, >31.1	0.91	0.90	0.98	0.49
16.1–21, 21.1–26	0.15	0.27	0.56	0.06
16.1–21, 26.1–31	0.35	0.47	0.68	0.40
16.1–21, ≥31.1	0.85	0.83	0.77	0.21
21.1–26, 26.1–31	0.06	0.08	0.63	0.22
21.1–26, ≥31.1	0.65	0.66	0.64	0.01
26.1–31, ≥31.1	0.66	0.44	0.02	–0.06

Note: *R*-values < 0.25 indicate almost no separation between groups, *R*-values of 0.25–0.5 indicate different groups but with considerable overlap, *R*-values of 0.5–0.75 indicate clearly different group with some overlap, and *R*-values > 0.75 indicate clear separation between groups (Clarke & Gorley, 2001, 2006).

groups (Figure 2). Available prey abundances were low for all size groups in 2015. Overall, cyclopoid copepods were the most abundant prey, but Bosminidae made a sizeable contribution to the available zooplankton community in some years, especially for larger size groups of Lake Whitefish. The smallest prey (Table 4), nauplii and veligers were occasionally abundant as well, but they were rarely or never eaten respectively.

Gill rakers were poorly developed for fish smaller than 20 mm, and no GRS measurements could be made for these fish. For fish 21–31 mm long, GRS increased with length: $GRS \text{ (mm)} = 0.007 \text{ TL (mm)} - 0.115$ ($p < 0.001$, $R^2 = 0.54$, $n = 25$). The predicted GRS increased from 0.03 to 0.10 mm between 21 and 31 mm, so these fish were capable of eating veligers and nauplii, but did not. GRS did not change with fish length for fish 32–45 mm long ($p = 0.22$, $n = 27$). Mean GRS for fish 32–45 mm long was 0.11 mm, so even

the smallest prey were at least somewhat accessible to the largest fish in the study.

The frequency occurrence of cyclopoid copepods in diets was never less than 83% for any size group/year. Cyclopoid copepods were selected by over half the fish for any given size group each year (Figure 2). In 2014 and 2017, the percentage of fish that selected cyclopoids decreased with fish size, and prey such as calanoid copepods, Daphniidae and Bosminidae were selected more frequently. In 2015 and 2016, patterns in selectivity were less clear, with cyclopoids a highly selected prey along with calanoids, Daphniidae and other prey (i.e., Harpacticoida and Chydoridae) for certain size groups.

Most fish (96%) had food in their stomachs, and most fish with empty stomachs were in the smallest size group (62%). The incidence of empty stomachs for the ≤16 mm size group was 2%, 17%, 28% and 50% in 2014, 2015, 2016 and 2017 respectively. For food mass/fish, there was a significant interaction between the covariate (length or weight) and year ($p < 0.03$), so that food mass/fish was highest in 2014 for the smallest fish, but in 2015 and 2016 for the largest fish (Figure 3). The slope relating food mass/fish to fish mass indicated that the increase in food mass/fish was simply a function of fish growth in 2017 ($b = 1.00$, 95% CI = 0.90–1.11), but factors other than fish growth affected the relationship in 2014–2016. Food mass/fish as a function of fish mass increased at a slower rate in 2014 ($b = 0.66$, 95% CI = 0.56–0.76) than in 2015 ($b = 1.29$, 95% CI = 1.16–1.42) or 2016 ($b = 1.30$, 95% CI = 1.17–1.42). The number of prey eaten/fish also increased with fish size, with significant differences among years within all size groups ($p < 0.030$) except for the largest size group (Figure 3). The number of prey eaten/fish was highest in 2014 for the ≤16 mm, 16.1–21 mm, and 21.1–26 mm size groups and in 2016 for the 26.1–31 mm size group. There was some evidence that the number of zooplankton eaten/fish was positively related to the abundance of cyclopoid copepods (Figure 4), with significant relationships found for the ≤ 16, 16.1–21 and 26.1–31 mm size groups ($R^2 > 0.51$, $p < 0.01$).

4 | DISCUSSION

Although there was a general tendency for the importance of cyclopoid copepods in each index to decline as fish grew, cyclopoid copepods were clearly an important food source for all sizes of age-0 Lake Whitefish. The importance of cyclopoid copepods in diets from this study is consistent with results from other studies in various systems (Chouinard & Bernatchez, 1998; Hart, 1930; Hoyle et al., 2011; Johnson, McKenna, Chalupnicki, Wallbridge, & Chiavelli, 2009; Pothoven, Höök, & Roswell, 2014). A study in the Bay of Quinte, Lake Ontario, found a correlation between cyclopoid and juvenile Lake Whitefish abundances (Hoyle et al., 2011). Cyclopoids were the primary prey for the smallest larval Lake Whitefish each year in this study despite strong variation in their abundance. Cyclopoids were the dominant food eaten just after the yolk sac had been absorbed

and fish were entirely dependent on exogenous feeding, a time frame when mortality for larval coregonids is thought to be highest (Freeberg et al., 1990; Sutela & Huusko, 1997; Taylor & Freeberg, 1984). Thus, cyclopoids may represent a critical food source for the survival of the earliest stages of larval Lake Whitefish (Freeberg et al., 1990).

Ongoing changes in the lower food web of Lake Michigan have impacted cyclopoid copepod populations, and in turn, could threaten recruitment success for Lake Whitefish. The proliferation of invasive

dreissenid mussels in the Great Lakes has been associated with declines in cyclopoid copepod abundance and shifts in zooplankton community composition favouring calanoid copepods, which are more tolerant of oligotrophic conditions (Pothoven, Höök, Nalepa, Thomas, & Dyble, 2013; Stewart, Johannsson, Holeck, Sprules, & O’Gorman, 2010; Vanderploeg et al., 2012). However, cyclopoids were the dominant zooplankton in the very shallow beach site in this study, a depth region that is rarely sampled for zooplankton. It is possible that other nursery areas that are not as productive as this study site, which was adjacent to the outflow from a drowned river mouth, could have zooplankton communities dominated by calanoid copepods.

The importance of cyclopoid copepods over calanoid copepods in larval Lake Whitefish diets could be related in part to differences in prey swimming behaviour. A study on the closely related *Coregonus lavaretus* found that cyclopoids might be passively selected by larval Lake Whitefish because of poor capture success on larger prey, the small size of cyclopoids, and the relatively high abundance of cyclopoids in the spring, whereas the swimming behaviour of calanoids might reduce encounter rates and the probability that this prey would be eaten (Anneville et al., 2011). In a laboratory study, Teska and Behmer (1981) found that larval lake whitefish (14–18 mm) did

TABLE 3 Diet overlap (R-values) from ANOSIM between pairs of years for each Lake Whitefish size group

Years	Size group (mm)				
	≤16	16.1–21	21.1–26	26.1–31	≥31.1
2014, 2015	0.44	0.31	−0.02	0.44	0.47
2014, 2016	0.47	0.02	0.12	0.31	0.59
2014, 2017	0.53	0.02	0.62	0.26	0.00
2015, 2016	−0.09	0.64	0.09	0.26	0.72
2015, 2017	0.11	0.25	0.56	0.44	0.70
2016, 2017	0.12	0.20	0.41	0.49	0.44

Note: See Table 2 for explanations of R-values.

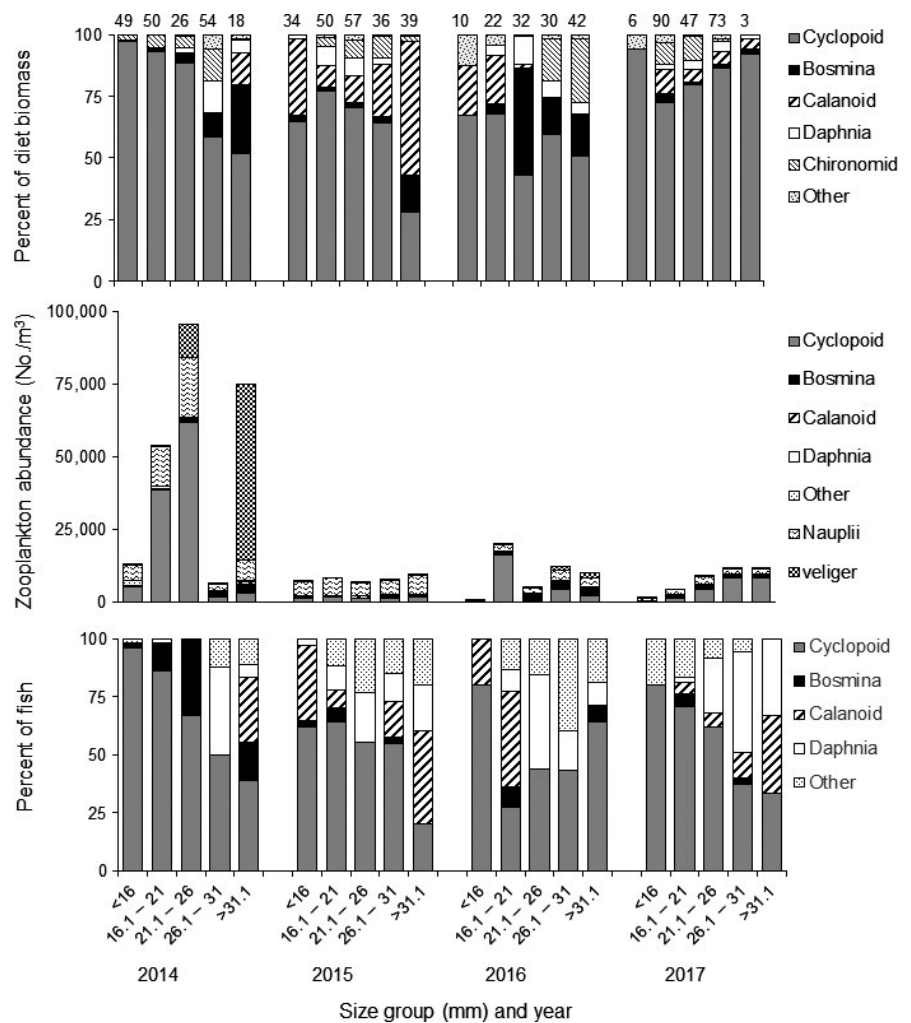


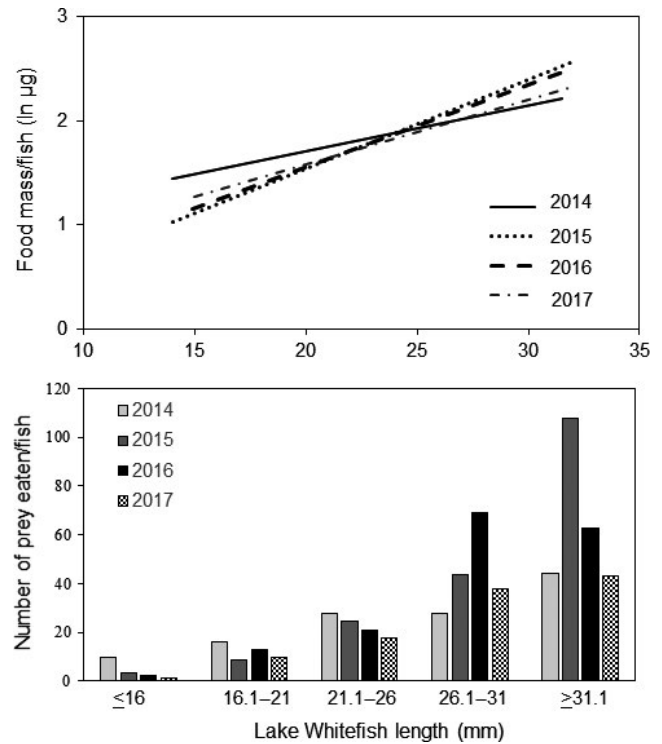
FIGURE 2 Diet composition (percent dry biomass, top), available zooplankton abundance (middle), and percent of fish that selected each zooplankton type (bottom) for five size groups of Lake Whitefish in southeastern Lake Michigan during 2014–2017. The number of fish with food in their stomachs is provided above each bar on the top panel

TABLE 4 Mean length of various zooplankton prey groups collected in a 64- μ m mesh zooplankton net during 2014–2017

Prey group		Length (mm)
Copepod	Copepod nauplii	0.19
Cyclopoid copepod	Cyclopoid juvenile	0.56
	<i>Diacyclops thomasi</i> adult	0.95
Calanoid copepod	Diaptomid juvenile	0.64
	<i>Leptodiaptomus ashlandi</i> adult	0.95
	<i>Leptodiaptomus sicilis</i> adult	1.40
	<i>Eurytemora affinis</i> juvenile	0.65
Cladoceran	<i>Bosmina longirostris</i>	0.34
	<i>Chydorus</i> spp.	0.31
	<i>Daphnia galeata mendotae</i>	0.76
	<i>Daphnia longiremus</i>	0.51
	<i>Daphnia retrocurva</i>	0.74
Other	<i>Dreissena veliger</i>	0.10

select the calanoid copepod *Diaptomus sicilis* over cyclopoids and cladocerans when *D. sicilis* were relatively abundant. However, in Saginaw Bay, Lake Huron, calanoids were rarely eaten by larval Lake Whitefish despite being relatively abundant (Pothoven et al., 2014). In this study, although calanoid copepods were eaten by the smallest age-0 Lake Whitefish during some years, those years were also associated with lower amounts of food/fish, suggesting that calanoids are not necessarily a suitable substitute for cyclopoids, especially for the smallest Lake Whitefish larvae.

Even though cyclopoids were the dominant food item, other prey became increasingly important as Lake Whitefish larvae grew. However, the degree of diet variation across fish sizes (Anneville, Laine, Benker, Ponticelli, & Gerdeaux, 2007; Pothoven et al., 2014) or years (Anneville et al., 2007) in this study was not as strong as in some other coregonid diet studies, due to the consistently high contribution of cyclopoids to the diet in this study. The ability to shift to large prey may facilitate growth and survival of age-0 fish (Crowder, McDonald, & Rice, 1987; Miller et al., 1988), but individuals can still focus on relatively small but abundant prey. The GRS for Lake Whitefish indicates that most zooplankton would still be vulnerable to even the largest fish in the study. Ponton and Müller (1990) found that larval coregonids ate abundant, small prey even when larger prey were available in order to decrease the costs of prey capture. In Saginaw Bay, Lake Huron, there was a shift in Lake Whitefish diets around 17–18 mm, when cyclopoids declined from 50% of the diet to < 20% as *Daphnia* spp. increased in importance in both diets and the environment (Pothoven et al., 2014). By contrast, in this study, *Daphnia* spp. abundance was low throughout the sampling season and the feeding strategy of Lake Whitefish did not shift towards feeding on them, although they were selected more

**FIGURE 3** Regression lines relating $\ln(\text{prey mass}/\text{fish})$ to Lake Whitefish total length (top) and the average number of prey eaten/fish for five size groups of Lake Whitefish (bottom) during 2014–2017

frequently as fish grew. It is possible that the diet shifts to large cladocerans by coregonids is a result of increased encounter rates and vulnerability of these prey, rather than a critical ontogenetic shift. For example, even though larger fish did not shift towards feeding on *Daphnia* spp. in this study, the percentage of empty stomachs was still low for fish in the 16–21 mm size group and there was a steady increase in prey/stomach.

As expected, there was a relationship between the number of zooplankton eaten/fish and cyclopoid abundance, especially for the smallest fish. This finding is consistent with previous work that has linked survival and growth with prey availability for European coregonids (Dabrowski, 1989; Karjalainen, 1992; Naesje et al., 1986; Rellstab et al., 2004) as well as Lake Whitefish (Freeberg et al., 1990; Hoyle et al., 2011; Taylor & Freeberg, 1984; Taylor et al., 1987). Further support that prey abundance impacts the early life history of Lake Whitefish was based on a number of other findings in this study. Most notably, food mass/fish was highest and the percentage of fish with empty stomachs was lowest in 2014, the year with the highest available prey abundances, including cyclopoids, for the small size groups of fish. When considered as a whole, these results indicate that food abundance can affect feeding success of early stage larval Lake Whitefish. Interestingly, the impact of food abundance on feeding success appeared to diminish as Lake Whitefish grew into the larger size classes, indicating that there may be ontogenetic shifts in the relationship between feeding success and prey availability.

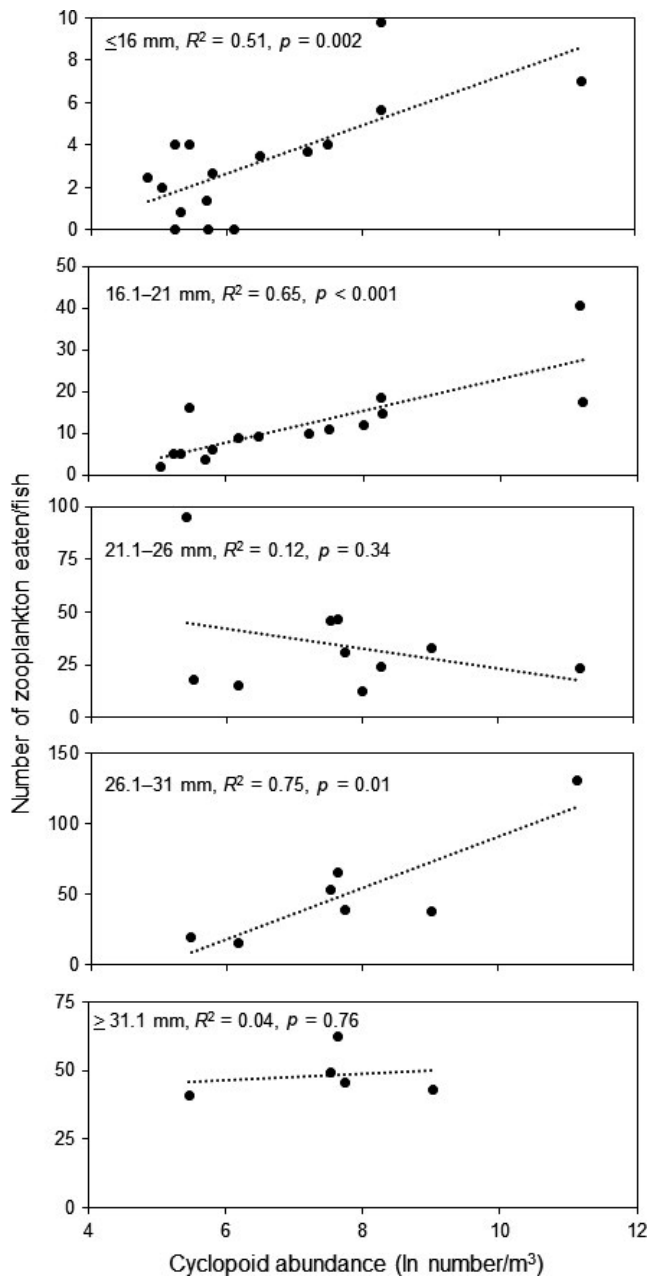


FIGURE 4 Number of zooplankton eaten/fish as a function of $\ln(\text{cyclopid copepod abundance})$ for five size groups of Lake Whitefish

Food availability depends on fish density as well as zooplankton abundance (Claramunt, Muir, Sutton, et al., 2010; Freeberg et al., 1990; Karjalainen, 1992; Taylor et al., 1987). Zooplankton abundance was used in this study to evaluate relationships between feeding and prey because fish were collected with two different methods, including seining which does not lend itself well to assessing the volume of water sampled. However, Lake Whitefish abundance estimates could be determined from the neuston net, which sampled a relatively estimable volume of water. Based on Lake Whitefish abundance in the neuston net, the average ratio of zooplankton (excluding nauplii and veligers) to Lake Whitefish (z/f) was

223,819, 20,686, 10,403 and 2,746 in 2014, 2015, 2016 and 2017 respectively, so in the context of this study, the high zooplankton abundance in 2014 was not diluted despite relatively high fish abundance. The highest catches in the neuston net were in 2015, when prey abundance was also low, and in turn, food mass/fish was low for the smallest fish.

Abiotic factors, such as temperature, can also play a role in recruitment success for Lake Whitefish (Brown, Taylor, & Assel, 1993; Taylor et al., 1987). Water temperatures in 2014 were much colder and the initial appearance of Lake Whitefish was later than during other years, but temperatures warmed up quickly compared with other years. Water temperature can also play an important role when considering the match–mismatch of larval fish with zooplankton resources (Anneville, Souissi, Molinero, & Gerdeaux, 2009). An advanced hatch due to early warming can lead to a mismatch with prey for Lake Whitefish (Patrick et al., 2013), which may have occurred during 2015–2017 compared with 2014, when a late hatch coincided with high zooplankton abundance as water temperatures warmed up quickly. A mismatch with the spring zooplankton pulse during early life can lead to slow growth or starvation for coregonids (Dabrowski, 1989).

Multiple factors affect year class formation for Lake Whitefish, including egg deposition, egg survival and larval survival (Taylor et al., 1987). This study indicated that variation in food availability, and in particular, the availability of cyclopid copepods could be important for larval feeding, especially during the earliest part of the larval period soon after the yolk sac disappears. Although starvation is thought to be rare among coregonids, food shortages could lead to slow growth and ultimately, low survival (Karjalainen, 1992). Survival for larval fish is size dependent, with larger fish having a competitive advantage, better tolerance to food shortages, and lower vulnerability to predation (Miller et al., 1988). Long-term assessments of Lake Whitefish recruitment into the fishery combined with early life feeding ecology and growth studies could provide additional insight into how zooplankton availability and composition ultimately affect Lake Whitefish populations over time.

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DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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