Ecology of
FRESHWATER FISH **WILEY**

Food web changes reflected in age-0 piscivore diets and growth

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Abstract

Lake Erie walleye (*Stizostedion vitreum*) recruitment fluctuates annually and depends partially on their diet and growth during their first year of life. In recent decades, age-0 walleye diet and growth may be responding to food web changes in western Lake Erie. To determine how age-0 walleye have responded to changes in prey species and abundance, we compared diet between 2019, 2014 and 1994–1999. Larval walleye ate predominantly cyclopoids in 2019, compared to 1994–1999 when calanoids were the most consumed copepod. Juvenile walleye ate predominantly large cladocerans and benthic invertebrates in 2019, compared to 2014 and 1994 when fish was the most consumed prey. Additionally, in 2019 and 2014, age-0 walleye ate two of the current aquatic invasive species (AIS), *Bythotrephes longimanus* and *Neogobius melanostomus*, and the historical AIS, *Osmerus mordax*. Age-0 walleye were smaller in 2019 than in 2014 and switched to consuming more AIS and less fish suggesting that more energetically favourable prey were not available. While age-0 walleye showed adaptation to new prey and conditions, they had a lower quality diet because they consumed less fish, but also because the invasive fish they now consume have a lower energy density than native species. However, lower quality diet and size may not result in reduced survival, if adequate alternative prey is available. Continued monitoring of age-0 walleye diet could provide confirmation that lower diet quality during the first year decreased walleye growth and aid to identify any effects changes in age-0 diets has on recruitment to the adult population.

KEYWORDS
age-0, *Bythotrephes longimanus*, diet, invasive species, Lake Erie, larval fish, *Neogobius melanostomus*, round goby, spiny water flea, *Stizostedion vitreum*, walleye

1 | INTRODUCTION

Walleye (*Stizostedion vitreum*) is an ecologically, economically, and recreationally important fish species in Lake Erie with fluctuating levels of annual recruitment (Lake Erie Walleye Task Group, 2022). Most Lake Erie walleye spawn in the western basin (Figure 1) during

early spring and spawning peaks when water temperatures reach 5.0 to 8.5°C (Baker & Manz, 1971; Roseman et al., 1996). Spawning occurs over rocky substrate on mid-lake reefs (Roseman et al., 1996) and in tributaries such as the Sandusky (DuFour et al., 2015), Maumee (Mion et al., 1998; Schmidt et al., 2020), and Detroit rivers (Prichard et al., 2017). Eggs typically hatch in 1 to 2 weeks and
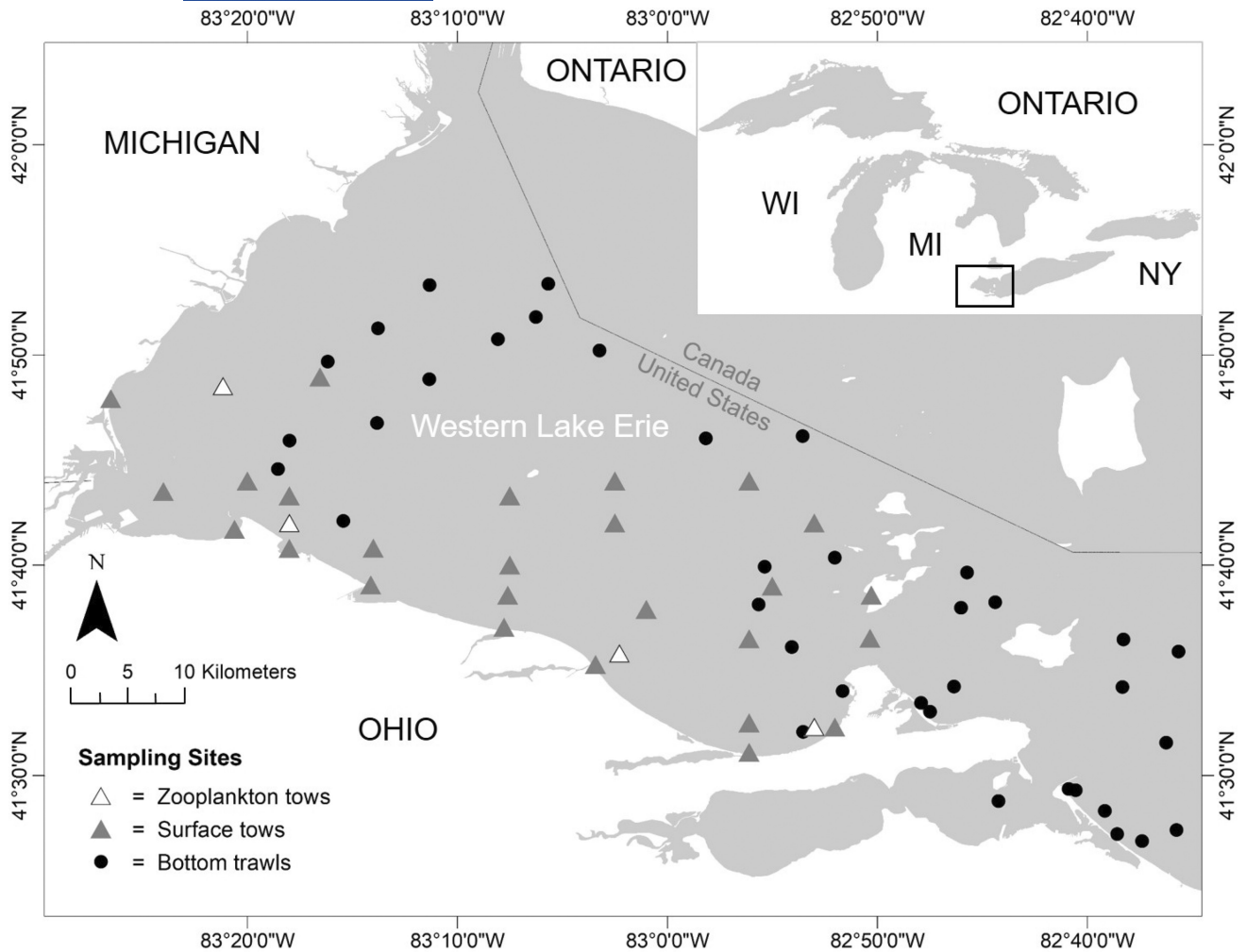
FIGURE 1 Map of western Lake Erie showing 2019 sampling sites for pelagic (grey and white triangles) and demersal (black circles) age-0 walleye (*Stizostedion vitreum*). White triangles indicate zooplankton sampling sites in addition to being pelagic age-0 walleye sites.

pelagic larvae begin exogenous feeding when yolk sac is absorbed in about 5 days to one week following hatch, depending on spring warming rates (Roseman et al., 1996). Pelagic larvae are zooplanktivorous until metamorphosis at about 25 mm total length when they become demersal and generally piscivorous (Galarowicz et al., 2006; Hokanson & Lien, 1986; Houde, 1967).

Walleye recruitment into adulthood at age-2 in Lake Erie is dependent on their growth and survival, which is directly affected by their diet during the first year of life (Hokanson & Lien, 1986.; Hoxmeier et al., 2004, May et al., 2021). During their first growing season, walleye undergo an ontogenetic diet shift from consuming zooplankton and benthic invertebrates to fish prey (Galarowicz et al., 2006; Madenjian et al., 1996; Parsons, 1971; Roseman, 1997). A quicker shift to consuming fish prey provides more energy for growth, which is especially important for their survival. With increased size, walleye can consume bigger and more energetically beneficial prey and are less likely to be preyed upon, thereby contributing to larger annual cohorts (Madenjian et al., 1996; May et al., 2020).

Walleye cohorts in recent years have been some of the largest since 2003 (Lake Erie Walleye Task Group, 2022) and therefore the

ratio of predators to prey, in addition to the composition of prey, may have changed. In recent years, age-0 *Morone* in western Lake Erie have remained high whereas age-0 cyprinids, such as emerald shiners (*Notropis atherinoides*), have been low (Figure 2; Lake Erie Forage Task Group, 2022). Historically, native soft-rayed fishes such as emerald shiners and gizzard shad (*Dorosoma cepedianum*) contributed the most (52%–83%) to young walleye diets at the end of their growing season and were an important factor for walleye growth whereas spiny rayed fishes contributed less (5.4%–25.3%) (Knight et al., 1984; Roseman, 1997). The reduction in preferred forage fish availability combined with a changing fish community could have implications for walleye diet and growth.

The suite of prey items available to age-0 walleye in Lake Erie include zooplankton, benthic invertebrates, and small forage fish at any given time. In the last few decades, Lake Erie has experienced several unintentional introductions of aquatic invasive species (AIS) that have likely led to environmental and food web changes (Bunnell et al., 2014; Mills et al., 1994; Munawar et al., 2005). Notable AIS, in terms of impact, abundance, and spread, include the spiny water flea (*Bythotrephes longimanus*) that invaded in the mid-1980s, the zebra
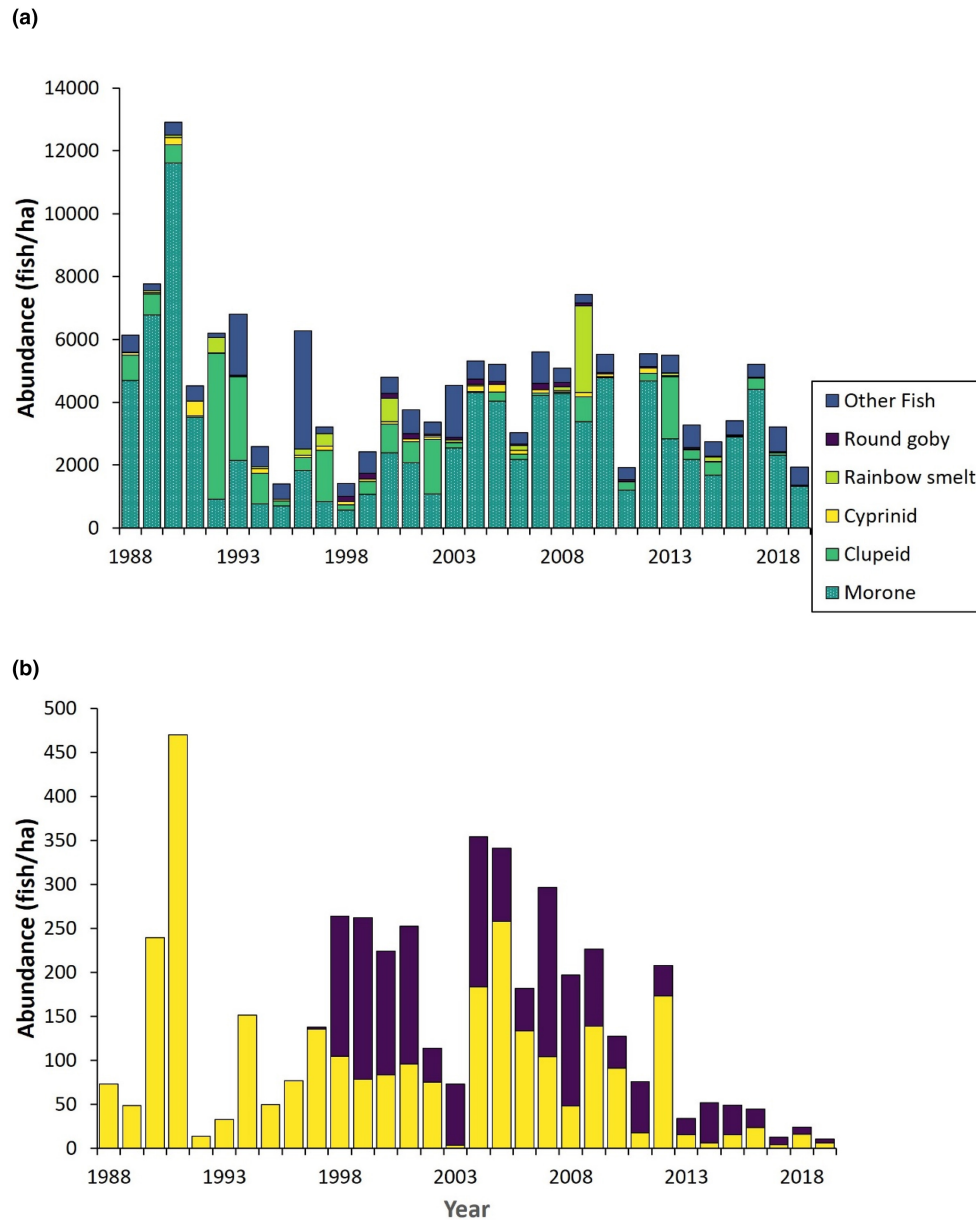
(a)

(b)

FIGURE 2 Abundance of prey fish (round goby *Neogobius melanostomus* – all ages, others – age-0) (a) and only age-0 cyprinid and round goby (all ages) (b) captured in Ohio waters of western Lake Erie for years 1988–2019. Fish were collected by the Ohio Department of Natural Resources-Division of Wildlife as part of their fall trawl survey to assess major predator and forage fish abundance and distribution (Ohio Department of Natural Resources-Division of Wildlife, 2022).

and quagga mussels (*Dreissena polymorpha, D. bugensis*) in the late-1980s, and the round goby (*Neogobius melanostomus*) in the early to mid-1990s. The composition of available prey, both native and introduced, likely affect the growth rate of young walleye (Mayer & Wahl, 1997) and is therefore important to individual survival and cohort recruitment.

The presence of AIS is likely to have direct effects on predator diets through consumption, quality, and competition with the novel species. For example, in the 1990s, age-0 walleye consumed rainbow smelt (*Osmerus mordax*), a long-established AIS in Lake Erie but made up less than 1% of diet by dry weight (Roseman, 1997). However, in Saginaw Bay, Lake Huron

(43.841324 N, −83.672824 W), pelagic larval walleye consumed *Dreissena* veligers and demersal walleye consumed *Bythotrephes* and round goby until the end of their first growing season (Stein et al., 2017). Although age-0 walleye may consume AIS, these novel prey species may not support high growth rates since the energy density of round goby is lower than native fish prey (Johnson et al., 2005; Van Guilder & Seefelt, 2013). Additionally, round goby and *Bythotrephes* have been found to compete with walleye for prey resources (Barbiero & Tuchman, 2004; Johnson et al., 2005; Pangle et al., 2007), especially when age-0 walleye are demersal and dependent on benthic prey commonly found in round goby diets (Johnson et al., 2005).

In addition to the direct effects of AIS as potential prey, these species can indirectly affect a predator by altering the food web. For example, *Dreissena* can shift productivity from the pelagic to benthic zone (Burlakova et al., 2014; Munawar et al., 2005) possibly shifting the availability and consumption of zooplankton and larger benthic invertebrates (Mayer et al., 2001). *Bythotrephes* can not only compete with young walleye for large-bodied zooplankton (Barbiero & Tuchman, 2004; Pangle et al., 2007), but also alter the behaviour of native zooplankton (Bourdeau et al., 2011), reducing zooplankton densities available for walleye consumption. Following *Dreissena* and *Bythotrephes* invasions in several Minnesota lakes, age-0 walleye grew more slowly (Hansen et al., 2020), suggesting that current AIS may reduce growth of young walleye. The aggregate disruptive effects of AIS on Lake Erie's food web and on the diet and growth of age-0 walleye are difficult to predict and therefore requires an empirical evaluation. Consequently, documenting the diet of age-0 walleye since establishment of current AIS is an important step for determining and understanding the possible direct and indirect interactions of the current food web.

Prior to the establishment of current AIS in Lake Erie, age-0 walleye diets mainly consisted of native zooplankton during the pelagic larval stage and native benthic invertebrates and fish prey during the demersal juvenile stage (Roseman, 1997). In other systems where AIS have established, young walleye diets differed spatially. For example, walleye in Lake Winnipeg, Manitoba, Canada (52.9105 N, −98.0345 W) consumed mainly introduced rainbow smelt in the north basin and native emerald shiners in the south basin (Sheppard et al., 2015). Sheppard et al. (2015) also observed differences in diet from spring to winter in the southern basin, suggesting a spatial dominance of different prey species and a seasonal change of available prey for walleye to consume. Such findings warrant further investigation into determining if diets differ spatiotemporally in western Lake Erie since the establishment of current AIS.

It is unclear how a changing food web, including the addition of current AIS, has spatially impacted diet and growth of contemporary age-0 walleye in western Lake Erie. To determine how these fish are adapting, we examined diet composition of age-0 walleye (pelagic to fall young-of-year) collected from western Lake Erie across a range of sampling years. Specifically, we aimed to (1) describe changes in diet composition, ontogenetic diet shift, and growth between 1990s (historical data), 2014, and 2019 (new data); (2) determine the importance of current AIS on contemporary age-0 walleye diets; and (3) explore spatial trends in diet for 1994, 2014, and 2019 demersal walleye collected during August. These findings will help researchers and managers better understand the impact of food web changes during this critical transitional period.

2 | METHODS

2.1 | Study area description

This study encompasses the Ohio, USA waters of western Lake Erie (Figure 1). Lake Erie is the fourth largest Laurentian Great Lake by surface area and the eleventh largest globally. Of the five Laurentian Great Lakes, it is the southernmost, shallowest, and has the least volume (Bolsenga & Herdendorf, 1993). The western basin, where most walleye spawning and nursery exist in the lake, has a mean depth of 7.4 m and a total surface area of about 3700 km². Mean water residence time of the basin is about 51–73 days (Bolsenga & Herdendorf, 1993; Burns, 1985). Bottom substrates consist primarily of sand and clay, with dolomite limestone forming several major reef complexes (Bolsenga & Herdendorf, 1993; Herdendorf & Braidech, 1972) where walleye spawn (Baker & Manz, 1971; May et al., 2021; Roseman et al., 1996).

2.2 | Historical field sampling

Historic pelagic larval walleye were collected in the western basin of Lake Erie during 1994–1999 from 15 to 40 sites weekly from April through June (Figure 1). Larvae were collected using a 2.0 m² framed ichthyoplankton net fitted with 583 μm mesh, towed horizontally in the upper 2 m of the water column. Zooplankton were collected concurrently with larval fish at four to 12 sites using a 0.5 m diameter conical plankton net fitted with 153 μm mesh, towed vertically through the water column and preserved in a 10% formalin solution for later analysis. In 1994, demersal juvenile walleye were sampled at 5 sites monthly from June to October using a semi-balloon bottom trawl with a 3.4 m head rope and 12.7 mm cod end. Collected walleye were brought back to the lab, dissected, and analysed for stomach contents. For a more detailed field sampling and diet content analysis of historical age-0 walleye, see Roseman (1997).

2.3 | 2019 and 2014 field sampling

Pelagic larval walleye were collected in western Lake Erie (Figure 1) as part of the 2019 Lake Erie Cooperative Science and Monitoring Initiative (CSMI), which is a binational effort between the U.S. and Canada to monitor and measure environmental conditions in one of the five Laurentian Great Lakes each year. Larval fish were sampled at 30 sites weekly from April 1st to June 26th using a 0.6 m diameter, paired bongo net fitted with 500 μm mesh, towed horizontally at a speed of 1.0 m/s in the upper 2 m of the water column for 5 min. Most larval sites were the same sites sampled in the 1990s. Fish were preserved in 95% ethanol for later analysis. Zooplankton were collected concurrently with larval fish at four sites using a 0.5 m diameter conical plankton net fitted with 153 μm mesh, towed vertically through the water column and preserved in a 10% formalin solution for later analysis.

Demersal age-0 walleye from 2014 and 2019 were collected in western Lake Erie by the Ohio Department of Natural Resources-Division of Wildlife (ODNR-DOW) as part of their Fall trawl survey to assess major predator and forage fish abundance and distribution (Ohio Department of Natural Resources-Division of Wildlife, 2022). Juvenile fish were sampled at 37 sites monthly from late June to September using a flat-bottom semi-balloon otter trawl with a 10.7 m

head rope and 13 mm bar mesh in the cod end towed for 10 min. Fish were identified in the field and walleye were put on ice and preserved in a freezer for later analysis.

2.4 | Laboratory analysis

Larval walleye were identified following dichotomous keys in Auer (1982) before diet analysis. A random sample of 20 walleye per site per sampling date was selected for diet analysis and each fish was measured for total length (0.01 mm for larval, nearest 1.0 mm for juvenile). Larval and juvenile fish stomachs were extracted and preserved in 95% ethanol.

All prey items were identified to the lowest taxonomic level possible under a dissecting microscope, counted, and up to 20 prey items from each taxa per fish were measured (0.01 mm) using a digital computer image analysis system. Zooplankton prey were identified to order, family, or genus following Balcer et al. (1984) and body length, excluding spine, was measured. Invertebrate prey items were identified to order, family, or genus following Thorp and Covich (2001) and measured for body length and/or head capsule width. Fish prey items were measured for total length, standard length, and/or backbone length. Heavily decomposed fish prey items were identified using Traynor et al.'s (2010) cleithra identification key when possible. Fish that were too digested to identify were classified as unidentified fish remains (UFR) and average lengths of the most common fish prey found in the same walleye stomach were assigned. If no other fish prey were found in the same stomach, the average length of the most common fish prey from the same date and/or site was assigned.

Species specific length-dry weight regression equations were used to estimate the dry weight (g) of each prey that was measured. For zooplankton, equations from Watkins et al. (2011) were used. For benthic invertebrates, equations from Benke et al. (1999), Bowen et al. (2018), Krynak (2012), and Méthot et al. (2012) were used. Dry weights of terrestrial invertebrates were estimated using Sabo et al. (2002) and Rogers et al. (1976). Standard lengths of fish prey were used to estimate dry weight following equations from Roseman (1997). Because no length-dry weight equations existed for round goby, one was developed. Round gobies ($n = 101$), sizes ranging from 8 mm to 85 mm, were collected using beach seines in the shallow (<0.5 m), rocky edges of the Portage River, Ohio (49.1557 N, −83.221647 W). Fish were measured for total length, standard length, and backbone length (0.01 mm), then dried and weighed (0.0001 g). Standard lengths were used for estimating dry-weight using $\ln(DW) = 3.3886(\ln SL)$ – 14.083 where DW is dry-weight and SL is standard length of round goby ($p < .001$, $R^2 = .9823$).

Zooplankton samples were sub sampled, identified to the lowest taxonomic level possible using a dissecting microscope, counted, and up to 20 zooplankton from each taxa were measured (nearest 0.01 mm). Copepod nauplii, *Dreissena* veligers, and rotifers were counted and copepod nauplii and *Dreissena* veligers were measured; however it should be noted that reported densities of these organisms are likely underestimated due to the large mesh size used for sample collection. Once one hundred individuals of the most common genus or species were counted, the rest of the sample was examined to get a whole sample count of *Leptodora kindtii* and *Bythotrephes*, and the first 20 individuals of each species encountered were measured. To ensure taxonomic accuracy, one in 10 samples were checked by a zooplankton taxonomy expert.

2.5 | Data analysis

2.5.1 | Ontogenetic diet shift

To describe possible changes in timing of the ontogenetic diet shift between 1994 and 2019, percent frequency of occurrence (FOC) for consumed prey types was calculated and compared following Chipps and Garvey (2006) for each sampling week. Frequency of occurrence was calculated as:

$$FOC_i = \frac{J_i}{P}, \tag{1}$$

where J = the number of fish containing prey type i. P = the number of fish examined (including empty stomachs).

Because we were only interested in describing the ontogenetic diet shift, all prey were grouped into either *Dreissena* veliger, zooplankton, benthic invertebrate, or fish. Stacked bar graphs were used to visualise weekly FOC_i for both years. FOC_i typically ranges from 0–1 (0%–100%), but because stacked bar graphs were used, it can exceed 1 because FOC is cumulative in this case.

2.5.2 | Diet composition

To assess if age-0 walleye diet composition has changed since establishment of current AIS, the mean percent composition by dry weight (MW_i) of each prey type was calculated and compared between 1994, 2014, and 2019 following Chipps and Garvey (2006) for each sampling week for pelagic larval walleye and sampling month for demersal juvenile walleye. Pelagic larval walleye diets from 1995–1999 are included (Roseman, 2000) to examine patterns in zooplankton consumption. Pelagic walleye in 2014 were not sampled. MW_i is useful for statistical analysis because it combines the percent composition by dry weight of each prey type for individual fish and the mean for each prey type among all fish sampled. Mean percent composition by dry weight was calculated as:

$$MW_i = \frac{1}{P} \sum_{j=1}^{P} \left(\frac{W_{ij}}{\sum_{i=1}^{n} W_{ij}} \right), \tag{2}$$

where P = the number of fish examined (excluding empty stomachs). W = the weight of prey type i in fish j. j = fish. n = the number of unique prey types i.

To describe overall diet composition, prey from pelagic larval walleye were grouped into rotifer, nauplii, small cladoceran, calanoid, cyclopoid, *Daphnia*, benthos (benthic invertebrate), freshwater drum (*Aplodinotus grunniens*), *Morone*, clupeid, UFR, or *Dreissena* veliger. Prey from demersal juvenile walleye were grouped into other zoop (zooplankton), *Daphnia*, *Leptodora*, *Bythotrephes*, benthos, other invert (invertebrate), yellow perch (*Perca flavescens*), freshwater drum, *Morone*, centrarchid, clupeid, cyprinid, rainbow smelt, round goby, and UFR. Stacked bar graphs were used to visualise weekly and/or monthly MW_i for both years.

An analysis of similarities (ANOSIM) was used to test for differences in diet composition between 1994 and 2014/2019. ANOSIM uses a nonparametric permutation applied to a Bray–Curtis rank dissimilarity matrix. Percent composition by dry weight of each prey type calculated for individual fish was square root transformed before running the ANOSIM to reduce the importance of dominant prey types (Clarke & Warwick, 2001). ANOSIM outputs a *p*-value that indicates whether diet composition between groups is significantly different and an *R*-value that indicates the extent of prey type overlap between groups. *R*-values typically range from 0 to +1, but can be −1 if overlap within groups is greater than overlap between groups (Clarke & Gorley, 2001). *R*-values are interpreted as follows:

$$R-\text{value} < .25 = \text{a lot of overlap}$$

$$.50 < R-\text{value} < .75 = \text{some overlap}$$

$$R > .75 = \text{little to no overlap}$$

For weeks and/or months between years where *p*-value were significant ($p < .05$), a similarity percentage routine (SIMPER) test was performed to determine which prey type contributed the most to the observed differences (Clarke, 1993). Only prey types that cumulatively contributed to more than 70% of the observed difference were considered most influential. Unidentified fish remains were not included for the analysis. All analyses were done in R with the *vegan* package.

2.5.3 | Importance of AIS

There are three traditional diet indices used to analyse fish diets, with each one emphasising the importance of different diet information. For example, the frequency of occurrence calculates how many fish contained a certain prey type. Second, the percent composition by number calculates the count of prey type found in fish diets. Third, the percent composition by weight calculates the weight of each prey found in fish diets. To determine the overall importance of current AIS on contemporary fish diet, an index of relative importance (IRI_i) was calculated following Chipps and Garvey (2006) for each sampling week or month and compared between 1994, 2014, and 2019. The IRI is advantageous in that it combines all three diet indices to provide a more complete and less biased interpretation

of prey contribution to fish diet. For example, using only percent composition by number (N_i) could overemphasise the importance of many small prey, such as zooplankton, while using only percent composition by weight (W_i) could overemphasise few big prey, such as fish. IRI was calculated as:

$$IRI_i = FOC_i \times (N_i + W_i), \tag{3}$$

where FOC = frequency of occurrence of prey *i*. N = percent composition by number of prey *i*. W = percent composition by dry-weight of prey *i*.

Further, percent IRI (%IRI) was calculated for ease of interpretation and visualisation, with 0 indicating no importance and 100 indicating most important (only prey type consumed). %IRI was calculated as follows (Cortés, 1997):

$$\%IRI_i = \frac{100 \times IRI_i}{\sum_{i=1}^{n} IRI_i} \tag{4}$$

2.5.4 | Spatial diet trend

To explore spatial trends in diet of 1994, 2014, and 2019 demersal walleye, diet composition from August was plotted in ArcMap 10.7.l. The display XY data function was used to visualise diets using graduated symbols with six breaks at 20 percent intervals. Prey types were grouped into fish prey, round goby, rainbow smelt, and *Bythotrephes*.

3 | RESULTS

Zooplankton density in 1994 increased gradually from April to early May, had large increases from mid-May to late-June, decreased slightly from early July to late August, gradually increased from late August to late September, and decreased from late September to late October (Figure 3a). Cyclopoid and calanoids combined were the most abundant zooplankton species from April to late May. From late May to mid-June, cyclopoids, calanoids and *Daphnia* were the most abundant zooplankton species. From late June to late July, *Daphnia* become the most abundant zooplankter until late July to late August when small cladocerans, cyclopoid, calanoid, and *Daphnia* were similar in abundance. From late August to late October, small cladocerans became the most abundant zooplankton species.

Zooplankton density in 2019 increased gradually from April to June, had large increases in early-mid July, then decreased into August (Figure 3b). Cyclopoid and calanoids combined were the most abundant zooplankton species from April to late May. From late May to early June, *Daphnia* became the most abundant zooplankter. From early June to mid-July, *Daphnia* continued to be the most abundant peaking in late-June. From mid-July through August, all zooplankton abundance were similar and continued toward an upward trend.

A total of 732 walleye stomachs were examined in 1994 collected from May 2nd to October 22nd (Roseman, 1997). Of the 204 pelagic larval walleye examined, 86 were yolk-sac larvae and 21 contained empty stomachs. Of the 528 demersal juvenile walleye, 112
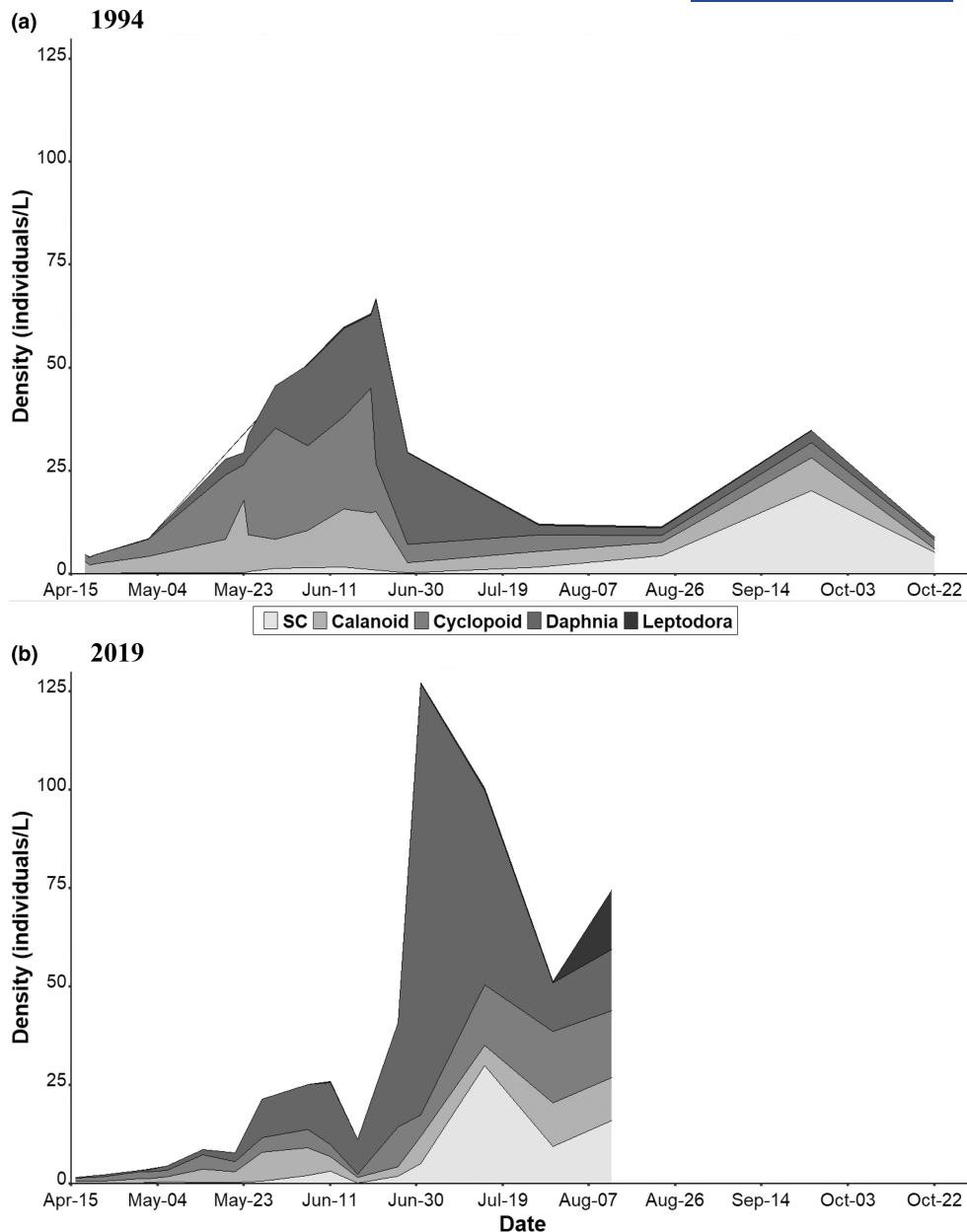
FIGURE 3 Density (individuals/L) of zooplankton collected in 1994 (a) and 2019 (b) from four locations in western Lake Erie in vertical tows. SC, small cladoceran. In 2019, zooplankton sampling stopped after August 12th.

contained empty stomachs. A total of 495 demersal juvenile walleye stomachs were examined in 2014 collected from July 14th to September 24th, where 125 had empty stomachs. A total of 1769 walleye stomachs were examined in 2019 collected from April 22nd to October 8th. Of the 736 pelagic larval walleye examined, 398 were yolk-sac larvae, and 60 had empty stomachs. Of the 1033 demersal juvenile walleye, 222 had empty stomachs.

3.1 | Ontogenetic diet shift

In 1994, yolk-sac pelagic walleye first appeared on April 30th when fish were 7.0 mm average total length and began exogenously feeding

on zooplankton on May 2nd (Figure 4a) when fish were 9.2 mm average total length. A majority of pelagic walleye continued to consume zooplankton near the surface until demersal walleye were captured on the bottom starting June 9th when fish were 24.2 mm average total length and almost half of walleye with non-empty stomachs ate fish (Figure 4a). Demersal juvenile walleye were sampled from June 9th to October 23rd and almost all walleye had shifted to consuming fish prey by June 29th when fish were 48.0 mm average total length, and consumption of fish continued through October 23rd (Figure 4a). The mean total length of age-0 walleye in October was 175.0 mm (Figure 5).

In 2014, no pelagic walleye were collected for diet analysis. Demersal juvenile walleye were sampled from July 14th to
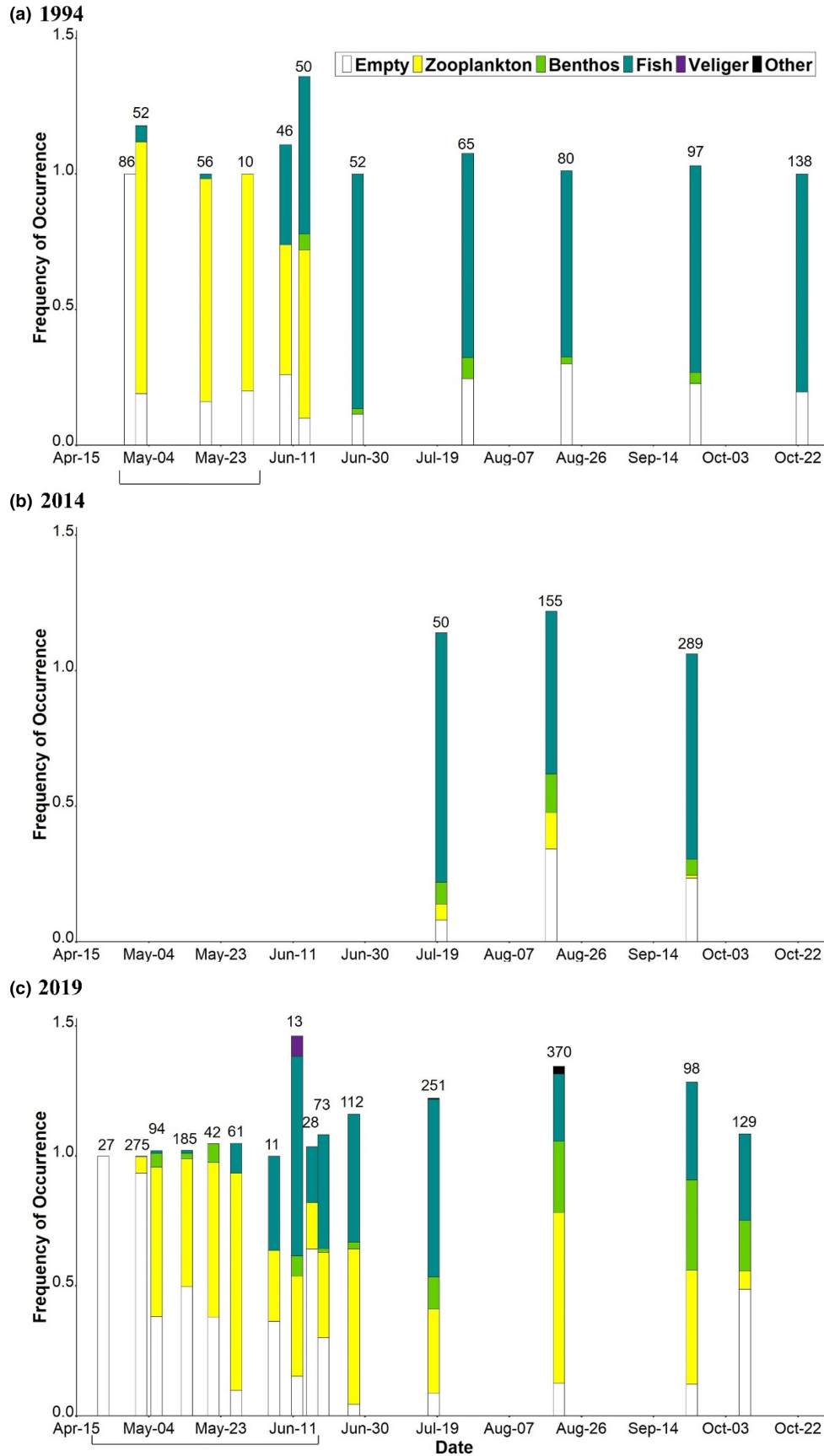
FIGURE 4 Frequency of occurrence (FOC) of prey found in age-0 walleye (*Stizostedion vitreum*) diets in 1994 (a), 2014 (b), and 2019 (c) collected in western Lake Erie during surface tows (pelagic stage, line under dates) and bottom trawls (demersal stage, no line under dates). The number above each bar indicates the number of fish examined (including empty stomachs). Benthos, benthic invertebrates; Veliger, *Dreissena* veliger; Other, other invertebrates. FOC typically ranges from 0–1 (0%–100%), but can exceed 1 because FOC is cumulative in this case.

September 24th where the majority of age-0 walleye consumed fish prey (Figure 4b). The mean total length of age-0 walleye in September was 174.0 mm (Figure 5).

In 2019, yolk-sac pelagic walleye first appeared in samples on April 22nd when they were 7.0 mm average total length and most fish began exogenously feeding on zooplankton by May 6th (Figure 4c) when they were 9.1 mm average total length. A majority of pelagic walleye continued to consume zooplankton until June 6th when more than half of walleye with non-empty stomachs consumed fish (Figure 4c) at 18 mm average total length. Sampling for pelagic walleye continued throughout June but none were captured near the surface after June 17th, suggesting most walleye had metamorphosed to the demersal juvenile stage. Demersal juvenile walleye were sampled from June 12th to October 8th, and, although many demersal walleye switched to consuming fish prey, a large proportion continued to consume zooplankton and benthic invertebrates (Figure 4c). The mean total length of age-0 walleye in October was 115 mm (Figure 5).

Pelagic larval walleye diets during 1995–1999 showed similar repeating patterns in zooplankton consumption as observed in 1994 and 2019. First-feeding larvae made use of copepod prey then consumed larger cladocerans during late spring and early summer before becoming mostly piscivorous after metamorphosis (Figure 6).

3.2 | Diet composition

Larval pelagic walleye diet data from 1994 were only available for 2 weeks (May 19th and May 30th) to compare with the same weeks in 2019. Similar prey types were found in both years (Figure 6). In

1994, copepod prey dominated the diet by mean dry weight during both pelagic sampling weeks, with higher proportions of calanoid than cyclopoid copepods (Figure 6a). In 2019, copepod prey dominated the diets by mean dry weight during the pelagic phase, with higher proportions of cyclopoid than calanoid copepods (Figure 6g). Calanoid and cyclopoid copepod mean dry weights were similar between 1994 and 2019 until June 3rd when 2019 consumption switched to primarily *Daphnia* and fish prey.

Juvenile demersal walleye diets in 1994 contained only a few different prey types (Figure 7a). Fish prey made up nearly 100% of mean dry weight from late June to October. Walleye consumed mostly spiny-rayed fish from late June to July and soft-rayed fish from August to October. Cyprinid species were the most dominant fish species in the later months. Diets for 2014 juvenile demersal walleye were similar to 1994 where fish prey made up nearly 100% of mean dry weight from July to September (Figure 7b). Walleye consumed mostly spiny-rayed fish from July to August and soft-rayed fish in September. In 2019, juvenile demersal walleye diets contained a mix of several different prey types (Figure 7c) and less fish compared to 1994 and 2014. Invertebrate prey made up more than 40% of the mean dry weight in all months except July.

3.3 | ANOSIM and SIMPER

3.3.1 | 2019 and 1994

ANOSIM results indicated that diet composition between 2019 and 1994 was significantly different with high prey type overlap for the
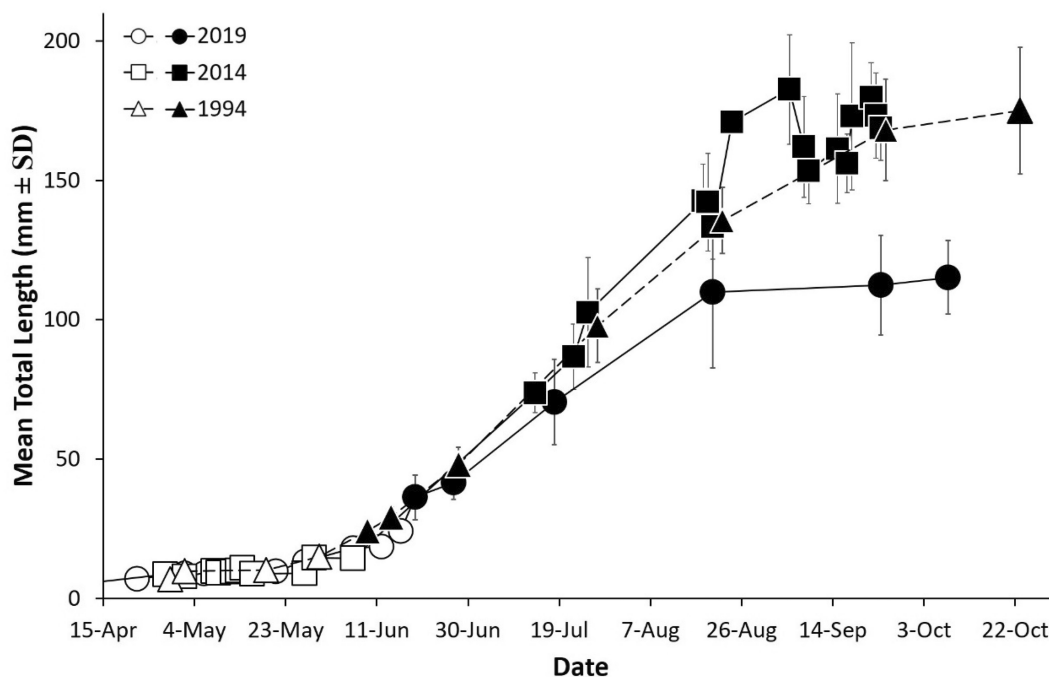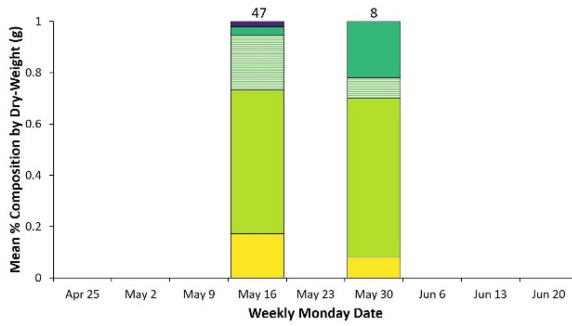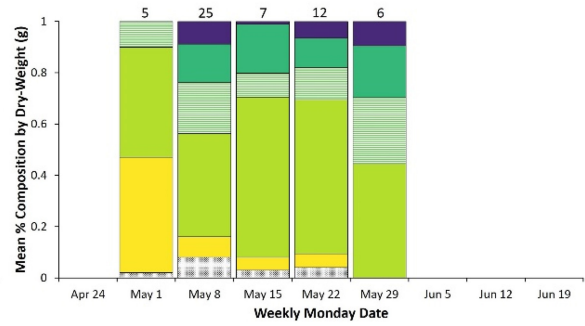

FIGURE 5 Mean total length (mm ± SD) of age-0 walleye (*Stizostedion vitreum*) collected from western Lake Erie in 1994, 2014, and 2019. White symbols indicate pelagic walleye caught in surface tows while black symbols indicate demersal walleye caught in bottom trawls.
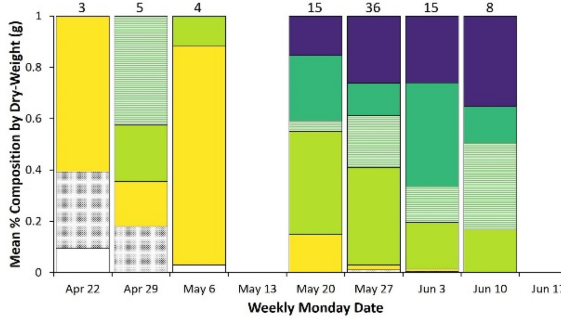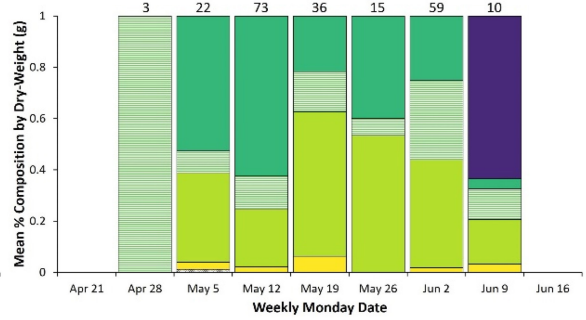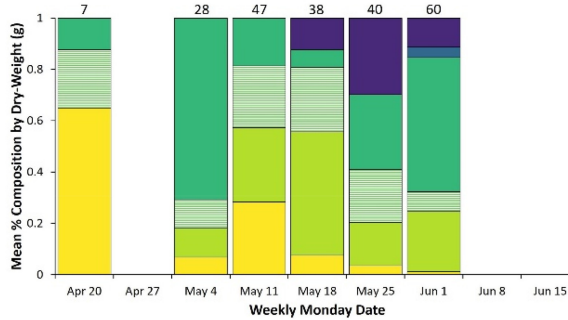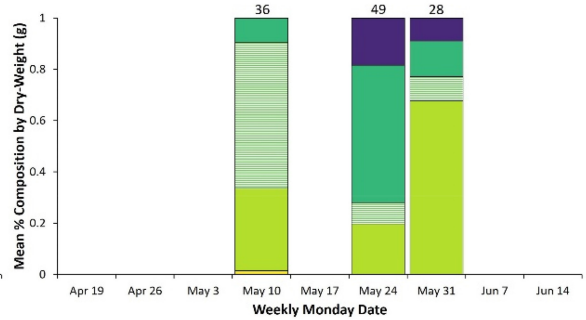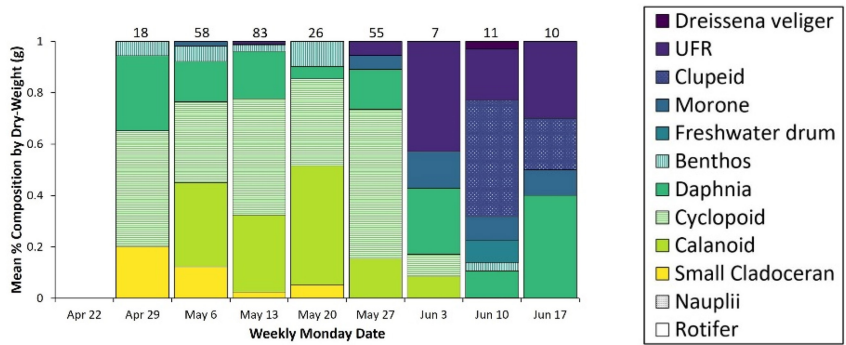
FIGURE 6 Weekly percent diet composition by dry-weight (g) during 1994 (a), 1995 (b), 1996 (c), 1997 (d), 1998 (e), 1999 (f), and 2019 (g) for pelagic larval walleye (*Stizostedion vitreum*) collected from western Lake Erie. The number above each bar indicates the number of fish examined from each week that contained at least one prey item. Benthos, benthic invertebrate; UFR, unidentified fish remains.

FIGURE 7 Monthly percent diet composition by dry-weight (g) during 1994 (a), 2014 (b), and 2019 (c) for demersal age-0 walleye (*Stizostedion vitreum*) collected from western Lake Erie in bottom trawls. The number above each bar indicates the number of fish examined from each week that contained at least one prey item. Benthos, benthic invertebrate; Other zoop, other zooplankton; UFR, unidentified fish remains.

week of May 13 (2019) and May 16 (1994) and as well as for the weeks of May 27 (2019) and May 30 (1994) (Table 1). SIMPER results indicated copepods and small cladocerans cumulatively contributed to more than 70% of the observed diet differences for May 13 and May 16 while copepods and *Daphnia* accounted for differences during May 27 and May 30 (Table 1).

ANOSIM results for demersal fish indicated that diet composition between 2019 and 1994 was significantly different for all months except July (Table 1), with varying consumption of cyprinid accounting for the difference in 1994 and zooplankton and benthic invertebrates being different in 2019 (Figure 7). SIMPER results indicated that in addition to fish prey, zooplankton and benthic invertebrates cumulatively contributed to more than 70% of the observed difference in all months (Table 1).

3.3.2 | 2014 and 1994

ANOSIM and SIMPER were only performed for demersal stage walleye between 2014 and 1994 during the months of July, August, and September. ANOSIM results between 2014 and 1994 indicated that diet composition between both years was significantly different for July and August, but not September (Table 2). SIMPER results

indicated that cyprinid, yellow perch, and *Morone* cumulatively contributed to more than 70% of the observed difference, with the percent contribution of each prey type differing for each month (Table 2).

3.3.3 | 2014 and 2019

ANOSIM and SIMPER were only performed for demersal stage walleye between 2014 and 2019 during the months of July, August, and September. ANOSIM results between 2014 and 2019 indicated that diet composition between both years was significantly different for all months (Table 3). In July, diets were significantly different with a lot of overlap in prey types ($p=.001$, $R=.18$). SIMPER results indicated that mostly fish prey contributed to more than 70% of the observed difference in July while zooplankton and benthic invertebrates contributed most for August and September (Table 3).

3.4 | Importance of AIS

Pelagic larval walleye from May 2nd to May 29th in 1994 contained no AIS. Demersal juvenile walleye collected from late June through

TABLE 1 Analysis of similarities (ANOSIM) and similarity percentage routine (SIMPER) test results for western Lake Erie age-0 pelagic and demersal walleye (*Stizostedion vitreum*) diet composition between 2019 and 1994.

Life stage	Week/month paired for analysis	ANOSIM		SIMPER	
		p-Value	R-value	Taxon	% Contribution
Pelagic	Week 20 (May 13/May 16)	**<.001**	.133	Calanoid	32
				Cyclopoid	28
				SC	18
	Week 22 (May 27/May 30)	**.003**	.2729	Calanoid	36
				Cyclopoid	32
				Daphnia	19
Demersal	Late-June	**.001**	.497	Daphnia	35
				MOR	30
				FWD	14
	July	.534	−.003		
	August	**.001**	.405	Cyprinid	32
				Daphnia	15
				Leptodora	12
				MOR	11
	September	**.001**	.657	Cyprinid	44
				Bythotrephes	19
				Benthos	19
	October	**.001**	.698	Cyprinid	48
				Benthos	21
				RAS	12

Note: *p*-Value <.05 indicates significant differences (bolded) between groups while *R*-value indicates the extent of prey taxa overlap between groups. Taxa that cumulatively explain at least 70% of the observed dissimilarity between groups are listed in the table.

Abbreviations: Benthos, benthic invertebrates; FWD, freshwater drum (*Aplodinotus grunniens*); MOR, *Morone*; RAS, rainbow smelt (*Osmerus mordax*); SC, small cladoceran.

end of the Fall 1994 contained no AIS except for October when rainbow smelt was found. Although rainbow smelt is a non-native fish, its IRI in October 1994 was less than 1%.

In 2014, in addition to the already established rainbow smelt, juvenile demersal walleye diets contained two new current AIS, round goby and *Bythotrephes*. In July, the only AIS found was round goby (%IRI=0.17). In August, the IRI of round goby (%IRI=0.9), rainbow smelt (%IRI=0.004), and *Bythotrephes* (%IRI=0.83) was cumulatively less than 2%. In, September, the IRI of round goby (%IRI=0.33), rainbow smelt (%IRI=.002), and *Bythotrephes* (%IRI=0) was cumulatively less than 0.5%.

In 2019, no AIS were found in larval pelagic walleye, but the stomach contents of one juvenile caught near the surface on June 12th contained *Dreissena* veligers. Although *Dreissena* veligers were consumed, their IRI was low at only 1%. Similar to 2014, juvenile demersal

walleye in 2019 contained some current AIS: rainbow smelt, round goby and *Bythotrephes*. In July, the IRI ofrainbow smelt (%IRI<0.001), round goby (%IRI<0.001), and *Bythotrephes* (%IRI=0.28) was cumulatively less than 0.5%. In August, the IRI of round goby (%IRI<0.05), rainbow smelt (%IRI=0.1), and *Bythotrephes* (%IRI=3.2) was cumulatively less than 4%. In, September, the IRI of round goby (%IRI=21.3) and *Bythotrephes* (%IRI=25.3) was cumulatively 46.6%. In October, the IRI of rainbow smelt (%IRI=14.4), round goby (%IRI=21), and *Bythotrephes* (%IRI=5.4) was cumulatively 40.8%.

3.5 | Spatial diet trend

The mean percent composition by dry-weight of fish prey consumed by demersal juvenile walleye was nearly 100% in August 1994 and

TABLE 2 Analysis of similarities (ANOSIM) and similarity percentage routine (SIMPER) test results for western Lake Erie age-0 demersal walleye (*Stizostedion vitreum*) diet composition between 2014 and 1994.

| Life stage | Month paired for analysis | ANOSIM | | SIMPER | |
		p-Value	*R*-value	Taxon	% Contribution
Demersal	July	**.001**	.348	MOR	44
				YEP	22
				Cyprinid	20
	August	**.001**	.1	Cyprinid	40
				YEP	23
				MOR	10
	September	.99	−.07		

Note: *p*-Value <.05 indicates significant differences (bolded) between groups while *R*-value indicates the extent of prey taxa overlap between groups. Taxa that cumulatively explain at least 70% of the observed dissimilarity between groups are listed in the table.

Abbreviations: MOR, *Morone*; YEP, yellow perch (*Perca flavescens*).

TABLE 3 Analysis of similarities (ANOSIM) and similarity percentage routine (SIMPER) test results for western Lake Erie age-0 demersal walleye (*Stizostedion vitreum*) diet composition between 2019 and 2014.

| Life stage | Month paired for analysis | ANOSIM | | SIMPER | |
		p-Value	*R*-value	Taxon	% Contribution
Demersal	July	**.001**	.18	YEP	24
				MOR	23
				Cyprinid	15
				Daphnia	13
	August	**.001**	.299	YEP	17
				Daphnia	15
				Leptodora	12
				Cyprinid	11
				Bythotrephes	11
				Benthos	10
	September	**.001**	.499	Cyprinid	34
				Bythotrephes	21
				Benthos	21

Note: *p*-Value <0.05 indicates significant differences (bolded) between groups while *R*-value indicates the extent of prey taxa overlap between groups. Taxa that cumulatively explain at least 70% of the observed dissimilarity between groups are listed in the table.

Abbreviations: Benthos, benthic invertebrates; MOR, *Morone*; YEP, yellow perch (*Perca flavescens*).

piscivory was highest along the southern shore of the western basin (Figure 8a). No round goby, rainbow smelt, nor *Bythotrephes* were found in diets during August 1994.

Similarly, the mean percent composition by dry-weight of fish prey consumed by demersal juvenile walleye was nearly 100% in August 2014 with high piscivory occurring throughout the western basin (Figure 8a). Among the fish prey consumed, consumption

of round goby was concentrated on the western part of the basin (Figure 8b) and rainbow smelt was concentrated on the eastern part of the basin (Figure 8c), although only 1 out of 75 walleye examined from the eastern part of the basin consumed rainbow smelt. *Bythotrephes* consumption was higherin the eastern part of western Lake Erie and were only found in 5 out of 75 walleye examined during 2014 (Figure 8d).
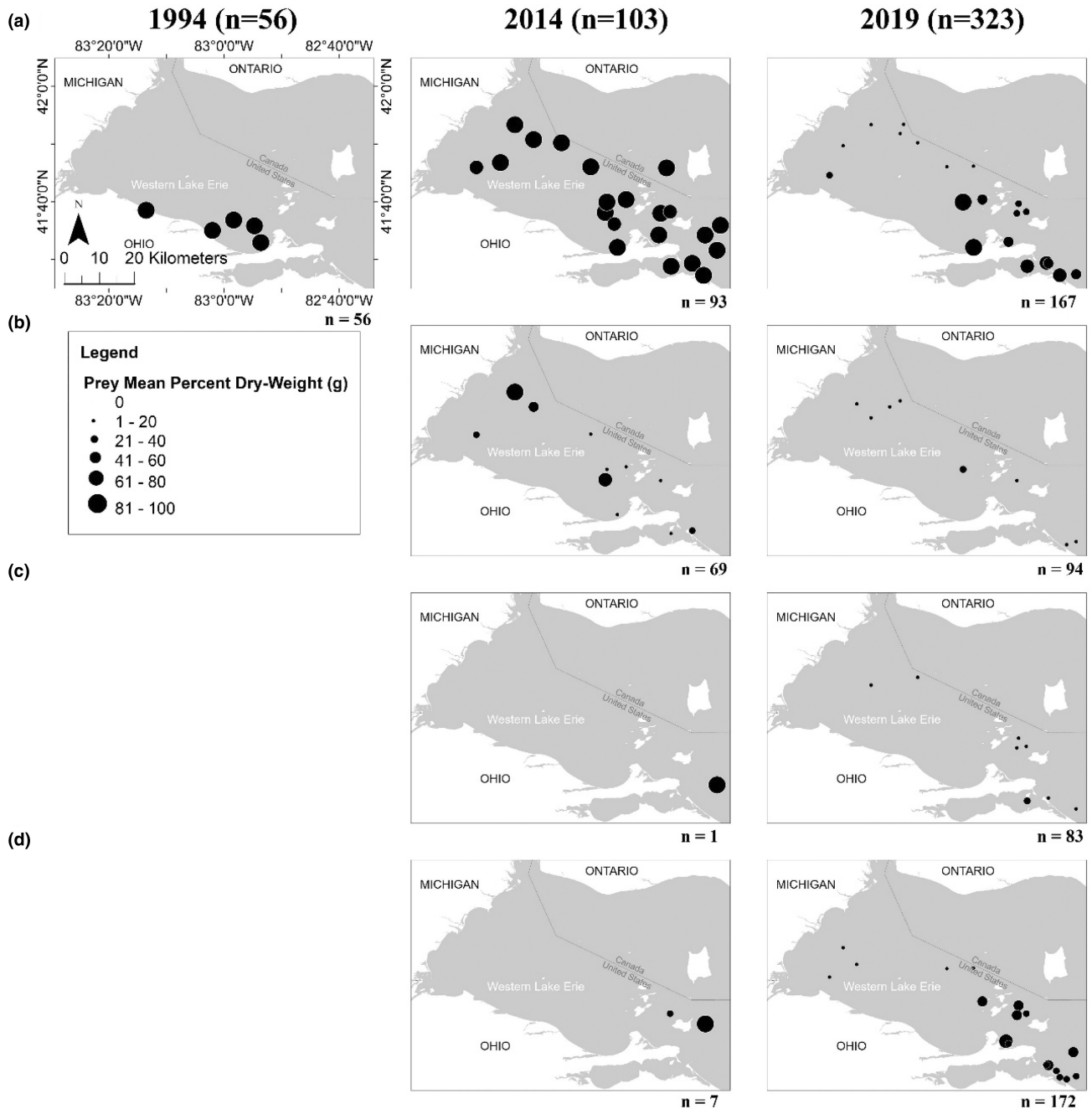

FIGURE 8 Spatial distribution of mean percent composition by dry weight (g) of prey consumed by western Lake Erie demersal age-0 walleye (*Stizostedion vitreum*) during August 1994, 2014, and 2019 where rows are (a) all fish prey, (b) round goby (*Neogobius melanostomus*), (c) rainbow smelt (*Osmerus mordax*), and (d) *Bythotrephes* prey. Missing panels indicate no prey of that type was consumed. *n* next to each year indicates the number of fish examined from August that contained at least one prey item. *n* below each panel indicates the number of fish that contained that specific prey type (row; fish prey, round goby, rainbow smelt, or *Bythotrephes* prey) for that year (column; 1994, 2014, 2019).

In 2019, most demersal juvenile walleye in the east part of western Lake Erie consumed fish (Figure 8a). Round goby were found in diets of walleye throughout western Lake Erie, but comprised less than 40% by mean percent dry-weight (in maximum; Figure 8b). Rainbow smelt were also consumed, with highest frequency of consumption occurring in the east part of western Lake Erie and also less than 40% by mean percent dry-weight (in maximum; Figure 8c). *Bythotrephes* consumption was concentrated in the east part of western Lake Erie and made up almost 80% of mean dry-weight (in maximum; Figure 8d).

4 | DISCUSSION

During the first year of life, walleye in western Lake Erie are broadly opportunistic predators, utilising various food sources. Diet composition changed over the more than two decades of our study, largely in response to AIS influence on the food web. Within the season, age-0 walleye shifted from consuming zooplankton and benthic invertebrates to fish prey as they progressed through ontogenetic developmental stages. The shift to consuming fish at an earlier size and developmental stage in 1994 produced higher growth, and potentially higher survival (Hoxmeier et al., 2006). However, walleye in 2019 continued to consume non-fish prey through October which contributed to the smaller size at the end of the 2019 growing season, but also higher abundance and survival. It is likely that age-0 walleye consumed more invertebrates and AIS because preferred and energetically more profitable prey, like age-0 cyprinids, were not available due to low abundance (Lake Erie Forage Task Group Report, 2022) in the 2019 food web. In addition, the high abundance of young walleye in 2019 (Lake Erie Walleye Task Group Report, 2022) likely caused density-dependent competition for prey.

Pelagic larval walleye growth was similar between 1994 and 2019, as fish began exogenously feeding at similar dates and zooplankton (e.g., copepods) contributed the most biomass to their diet. Similar larval growth during the pelagic stage across years suggests that calanoid and cyclopoid copepod species provide equal quality diet items. A high copepod biomass during the larval stage has been linked to strong recruitment (May et al., 2021) and 2019 age-0 walleye fall abundance was the third highest on record since 1988 (Lake Erie Forage Task Group, 2022). Small cladocerans were consumed less than copepods, possibly due to their lower abundance or due to larger prey size (e.g. *Daphnia*) (Mayer & Wahl, 1997). It is likely that in western Lake Erie the size distribution of copepods falls into the preferred range for larval walleye and, during 2019, were available in sufficient abundance to support walleye growth and survival during their larval stage.

Demersal juvenile walleye growth was similar between 1994 and 2014 but diverged in 2019 when the diet composition changed and less than 50% of prey biomass included fish. Previous studies showed that demersal juvenile walleye in Lake Erie relied on fish prey over non-fish prey for optimum growth, initially consuming clupeid and *Morone* species and then switching to mostly cyprinids

in August (Knight et al., 1984; Roseman, 1997). During our study, young walleye in western Lake Erie did not consume *Morone* at the end of their growing season, even though age-0 *Morone* abundance remained high when emerald shiner and gizzard shad abundances were low (Lake Erie Forage Task Group, 2022), suggesting *Morone* may not be a preferred prey. Although age-0 walleye will select fish over invertebrate prey (Galarowicz et al., 2006), they can switch to lower quality prey when necessary (Ward et al., 2008). The typical high quality fish prey (i.e. age-0 cyprinids) was replaced in 2019 with lower quality AIS fish prey (round goby; Johnson et al., 2005) as well as zooplankton and benthic invertebrate prey including the invasive *Bythotrephes*. *Bythotrephes* have low nutritional value due to their small body size and large caudal spine (Parker Stetter et al., 2005), and likely contributed to the slower age-0 walleye growth observed in 2019 compared to 1994 and 2014. Similarly, walleye populations in inland lakes had reduced growth when invertebrates were consumed during periods of reduced fish prey abundance (Paradis et al., 2006; Slipke & Duffy, 1997). Results from this study and others demonstrate the importance of fish prey for walleye, especially for growth and survival during their first year of life.

Despite high consumption of non-preferred items in the diet after the pelagic larval stage and slower demersal stage growth, the 2019 walleye year-class had high fall abundance (Lake Erie Walleye Task Group, 2022). The average size of 2019 age-0 walleye was the smallest recorded since 2003 reflecting the inverse relationship between size and abundance (Figure 9). Consecutive years of high walleye abundance may heighten the potential for density-dependent reductions in growth. Although 2019 age-0 walleye were smaller during fall than 1994 and 2014 fish, the high proportion of non-empty stomachs and high abundance of demersal juvenile walleye at the end of the first growing season suggests fish were consuming enough prey to avoid starvation. Lake Erie is a productive system and can provide multiple alternative prey to buffer from starvation. In less eutrophic lakes (e.g. Paradis et al., 2006), the lack of preferred fish prey available to piscivores may negatively impact their growth and survival if abundant alternative prey is not available. Consequently, the prey availability and growth likely interact with other factors (e.g. temperature and predator abundance; Gopalan et al., 1998) that set overall recruitment and cannot be interpreted in isolation.

In other systems where growth of young walleye was slow, cannibalism by older walleye was a factor for poor recruitment (Forney, 1976). For example, in Oneida Lake, New York, Forney (1976) found that slow growing age-0 walleye experienced a longer duration of predation by older walleye than faster growing age-0 walleye. In western Lake Erie, however, we found no evidence of cannibalism by older walleye even though 2019 walleye were much smaller than historical walleye by the end of their first growing season. Similar studies in western Lake Erie found no evidence of cannibalism (Knight et al., 1984; Roseman, 1997), suggesting that although availability of preferred prey may be low, there exists other alternative prey to avoid cannibalism, including current AIS.
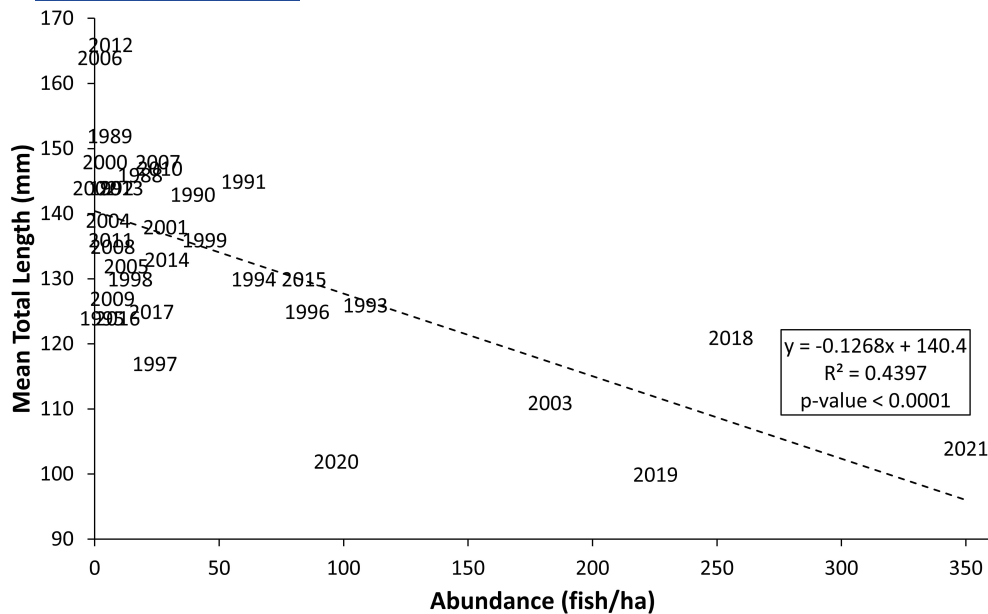
FIGURE 9 Relationship between August demersal age-0 walleye (*Stizostedion vitreum*) abundance and mean total length in western Lake Erie, 1988–2021. Data from Lake Erie Forage Task Group Report (2022). Line represents simple linear regression to show direction and strength of relationship where *y* represents Mean Total Length (mm) and *x* represents Abundance (fish/ha) (*p*-value < .0001).

It is important to mention that although we looked at diet as it relates to growth and survival, there are other factors that likely contribute to overall walleye recruitment. For example, environmental variables such as water temperature were important in predicting walleye recruitment in several Minnesota lakes (Honsey et al., 2020). Honsey et al.'s (2020) model predicted weak year classes with cold first growing seasons and severe first winters. In Escanaba Lake, Wisconsin, variable May temperatures explained 24% of annual variation in recruitment of walleye but combined with spawning population of walleye and yellow perch longer than 152.4 mm, 89% was explained (Hansen et al., 1998). Recruitment for walleye across their range is complex and difficult to predict requiring examination of a combination of spatially and temporally varying factors to more fully understand causes of variability.

Our results indicate that age-0 walleye are spatially adapting to food web changes in western Lake Erie as the distribution of percent AIS incorporated into diets varied between 1994, 2014, and 2019. In general, we found age-0 walleye in the eastern part of the western basin contained higher proportions of fish in their diets. Continued spatial monitoring and analysis of age-0 walleye diets and growth could confirm that reduced fish prey consumption in some areas during the first year is linked to decreased growth but may not result in lower survival if adequate alternative prey is available. For example, during 2019 when preferred native prey fish abundances were near historic lows (e.g., cyprinids; Figure 2b), age-0 walleye incorporated a higher percentage of non-native fishes (e.g., round goby and rainbow smelt; Figure 8) and *Bythotrephes* into their diets over a greater spatial range. The availability of non-native prey across the western basin led to reduced growth on average but may have helped buffer fish from starvation. Future work focusing on detailed spatiotemporal trends of age-0 walleye diet and growth in western

Lake Erie could help identify other factors affecting diet such as seasonal shifts in prey-specific abundances at sampling locations. Such quantitative comparisons of location-specific consumption and prey abundances would improve our understanding of food web dynamics in western Lake Erie and be useful for ecosystem modellers and environmental managers.

Our results also show repeated patterns in zooplankton consumption during the pelagic larval stage. While differences in zooplankton taxa consumed occurred across years, our data show that copepods are an important first-food for larval walleye, complementing May et al. (2021) and emphasising the need for early spring zooplankton community surveys. Predictable ontogenetic diets shifts were documented in our study, and the switch from zooplanktivory to piscivory seemed dependent on the availability of suitable fish prey. For example, in 2019, in the absence of suitable fish prey (Lake Erie Forage Task Group Report, 2022) and with high age-0 walleye abundance (Lake Erie Walleye Task Group Report, 2022), age-0 walleye adapted by consuming more invertebrates and AIS, but growth was retarded resulting in small average size by October. However, based on walleye recruitment indices (Lake Erie Walleye Task Group Report, 2022), the 2019 walleye year class is among the highest on record suggesting that diets including invertebrates and AIS during the age-0 and juvenile stages are adequate for survival.

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AUTHOR CONTRIBUTIONS

CMM and RLD provided substantial advising, conception, input, and drafting and revising of the manuscript. EFR provided acquisition of data as well as input and revising the manuscript. MRD provided input, creating figures, and revising the manuscript. EJW provided acquisition of data as well as input and revising of the manuscript.

CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in at https://doi.org/10.5066/P9A4NK3J.

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REFERENCES

Auer, N. A. (1982). *Identification of larval fishes of the Great Lakes basin with emphasis on the Lake Michigan drainage* (744 p). Great Lakes Fishery Commission.

Baker, C. T., & Manz, J. V. (1971). *Walleye spawning area study in western Lake Erie*. Ohio Department of Natural Resources Division of Wildlife. Final Report Research. Project F-35-R-10, 23 p.

Balcer, M. D., Korda, N. L., & Dodson, S. I. (1984). *Zooplankton of the Great Lakes: A guide to the identification and ecology of the common crustacean species* (174 p). University of Wisconsin Press.

Barbiero, R. P., & Tuchman, M. L. (2004). Changes in the crustacean communities of lakes Michigan, Huron, and Erie following the invasion of the predatory Cladoceran *Bythotrephes longimanus*. *Canadian Journal of Fisheries and Aquatic Sciences*, 61, 2111–2125.

Benke, A. C., Huryn, A. D., Smock, L. A., & Wallace, J. B. (1999). Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society*, 18, 308–343.

Bolsenga, S. J., & Herdendorf, C. E. (1993). *Lake Erie and Lake St. Clair handbook*. Wayne State University Press.

Bourdeau, P. E., Pangle, K. L., & Peacor, S. D. (2011). The invasive *Bythotrephes* induces changes in vertical distribution of native copepods in Lake Michigan. *Biological Invasions*, 13, 2533–2545.

Bowen, K. L., Conway, A. J., & Currie, W. J. S. (2018). Could dreissenid veligers be the lost biomass of invaded lakes? *Freshwater Science*, 37(2), 315–329.

Bunnell, D. B., Barbiero, R. P., Ludsin, S. A., Madenjian, C. P., Warren, G. J., Dolan, D. M., Brenden, T. O., Briland, R., Gorman, O. T., He, J. X., Johengen, T. H., Lantry, B. F., Lesht, B. M., Nalepa, T. F., Riley, S. C., Riseng, C. M., Treska, T. J., Tsehaye, I., Walsh, M. G., … Weidel, B. C. (2014). Changing ecosystem dynamics in the Laurentian Great Lakes: Bottom-up and top-down regulation. *Bioscience*, 64, 26–39.

Burlakova, L. E., Karatayev, A. Y., Pennuto, C., & Mayer, C. (2014). Changes in Lake Erie benthos over the last 50 years: Historical perspectives, current status, and main drivers. *Journal of Great Lakes Research*, 40, 560–573.

Burns, N. M. (1985). *Erie: The Lake that survived* (320 pp). Rowman and Allanhead.

Chipps, S. R., & Garvey, J. E. (2006). Assessment of diets and feeding patterns. In C. S. Guy & M. L. Brown (Eds.), *Analysis and interpretation of freshwater fisheries data* (pp. 473–514). American Fisheries Society.

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 19, 117–143.

Clarke, K. R., & Gorley, R. N. (2001). *Primer V5 (Plymouth routines in multivariate ecological research): User manual/tutorial.* Primer-E.

Clarke, K. R., & Warwick, R. M. (2001). *Changes in marine communities: An approach to statistical analysis and interpretation* (2nd ed.). Primer-E.

Cortés, E. (1997). A critical review of methods of studying fish feeding based on analysis of stomach contents: Application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 726–738.

DuFour, M. R., May, C. J., Roseman, E. F., Mayer, C. M., Ludsin, S. A., Vandergoot, C. S., Pritt, J. J., Fraker, M. E., Davis, J. J., Tyson, J. T., Miner, J. G., & Marschall, E. A. (2015). Portfolio theory as a management tool to guide conservation and restoration of multi-stock fish populations. *Ecosphere*, 6(12), 1–21. https://doi.org/10.1890/ES15-00237.1

Forney, J. L. (1976). Year-class formation in the walleye (*Stizostedion vitreum vitreum*) population in Oneida Lake, New York, 1966–1973. *Journal of the Fisheries Board of Canada*, 33(4), 783–792.

Galarowicz, T. L., Adams, J. A., & Wahl, D. H. (2006). The influence of prey availability on ontogenetic diet shifts of a juvenile piscivore. *Canadian Journal of Fisheries and Aquatic Sciences*, 63, 1722–1733.

Gopalan, G., Culver, D. A., Wu, L., & Taruben, B. K. (1998). Effects of recent ecosystem changes on the recruitment of young-of-the-year fish in western Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 2572–2579.

Hansen, G. J. A., Ahrenstorff, T. D., Bethke, B. J., Dumke, J. D., Hirsch, J., Kovalenko, K. E., LeDuc, J. F., Maki, R. P., Rantala, H. M., & Wagner, T. (2020). Walleye growth declines following zebra mussel and *Bythotrephes* invasion. *Biological Invasions*, 22, 1481–1495.

Hansen, M. J., Bozek, M. A., Newby, J. R., Newman, S. P., & Staggs, M. D. (1998). Factors affecting recruitment of walleyes in Escanaba Lake, Wisconsin. *North American Journal of Fisheries Management*., 18(4), 764–774.

Herdendorf, C. E., & Braidech, L. L. (1972). *A study of the physical characteristics of the major reef areas in western Lake Erie*. Ohio Dept. Nat. Res., Div. Geol. Surv., Proj. AFCS-1 139 p.

Hokanson, K. E., & Lien, G. G. (1986). Effects of diet on growth and survival of larval walleyes. *Progressive Fish-Culturist*, 48, 250–258.

Honsey, A. E., Feiner, Z. S., & Hansen, G. J. (2020). Drivers of walleye recruitment in Minnesota's large lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 77(12), 1921–1933.

Houde, E. D. (1967). Food of pelagic young of the walleye, *Stizostedion vitreum vitreum*, in Oneida Lake, New York. *Transactions of the American Fisheries Society*, 96(1), 17–24.

Hoxmeier, R. J. H., Wahl, D. H., Brooks, R. C., & Heidinger, R. C. (2006). Growth and survival of age-0 walleye (*Sander vitreus*): Interactions among walleye size, prey availability, predation, and abiotic factors. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(10), 2173–2182.

Hoxmeier, R. J. H., Wahl, D. H., Hooe, M. L., & Pierce, C. L. (2004). Growth and survival of larval walleyes in response to prey availability. *Transactions of the American Fisheries Society*, 133(1), 45–54.

Johnson, T. B., Bunnell, D. B., & Knight, C. T. (2005). A potential new energy pathway in central Lake Erie: The round goby connection. *Journal of Great Lakes Research*, 31, 238–251.

Knight, R. L., Margraf, F. J., & Carline, R. F. (1984). Piscivory by walleyes and yellow perch in western Lake Erie. *Transactions of the American Fisheries Society*, 113, 677–693.

Krynak, E. M. (2012). *Aquatic mesohabitats: Abiotic and biotic comparisons in a sand dominated, 3rd order, Michigan stream.* M.S. thesis, Grand Valley State University, Allendale, MI, 79 pp.

Lake Erie Forage Task Group. (2022). *Report of the Lake Erie forage task group.* Great Lakes Fishery Commission.

Lake Erie Walleye Task Group. (2022). *Report of the Lake Erie Walleye Task Group to the Great Lakes.* Great Lakes Fishery Commission.

Madenjian, C. P., Tyson, J. T., Knight, R. L., Kershner, M. W., & Hansen, M. J. (1996). First-year growth, recruitment, and maturity of walleyes in western Lake Erie. *Transactions of the American Fisheries Society*, 125, 821–830.

May, C. J., Budnik, R. R., Ludsin, S. A., O'Donnell, D. R., Hood, J. M., Roseman, E. F., & Marschall, E. A. (2021). Evidence that copepod biomass during the larval period regulates recruitment of Lake Erie walleye. *Journal of Great Lakes Research*, 45, 1241–1250.

May, C. J., Ludsin, S. A., Glover, D. C., & Marschall, E. A. (2020). The influence of larval growth rate on juvenile recruitment in Lake Erie walleye (*Sander vitreus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 77(3), 548–555.

Mayer, C. M., Rudstam, L. G., Mills, E. L., Cardiff, S. G., & Bloom, C. A. (2001). Zebra mussels (*Dreissena polymorpha*), habitat alteration, and yellow perch (*Perca flavescens*) foraging: System-wide effects and behavioral mechanisms. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 2459–2467.

Mayer, C. M., & Wahl, D. H. (1997). The relationship between prey selectivity and growth and survival in a larval fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 1504–1512.

Méthot, G., Hudon, C., Gagnon, P., Pinel-Alloul, B., Armellin, A., & Poirier, A. M. T. (2012). Macroinvertebrate size–mass relationships: How specific should they be? *Freshwater Science*, 31, 750–764.

Mills, E. L., Leach, J. H., Carlton, J. T., & Secor, C. L. (1994). Exotic species and the integrity of the Great Lakes. *Bioscience*, 44(10), 666–676.

Mion, J. B., Stein, R. A., & Marschall, E. A. (1998). River discharge drives survival of larval walleye. *Ecological Applications*, 8, 88–103.

Munawar, M., Munawar, I. F., Mandrak, N. E., Fitzpatrick, M., Dermott, R., & Leach, J. (2005). An overview of the impact of non-indigenous species on the food web integrity of North American Great Lakes: Lake Erie example. *Aquatic Ecosystem Health & Management*, 8, 375–395.

Ohio Department of Natural Resources - Division of Wildlife. (2022). *Ohio's Lake Erie Fisheries, 2021.* Annual data report. Federal Aid in Fish Restoration Project F-69-P. Ohio Department of Natural Resources, Division of Wildlife, Lake Erie Fisheries Units, Fairport Harbor and Sandusky, 91 pp.

Pangle, K. L., Peacor, S. D., & Johannsson, O. E. (2007). Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. *Ecology*, 88, 402–412.

Paradis, Y., Bertolo, A., Perot, A., Debas, S., & Magnan, P. (2006). Do benthivory and piscivory result in similar growth in walleye? *Journal of Fish Biology*, 69, 1317–1329.

Parker Stetter, S. L., Witzel, L. D., Rudstam, L. G., Einhouse, D. W., & Mills, E. L. (2005). Energetic consequences of diet shifts in Lake Erie rainbow smelt (*Osmerus mordax*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 145–152.

Parsons, J. W. (1971). Selective food preferences of walleyes of the 1959 year class in Lake Erie. *Transactions of the American Fisheries Society*, 100, 474–485.

Prichard, C. G., Craig, J. M., Roseman, E. F., Fischer, J. L., Manny, B. A., & Kennedy, G. W. (2017). *Egg deposition by lithophilic-spawning fishes in the Detroit and Saint Clair Rivers, 2005–14: U.S. Geological Survey Scientific Investigations Report 2017 5003*, 20 p. https://doi.org/10.3133/sir20175003

Rogers, L. E., Hinds, W. T., & Buschborn, R. I. (1976). General weight vs length relationship for insects. *Annals of the Entomological Society of America*, 69, 387–389.

Roseman, E. F. (1997). *Factors influencing the year-class strength of reef spawned walleye in western Lake Erie.* M.S. thesis, Michigan State University, East Lansing, MI, 140 pp.

Roseman, E. F. (2000). *Physical and biological processes influencing walleye early life history in western Lake Erie.* Doctoral dissertation, Michigan State University, East Lansing, MI, 147 pp.

Roseman, E. F., Taylor, W. W., Hayes, D. B., Haas, R. C., Knight, R. L., & Paxton, K. O. (1996). Walleye egg deposition and survival on reefs in western Lake Erie. Proceedings of the Second International Percid Fishes Symposium. *Annales Zoologici Fennici*, 33, 341–351.

Sabo, J. L., Bastow, J. L., & Power, M. E. (2002). Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. *Journal of the North American Benthological Society*, 21, 336–343.

Schmidt, B. A., Tucker, T. R., Collier, J. J., Mayer, C. M., Roseman, E. F., Stott, W., & Pritt, J. J. (2020). Determining habitat limitations of Maumee River walleye production to western Lake Erie fish stocks: Documenting a spawning ground barrier. *Journal of Great Lakes Research*, 46(6), 1661–1673. https://doi.org/10.1016/j.jglr.2020.08.022

Sheppard, K. T., Davoren, G. K., & Hann, B. J. (2015). Diet of walleye and sauger and morphological characteristics of their prey in Lake Winnepeg. *Journal of Great Lakes Research*, 41, 907–915.

Slipke, J. W., & Duffy, W. G. (1997). Food habits of walleye in Shadehill Reservoir, South Dakota. *Journal of Freshwater Ecology*, 12(1), 11–17.

Stein, S. R., Roswell, C. R., Pothoven, S. A., & Höök, T. O. (2017). Diets and growth of age-0 walleye in a recently recovered population. *Journal of Great Lakes Research*, 43, 100–107.

Thorp, J. H., & Covich, A. P. (2001). *Ecology and classification of North American freshwater invertebrates.* Academic Press.

Traynor, D., Moerke, A., & Greil, R. (2010). *Identification of Michigan fishes using cleithra.* Great Lakes Fishery Commission Miscellaneous Publication.

Van Guilder, M. A., & Seefelt, N. A. (2013). Double-crested Cormorant (*Phalacrocorax auritus*) chick bioenergetics following round goby (*Neogobius melanostomus*) invasion and implementation of cormorant population control. *Journal of Great Lakes Research*, 39, 153–161.

Ward, M. C., Willis, D. W., Herwig, B. R., Chipps, S. R., Parsons, B. G., Reed, J. R., & Hanson, M. A. (2008). Consumption estimates of walleye stocked as fry to suppress fathead minnow populations in west-central Minnesota wetlands. *Ecology of Freshwater Fish*, 17, 59–70.

Watkins, J., Rudstam, L. G., & Holeck, K. (2011). *Length-weight regressions for zooplankton biomass calculations – A review and a suggestion for standard equations.* Cornell Biological Field Station Publications and Reports.