ARTICLE

Freshwater Ecology

Lakescape connectivity: Mobile fish consumers link Lake Michigan coastal wetland and nearshore food webs

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Abstract

In large lake ecosystems, fish movement between coastal littoral habitats such as wetlands and the adjacent open-water nearshore represents an understudied but potentially important linkage supporting energy flow and fisheries production. We hypothesized that yellow perch (*Perca flavescens*), an ecologically and economically important sport fish in the Laurentian Great Lakes, transport energy from highly productive wetlands to nearshore food webs, but that their role changes with ontogenetic shifts in diet and habitat use. We also predicted that the relative strength of such fish-mediated habitat linkages would vary depending on physical connectivity across habitats. We collected perch and potential prey resources from seven paired coastal wetland–nearshore sites across three regions of Lake Michigan and quantified resource and habitat use with Bayesian stable isotope mixing models and otolith microchemistry. We found that juvenile perch collected in nearshore habitats showed high use of wetland resources, and that diets of wetland-collected juveniles typically contained a smaller proportion of nearshore resources than did more mobile adults from the same wetland. The least hydrologically connected sites had lower cross-habitat resource use (e.g., wetland-collected perch consumed fewer nearshore resources and vice versa) compared with sites with greater levels of hydrological connectivity. Otolith microchemistry confirmed the linkages revealed by stable isotopes, suggesting that a dual approach can increase understanding of habitat linkages in large lakes. Quantifying the importance of multiple lentic habitats (i.e., "lakescape connectivity") for fisheries production is critical for developing comprehensive large lake food web models and providing managers with information to prioritize locations for conservation and restoration.

INTRODUCTION

Mobile consumers can promote coupling of spatially separated food webs by foraging across a large range of habitats and providing links between the prey items found within them (Polis et al., 1997; Schindler & Scheuerell, 2002). Food webs coupled in space are able to enhance consumer biomass beyond the internal production of a single system; therefore, factors controlling access to habitats and resources (e.g., landscape features) can affect system productivity (Polis et al., 1997). The magnitude and timing of such flows may also be influenced by differential habitat use of mobile consumers such as fishes. While the role of fish in linking natal and adult habitat food webs has been studied extensively in marine coastal ecosystems (e.g., Janetski et al., 2009), similar work is limited within freshwater ecosystems such as large lakes (but see Vander Zanden & Vadeboncoeur, 2002). In marine ecosystems, fishes are often important vectors of energy flow among habitats, with coastal wetlands such as salt marshes and mangroves serving as nursery habitats for juveniles who then transport wetland-derived biomass and energy upon moving to adult habitats (Beck et al., 2001). For many marine fishes, access to multiple habitats (seascape connectivity) is critical across ontogenetic shifts (Gillanders et al., 2003). Fish use of different habitats within a seascape may, however, be facultative and spatially complex, and these flows are increasingly disrupted by anthropogenic environmental change with cascading effects on ecology and biogeochemistry (Schmitz et al., 2018).

Understanding and quantifying fish-mediated energy exchange across aquatic habitats therefore require information about both cross-habitat resource use (i.e., use of resources from multiple habitats) and movement throughout life. These types of data can be difficult to obtain as stomach contents may provide only a snapshot of prey items consumed with little indication of prey origin (Vander Zanden & Vadeboncoeur, 2002), and movement measurements using artificial tags can be expensive and impractical for juvenile fishes or for long-term tracking (Cooke et al., 2004). As such, increasing focus has been placed on the use of natural markers such as stable isotope signatures in fish muscle tissue and the elemental composition of fish otoliths. Stable isotope analysis (SIA) of consumer tissues and potential prey items provides an effective method for indirectly determining animal diets and estimating proportional contributions of food sources (i.e., "resource use," sensu Newsome et al., 2007) from different habitats when food sources are isotopically distinct. Information about resource use inferred by SIA can be combined with habitat use data obtained independently with otolith microchemistry. Movements among habitats over a fish's lifetime can be reconstructed using otolith microchemistry because fish can incorporate a detectable chemical signature into their otoliths if they reside in a chemically distinct environment for a sufficient period of time (e.g., Thorrold et al., 1998). The use of otoliths as natural tags is possible due to continuous growth, metabolic inertness, and because trace elements (e.g., strontium and barium) are incorporated into the otolith's crystalline structure proportional to concentrations in the surrounding environment (Campana, 1999). Patterns in trace element incorporation therefore can be associated with temporal landmarks (i.e., annuli) to understand habitat use across life stages (Thorrold et al., 1998). The combined use of SIA and otolith microchemistry can help reconstruct previous environmental and dietary histories and understand energy exchange among habitats.

In the Laurentian Great Lakes (hereafter, Great Lakes), fish movement between coastal wetlands and adjacent open-water habitats of the nearshore lake represents an understudied but potentially important linkage supporting fisheries production. A broader understanding of such fish-mediated habitat linkages is particularly important in the context of dramatic and complex changes to native food webs over the last century including overfishing and eutrophication in the mid-20th century, as well as subsequent oligotrophication following the reduction of nutrient loading (Warner & Lesht, 2015) and introduction of non-native species such as dreissenid mussels in the second half of the century (Hecky et al., 2004). In Lake Michigan, the introduction and spread of non-native filter-feeding dreissenid mussels (*Dreissena bugensis* and *Dreissena polymorpha*) beginning in the 1990s has contributed to increased nutrient concentrations in localized nearshore benthic areas (the "nearshore shunt," Hecky et al., 2004) and declines in offshore pelagic primary production (Fahnenstiel et al., 2010; Warner & Lesht, 2015). This reduced productivity has significantly impacted overall fisheries production (Hecky et al., 2004; Warner & Lesht, 2015), and pelagic fishes have responded to dreissenid-induced

changes in nutrient and energy pathways by increasing their reliance on coastal nearshore energy subsidies (Turschak et al., 2014).

While many large-scale changes have been documented in the pelagic offshore habitats of Lake Michigan, changes to the trophic structure of coastal wetlands have received comparatively less study (Ives et al., 2018; Vadeboncoeur et al., 2011), despite their ecological importance and potential role in sustaining sport fish populations (Hoffman et al., 2010; Keough et al., 1998). Great Lakes coastal wetlands can have high rates of primary productivity relative to the pelagic lake (Cooper et al., 2013) and often support diverse biological communities, with up to 90% of Great Lakes fish species using coastal wetlands at some point during life (Chubb & Liston, 1986; Cvetkovic & Chow-Fraser, 2011). Because coastal wetlands occupy only a small fraction (<1%) of the total surface area of the Great Lakes, it has generally been assumed that ecological linkages between wetlands and the adjacent lake would be minimal (Brazner et al., 2004), but fish use of these habitats can be disproportionate to their available area (Wei et al., 2004). Differences in wetland hydrogeomorphology and distance between wetland and nearshore habitats (i.e., "hydrological connectivity") may therefore affect the strength of fish-mediated linkages, as landscape features limit the duration and spatial distribution of wetland habitats available to consumers (Albert et al., 2005; Jude & Pappas, 1992; Keough et al., 1999).

The main objective of this study was to examine the role of mobile consumers in transporting wetland-derived productivity to nearshore food webs using yellow perch (*Perca flavescens*, hereafter perch) as a model organism that uses both coastal wetland and open-water nearshore Lake Michigan habitats throughout life. Perch provides a useful model because this species is highly mobile, frequently uses both coastal wetland and nearshore habitats (Schoen et al., 2016; Trebitz et al., 2009), and is able to prey on resources from both pelagic and benthic habitats (Happel et al., 2015). Many perch that are spawned in coastal wetlands appear to stay within the wetland habitats as young-of-the-year (age-0) and age-1 juveniles before dispersing to deeper open-water nearshore habitats as adults (Brazner et al., 2001). Adult perch may return to wetlands in spring to spawn, although little information exists on their movement before and after spawning events (Brazner et al., 2004).

Perch movement may therefore be viewed as one aspect of "lakescape connectivity" (i.e., connectivity between lake habitats such as the multiple types of coastal habitats found within Lake Michigan), which could contribute to the high level of fish production and diversity found within the nearshore and potentially provide energy to the pelagic zone. We quantified perch use of Lake Michigan coastal wetland and nearshore habitats as a model for understanding the role of mobile consumers in mediating energy exchange between food webs of coastal wetlands and the nearshore lake. If such a role exists, we additionally sought to determine (1) whether this role changes with ontogeny, as fish can use habitats differentially over life; and (2) whether the relative strength of these linkages varies among wetland geomorphic types and hydrological connectivity. We quantified perch use of wetland resources using Bayesian stable carbon and nitrogen isotope mixing models and otolith microchemistry at paired wetland–nearshore sites that varied in hydrological connectedness. We hypothesized that there would be distinct differences in resource use across ontogeny, with higher wetland resource use by juveniles due to the protection from predation provided by macrophyte structure, and because abiotic conditions in wetlands (e.g., lower oxygen, higher water temperatures) can restrict adult use (e.g., Robb & Abrahams, 2003). We also hypothesized that the strength of cross-habitat linkages (i.e., resource and habitat use) would be lowest in wetlands that had low hydrological connectedness to the nearshore lake.

METHODS

Study sites

Food web components and perch were collected from seven paired coastal wetland–adjacent nearshore sites (Figure 1, Table 1) representing different wetland geomorphic types in Lake Michigan: (1) southern riverine wetlands (Burns Harbor and Calumet), (2) eastern drowned river-mouth (DRM) wetlands (Muskegon, Pentwater, and White), and (3) western lacustrine wetlands of Green Bay (Cedar River, Little Sturgeon, and Peshtigo). Specific paired wetland–nearshore sites were selected using data from the Great Lakes Coastal Wetland Monitoring Program (https://www.greatlakeswetlands.org; Uzarski et al., 2017; Appendix S1: Table S1) and sampled twice in the summers (June and July) of two consecutive years (2014 and 2015). At eastern DRM wetland sites, an estuarine-DRM lake habitat between the coastal wetland and the open waters of the nearshore was also sampled, as this may represent an important habitat for perch (Senegal et al., 2020). Additionally, the extent to which systems were exposed to wave action and susceptible to exchange with Lake Michigan was characterized by calculating modified effective fetch following Howes et al. (1999) (Table 1). South-region sites were representative of riverine coastal wetlands that form at the lake terminus of
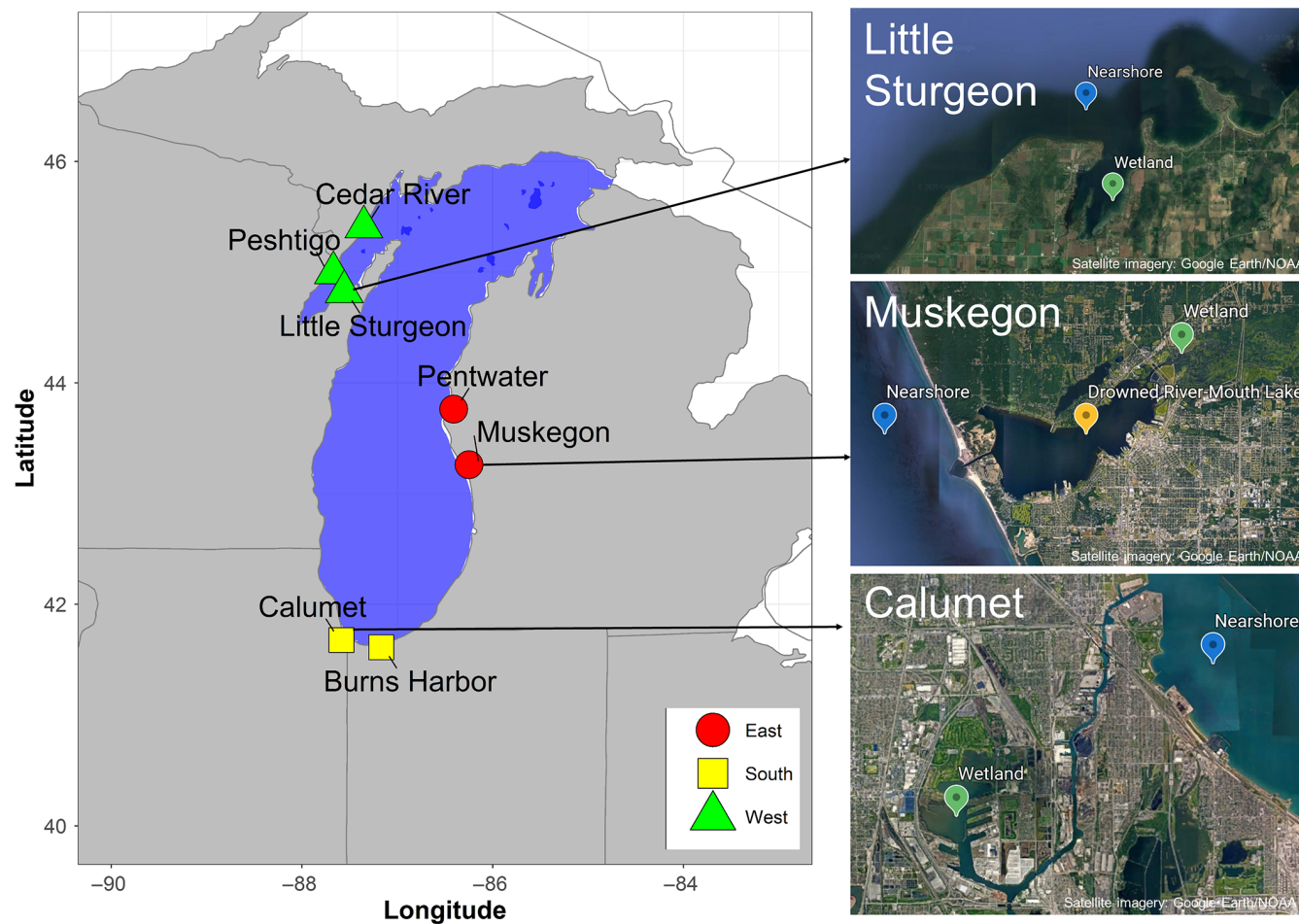
FIGURE 1 Locations of the seven sampled paired wetland–nearshore sites. Regions represent typical wetland hydrogeomorphology: lacustrine and riverine wetlands of the west region, drowned river-mouth wetlands of the east region, and riverine wetlands of the south region. The right-hand panels show satellite imagery of three sites representative of each region (Little Sturgeon, Muskegon, and Calumet) with sampled habitats.

tributaries and characterized by high levels of anthropogenic activity (Albert et al., 2005). Sites in the east region were representative of DRM wetland complexes commonly found along the eastern shore of Lake Michigan where tributaries course through extensive wetlands and into a DRM lake habitat before entering the lake through a restricted channel (Wetzel, 1992). West region sites were located within Green Bay, an elongated, shallow (20 m mean depth) estuary with a hypereutrophic lower bay and a strong declining south-to-north trophic gradient (Sager & Richman, 1991).

Field methods

Measurements of physical and chemical parameters were collected in situ, as well as water samples for dissolved inorganic carbon isotope (DIC-δ^{13}C) analysis, and food web components from each trophic level

(i.e., seston, benthic macroinvertebrates, prey fish, and perch) for stable carbon and nitrogen isotope analysis (SIA) from each habitat (nearshore, wetland, or DRM lake). Perch with a spectrum of lengths (total length range: 39–344 mm) and ages (age-0 to age-7) were collected to examine ontogenetic variation in resource and habitat use, and a subset of perch collected for SIA was also used for otolith microchemistry analysis. Seston samples were collected using horizontal net tows with an 80-μm mesh plankton net, and samples were transferred to a 1-L polyethylene bottle and placed on ice for transport to the lab. Wetland macroinvertebrates were qualitatively sampled from macrophyte zones using standard 0.5-mm mesh D-frame dip net sweeps, while nearshore and DRM lake macroinvertebrates were collected using PONAR dredge grabs. For all habitats, contents of net sweeps or PONAR grabs were placed in plastic bags, transported to the laboratory on ice, and frozen until processing. Fish species representative of all trophic levels present in a

T A B L E 1 Site attributes of drowned river-mouth (DRM) lake (where present), nearshore (NS), and wetland (WL) habitats sampled in this study.

Site	HGM	Distance (km)	Mod. eff. fetch (km)	ΔDIC-δ^{13}C (‰)	Prey taxa present	Site characteristics
South						
Burns Harbor	Riverine	4.9	0.069	−4.56*	NS fish: Alewife (*Alosa pseudoharengus*), spottail shiner (*Notropis hudsonius*); NS invertebrates: Chironomidae; WL fish: Bluegill (*Lepomis macrochirus*), bluntnose minnow (*Pimephales notatus*), golden shiner (*Notemigonus crysoleucas*); WL invertebrates: Amphipoda, Chironomidae, Decapoda crayfish, Isopoda, Gastropoda	Wetland connected to Lake Michigan via East Arm of Little Calumet River; intensive anthropogenic development (site located immediately adjacent to a steel factory and national park)
Calumet	Riverine	20.1	0.150	−1.52	NS fish: Alewife, spottail shiner; NS invertebrates: Amphipoda, Chironomidae, Dreissenidae; WL fish: Alewife, banded killifish (*Fundulus diaphanus*), bluegill, bluntnose minnow, golden shiner, mimic shiner (*Notropis volucellus*), pumpkinseed (*Lepomis gibbosus*); WL invertebrates: Amphipoda, Chironomidae, Dreissenidae, Ephemeroptera, Gastropoda, Hydrachnidia mites, Lepidoptera, Odonata, Trichoptera	Wetland connected to Lake Michigan via Calumet River; shallow (most areas <2 m) with some areas dredged to 10 m for ship traffic; intensive anthropogenic development surrounding wetland includes petroleum refineries and chemical plants
East						
Muskegon	DRM	15.2	0.170	−9.70* −1.25* (WL–DRM)	DRM fish: Spottail shiner; DRM invertebrates: Amphipoda, Chironomidae, Dreissenidae, Gastropoda; NS fish: Spottail shiner; NS invertebrates: Chironomidae, Dreissenidae, Sphaeriidae; WL fish: Spottail shiner, yellow perch (*Perca flavescens*, <100 mm); WL invertebrates: Amphipoda, Chironomidae, Decapoda crayfish, Dreissenidae, Ephemeroptera, Gastropoda, Isopoda	Wetland forms at mouth of Muskegon River and is connected to Lake Michigan via DRM lake habitat; part of system designated as an area of concern (AOC) by the US Environmental Protection Agency because of degraded water and sediment quality because of industrial pollution, but has undergone remediation

(Continues)

TABLE 1 (Continued)

Site	HGM	Distance (km)	Mod. eff. fetch (km)	ΔDIC-δ^{13}C (‰)	Prey taxa present	Site characteristics
Pentwater	DRM	6.3	0.058	−10.86* (WL–NS) −1.58* (WL–DRM)	DRM fish: Yellow perch (<100 mm); DRM invertebrates: Amphipoda, Chaoborous, Chironomidae, Dreissenidae, Hydrachnidia mites, Trichoptera; NS fish: Alewife, round goby (*Neogobius melanostomus*), spottail shiner; NS invertebrates: Chironomidae, Gastropoda; WL fish: Alewife, bluegill, spottail shiner; WL invertebrates: Amphipoda, Chironomidae, Decapoda crayfish, Dreissenidae, Gastropoda, Isopoda, Trichoptera	Wetland forms at confluence of north and south branches of Pentwater River; water exiting the wetland flows through DRM lake habitat which empties into Lake Michigan via a small channel
West						
Cedar River	Lacustrine	1.9	8.659	−7.14*	NS fish: Alewife; NS invertebrates: Chironomidae, Isopoda; WL fish: Common shiner (*Luxilus cornutus*), pumpkinseed; WL invertebrates: Amphipoda, Chironomidae, Gastropoda, Hemiptera, Isopoda, Trichoptera	Open DRM/open shoreline system on northwestern shore of Green Bay; adjacent upland land use is primarily upland forest
Little Sturgeon	Lacustrine	6.3	0.773	−6.40*	NS fish: Alewife, round goby; NS invertebrates: Chironomidae; WL fish: Pumpkinseed, round goby; WL invertebrates: Amphipoda, Chironomidae, Ephemeroptera, Hemiptera, Isopoda	Open embayment on eastern shore of Green Bay; adjacent upland land use is primarily agriculture
Peshtigo	Riverine	2.2	14.434	−7.67*	NS fish: Alewife; NS invertebrates: Chironomidae; WL fish: Bluntnose minnow, common shiner, pumpkinseed, spotfin shiner (*Cyprinella spiloptera*), yellow perch (<100 mm); WL invertebrates: Coleoptera, Isopoda	Riverine wetland located along northwestern shore of Green Bay; wetland extends upstream along the Peshtigo River for 3 km from the mouth

Note: Distance (in kilometers) is measured as river kilometer distance between the wetland and lake measured using ArcGIS. An estimate of exposure to lake waves (i.e., modified effective fetch [mod. eff. fetch]) is provided for wetland habitats based on Howes et al. (1999). ΔDIC-δ^{13}C is the difference in mean dissolved inorganic carbon (DIC) δ^{13}C between WL–NS (or WL–DRM where applicable) habitats; significance based on *t* tests (ANOVA for DRM sites) is noted with an asterisk (*). Prey taxa collected from each site are presented as species (for fish) and order (for invertebrates). Sites are classified by hydrogeomorphology (HGM) as described in Albert et al. (2005).

community were collected from wetland sites using boat electroshocking or modified fyke nets (depending on water depth) and from nearshore and DRM lake habitats using gillnets set perpendicular to the shoreline at depths of approximately 5–7 m. Fish total length was recorded before euthanizing following Institutional Animal Care and Use Protocol (IACUC) 12-04-1712 and freezing. While specific prey fish species assemblages varied among sites, species collected in all habitats included common species consumed by Lake Michigan perch including small cyprinids (e.g., *Notropis* spp. shiners, particularly spottail shiner *N. hudsonius*), clupeids (alewife *Alosa pseudoharengus*), and round goby (*Neogobius melanostomus*) (Turschak et al., 2019). Additionally, we examined gut contents from a subset of perch collected in 2015 from wetland and DRM habitats, but found only invertebrate prey (Appendix S1: Table S2).

Laboratory procedures

Water samples for DIC-δ^{13}C analysis were prepared following methods outlined in Atekwana and Krishnamurthy (1998), but briefly; water from the site was collected in an acid-rinsed container and a syringe was used to add sample water to an evacuated 12-ml glass vial prefilled with 85% phosphoric acid. Isotope ratios of CO_2 produced by the resulting acid-water reaction were determined using an isotope ratio mass spectrometer (IRMS) (Thermo Delta V Advantage, Thermo Fisher) interfaced with a Thermo Gasbench II/Precon located in the University of Notre Dame Center for Environmental Science and Technology (CEST). Carbon isotope ratios were reported in δ notation:

$$\delta\,(‰) = \left(\left[R_{\text{sample}}/R_{\text{standard}}\right] - 1\right) \times 10^3,$$

where R was ^{13}C/^{12}C and δ values were reported as enriched (more positive) or depleted (more negative) relative to the standard Vienna Pee Dee Belemnite (VPDB) via the NBS-19 standard (Atekwana & Krishnamurthy, 1998). The observed analytical precision of δ^{13}C was ±0.11‰ based on an internal laboratory carbonate standard.

In the laboratory, each seston sample was separated into size fractions using stacked 50-, 160-, and 253-µm sieves. Fractions were backwashed onto 50-µm Nitex filters and vacuum-filtered to remove water before being frozen for storage. Benthic macroinvertebrate samples were thawed in enamel pans and individual invertebrates were sorted and identified to family (if possible) or order under a dissecting microscope. Multiple individuals of the same taxonomic class (i.e., between 2 and

20 individuals) were pooled across sweep net samples to obtain sufficient biomass for SIA. Gastropod soft tissues were removed from shells to avoid carbonate fragments. Fish were identified to species, and muscle samples for SIA were taken from the anterior white dorsal muscle of individual fish and rinsed in deionized water. All seston, macroinvertebrate, and fish samples were oven-dried at 70°C for 48 h and homogenized using a ceramic mortar and pestle. Dry sample material was packed into tin capsules for analysis using a Thermo Scientific Delta Plus IRMS coupled with an Elemental Analyzer Trace GQ, also located at CEST. As with the DIC-δ^{13}C measurements, isotopic composition was denoted in δ notation, that is, differences between isotopic ratios in samples and in international standards (VPDB for δ^{13}C and atmospheric nitrogen for δ^{15}N). The observed analytical precisions of δ^{13}C and δ^{15}N were ±0.33‰ and ±0.22‰, respectively, based on replicates of laboratory standards included with every instrument run. To avoid bias resulting from chemical interference in isotopic signatures (Post et al., 2007), we did not extract lipids using chemical solvents, but instead corrected δ^{13}C signatures of lipid-rich samples (i.e., those with C:N > 3.5) following Post et al. (2007):

$$\delta^{13}C_{\text{corrected}} = \delta^{13}C_{\text{uncorrected}} - 3.32 + 0.99 \times C:N.$$

Microchemistry of sagittal otoliths was analyzed using a subset of large perch (TL > 150 mm) collected from wetland and nearshore habitats at three sites—Calumet (south), Muskegon (east), and Little Sturgeon (west)—from 2014, only to avoid confounding analyses with the potential for otolith microchemistry to vary among years (e.g., Tanner et al., 2012). Analytical methods were modified from those described in Schoen et al. (2016) and are detailed in Appendix S1. Briefly, otoliths were cleaned using ultrapure water, mounted in epoxy resin, and longitudinally sectioned using a low-speed wafering saw to create a dorsoventral cross section through the nucleus (i.e., core) that exposed all growth annuli (Pangle et al., 2010). Cross sections were polished and mounted onto glass slides for analysis using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) in the Center for Elemental and Isotopic Analysis (CELISA) at Central Michigan University. LA lines were run perpendicular to annuli, starting across the otolith core and ending at the outer edge (Appendix S1: Figure S1). Analyses of otoliths were bracketed by NIST-612 standard analyses for trace element concentration determinations, and MACS3 (United States Geological Survey carbonate standard) reference material was also analyzed at the beginning and end of each daily session as an internal standard

(Jochum et al., 2005). For every sample and standard analysis, the carrier/makeup gas background signal was measured prior to ablation to quantify background trace elements that were then subtracted from the measured raw isotope count rates. Background-corrected isotope count rates were adjusted and converted to parts per million (ppm) based upon the known and measured isotope:Ca ratios in the NIST 612 standards bracketing each sample (Iolite software, version 2.31; Paton et al., 2011). Otolith elemental concentrations were converted into molar equivalents and normalized to mmol $X \times$ mol Ca^{-1} (where "X" is the element of interest) prior to statistical analyses.

Data analysis

Data from both sampling years (2014 and 2015) were pooled for all statistical analyses because t tests indicated no difference in seston, primary consumer, or fish isotope values within sites between the two years of sampling. Because we determined that water column DIC and prey $\delta^{13}C$ values differed between the wetland and nearshore lake habitats (Table 1, Figure 2a; Appendix S1: Figure S2) and little fractionation occurs between prey and predators (Hecky & Hesslein, 1995), this distinct isotope "signal" for each habitat should be conserved throughout trophic levels and allow for the use of mixing models to
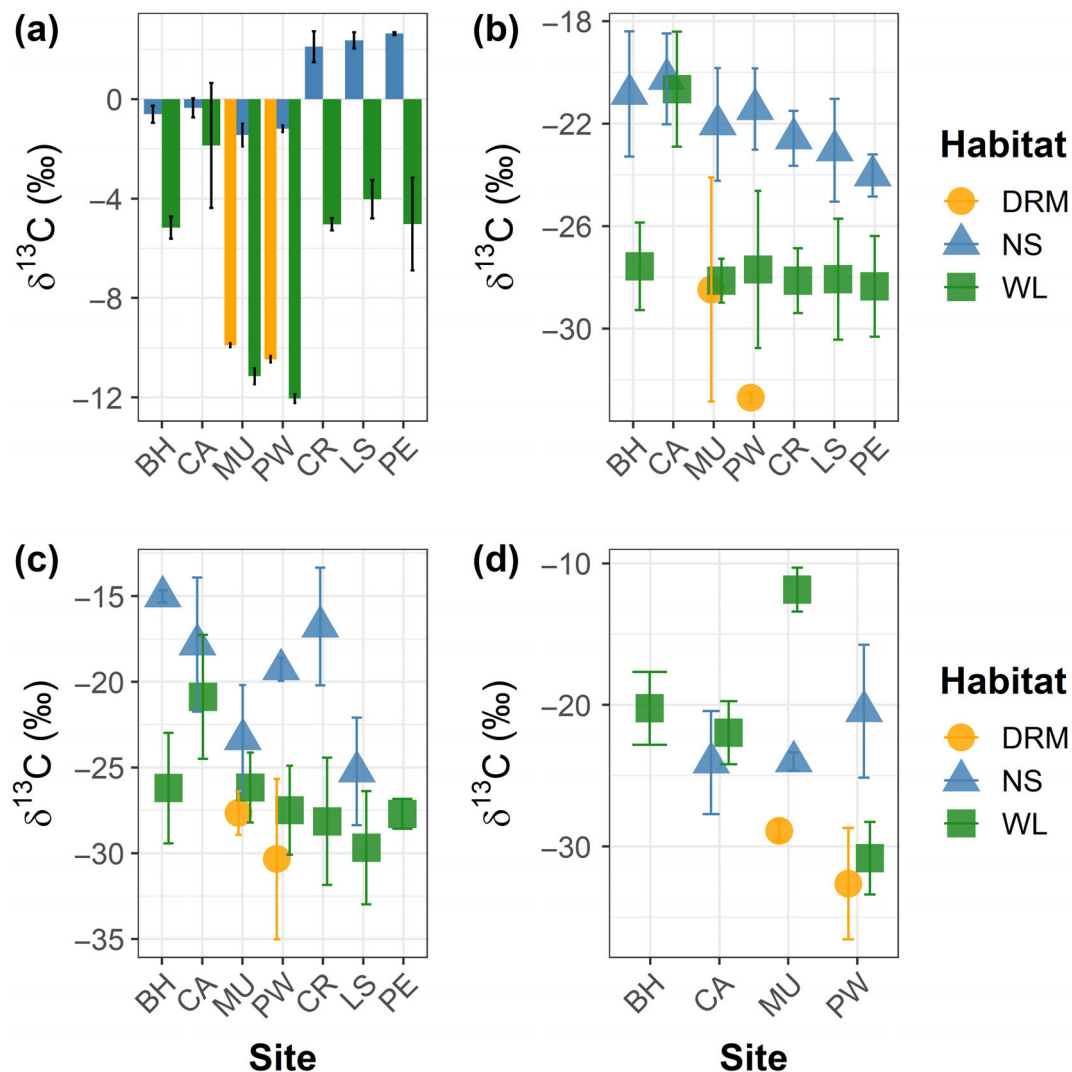
FIGURE 2 Differences in $\delta^{13}C$ among food web components collected from drowned river-mouth (DRM), nearshore (NS), and coastal wetland (WL) habitats in Lake Michigan. Plots show mean ± standard deviation of $\delta^{13}C$ measured in (a) water column dissolved inorganic carbon (DIC), (b) prey fish, (c) benthic invertebrates, and (d) seston. WL DIC was significantly ^{13}C-depleted relative to the adjacent NS at all sites except Calumet (CA) where habitat DIC-$\delta^{13}C$ values were not significantly different (t test, $p = 0.08$). WL prey fish and invertebrates were typically ^{13}C-depleted relative to the same resources found in the adjacent NS habitat, except at CA. At east sites with DRM habitats, DRM resources were ^{13}C-depleted relative to those from the WL. Seston $\delta^{13}C$ did not follow a consistent trend across habitats. BH, Burns Harbor; CR, Cedar River; LS, Little Sturgeon; MU, Muskegon; PE, Peshtigo; PW, Pentwater.

estimate the relative importance of wetland and nearshore resources to perch populations (Vander Zanden & Vadeboncoeur, 2002). Although alewife mobility can be high compared with the other species of prey fishes collected (e.g., Turschak et al., 2019), other work has found that movements of alewife between nearshore areas of Lake Michigan and DRM lake habitats are limited (Dufour et al., 2008); therefore, species collected in a habitat were considered spatially representative of that habitat. Bayesian stable isotope mixing models were run in R version 3.4.2 (R Core Team, 2020) using the package MixSIAR (version 3.1.10; Stock et al., 2018) to determine the relative contributions of wetland, DRM lake, and nearshore resources to four groups of perch: nearshore-collected large perch (i.e., TL > 150 mm, NS Large Perch), nearshore-collected small perch (i.e., TL < 150 mm, NS Small Perch), wetland-collected large perch (WL Large Perch), and wetland-collected small perch (WL Small Perch). Mixing models were run separately for each of these size class–habitat combination groups at each site. We used TL of 150 mm as the cutoff length between small and large perch because yellow perch generally switch to piscine prey items at or near this length (Clady, 1974), while smaller perch primarily consume zooplankton and soft-bodied benthic invertebrates (Tyson & Knight, 2001). In southern Lake Michigan, zooplankton and invertebrates typically consumed by small perch include Copepoda and Chironomidae (larvae and pupae) (Happel et al., 2015).

Mixing models for each size class–habitat group at each site were developed using MixSIAR and three types of data: (1) the mean $\delta^{13}C$ and $\delta^{15}N$ values of potential sources in the wetland (WL), nearshore (NS), or DRM habitat (mean ± standard deviation [SD]; Appendix S1: Table S3); (2) the $\delta^{13}C$ and $\delta^{15}N$ values of individual perch consumers (Appendix S1: Table S4); and (3) consumer-specific trophic enrichment factors (TEFs, mean ± SD). The use of a Bayesian mixing model approach allowed us to incorporate uncertainty in the isotopic signatures of sources, consumers, and TEFs, and report output source contributions as the median estimates of probability distributions (Parnell et al., 2010; Stock et al., 2018). Because we had limited stomach content data from perch consumers, an uninformative prior was used in the models to give an equal probability of consumption among sources and TEFs of 1.3 (±0.3)‰ and 2.9 (±0.32)‰ for carbon and nitrogen, respectively (McCutchan et al., 2003). Models converged after 1,000,000 iterations of three chains with a burn-in of 500,000 iterations, and chain convergence was checked using Gelman–Rubin and Geweke diagnostics.

Because stable isotope mixing models make several assumptions (e.g., every source in the model contributes to the consumer's diet), violations of these assumptions (e.g., missing dietary source) have traditionally been assessed using the "point-in-polygon" approach (e.g., Benstead et al., 2006); that is, for mass balance to be established in a linear mixing model, a consumer's isotopic signature must be within a polygon bounding the signatures of the sources. Because Bayesian mixing models will calculate source contributions even when a model is unlikely to satisfy point-in-polygon for every consumer (Parnell et al., 2010), we performed a priori model evaluations following the simulation procedure detailed in Smith et al. (2013). Briefly, we generated a large number of possible mixing polygons with a Monte Carlo simulation using the same uncertainty incorporated in the mixing models and tested these polygons for point-in-polygon. The proportion of iterated polygons that satisfied the point-in-polygon assumption was calculated for each consumer and was interpreted as the probability (in a frequentist sense) that a consumer's isotopic signature was explained by the proposed model. This probability provided a quantitative basis for correction of TEFs or consumer exclusion (e.g., any consumer outside the 95% mixing region; Smith et al., 2013).

We analyzed otolith edge microchemistry following the assumption that the edge (i.e., the last 10 μm of ablated otolith material) would reflect the most recently encountered environmental conditions (Thorrold et al., 1998). Previous work in Great Lakes coastal wetlands has found that concentrations of barium (Ba), magnesium (Mg), manganese (Mn), and strontium (Sr) in perch otolith edge separated individuals among wetland types in multivariate space (Schoen et al., 2016). Mn and Ba concentrations for Muskegon perch and Mn concentrations for Little Sturgeon perch were natural log-transformed to normalize distributions prior to statistical analysis. All other element concentrations were normally distributed and not transformed. We used nonmetric multidimensional scaling (NMDS) with permutational multivariate analysis of variance (PERMANOVA) to compare an otolith edge "fingerprint" between wetland and nearshore habitats for each site. We then evaluated the ability of a classification method (linear discriminant analysis [LDA]) to assign an individual to its collection habitat using otolith edge microchemistry with a jackknife procedure to estimate classification accuracy (e.g., Pangle et al., 2010). Otolith edge analyses were performed using the R packages vegan (Oksanen et al., 2019) and MASS (Venables & Ripley, 2002).

RESULTS

Basal resources

Water column DIC-$\delta^{13}C$ values generally indicated depletion of ^{13}C in wetland habitats relative to the nearshore

Lake Michigan habitat (Table 1, Figure 2a), likely due to in situ biogeochemical processes including exchange with atmospheric CO_2 and decomposition and respiration of organic matter that decreases $\delta^{13}C$ of DIC (Bade et al., 2004). The south-region site Calumet was the only location where habitat DIC-$\delta^{13}C$ values did not differ significantly between nearshore and wetland due to high intra-wetland variability. DIC-$\delta^{13}C$ values of the DRM lake habitats in the east region were intermediate between nearshore and wetland values (Table 1), suggesting possible mixing of water or a level of in situ biogeochemical processing in this intermediary habitat (Larson et al., 2013).

Prey fish resources collected from the coastal wetland habitats were depleted in $\delta^{13}C$ compared with prey fish resources collected from the adjacent paired nearshore Lake Michigan habitat (Figure 2b; Appendix S1: Table S3 and Figure S2). The most commonly collected species across all sites and habitats were alewife and spottail shiner (*N. hudsonius*); however, we also included other soft-rayed cyprinid species (e.g., bluntnose minnow *Pimephales notatus* and golden shiner *Notemigonus crysoleucas*), young-of-year yellow perch, and small pumpkinseed (*Lepomis gibbosus*) as prey fish resources for sites where alewife and spottail shiners were not found. Mean $\delta^{13}C$ values of prey fish resources ranged from $-20.7‰$ to $28.4‰$ in coastal wetland habitats ($n = 7$), $-20.3‰$ to $-24.0‰$ in nearshore pelagic Lake Michigan ($n = 7$), and $-28.5‰$ to $-32.7‰$ in DRM lakes ($n = 2$). The mean difference in prey fish $\delta^{13}C$ between paired wetland–nearshore habitats was $4.9‰$, but ranged from $0.40‰$ (Calumet) to $6.7‰$ (Burns Harbor). DRM lake prey fish resources were on average $-2.7‰$ ^{13}C-depleted relative to the adjacent wetland.

Wetland benthic invertebrate resources were also depleted in $\delta^{13}C$ compared with benthic invertebrates collected from the adjacent paired nearshore habitat (Figure 2c; Appendix S1: Table S3 and Figure S2). The most commonly collected taxon across all sites and habitats was Chironomidae larvae; however, we also included Amphipoda, Isopoda, Gastropoda, and Ephemeroptera as invertebrate resources for sites where Chironomidae larvae were not found. Mean $\delta^{13}C$ values of benthic invertebrate taxa ranged from $-26.2‰$ to $27.5‰$ in coastal wetland ($n = 7$), $-15.0‰$ to $-25.2‰$ in nearshore pelagic lake ($n = 6$), and $-27.7‰$ to $-30.3‰$ in DRM lake habitats ($n = 2$). The mean difference in invertebrate $\delta^{13}C$ between wetland and nearshore resources was $6.8‰$, but ranged from $2.8‰$ (Muskegon) to $11.4‰$ (Cedar River). DRM lake benthic invertebrate resources were on average $2.2‰$ depleted in ^{13}C relative to the wetland. In contrast to prey fish and invertebrate resources, mean seston $\delta^{13}C$ did not follow a consistent trend across habitats (Figure 2d)

and showed high variability among habitats and sites, ranging from $-11.9‰$ (Muskegon WL) to $-32.6‰$ (Pentwater DRM).

Mixing models

Results of the stable isotope mixing models indicated that large perch collected in nearshore habitat (NS Large Perch) can have up to a quarter of their diet on average originating in the adjacent wetland habitat (Figure 3; Appendix S1: Table S5). Little Sturgeon NS Large Perch ($n = 3$, mean TL [SD] = 149 [5.3] mm) were primarily piscivorous, with the largest median resource contributions coming from nearshore prey fish (median posterior estimate = 43.5%, 95% Bayesian credible interval = 5.0%–75.8%) and wetland prey fish (28.8%, 1.7%–71.1%). In contrast, the largest resource contributions to diets of Burns Harbor NS Large Perch ($n = 3$, 228 [30.6] mm) were from lower trophic levels, that is, nearshore invertebrates (26.0%, 2.0%–51.0%) and wetland seston (22.4%, 3.0%–45.4%), despite the consumers' large body size. Similar to Burns Harbor, Calumet NS Large Perch ($n = 4$, 201 [16.2] mm) also had the largest single contribution from nearshore invertebrates (30.5%, 3.6%–56.6%). Muskegon NS Large Perch ($n = 5$, 222 [23.6] mm) used mostly nearshore shiners (33.2%, 5.9%–51.7%) and seston (33.1%, 6.9%–50.4%). The mixing model for Muskegon NS Large Perch converged only when two wetland sources were included (wetland invertebrates and smaller conspecifics, i.e., perch <100 mm TL), although these sources together represented approximately 15% of the overall assimilated energy.

Small perch were only collected from the nearshore habitat at two sites: Little Sturgeon and Burns Harbor (NS Small Perch; Figure 4; Appendix S1: Table S5). Although Little Sturgeon NS Small Perch ($n = 3$, 110 [20.8] mm) had total lengths of <150 mm, they appeared to be primarily piscivorous with the largest contribution being prey fish collected in the adjacent wetland (23.5%, 1.7%–60.4%). The largest contribution to Burns Harbor NS Small Perch ($n = 6$, 120 [8.2] mm) was wetland seston (56.6%, 40.2%–69.6%). No NS Small Perch were collected from east region sites.

Large perch were collected from wetland habitats at all sites except Burns Harbor, and often had low use of resources from outside their habitat of collection (Figure 5; Appendix S1: Table S5). WL Large Perch from Little Sturgeon ($n = 3$, 158 [16.5] mm) had the highest nearshore resource use within this group, with approximately equal contributions from nearshore prey fish (18.9%, 1.0%–53.9%) and nearshore invertebrates
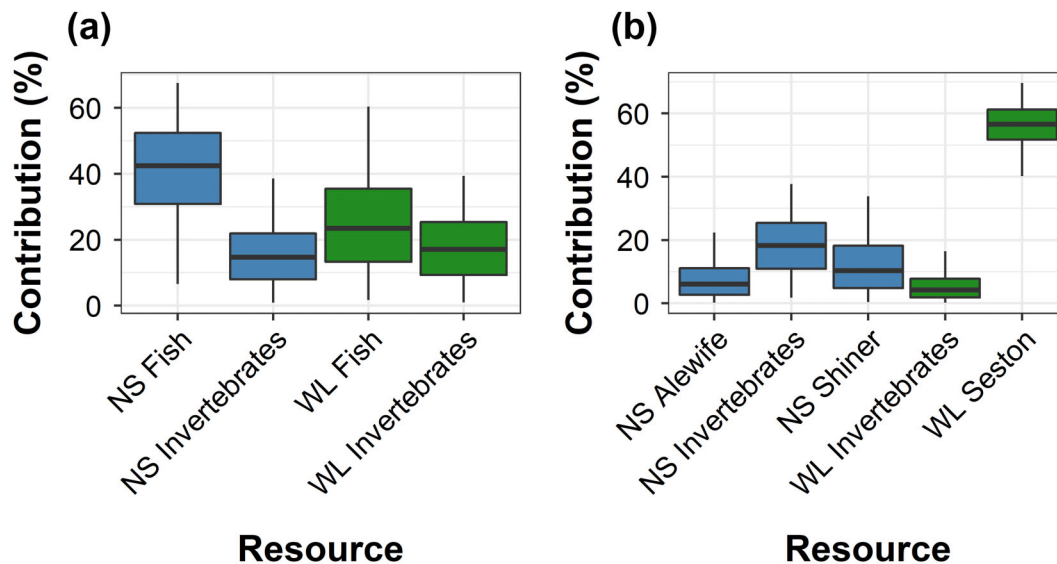
(a)

(b)

(c)

(d)
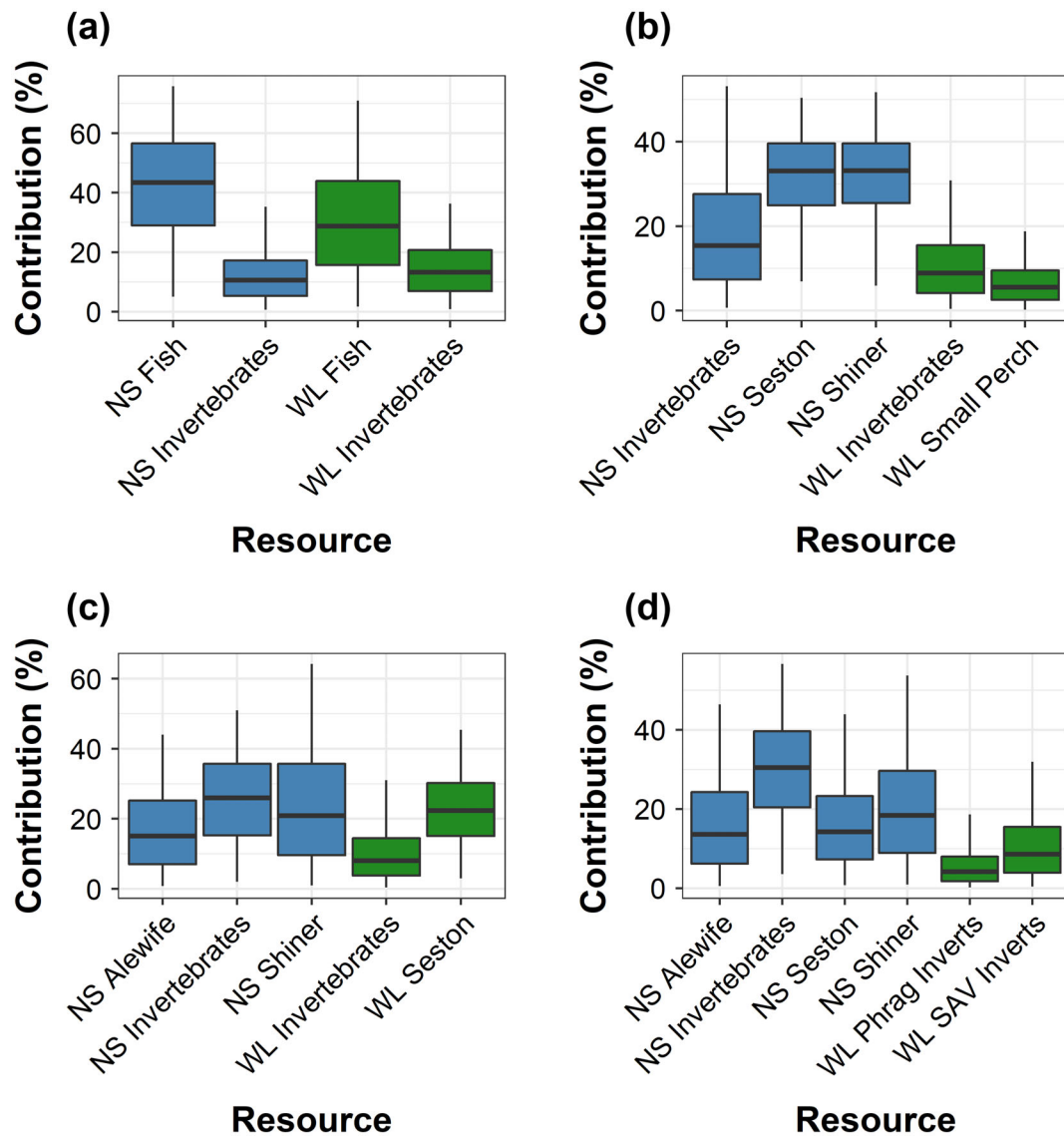
FIGURE 3 Diet contributions to nearshore (NS)-collected large perch (TL > 150 mm) estimated by stable carbon and nitrogen isotope Bayesian mixing models. Box plots show median posterior estimates of resource use (with 95% Bayesian credible intervals) for NS Large Perch collected from (a) Little Sturgeon, (b) Muskegon, (c) Burns Harbor, and (d) Calumet. Box colors indicate resource origin (NS or wetland [WL]). At Calumet, WL invertebrates were collected from both emergent vegetation ("Phrag") and submerged aquatic vegetation ("SAV") microhabitats.

(17.9%, 1.0%–51.3%). WL Large Perch from the two other west region sites, Cedar River ($n = 3$, 189 [7.5] mm) and Peshtigo ($n = 2$, 150 [13.4] mm), had nearshore resource contributions totaling approximately 20%, mostly consisting of nearshore alewives (Cedar River: 18.1%, 1.0%–51.0%; Peshtigo: 19.1%, 1.2%–49.7%). The largest single-resource contribution to Muskegon WL Large Perch ($n = 8$, 193 [25.1] mm) was seston from the adjacent DRM habitat (39.7%, 14.3%–62.3%), although the best-fit models also included smaller contributions of nearshore invertebrates (13.8%, 1.0%–34.6%) and nearshore shiners (15.0%, 1.0%–35.8%). The best-fit models for WL Large Perch from Calumet ($n = 15$, 183 [33.7] mm) and Pentwater ($n = 4$, 210 [40.7] mm) did not include

any nearshore resources, although perch at Pentwater did appear to consume small perch living in the adjacent DRM habitat (24.4%, 1.6%–50.8%).

Small perch collected in wetland habitats (WL Small Perch) had the lowest average posterior estimates of nearshore resource use of the four size class–habitat groups, although those from east region sites did have significant use of adjacent DRM lake resources (Figure 6; Appendix S1: Table S5). Little Sturgeon WL Small Perch ($n = 4$, 48 [7.1] mm) had about equally small contributions of nearshore prey fish (8.8%, 0.4%–43.8%) and nearshore invertebrates (9.2%, 0.4%–36.2%). While Muskegon WL Small Perch ($n = 3$, 117 [18] mm) received most of their diet from prey fish collected from the adjacent DRM

FIGURE 4 Diet contributions to nearshore (NS)-collected small perch (TL < 150 mm) estimated by stable carbon and nitrogen isotope Bayesian mixing models. Boxplots show median posterior estimates of resource use (with 95% Bayesian credible intervals) for NS Small Perch collected from (a) Little Sturgeon and (b) Burns Harbor. Box colors indicate resource origin (NS or wetland [WL]).

lake (45.3%, 4.0%–72.2%), the best-fit mixing model also included nearshore shiners (11.5%, 0.7%–39.8%). No nearshore resources were included in the best-fit mixing model for Pentwater WL Small Perch ($n = 6$, 128 [24.1] mm), and like Muskegon, the largest contribution to this consumer group came from prey fish collected from the DRM lake (specifically small conspecifics, 34.7%, 3.2%–60.2%). The best-fit model for Calumet WL Small Perch ($n = 12$, 107 [29.6] mm) also did not include any nearshore resources, and the largest single-resource contribution came from wetland alewives (44.3%, 7.3%–70.1%).

Otolith edge microchemistry

For large perch collected from Calumet ($n = 15$), the otolith edge elemental "fingerprint" (i.e., Sr, Mg, Ba, and Mn) was distinct between nearshore- and wetland-collected perch (PERMANOVA, $p = 0.002$, $F = 70.681$; Figure 7a; Appendix S1: Figure S3). All perch at this site (100%) could be classified to the correct habitat of collection using either Sr alone or Mn and Mg. The otolith edge fingerprint of large perch collected from Muskegon ($n = 19$), however, did not differ significantly between habitats ($p = 0.15$, $F = 2.11$; Figure 7b; Appendix S1: Figure S4). While Sr- and ln-transformed Ba were able to classify perch to the habitat of collection with 84% accuracy, the addition of Mg- and ln-transformed Mn reduced classification accuracy to 79%, largely due to high within-habitat variability of these elements. The elemental fingerprint for Little

Sturgeon perch was also not significantly different between habitats ($p = 0.7$, $F = 0.33$; Figure 7c; Appendix S1: Figure S5), but our inferences were limited by small sample size ($n = 5$).

DISCUSSION

Fish promote lakescape connectivity in Lake Michigan

Our results demonstrated that yellow perch promoted the flux of energy between coastal wetlands and nearshore Lake Michigan by consuming resources across a mosaic of habitats (i.e., "lakescape connectivity"), and that the magnitude of this flux likely varies with perch ontogeny and habitat connectedness. While many ecosystems are naturally linked by fluxes across habitat boundaries (see Lamberti et al., 2010), few previous studies have explicitly addressed fish-mediated wetland–nearshore linkages in the Great Lakes, and exceptions generally have focused on relatively pristine systems in Lake Superior (e.g., Hoffman et al., 2010; Sierszen et al., 2004; but see Sierszen et al., 2018). We found that nearshore-collected perch in three regions of Lake Michigan had substantial dietary contributions from resources originating in coastal wetlands. NS Large Perch relied on wetland-derived resources for up to 40% of their overall diet. This high use of wetland resources is consistent with the characterization of coastal wetlands as energy-rich systems that export resources to adjacent habitats either directly (e.g., physical movement of
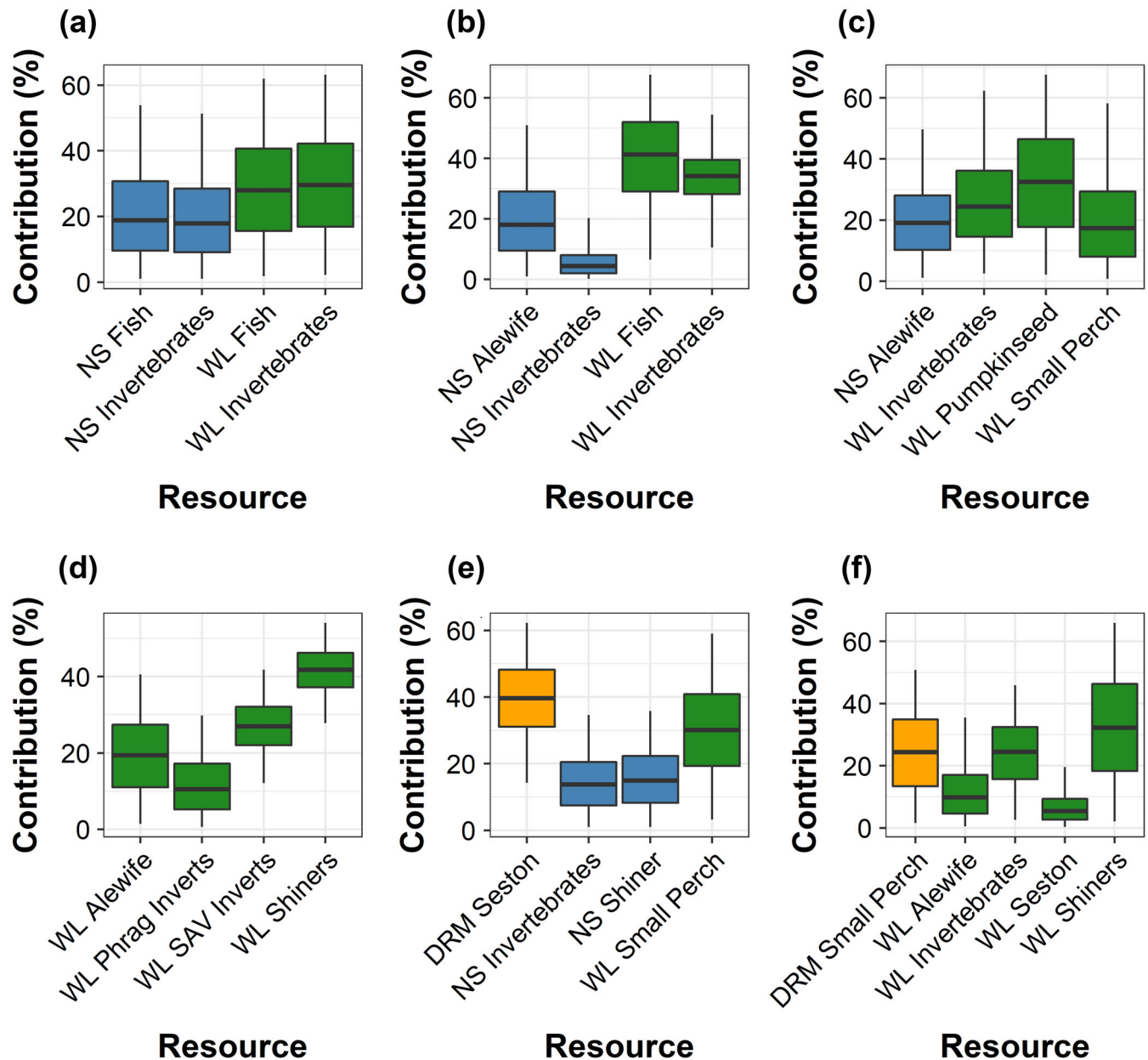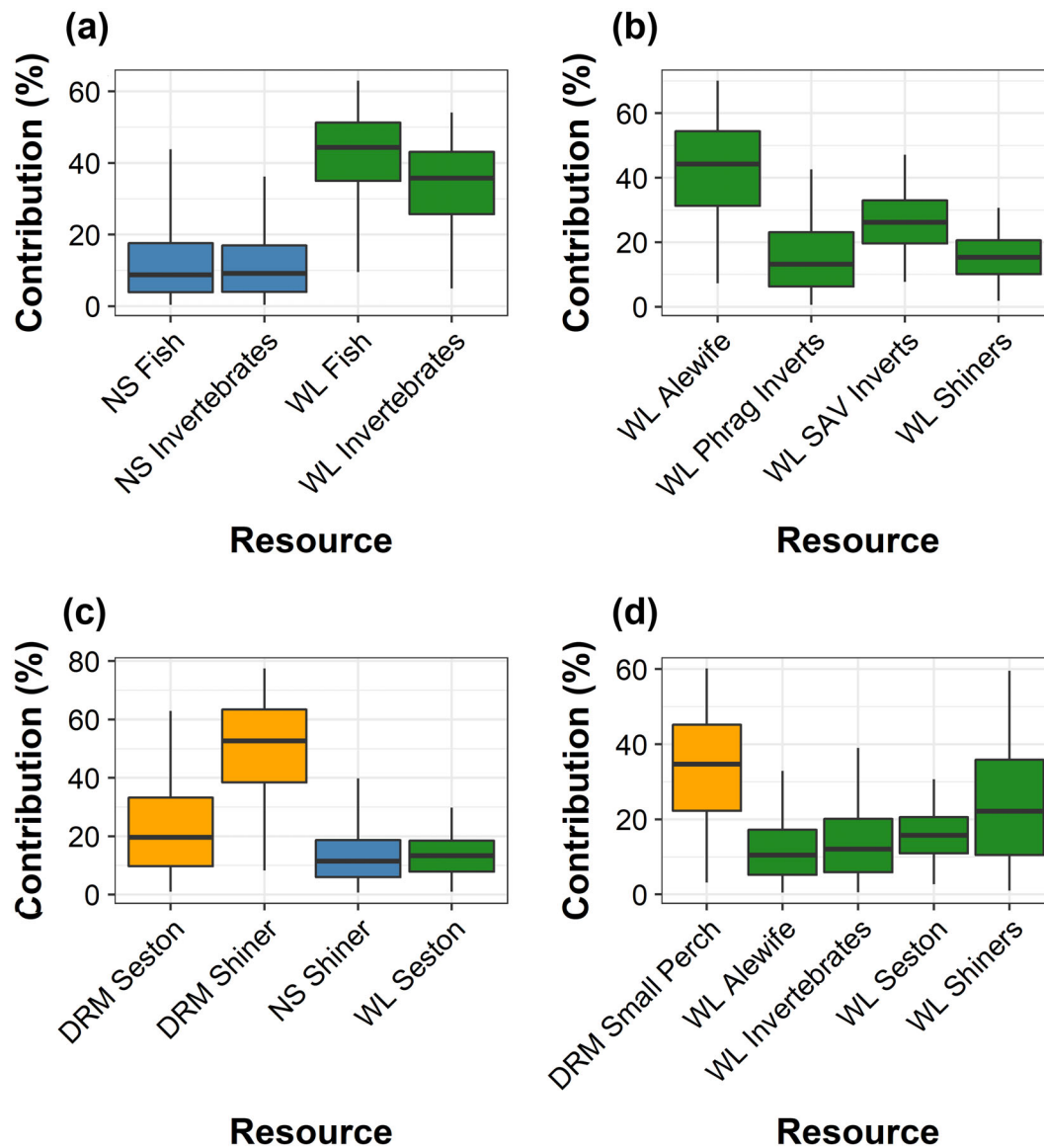
FIGURE 5 Diet contributions to wetland (WL)-collected large perch (TL > 150 mm) estimated by stable carbon and nitrogen isotope Bayesian mixing models. Boxplots show median posterior estimates of resource use (with 95% Bayesian credible intervals) for WL Large Perch from (a) Little Sturgeon, (b) Cedar River, (c) Peshtigo, (d) Calumet, (e) Muskegon, and (f) Pentwater. Box colors indicate resource origin (drowned river-mouth [DRM], nearshore [NS], or WL). At Calumet, WL invertebrates were collected from both emergent vegetation ("Phrag") and submerged aquatic vegetation ("SAV") microhabitats.

organic matter via wave action) or indirectly (e.g., through consumer use of multiple habitats; Odum, 1968; Wetzel, 1992). In contrast, wetland-collected perch in our study often had low use of nearshore-derived resources, possibly due to the high natural productivity of wetlands (Cooper et al., 2013). However, the use of nearshore resources by wetland perch at some sites suggests some level of reciprocal exchange of energy between habitats, not solely that wetlands are one-way exporters (Odum, 1968; Wetzel, 1992). In fact, our estimates of

nearshore resource use by wetland-collected perch were generally lower than estimates for perch from other wetland sites in lakes Michigan and Huron (Sierszen et al., 2018).

Habitat use changes with ontogeny

Perch appear to use wetland resources differentially across life stages, supporting our hypothesis that their

FIGURE 6   Diet contributions to wetland (WL)-collected small perch (TL < 150 mm) estimated by stable carbon and nitrogen isotope Bayesian mixing models. Box plots show median posterior estimates of resource use (with 95% Bayesian credible intervals) for WL Small Perch from (a) Little Sturgeon, (b) Calumet, (c) Muskegon, and (d) Pentwater. Box colors indicate resource origin (drowned river-mouth [DRM], nearshore [NS], or WL). At Calumet, WL invertebrates were collected from both emergent vegetation ("Phrag") and submerged aquatic vegetation ("SAV") microhabitats.

role connecting coastal wetland and nearshore food webs changes across life. In our study, NS Small Perch had higher wetland resource use than NS Large Perch, with about half of NS Small Perch assimilated energy originating in the wetland, although we acknowledge that our inferences are limited by only having NS Small Perch from two sites. However, we also observed variation in ontogenetic resource use among sites. NS Small Perch from Little Sturgeon assimilated about 20% of their energy from wetland benthic invertebrates, which suggests physical movement of young perch into the wetland to forage, given lower rates of invertebrate movement. In contrast, wetland resource use by NS Small Perch from

Burns Harbor was almost completely driven by wetland seston, likely exported to the nearshore via the Little Calumet River. Detrital carbon originating in both freshwater and marine coastal wetlands can be exported to adjacent open-water habitats via wave action, river flow, and tides/seiches (Odum, 1968). Further, small river plumes support highly localized hotspots of biological productivity and fish abundance in Lake Michigan, primarily within 2 km of river mouths (Smith & Simpkins, 2018). Our results support the idea that export of riverine wetland-derived primary production to the nearshore in the form of seston supports nearshore fisheries production, particularly in habitats with low
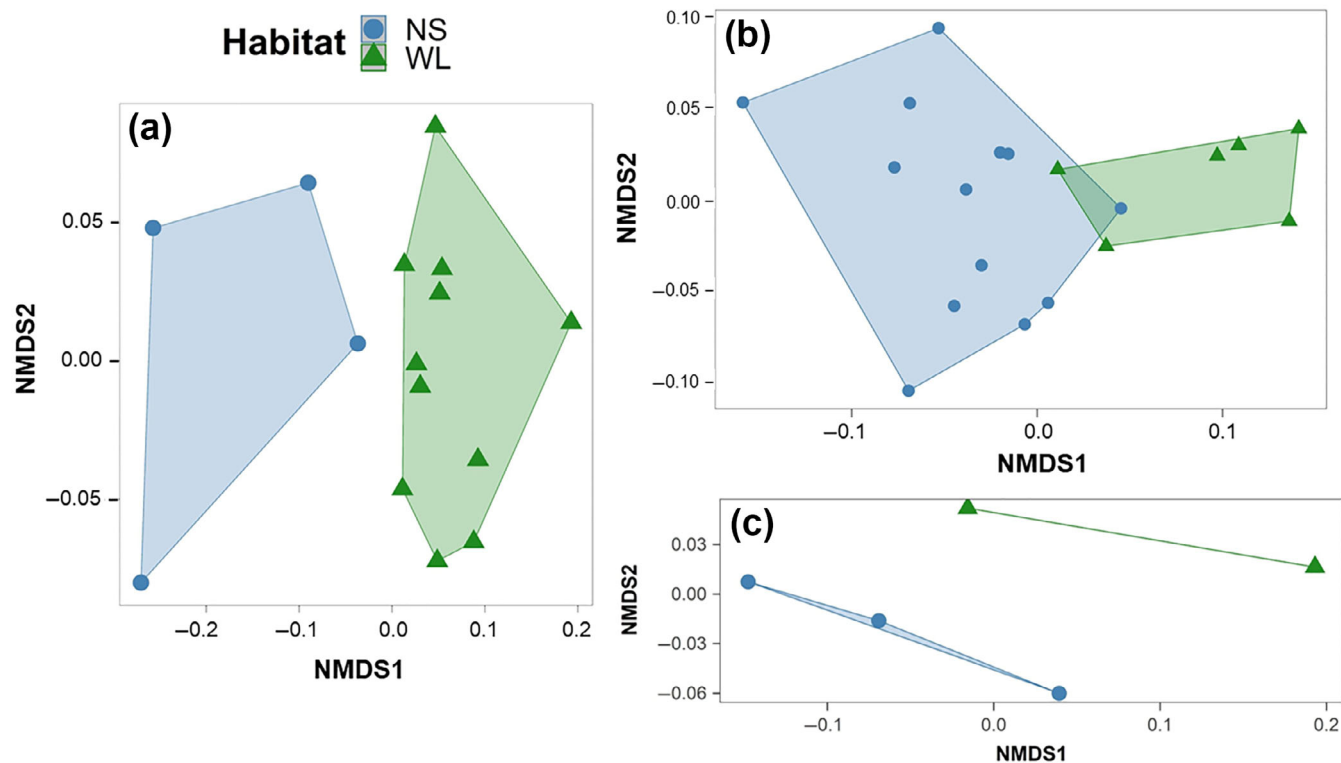
FIGURE 7 Ordination plots of otolith edge elements (Ba, Mg, Mn, and Sr) for nearshore (NS) and wetland (WL) Large Perch collected in 2014 from (a) Calumet, (b) Muskegon, and (c) Little Sturgeon. In (a), the elemental "fingerprint" differed significantly between habitats (permutational multivariate analysis of variance, $p = 0.002$). In (b), fingerprints did not differ significantly between habitats ($p = 0.15$). In (c), no significant difference was found in edge elemental composition ($p = 0.7$), but this was likely due to small sample size ($n = 5$). NMDS, nonmetric multidimensional scaling.

complexity such as the bare sand found in parts of southern Lake Michigan. Coastal wetlands therefore can either directly provide habitat and energy (e.g., Little Sturgeon) or indirectly provide foraging opportunities through physical export of wetland-generated energy (e.g., Burns Harbor) for young perch living in the nearshore lake.

Despite our assumption that small perch (TL < 150 mm) would primarily rely on invertebrates, prey fish (generally *Notropis* spp. shiners and smaller conspecifics) typically made up the largest contributions to WL Small Perch diets. WL Small Perch across all sites had the highest median prey fish use (62%), similar to WL Large Perch (60%) but higher than NS Small Perch (41%). Although the shift to piscivory is thought to occur in perch around 150-mm TL in small lakes such as those in Michigan (Clady, 1974), perch in Saginaw Bay coastal wetlands made the ontogenetic shift to piscivory at approximately 80 mm standard length (SL) (Parker et al., 2009). While the shift to piscivory has been shown to relieve intraspecific competition and increase growth (Headley & Lauer, 2008), its early onset in coastal wetlands might also be due to the high availability of different prey fish in these habitats (Parker et al., 2009) compared with the nearshore.

About a quarter of the assimilated energy for both NS and WL Large Perch originated in a habitat other than where they were collected, but this also varied with region and site. Despite their large size, NS Large Perch in the south region were generally less piscivorous than NS Large Perch from other regions. South-region NS Large Perch appear to consume roughly equal amounts of nearshore invertebrates and prey fish, which may reflect the time during which we sampled (June–July), as perch diets can vary seasonally. In nearshore Lake Erie, for example, both small and large perch primarily consumed invertebrates in spring (80%–100% of diet) but shifted to clupeids and shiners (40%–60% and 35%–40% of diet, respectively) in summer and fall, perhaps due to changes in prey availability (Knight et al., 1984). Although WL Large Perch in our study were primarily piscivorous, seston did appear to make up a large portion of the diet of perch from Muskegon. Although these large perch (mean TL = 193 mm) may be directly zooplanktivorous, perch of similar sizes in other Great Lakes coastal wetlands were almost exclusively piscivorous, although this was based on stomach contents and not assimilated energy estimated via stable isotopes (Parker et al., 2009). We may also be missing another resource such as a planktivorous prey fish

(e.g., alewife), as the other species of prey fish we collected in the DRM lake, *Notropis* shiners and small perch, had more enriched $\delta^{13}C$ signatures.

Coastal geomorphology affects resource exchanges

Our results were consistent with the hypothesis that the relative strength of perch-mediated linkages varies among wetland geomorphic types, with perch from riverine wetland sites typically having lower cross-habitat resource use than those from lacustrine wetlands. Landscape features that control access to an external subsidy (i.e., resources from another habitat) can alter the assembly of a food web and the trophic relationships among food web members (Polis et al., 1997), and the geomorphology of a landscape can exert control on the distribution and the structure of communities, which affects overall ecosystem trophic structure (i.e., the geomorphic–trophic hypothesis; Hershey et al., 1999). WL Small and Large Perch from the riverine Calumet site incorporated no nearshore resources based on the mixing models, and the distinct differences in otolith edge chemistry between NS and WL Large Perch suggest limited movement between the two habitats at this site. Calumet NS Large Perch, however, did have a small amount of wetland resource use (<15%), despite the large physical distance between wetland and nearshore habitats (20 km). The mixing model run without the wetland resources had low support, suggesting either these resources play a limited role or that we missed an isotopically similar nearshore source. In contrast, nearshore-collected perch from another riverine wetland in the south region (Burns Harbor) had higher reliance on wetland resources, but this use may have been driven by exported seston rather than direct movement of perch into the wetland to forage. While we did not collect any perch from the nearshore at Peshtigo (the only west region riverine wetland), WL Large Perch from this site had low cross-habitat resource use, especially compared with a lacustrine site in the same region (Little Sturgeon).

Contrary to our hypothesis, perch from the east region DRM wetland sites did not have intermediate cross-habitat resource use. Muskegon NS Large Perch had no use of DRM lake resources but some use of wetland resources, despite having to travel through the DRM lake to get to the wetland at this site. Otolith edge chemistry was less accurate at correctly classifying large perch from Muskegon to their habitat of collection than for Calumet, which may suggest adult perch have higher rates of movement across habitats at this site (i.e., they

do not stay in one habitat for a sufficient amount of time to incorporate a habitat chemical signature into the otolith). Lake Michigan perch have been observed using DRM lake habitats during autumn, possibly for feeding since these habitats have higher productivity than the nearshore lake (Janetski & Ruetz, 2014). Because perch diets vary seasonally, the DRM habitat may provide fewer preferred prey items or poor habitat (e.g., high temperatures, low oxygen) during the summer months when we sampled.

While we expected that lacustrine wetlands of the west region would have the highest level of cross-habitat use, habitat resource contributions differed among sites within the region. The only open embayment wetland in this study (Little Sturgeon) had the highest levels of cross-habitat resource use of all sites, with both NS Large and Small Perch from this site having approximately equal resource use from nearshore and wetland habitats. These perch were primarily piscivorous, and therefore either prey fish originating in the wetland could be entering the nearshore or perch from the nearshore could be entering the wetlands to forage before returning to the nearshore. Although small sample sizes of large perch otoliths at this site limit our conclusions, we hypothesize that we would have lower accuracy in classifying large perch to their habitat of collection because of frequent fish movement between habitats. At another west region site (Cedar River), the majority of nearshore resource use by WL Large Perch consisted of nearshore alewife with a small proportion of nearshore invertebrates. The low contribution of relatively sedentary invertebrates (e.g., amphipods and isopods) and higher contribution from more mobile prey fish could suggest that WL Large Perch at this site are not physically traveling to the nearshore habitat to forage, but instead that nearshore prey fish occasionally move into the wetland and transport nearshore-derived energy into the wetland food web.

A model for lakescape connectivity

Understanding the role of yellow perch in connecting food webs is particularly important because this species is ubiquitous in Great Lakes coastal wetlands (Trebitz et al., 2009). In Lake Superior, large numbers of young-of-year perch (>40,000) have been estimated to emigrate to the nearshore from a single wetland, representing a potential major seasonal pulse of wetland-derived energy to the nearshore food web (Brazner et al., 2001). Because we used perch as a model for quantifying wetland–nearshore linkages, our estimates of the overall importance of these linkages by fish

species are likely conservative, as more mobile species such as northern pike (*Esox lucius*) and walleye (*Sander vitreus*) have been shown to have even higher cross-habitat resource use in paired coastal wetland–nearshore sites (Sierszen et al., 2018). However, perch represent an important model for understanding cross-habitat use because this species is economically and ecologically important to the Great Lakes region and has historically supported a multi-million-dollar sport fishing industry and commercial fishery in Lake Michigan (Clapp & Dettmers, 2004). A decline in population abundance to historical lows in the 1990s and continued low recruitment, however, has resulted in closures of the commercial fishery and dramatically reduced sport harvests (Clapp & Dettmers, 2004). At sites with significant cross-habitat resource use (e.g., Little Sturgeon), fewer perch in Lake Michigan has likely resulted in reduced exchange between nearshore and coastal wetland habitats, particularly with lower recruitment of juveniles.

Managing the "lakescape"

Our findings suggest that in large lake ecosystems like the Great Lakes, management should strive to maintain "lakescape connectivity" across diverse habitats including coastal wetlands, rocky reefs, tributaries, the nearshore, and the pelagic offshore. Many sport fish species—and their prey items—travel across the lakescape throughout life for spawning and foraging (Wei et al., 2004). In marine ecosystems, the framework of "seascape connectivity" has been used for conservation and management where populations of mobile organisms are spatially linked and adjacent ecosystems are treated as linked units that form a vital habitat mosaic (Green et al., 2015). Similar to seagrass or mangrove habitats within the traditional seascape, Great Lakes coastal wetlands provide nursery habitats for larval and juvenile fish species (Brazner, 1997; Chubb & Liston, 1986; Jude & Pappas, 1992) as well as energy exchange with the nearshore lake (Sierszen et al., 2018, this study). Habitat diversity among coastal wetlands across the Great Lakes is large (Keough et al., 1999), and even within a wetland, different microhabitats can provide refugia and/or forage, such as submergent or emergent vegetation (Kovalenko et al., 2018). Therefore, maintaining lakescape connectivity by reconnecting diked wetlands (Kowalski et al., 2014) or reengineering coastal infrastructure (Bulleri & Chapman, 2010), in addition to protecting a diversity of wetland habitats, is likely crucial for preserving fish-mediated trophic linkages that support nearshore fisheries production, as well as for the physical exchange of resources (e.g., prey fishes and seston).

CONCLUSIONS

Our results enhance our understanding of habitat linkages in large lakes and their importance in supporting ecosystem services such as fisheries production, particularly in light of anthropogenic change. Similar to other large lake ecosystems across most of the globe, coastal wetlands of the Great Lakes have been extensively impacted by human development, with a loss of approximately 75% of historical area and the degradation of many remaining wetlands (Jude & Pappas, 1992). While our study focused on consumer ontogeny and habitat geomorphology, disturbance may also affect the strength of linkages across the lakescape. Urbanization and other land-use changes are major causes of coastal wetland loss globally (Lee et al., 2006), and reduced wetland area or lower quality habitat may result in lower fisheries production if wetland contributions to food webs are substantial (Sierszen et al., 2012). While all sites in our study had some level of human disturbance, sites in the south region (i.e., Burns Harbor and Calumet) were particularly modified (e.g., fragmented/reduced wetland area, evidence of dredging), dominated by invasive vegetation types (e.g., *Phragmites australisis*), and located near industry (e.g., Burns Harbor wetland was located immediately adjacent to a major steel production plant). Therefore, our estimates of wetland–nearshore linkages reflect a reduced number of consumers (i.e., declines in the Lake Michigan perch population) and anthropogenic changes to wetland habitats. Quantifying cross-habitat resource use by an economically important sport fish can provide information for managers to prioritize wetlands for conservation and restoration efforts that are focused on the maintenance or creation of resilient, functioning ecosystems. Our finding of the importance of wetland-derived resources to yellow perch across life suggests that the extensive loss and degradation of wetland area in Lake Michigan may be linked to the lower recruitment of perch documented by other studies (e.g., Clapp & Dettmers, 2004). Based on our findings of cross-habitat use by perch, conservation will likely require management of the mosaic of habitats (i.e., "lakescape connectivity") used by perch and other fish that sustain fisheries production.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code (O'Reilly, 2022) are available from Zenodo: https://doi.org/10.5281/zenodo.7261787.

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SUPPORTING INFORMATION

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