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Individual and spatial variation are as important as species-level variation to the trophic complexity of a lentic food web

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Abstract

Ecological complexity may improve ecosystem function, stability, and adaptability to natural and anthropogenic disturbances. Intraspecific trophic variation can represent a significant component of total community variation and can influence food web structure and function. Thus, understanding how trophic niches are partitioned between intraspecific and interspecific processes could improve our understanding of food web dynamics. We examined gut contents, fatty acids, and stable isotope ratios in round goby (*Neogobius melanostomus*) and yellow perch (*Perca flavescens*) across six sites in Lake Michigan, USA, to determine patterns in intra- and interspecific trophic composition (*i.e.*, mean gut or fatty acid composition) and diversity (*i.e.*, the diversity of gut items or fatty acids). We also examined relationships between fatty acid diversity and gut content characteristics to understand potential mechanisms shaping individual trophic phenotypes. There was significant variation in both trophic composition and diversity among sites, and individual and spatial variation was as important to total trophic variation as species identity. Round goby that consumed dreissenid mussels had more diverse fatty acid profiles than those that consumed other benthic invertebrates, whereas yellow perch fatty acid diversity was not related to gut content composition. Our results confirm that intraspecific variation in resource use can be as important to trophic dynamics as interspecific variation, and that spatial variation in lower level food web processes or habitat may strongly structure local food web dynamics. Individual-level examination of trophic diversity, in concert with trophic composition, could provide additional information about the resilience, function, and adaptability of local food webs.

1 | INTRODUCTION

Food web complexity, defined as the number of linkages of energy pathways in an ecosystem, may promote ecosystem stability by increasing the density of trophic linkages between food web components, coupling disparate habitats or energetic pathways, and increasing the functional overlap of niches, allowing for ecosystem function to be maintained even if species are lost (Hubbell, 2005; Layman et al., 2007; Schindler et al., 2010; McMeans et al., 2016). However, trophic complexity is most often considered at an interspecific level and regards species or populations as functionally homogenous, even though recent evidence suggests that intraspecific (i.e., within-species) complexity arising from spatial, seasonal, or ontogenetic variation in trophic niche use can represent a significant proportion of overall community functional variability (Violle et al., 2012; Faulks et al., 2015; Siefert et al., 2015). Such intraspecific variability in trophic niche size and position can alter community composition by influencing niche partitioning among functionally similar species (Pool et al., 2016; Allgeier et al., 2017) and facilitating occupancy of otherwise unfilled trophic niches (Eklöv & Jonsson, 2007; Quevedo et al., 2009). Not accounting for intraspecific trophic variation may therefore lead to biologists missing a major source of functional adaptability in food webs (Violle et al., 2012; Allgeier et al., 2017).

The extent of intra- and inter-specific trophic complexity can be driven not only by inherent foraging behaviors, but also by individual responses to environmental factors, such as spatial or temporal heterogeneity in resource availability (Crowder & Cooper, 1982; Svanbäck & Eklöv, 2006; Larson et al., 2015; Eloranta et al., 2017). The importance of individual niche variation to total community trophic complexity remains poorly understood, but there is some evidence that individual responses to environmental conditions can influence food web structure (Svanbäck & Eklöv, 2003; Quevedo et al., 2009). For example, individuals inhabiting large, deep lakes may exhibit increased specialization on littoral or pelagic resources, decreasing within-individual trophic complexity (Snorrason et al., 1994; Eloranta et al., 2017) with the overall effect of decreasing connectivity between benthic and pelagic energy pathways (Quevedo et al., 2009). Understanding broad-scale spatial patterns in the responses of individuals and species to environmental variation could help predict food web adaptability to major anthropogenic stressors, providing a foundation for understanding the importance of underlying energy pathways in shaping food web complexity.

Measures of trophic niche, such as gut contents, fatty acid composition, and stable isotope ratios, can be considered components of an expanded trophic phenotype (Houle, Govindaraju & Omholt, 2010). These metrics have been primarily used to understand the average trophic position of consumers (e.g., Jackson *et al.*, 2011; Happel *et al.*, 2015; Foley *et al.*, 2017), but there is increasing interest in using these metrics to understand how trophic diversity is partitioned among individuals, populations, and species (Price & Guglielmo, 2009; Bolnick et al., 2011). Understanding variability in individual-level trophic diversity (Bolnick et al., 2002, 2014) could also provide insights into the impacts of resource use on individual fitness. Fatty acid diversity has been linked to measures of performance like peak metabolic rate in birds (Price & Guglielmo, 2009) and swimming speed and cardiac output in fish (Chatelier et al., 2006) whereas diet mixing improved growth and fecundity in an amphipod (Cruz-Rivera & Hay, 2000). At the community level, treating trophic characteristics as complex traits could enable partitioning of trophic complexity across levels of organization (Marion et al., 2015), allowing for the quantification of energy flows through food webs and improved assessments of true community functional diversity (Hubbell, 2005; Bolnick et al., 2011).

We used a set of observations from six spatially distinct sites in Lake Michigan, USA, to investigate patterns in the trophic composition (i.e., the abundance and types of resources used) and trophic complexity (i.e., the distribution of different resources used, regardless of identity) of two fishes that occupy similar nearshore habitats: invasive round goby (*Neogobius melanostomus*) and native yellow perch (*Perca flavescens*). We did so by evaluating the composition of gut contents, fatty acids, and stable isotopes using multivariate comparison and ordination, and by using a complexity-as-diversity approach to quantify gut content and fatty acid complexity in terms of Shannon's effective diversity (Marion, Fordyce & Fitzpatrick 2015). Round goby and yellow perch are highly abundant in nearshore Lake Michigan and serve important ecological roles in the nearshore food web (Marsden & Robillard, 2004; Truemper & Lauer, 2005; Houghton & Janssen, 2015). Round goby are restricted to the substrate and thus prey most heavily on benthic resources while yellow perch are highly mobile and able to prey on both planktonic and benthic resources (Happel et al., 2015; Foley et al., 2017). Yellow perch and closely related Eurasian perch (*P. fluviatilis*) have demonstrated considerable plasticity in foraging strategies and morphology in response to environmental conditions (Svanbäck & Eklöv, 2003, 2006; Olsson et al., 2007; Roswell et al., 2013). However, less is known about the plasticity of round goby. Comparing spatio-temporal patterns in the trophic niches exploited by these two species with potentially different abilities to respond to resource variation allowed us to address several questions about how trophic niches are partitioned in complex aquatic food webs, including 1) Does trophic composition vary spatially, and how is it partitioned among seasons, sites, and species?; 2) Does trophic diversity vary spatially, and how is it partitioned among individuals, seasons, sites, and species?; and 3) Does diet drive fatty acid diversity in individuals? Examining the trophic composition and diversity of these species across three trophic markers allowed us to elucidate the importance of individual, spatial, and taxonomic differences in trophic niche construction in a large and complex freshwater food web.

2 | MATERIALS AND METHODS

2.1 | Study sites

Fish and benthic invertebrate samples were collected in July and September 2010 at six nearshore sites around Lake Michigan: Fox Point, WI (FP); Highland Park, IL (HP); Calumet, IN (CA), Saugatuck, MI (SA), Arcadia, MI (AR), and Sturgeon Bay, WI (SB) (Figure 1). While these sites were all considered to have hard substrate, they varied in the specific habitat types available. Fox Point is Devonian mudstone/shale bedrock with pockets of cobble, and Highland Park and Calumet are Niagaran bedrock with cobble-filled glacial grooves and depressions. Saugatuck and Arcadia are dominated by loose cobble and located near primarily sandy substrate, whereas Sturgeon Bay is loose cobble with nearby Niagaran bedrock. In addition, eastern sites (Arcadia and Saugatuck) receive riverine inputs from multiple large watersheds, whereas southern and western sites have limited riverine inputs and Sturgeon Bay receives tidal cycle influxes of water from the warmer and more productive Green Bay. The northern basin of Lake Michigan is primarily forested while the southern basin is dominated by agriculture and urban watersheds (NOAA CSC, 2013).

2.2 | Fish and invertebrate collection

The yellow perch, round goby, and invertebrate samples used in this study were collected as part of a larger study to examine the nearshore Lake Michigan food web, and all relevant sampling protocols are detailed in previous studies (Happel et al., 2015; Foley et al., 2017). Fish were collected via experimental micromesh gill nets. At Wisconsin sites and SA, we used 60-m long nets with two panels of 6 and 8 mm bar mesh, whereas all other sites were sampled with 40-m long nets with four panels of 6, 8, 10, and 12 mm bar mesh. Nets were set parallel to shore at 3, 7 to 9, and 12 to 15 m depth contours and allowed to fish either for two hours or overnight. We only kept living fish for analysis, which were euthanized via overdose of MS-222. We collected benthic invertebrate samples via either ponar grab sampling, benthic scrapes, or diving lifts, depending on the substrate at each site. All samples were immediately frozen on dry ice, then stored at -80 °C until processing.

In the lab, all fish were thawed and measured to the nearest 1 mm total length (TL; Table 1). Either the stomach (from yellow perch) or entire digestive tract (for round goby) was removed from each fish and stored in 95% ethanol until processing. Following gut removal, we homogenized whole fish for stable isotope and fatty acid analysis. We analyzed gut contents by first removing all prey items from the digestive tract of each fish, identifying each item to the lowest possible taxon, and enumerating their abundance (for further details, see Happel *et al.*, 2015; Foley *et al.*, 2017). We developed a standardized set of 17 prey items from the taxa present in the guts of both species for use in comparing between-species patterns in gut content diversity and composition (Table S1). We classified prey items in terms of taxonomic (primarily family or order), functional (e.g., trophic position, metabolism), and behavioral (e.g., feeding, habitat use, position in the water column) traits as accurately as possible given limitations in identifying often partially digested organisms (Czesny et al., 2011; Feiner et al., 2018a). For example, we distinguished between Chironomidae larvae and pupae because of evidence that metabolic processes during metamorphosis lead to distinct fatty acid and isotopic signatures in each (Hanson et al., 1985; Doi et al., 2007). These gut content categorizations therefore represent the scope of potential gut content diversity on an ecologically relevant scale, allowing us to investigate how diversity and composition of diets potentially influence diversity and composition of biochemical markers.

The fatty acid composition of each fish was determined by extracting lipids from homogenized tissue (Folch et al., 1957), transmethylating fatty acids (Metcalfe & Schmitz, 1961), and analyzing the abundance of 28 fatty acids using gas chromatography/mass spectrometry (Agilent 7890A GC and 5975C inert XL EI/CI/ MSD, Agilent Technologies, Inc., Santa Clara, CA, USA), as described in previous studies (Turschak et al., 2014; Happel et al., 2015; Foley et al., 2017). We quantified fatty acid relative abundance as the proportion by mass of all fatty acids detected (Table S2).

We performed stable carbon and nitrogen isotope analyses by freeze-drying homogenate samples for 48 h and measuring isotope ratios using a mass spectrometer (Finnigan MAT delta S SIR-MS, with elemental analyzer front end and ConFlo II interface, Bremen, Germany). Results are reported in relation to Pee Dee Belemnite and atmospheric nitrogen reference standards using the conventional $\delta^{13}C$ and $\delta^{15}N$ notation (Turschak et al., 2014; Happel et al., 2015; Foley et al., 2017). Carbon isotope ratios were corrected for lipid content in each fish as reflected in C:N ratios using species-specific equations developed for yellow perch and round goby in Lake Michigan (Turschak et al., 2014).

Benthic invertebrate samples (whole bodies for Arthropoda, foot muscle for Gastropoda and Dreissenidae) were dried, ground, and analyzed for stable isotope signatures using the same methods as fish samples. Isotopic signatures of abundant taxa (quagga mussel [*Dreissena rostriformis bugensis*], Chironomidae larvae, Gastropoda, Amphipoda, and Isopoda) were then used to determine the benthic and pelagic isotopic baselines for each site. We used the most ^{13}C-depleted values for filter-feeding quagga mussel (since filter-feeding mussels have been shown to act as a reliable primary consumer of pelagic production; Post, 2002) as a pelagic baseline and the most ^{13}C-enriched chironomid, gastropod, amphipod, or isopods as a benthic baseline to completely encapsulate the full potential isotopic range of the food web at each site. We used the most ^{15}N-depleted mussels as a pelagic baseline and the most ^{15}N-depleted benthic invertebrates as a benthic baseline (Table S3).

We estimated benthic reliance as the proportion of carbon individuals derived from benthic sources using a two-member mixing model based on the $\delta^{13}C$ signature of each fish and baseline consumer values at each respective site (Equation 1; Post, 2002; Ives et al., 2013)

$$(1) \qquad \alpha = 1 - \frac{(\delta^{13}C_{fish} - \Delta - \delta^{13}C_{benthic})}{(\delta^{13}C_{pelagic} - \delta^{13}C_{benthic})}.$$

The parameter Δ is a correction factor for trophic enrichment in $\delta^{13}C$ (Equation 2),

(2) $$\Delta = 0.4\left[\frac{(\delta^{15}N_{fish} - \delta^{15}N_{benthic})}{3.4} + 1\right],$$

where 0.4 and 3.4 are the assumed mean per mil fractionation per trophic position for δ^{13}C and δ^{15}N, respectively (Minagawa & Wada, 1984; Vander Zanden & Rasmussen, 2001). We then determined the relative trophic position of each individual fish at each site (Equation 3; Vander Zanden et al., 2000):

(3) $$Trophic\ position = 2 + \frac{\delta^{15}N_{fish} - [\delta^{15}N_{benthic} \times \alpha + \delta^{15}N_{pelagic} \times (1-\alpha)]}{3.4},$$

assuming a primary consumer trophic position of 2 and a δ^{15}N enrichment of 3.4‰ per trophic transfer (Minagawa & Wada, 1984). Two round gobies (out of N = 95) were more δ^{13}C enriched or depleted than the baselines and were corrected by setting α to one and zero, respectively. We did not assess isotopic niche metrics at site AR because no baseline data were collected from that site for either species.

2.2 | Data analysis

2.2.1 | Spatial variation and partitioning of in trophic composition

We used a series of analyses to investigate individual, seasonal, spatial, and interspecific patterns in trophic composition in this study (see Table 2 for a summary of methods and general conclusions). Site-level differences in the multivariate composition of gut content, fatty acid, and isotopic niche (in benthic reliance – trophic position space) within each species were assessed using PERMANOVA (999 permutations, R package ‘vegan’, v. 2.4-1; Oskansen *et al.*, 2013) with site as the explanatory factor and fish length as a covariate. We did not consider seasonal variation in this analysis because seasonal variation was limited in other tests in this study and in previous research using these samples (Foley et al., 2017). We used Euclidean distances in analysis of fatty acid and stable isotope data and Bray-Curtis distances to analyze gut content data due to the increased incidence of zeroes. When the overall PERMANOVA indicated significant differences in a given trophic metric, we used post hoc pairwise PERMANOVA on all combinations of sites to test for specific significant differences after correcting for multiple comparisons (Holm-corrected P < 0.05; Aickin & Gensler, 1996).

We used species-specific principal components analysis (PCA, R package 'vegan') on gut content and fatty acids to visualize site-level differences and to generate simplified, orthogonal diet composition axes for use in subsequent analyses. All data were centered and scaled, and fatty acid data were further natural log + 1 transformed to meet the assumptions of a PCA. We identified and retained significant and interpretable principal components using a randomization test based on eigenvalues (λ_k) for each of the k possible principal components (PCs). The data were randomized 1000 times, a PCA was performed on each randomized dataset, and the proportion of randomized λ_k that were larger than the observed λ_k served as a test statistic significant at $\alpha = 0.05$ (R package 'PCDimension'; Peres-Neto et al., 2005; Coombes & Wang, 2018). Based on this test, the first two and one (although two were retained for visualization purposes) out of 11 gut content PCs explained 44% and 21% of round goby and yellow perch diet content variation, and the first two and three (out of 28) fatty acid PCs explained 50% and 62% of the variation in round goby and yellow perch fatty acid composition (Figure 2, Tables S4, S5). We visualized the isotopic niches of each species at each site in bivariate benthic reliance – trophic position space.

We were interested in determining how trophic composition and diversity were partitioned across individual, site, season, and species levels (Table 2). To do so, we compared trophic metrics of individuals of both species captured at the same sites and seasons (sites FP, HP, CA, SA, and AR for gut contents and fatty acids, and FP, HP, CA, and SA for stable isotopes; Figure 1). To determine variance partitioning of trophic composition, we used PERMANOVA with season, site, their interaction, and species as explanatory factors and either fatty acid, gut content, or stable isotopic composition as the response variables, and determined the explanatory power (R^2) and significance (χ^2) of each factor.

2.2.2 | Spatial variation and partitioning of in trophic diversity

We used the complexity-as-diversity approach to evaluate trophic diversity in gut contents and fatty acids (Marion et al., 2015). Briefly, the diversity of gut contents or fatty acids was described in terms of Shannon's effective diversity ${}^qD$ (Equation 4):

$$(4) \qquad {}^qD = \left(\sum_{i=1}^{K} p_i^q\right)^{1/(1-q)},$$

where p_i is the proportional abundance of gut item or fatty acid i across all K items or acids examined. Note that this index of diversity can be weighted by the abundances of each component by varying the parameter q, where $q = 0$ means weights are disregarded (and therefore ${}^{0}D$ represents richness), and the abundance of components becomes increasingly important as q increases. We assessed spatial variation in gut content and fatty acid diversity at two levels of q: first, we represented general diversity with weak abundance weighting by using $q = 1$ (for which the limit represents the exponentiated Shannon's diversity). Second, we emphasized the diversity of abundant (and therefore potentially more ecologically important) components by using diversity at $q = 4$ (diversity metrics also largely stabilized at $q > 4$). After determining trophic diversity using this method, we could then summarize and partition diversity using three metrics common in community ecology: α diversity, the mean "local" diversity observed within a hierarchical level (e.g., the mean number of diet components or fatty acids observed within individuals at a site); γ diversity, the total "regional" diversity observed across a hierarchical level (e.g., the total number of diet components or fatty acids observed across individuals at a site); and additive β diversity, the amount of excess diversity observed "regionally" that was not observed "locally" (e.g., the additional number of diet components or fatty acids observed across individuals at a site not present within the average individual; $\beta = \gamma - \alpha$) (also see Marion et al., 2015).

We tested for differences in gut content and fatty acid diversity among sites by determining α diversity at each site and using a bootstrap approach to estimate uncertainty in site-level means. We conservatively interpreted sites-level estimates of fatty acid and gut content diversity to be significantly different when bootstrapped 95% confidence intervals did not overlap. We determined isotopic niche size among sites estimating standard ellipse areas using Bayesian inference (SEA_B) encapsulating approximately 80% if the data in bivariate benthic reliance – trophic position space using R package 'SIBER' following the recommendations of Jackson et al. (2011). We compared SEA_B among sites within each species determining whether 95% credible intervals overlapped. For visualization of stable isotope niche size and position, we used small sample size corrected standard ellipse areas (SEA_C) also calculated in 'SIBER'.

We used the group-wise partitioning method to investigate the partitioning of trophic diversity across levels of organization (Marion et al., 2015). Using the ‘hierDiversity’ package, we estimated gut or fatty acid α, γ, and β diversity at five hierarchical levels. We first estimated α and β diversity within each combination of species, season, and site and averaged α and β diversity across groups to determine the mean individual diversity observed (e.g., the mean diversity of individuals of each species collected from one site and season) and the mean information gained by grouping individuals by sampling event (e.g., the mean excess diversity observed among individuals of the same species captured at the same site and season). We then estimated mean β diversity at each hierarchical level using the same process: species and site-specific β diversity (i.e., mean excess diversity observed across seasons for each species and site); mean species- and season-specific β diversity (i.e., mean excess diversity observed across sites within species and seasons), mean species-specific β diversity (i.e., mean excess diversity observed across seasons and sites within each species), and finally between-species β diversity (i.e., excess diversity observed between species). We then calculated the proportion of overall diversity (γ) contributed by each grouping. To understand how diversity partitioning varied with increasing component abundances, we performed partitioning at levels of q from $q = 0$ to $q = 6$.

2.2.3 | Mechanisms driving fatty acid diversity

We tested for relationships between fatty acid diversity and gut contents using linear mixed-modeling fit with maximum likelihood (R package ‘lme4’; Bates *et al.*, 2015) with individual fatty acid diversity ($q = 1$) as the response, fish total length as a covariate, and either gut content diversity ($q = 1$) or gut content composition (significant principal components of the diet PCA for each species) as continuous explanatory variables with random intercepts and slopes among sites,

$$y_{ij} = (\beta_0 + u_{0j}) + (\beta_1 + u_{1j})X_{ij} + \beta_2 TL_{ij}, \tag{5}$$

where y_{ij} represents the fatty acid or gut content diversity of fish i and site j, β_0 is the mean intercept, β_1 is the mean effect of the respective response variable (gut content diversity, PC 1, or PC 2), and β_2 is the fixed effect of fish total length (TL_{ij}). u_{0j} and u_{1j} are the random intercept and slope coefficients accounting for variation in mean fatty acid diversity or the relationships between fatty acid diversity and predictors among sites j. Random slopes were evaluated for significance using χ^2 tests comparing the full model (Equation 5) with a reduced model excluding random slopes (Equation 6) and dropped from the model when not significant to simplify interpretation of the effect of response variables:

$$(6) \qquad y_{ij} = (\beta_0 + u_{0j}) + \beta_1 X_{ij} + \beta_2 TL_{ij}.$$

The significance of the effects of total length and the indicator of trophic composition (gut content diversity and gut content PCs) were evaluated using bootstrapped 95% confidence intervals.

3 | RESULTS

3.1 | Spatial variation and partitioning of trophic composition

Round goby gut contents varied significantly among sites (pseudo-$F_{5,67}$ = 5.22, R^2 = 0.26, P = 0.001) and with fish length (pseudo-$F_{1,67}$ = 5.51, R^2 = 0.06, P = 0.001). After accounting for length variation, sites FP and HP were significantly different from sites CA, SA, and AR; site CA was different from AR and SB; and AR and SB differed from one another (Table S6). These differences were occurred largely along an axis trading off consumption of dreissenid mussels at sites CA, SA, and AR versus consumption of benthic arthropods (including chironomid larvae, pupae, and chydorid microcrustaceans) at sites FP and HP (Figure 2a, Tables S1, S4). Round goby fatty acids exhibited similar significant spatial variation (PERMANOVA site effect: pseudo-$F_{5,67}$ = 14.23, R^2 = 0.48, P = 0.001) and variation with fish length (PERMANOVA length effect: pseudo-$F_{1,67}$ = 9.76, R^2 = 0.07, P = 0.001). After accounting for variation in fish size, post hoc analyses revealed that round goby fatty acid composition at sites FP and HP was significantly different from that at every other site, and site SA was significantly different from CA and SB (site R > 0.14, P < 0.05 for all pairs; Table S7). Round goby at sites FP and HP exhibited higher levels of fatty acids attributable to benthic energy sources, like C16:0, C16:1n-7, and C18:1n-7 (Czesny et al., 2011), whereas other sites exhibited higher levels of long-chain polyunsaturated fatty acids often attributed to pelagic sources like C22:5n-3, C22:5n-6, and C22:6n-3 (Figure 2c, Table S2).

Yellow perch diet and fatty acid variation followed somewhat similar spatial patterns to those for round goby. Yellow perch gut contents demonstrated significant spatial variation (pseudo-$F_{4,31}$ = 2.38, R^2 = 0.21, P = 0.002) and varied with length (pseudo-$F_{1,31}$ = 5.79, R^2 = 0.12, P = 0.001), where sites CA and SA were significantly different after accounting for length differences (R = 0.23, P = 0.04; Table S6). Sites were effectively organized along two axes exhibiting primary predation on fish (FP), a mix of benthic invertebrates and zooplankton prey (HP and CA), or entirely zooplankton prey (SA and AR) (Figure 2b; Tables S1, S4). Yellow perch fatty acids exhibited significant variation in fatty acid composition among sites (pseudo-$F_{4,31}$ = 4.22, R^2 = 0.30, P = 0.002) and with length (pseudo-$F_{1,32}$ = 7.89, R^2 = 0.14, P = 0.005). After accounting for length, FP was significantly different from CA, and HP was significantly different from CA and AR (site R > 0.24, *P* < 0.05; Table S5, S7). Yellow perch fatty acid variation was similar to that observed in round goby – sites FP and HP were high in C16:0, C16:1n-7, and C18:2n-6, often associated with benthic production, whereas the other sites exhibited higher abundances of C22:6n-3, C22:5n-6, and C20:4n-6 (Figure 2d, Table S2).

Stable isotopes revealed relatively consistent spatial variation in trophic niches between species, but the spatial patterns differed from those identified with fatty acids or gut profiles. Round goby niches differed in multivariate space across sites and with length, where site explained 66% of the variation in isotopic niche position (pseudo-$F_{4,60}$ = 17.19, P = 0.001) and fish length explained 5.5% (pseudo-$F_{1,60}$ = 7.47, P = 0.007). Trophic niches varied significantly among all sites (R > 0.2, P < 0.05) except for FP and CA; CA and SB; and SA and SB (Table S8). Round goby at FP and HP fed at a lower trophic position and were more reliant on benthic production compared to those at SA, where they spanned a wide range of benthic reliance at while feeding at low trophic position, and SB and CA, where they fed at an elevated trophic position (Figures 3a, S1; Table S3). In yellow perch, length explained 50.7% (pseudo-$F_{1,24}$ = 42.73, P = 0.001) of the variation in isotopic niche and site explained an additional 20.9% (pseudo-$F_{3,24}$ = 5.88, P = 0.001), where site FP differed from HP and SA after accounting for length differences (Table S8). Fish at SA and HP fed at low trophic position and had higher benthic reliance compared to CA, where there was a wide range of trophic position, and FP, where, contrary to round goby or evidence from diets and fatty acids, yellow perch exhibited elevated trophic position and reduced benthic reliance (Figures 3b, S1; Table S3).

Partitioning trophic composition across levels of organization (from within-individual to between species) revealed surprising patterns. Variance in gut content composition was evenly partitioned between site (pseudo-$F_{4,91}$ = 4.06, R^2 = 0.12, P = 0.001) and species levels (pseudo-$F_{1,91}$ = 15.17, R^2 = 0.11, P = 0.001), with lessened (although significant) explanatory power of season (pseudo-$F_{1,91}$ = 7.08, R^2 = 0.05, P = 0.001) and the interaction of season and site (pseudo-$F_{2,91}$ = 2.14, R^2 = 0.03, P = 0.002). Variance in fatty acid composition followed a similar pattern to that of gut contents, with roughly equal explanatory power of site (pseudo-$F_{4,91}$ = 11.36, R^2 = 0.21, P = 0.001) and species (pseudo-$F_{1,91}$ = 61.82, R^2 = 0.29, P = 0.001), with little contribution from between-season variability (pseudo-$F_{1,91}$ = 14.82, R^2 = 0.07, P = 0.001) or the interaction between season and site (pseudo-$F_{2,91}$ = 0.99, R^2 = 0.01, P = 0.382), and 42.3% of the variation in individual fatty acid composition was unexplained. Like diet and fatty acid composition, variation in isotopic niche was largely reflective of variation among sites. Site identity explained almost half of the isotopic variation across species (pseudo-$F_{3,81}$ = 21.46, R^2 = 0.38, P = 0.001). The interaction of site and season (pseudo-$F_{3,81}$=4.58, R^2 = 0.08, P = 0.002) and species identity (pseudo-$F_{1,81}$ = 8.41, R^2 = 0.05, P = 0.003) contributed considerably less to isotopic variation. Temporal variation among seasons had almost no power to explain variation in isotopic niches and did not contribute significantly to the model (pseudo-$F_{1,81}$ = 1.20, R^2 = 0.007, P = 0.261).

3.2 | Spatial variation in trophic diversity and niche size

Gut content diversity exhibited essentially no spatial variability for either species – round gobies generally had 2 to 4 types of diet items in their guts, whereas yellow perch had generally consumed 1 to 2 types of diet items across sites (Figure 4a, c). Individuals of both species captured at FP and HP exhibited relatively lower fatty acid diversity at q = 1 than those at sites CA, SA, AR, and SB, with significant differences between those groups (Figure 4b,d). When examining the diversity of abundant fatty acids (q = 4), however, this spatial pattern held true for round goby but not yellow perch, as yellow perch fatty acid diversity was roughly equal across all sites (Figure 4d). Between species, round goby fatty acid diversity was higher than that of yellow perch at all sites, but these differences were only significant at site AR. Stable isotopes revealed variation in trophic niche size among sites. Round goby at sites FP, CA, and SA occupied significantly larger niches than gobies at HP or SB, which were not different from one another. Yellow perch isotopic niche size did not vary among sites, although yellow perch at site CA occupied a marginally larger niche compared to all other sites (Figure S2).

In partitioning trophic diversity, relatively little gut diversity variation was attributable to within-individual variation due to the relatively low diversity of individual gut contents (~15%). Instead, the largest contributors to gut content diversity were observed at the species (i.e., round goby and yellow perch were eating relatively dissimilar items; ~32%) and the site levels (i.e., individuals of either species were eating relatively dissimilar items at different sites; ~21%) (Figure 5a). Within season and site (~10%), within species (~15%), and seasonal (~7%) variation contributed less to overall diet diversity. The proportional contribution of each level to gut content diversity remained relatively unchanged across levels of *q*. Fatty acid diversity was almost entirely contained within individuals (~80% of total observed diversity) (Figure 5b). As *q* increased, the contribution of within-individual variation decreased from a high of 99% ($q = 0$) to 79% ($q = 6$) of total fatty acid diversity. The remaining fatty acid diversity was roughly evenly divided among within-season and site (0.6 – 5.7%), within site (0.4 – 5.4%), and between species (0 – 6.4%). The contribution of seasonal variation in diversity was limited (~1%).

3.3| Drivers of fatty acid diversity

Accounting for variation among sites and with fish length, round goby fatty acid diversity was negatively related to diet PC 1 (representing a gradient between consuming dreissenid mussels to consuming benthic arthropods), but not related to gut content PC 2 or gut content diversity (Table 3; Figure 6, S3). Yellow perch fatty acid diversity was not related to any indicator of gut content composition or diversity (Table 3, Figure S3).

4 | DISCUSSION

Variation in the trophic structure of food webs can have important implications for their stability (Paine, 1966; Layman et al., 2007; Faulks et al., 2015). By evaluating patterns in trophic composition and diversity in two species, we found that sites where fish were more reliant on benthic energy pathways exhibited reduced fatty acid diversity and isotopic niche size, potentially driven by differences in prey consumption. This suggests that underlying resource availability can have strong influences on these traits in individuals and populations. In addition, we found that intraspecific spatial variability in resource use can match or even exceed trophic variation observed among different species. Lastly, we determined that indices of trophic diversity may not incorporate similar information on the diversity of resources utilized by individuals or populations. Rather, diet composition (not diet diversity) appears to drive variation in fatty acid diversity. These results offer further support for the thesis that individual behavior can influence the realized trophic niche of a population, and that individual variation in trophic phenotypes can play a significant role in determining overall food web structure (Hubbell, 2005; Allgeier et al., 2017).

4.1 | Spatial variation in trophic diversity and niche size

Variation in habitat and resource use can have strong effects on local food web structure (Hessen & Leu, 2006; Lau et al., 2012; Galloway & Winder, 2015; Larson et al., 2015). We observed strong concordance in the spatial patterns of trophic composition and trophic diversity between round goby and yellow perch in Lake Michigan. Two sites on the west side of the lake exhibited lower fatty acid diversity and increased reliance on benthic invertebrates compared to all other sites even after accounting for differences in fish size. These western sites are dominated by bedrock and large cobble while generally experiencing weaker water currents, whereas other sites are composed of a mixture of rocky and sandy habitats and experience stronger water currents (Beletsky & Schwab, 2001; Janssen et al., 2005). Thus, rocky but calmer western habitats may have increased the availability of interstitial spaces for benthic invertebrates and improved searching ability of fish predators (Crowder & Cooper, 1982; Kuhns & Berg, 1999; Tierney et al., 2011). Dreissenid beds occupying rocky areas may also provide refuge for other macroinvertebrates, increasing their abundance and availability to fish predators (Ward & Ricciardi, 2007). Supporting this, a pattern of increased benthic reliance on the western side of Lake Michigan has been observed previously, meaning such differences in resource use are stable over time and may result from consistent spatial patterns in habitat and resource availability (Czesny *et al.*, 2011). The consistency of these patterns in two different species after considering ontogenetic differences among sites suggests that spatial variance in available resources can play a substantial role in structuring fish niches (Robinson & Wilson, 1998).

Spatial variation in lower food web processes can also exert strong influences on spatial heterogeneity in food web structure in aquatic systems (Crowder & Cooper, 1982; Sass et al., 2006; Rude et al., 2016). The southwest portion of the lake receives relatively little allochthonous nutrient input from different land use types (forested versus urban and agriculture) compared to other sites, which may affect fatty acid availability by changing primary production pathways from bacterial and detrital sources to phytoplankton production (Lau et al., 2012; Larson et al., 2013; Scharold et al., 2015; Rude et al., 2016). Similar west-to-east spatial patterns have been observed in the microbial communities, nitrogen cycling dynamics, and nearshore primary productivity in Lake Michigan (Gardner et al., 2004; Hutton Stadig, 2016; Turschak et al., 2018). The consistency of spatial patterns between both species suggests that these dynamics are likely shaping local variation in food web structure, with implications for whole food web function and, potentially, habitat quality (MacPherson et al., 2015; McMeans et al., 2016). Increased individual trophic diversity may potentially improve individual fitness (e.g., parasite loads, the composition of gut biota, and response to stress or exertion; Merrick, Chumbley & Byrd, 1997; Chatelier *et al.*, 2006; Ahlgren, Vrede & Goedkoop, 2009; Locke, Marcogliese & Valtonen, 2014; Bolnick *et al.*, 2014). Therefore, increased trophic diversity could be a potential indicator of habitat and resource quality for consumers, as sites exhibiting decreased trophic diversity may be less resilient to ecological change or represent lower quality sites compared to others representing a wider range of potential resources (Ghomi et al., 2014).

Although spatial patterns in trophic niches were similar between species, round goby exhibited greater consistency between metrics across sites than yellow perch (Fig. 2), which may be rooted in taxonomic differences in foraging behavior and fatty acid regulation. Round goby are highly territorial, less vagile, and largely limited to feeding on benthic prey compared to yellow perch, which can utilize benthic and planktonic prey and thereby potentially homogenize spatial variance in lower food web processes (Ray & Corkum, 2001; Feiner & Höök, 2015; Houghton & Janssen, 2015). However, round goby exhibited generally more diverse gut contents and fatty acids across sites than yellow perch, which suggests that, despite having access to a broader resource base, yellow perch individuals tend to specialize on variable local resources, which has been demonstrated in both yellow and Eurasian perch (Svanbäck & Eklöv, 2006; Roswell et al., 2013; Eloranta et al., 2017). Fatty acid assimilation and metabolism also likely differ between the two species – round goby contained relatively lower levels of polyunsaturated fatty acids and higher abundances of monounsaturated and saturated fatty acids than Eurasian perch in one study (Ghomi et al., 2014), and yellow perch have highly conserved fatty acid profiles in response to their thermal environment (Feiner et al., 2016, 2018b). This suggests that some species-specific variation in the composition and diversity of fatty acids is possible.

4.2 | Partitioning variance in trophic composition and diversity

We expected species identity to play a strong role in differentiating trophic composition and diversity between yellow perch and round goby, as species-specific differentiation in fatty acid profiles is often so extensive that fatty acids have been suggested as a potential method for species fingerprinting (Iverson et al., 2002; Czesny et al., 2011; Lau et al., 2012; Galloway & Winder, 2015). Instead, spatial variation in trophic metrics explained up to 50% of the total variation in composition or diversity (e.g., combining the red "season/site" and yellow "site" components in Fig. 5a), equal to or exceeding variation due to species, suggesting that intraspecific niche variation may play a significant role in food web structure and should not be ignored. Other studies across terrestrial and aquatic systems have found that trait variation within species can contribute as much to the total community variation as interspecific variation, and that taxonomic diversity or composition does not necessarily correlate well with trophic diversity among communities (Hubbell, 2005; Bolnick et al., 2011; Siefert et al., 2015; Pool et al., 2016; Allgeier et al., 2017). For example, individual trophic behavior in a complex parrotfish community accounted for a substantial amount of the total niche variation in the community and drove niche partitioning among species (Allgeier et al., 2017), habitat complexity influenced inter- and intraspecific niche partitioning in two percids (Eloranta et al., 2017), and variability in community structure was highest at local scales and varied among habitat types in coastal boulder fields (Leclerc, 2018). We note, however, that differences in resource availability among systems may influence the extent to which taxonomy and spatial heterogeneity influence niche partitioning. Lake Michigan is a large, diverse ecosystem presenting a range of potential prey to our study species (Garza & Whitman, 2004; Vanderploeg et al., 2012), potentially reducing interspecific interactions and niche partitioning (Svanbäck & Persson, 2004). Species inhabiting smaller systems with more limited resources may exhibit stronger taxonomic partitioning as a result of increased interspecific interactions (Griffin et al., 2008; Cardinale, 2011; Correa & Winemiller, 2014). Thus, understanding how individuals vary in their behavior across sites and systems could help to quantify the resilience of food webs to ecosystem change (Paterson et al., 2014; MacPherson et al., 2015; McMeans et al., 2016) and predict changes in ecosystem function (e.g., trophic cascades, Carpenter, Kitchell & Hodgson, 1985; Finke & Denno, 2004).

While variation in gut content diversity was strongly linked to spatial variation, virtually all fatty acid diversity was observed at the individual level – that is, a random fish sampled at any site could be expected to contain 80 to 90% of the total fatty acid diversity observed. Many essential fatty acids serve important roles in neural development, energy storage, and reproductive success, and therefore may be strongly regulated owing to fitness costs when fatty acid composition is sub-optimal (Bell et al., 1986; Ahlgren et al., 2009). Freshwater fishes are able to catabolize and synthesize important fatty acids to some extent, allowing individuals to modulate fatty acid variation based on available dietary fatty acids (Ahlgren et al., 2009), effectively homogenizing potential variability in diversity. Despite this, we were able to detect subtle differences in fatty acid diversity, especially between western and northern and eastern sites (Fig. 4b,d). As some fatty acids are metabolized preferentially and others require certain precursors for endogenous synthesis (Bell et al., 1986; Sawyer et al., 2016), locations exhibiting low fatty acid diversity could represent poor habitats or stressed populations (Merrick et al., 1997; Brown et al., 2005; Chatelier et al., 2006; Ahlgren et al., 2009). Further research investigating the potential fitness costs of reduced fatty acid diversity and potential environmental causes could offer insights into the use of fatty acid diversity as an indicator of habitat quality or individual health.

4.3 | Drivers of fatty acid diversity

We expected to observe a relationship between gut content diversity and fatty acid diversity among individuals; however, no such relationship was apparent in either species. This suggests that diets and fatty acids are relaying somewhat different information about the trophic diversity of individuals. One likely explanation, as previously mentioned, is that fatty acid diversity is more tightly regulated due to physiological constraints and therefore somewhat unresponsive to diet (Ahlgren et al., 2009; Sawyer et al., 2016). In addition, gut contents are snapshots of recent (<12 h) consumption, whereas fatty acids integrate diet composition over multiple days or weeks (Happel et al., 2016). Because we lack multiple diet samples over time, it is unclear how consistent diet specialization and individual diet diversity are in these species (although it may be extensive in other species; Bryan & Larkin, 1972), and therefore fatty acid signatures could be integrating a more diverse range of resources than what is reflected in the observed gut contents.

Variability in the fatty acid diversity of diet items, in addition to our limited ability to identify them with high taxonomic resolution, could also have led to the lack of an observable relationship between gut content and fatty acid diversity. For example, our diet item groupings of fish and Copepoda contain multiple species that we were unable to consistently differentiate due to digestion, but that may have disparate fatty acid profiles (Smyntek et al., 2008; Happel et al., 2017). Fatty acid analyses were not performed on the benthic invertebrates in this study. Instead, we relied on earlier observations of invertebrate fatty acid composition (e.g., Czesny et al., 2011) to make inferences about probable fatty acids available to our focal fish species. Deeper investigations into the fatty acid diversity of prey items and true diversity of predator gut contents (e.g., via genetic analysis of diets; King et al., 2008; Carreon-Martinez et al., 2011) could yield a more complete picture of the resource heterogeneity experienced by aquatic predators.

Rather than being linked to gut content diversity, round goby fatty acid diversity was instead related to dreissenid mussel consumption. The invasion of dreissenid mussels into the Great Lakes has caused severe ecological impacts (Hecky et al., 2004; Bunnell et al., 2009; Paterson et al., 2014; Turschak et al., 2014), and round goby are one of relatively few species that regularly consume dreissenid mussels (Foley et al., 2017). Our study suggests that the inclusion of dreissenids in round goby diets provides a highly diverse suite of fatty acids - in one study, dreissenids contained 17 different fatty acids at more than 2% relative abundance, while zooplankton had 13 fatty acids reach this threshold, and amphipods only 11 (Czesny et al., 2011). Many of these were long chain mono or polyunsaturated fatty acids (C20:1n-9, C18:4n-3, C22:5n-3, and C22:5n-6) important for a wide range of physiological functions in fish (Bell et al., 1986; Ahlgren et al., 2009; Czesny et al., 2011). By consuming dreissenids, round goby may be making these valuable fatty acids available to their predators, including important species like lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*) (Dietrich et al., 2006; Pothoven & Madenjian, 2013). Thus, round goby, though invasive, may represent an important re-linking of benthic and pelagic energy pathways that were decoupled through dreissenid benthification (Johnson et al., 2005; Almqvist et al., 2010; Turschak et al., 2014).

4.4 | Conclusions

We have shown congruent spatial patterns in the trophic composition and diversity of two sympatric freshwater fishes. As both species are highly locally abundant, they likely play a key role in food web interactions as both predator and prey. Therefore, intra- and interspecific variation in their trophic function can have significant impacts on the connectivity of benthic and pelagic production pathways (Happel et al., 2015; Foley et al., 2017). Our data suggest that spatial heterogeneity in habitat, resource availability, and other environmental conditions have a significant role in determining the feeding behavior of individuals, to the extent that trophic niches may be more a function of environment than of species identity (Paterson et al., 2014; Pool et al., 2016; Allgeier et al., 2017). Our results support the notion that elucidating functional diversity is at least as important to understanding food web structure as taxonomic diversity (Hubbell, 2005; Pool et al., 2016). As trophic diversity is potentially important for both niche partitioning and population resilience (Paterson et al., 2014; McMeans et al., 2016; Allgeier et al., 2017), variation in trophic diversity could be a useful indicator for understanding the impacts of environmental change on ecosystem function (Layman et al., 2007; MacPherson et al., 2015; Pool et al., 2016).

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AUTHOR CONTRIBUTION STATEMENT

Conceived and designed the investigation: ZSF, TOH, RKS. Performed field and/or laboratory work: CJF, TOH, JJ, HB, SC, JR. Analyzed the data: ZSF, CJF. Contributed materials, reagents, and/or analysis tools: TOH, JR, JJ, SC, HB. Wrote the paper: ZSF. Revised the paper: ZSF, CJF, RKS, HB, SC, JJ, JR, TOH

TABLES

TABLE 1 Sample size (N) and mean ± standard deviation (SD) of total length (TL, mm) of round goby and yellow perch collected at six sites during two seasons in Lake Michigan that were used for gut content, fatty acid, and stable isotope analyses. Note that, due to lack of isotopic baseline data, no isotopic information was used from site AR in either species.

	N		Mean ± SD TL	
	Summer	Fall	Summer	Fall
Site	Round Goby			
FP	4	6	87.8 ± 20.5	65.4 ± 4.8
HP	7	6	86.4 ± 22.3	59.2 ± 5.9
CA	5	25	65.4 ± 3.6	76.6 ± 15.4

SA	2	6	90.0 ± 45.3	92.3 ± 31.1
AR	0	8	--	84.8 ± 24.2
SB	2	3	66.3 ± 4.5	66.0 ± 1.5
		Yellow perch		
FP	8	0	247.2 ± 55.4	--
HP	3	3	96.1 ± 5.6	117.8 ± 13.7
CA	3	6	89.0 ± 15.1	106.7 ± 84.0
SA	2	4	238.5 ± 23.3	74.3 ± 2.2
AR	0	8	--	91.7 ± 23.0
SB	0	0	--	--

TABLE 2. Summary schematic of study focal questions, data uses (gut contents – GC, fatty acids – FA, stable isotopes – SI), analytical methods, general conclusions, and relevant tables and figures for investigations of patterns and relationships in trophic composition (i.e., mean abundances of identified components) and trophic diversity (i.e., diversity of components, measured using Shannon's effective diversity ${}^{q}D$) in round goby and yellow perch across six sites in Lake Michigan, USA.

Question	Data	Analysis	General Conclusions	Relevant section
Does trophic composition vary among sites?	GC, FA, SI	Species-specific PERMANOVA for differences in sites; visualization via PCA (GC, FA) or biplot (SI)	Yes - southwestern sites reliant on benthic energy, eastern sites reliant on pelagic energy	Tables S4-S8; Figures 2, 3, S1
How is trophic composition partitioned among seasons, sites, and species?	GC, FA, SI	Combined PERMANOVA with site, season, season × site, and species as predictors	Site-level variation equal to species-level variation, minor variation by season	Results Section 3.1
Does trophic diversity vary among sites?	GC, FA, SI	GC and FA: Bootstrapped site-level ${}^{q}D$; SI: Comparison of Bayesian standard ellipse areas among sites	Yes/No - FA diversity lower at southwestern sites; no differences in GC diversity; inconsistent differences in SI niche size	Figures 4, S2
How is trophic diversity partitioned among individuals, seasons, sites, and species?	GC, FA	Group-wise partitioning of ${}^{q}D$	Site-level variation equal to species-level variation, different contributions of individual variation (high in FA, low in GC)	Figure 5

Does diet drive fatty acid diversity?	GC, FA	Random effects regression between FA diversity and GC diversity or composition	Round goby fatty acid diversity related to diet content, no relationship in yellow perch	Table 3; Figures 6, S3

TABLE 3 Linear mixed-modeling results for relationships between fatty acid diversity and either diet diversity ($q = 1$) or gut content composition (significant principal components) for round goby and yellow perch sampled at six sites in Lake Michigan. Models with random intercepts for site and random slopes for the effect of the explanatory gut content variable within site were tested first; if random slopes were not significant (NS), a model including only random intercepts were fitted. Mean and bootstrapped 95% confidence intervals (CI) are given for the standard deviation of random intercepts ($\sigma_{\text{intercept}}$) and slopes ($\sigma_{\text{slope}}$; when significant), the effect of the given predictor variable (β_X), and the effect of total length (β_{TL}). Bold values indicate significant fixed effects (95% CI did not overlap zero).

Species	Parameter	Diet diversity	Diet PC 1	Diet PC 2
Round goby	$\sigma_{\text{intercept}}$	**1.3913**	**1.2645**	**1.4132**
	CI	**(0.5226 - 2.2681)**	**(0.4777 - 2.0446)**	**(0.5655 - 2.3046)**
	σ_{slope}	NS	NS	**0.3377**
	CI	NS	NS	**(0.0198 - 0.7136)**
	β_X	-0.1222	**-0.1496**	-0.0958
	CI	(-0.2742 - 0.0333)	**(-0.2618 - -0.0198)**	(-0.4558 - 0.2544)
	β_{TL}	**0.0085**	**0.0099**	**0.0088**
	CI	**(0.0011 - 0.0167)**	**(0.0026 - 0.0177)**	**(0.0003 - 0.0163)**
Yellow perch	$\sigma_{\text{intercept}}$	0.3246	0.49	
	CI	(0 - 0.9565)	(0 - 1.1198)	
	σ_{slope}	NS	NS	
	CI	NS	NS	
	β_X	-0.5543	-0.0225	
	CI	(-1.2867 - 0.2872)	(-0.3218 - 0.2747)	
	β_{TL}	-0.0047	-0.0033	
	CI	(-0.0103 - 0.0014)	(-0.0099 - 0.0029)	

FIGURES

FIGURE 1 Sample sites where round goby, yellow perch, benthic invertebrates, and zooplankton were collected in summer and fall 2010 in Lake Michigan, USA, including Fox Point, WI (FP); Highland Park, IL (HP); Calumet, IN (CA), Saugatuck, MI (SA), Arcadia, MI (AR), and Sturgeon Bay, WI (SB). Darkened area represents the extent of Lake Michigan watershed.

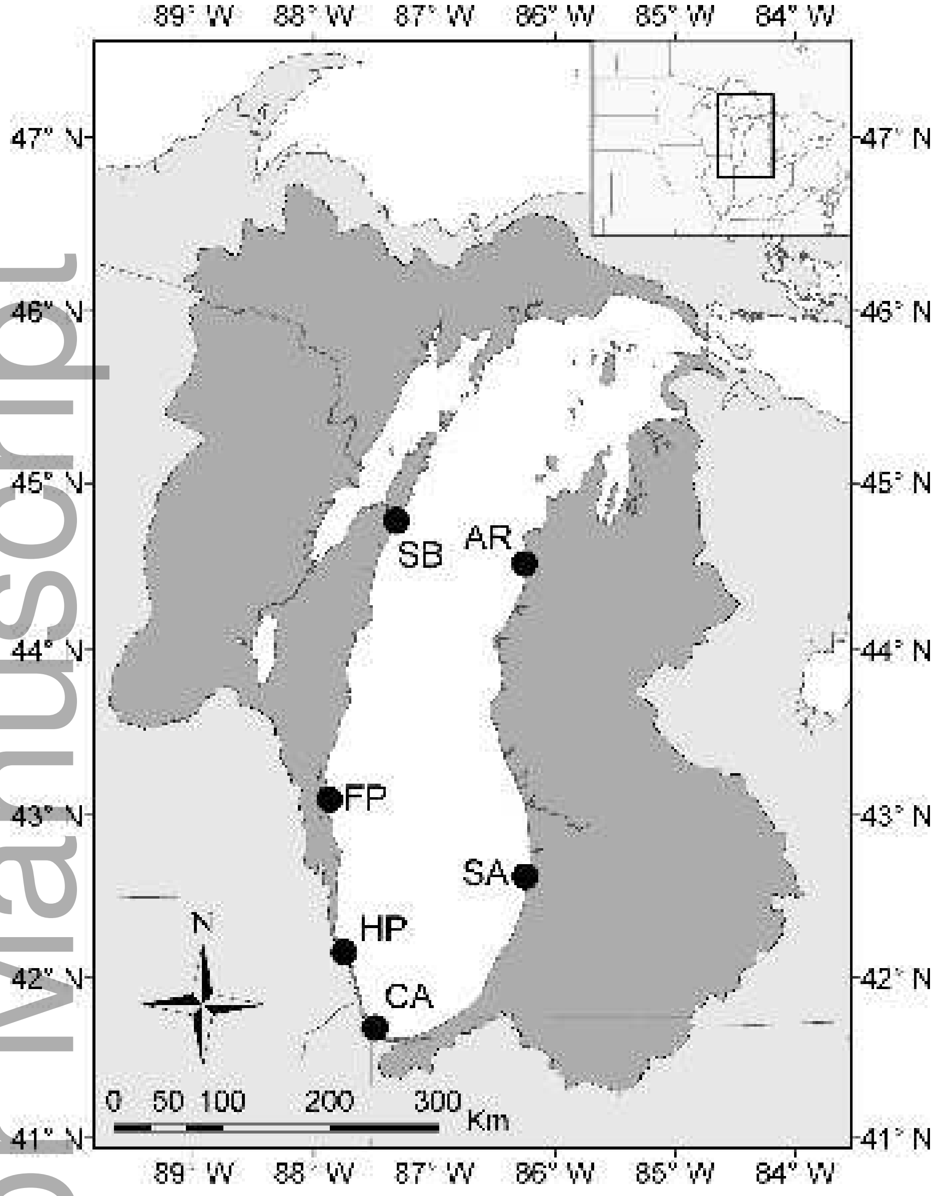
FIGURE 2 Principal components analysis biplots demonstrating spatial patterns in gut content (a,c) and fatty acid composition (b,d) of round goby (a,b) and yellow perch (c,d) sampled from Lake Michigan at six sites (FP: black points, HP: red circles, CA: green squares, SA: blue diamonds, AR: orange upward triangle, SB: pink inverted triangle; abbreviations for site names in Figure 1). Points represent individual fish and ellipses represent one standard deviation. Text indicates loadings of gut items and fatty acids multiplied by 6 and 15, respectively, for clarity.

FIGURE 3 Small sample size-corrected standard ellipse areas (SEA_C) corrected for spatial variation in baseline $\delta^{13}C$ and $\delta^{15}N$ for a) round goby and b) yellow perch collected from six Lake Michigan sites (FP: black points, HP: red circles, CA: green squares, SA: blue diamonds, SB: pink triangles; abbreviations for site names in Figure 1). Points are individual fish and ellipses encompass 80% of the data.

FIGURE 4 Variation in mean individual (α) diversity of gut contents (a, c; black and hatched bars) and fatty acids (b, d; gray and white bars) with low weighting ($q = 1$; a, b) and high weighting ($q = 4$; c, d) of component abundance for round goby (gray, black) and yellow perch (white, hatched) sampled at six sites in Lake Michigan. Error bars represent 95% confidence intervals, where non-overlapping intervals indicate significant differences denoted by different letters (A and B for round goby, C and D for yellow perch). No letters signify that there were no significant differences across all sites for that species.

FIGURE 5 Partitioning of total observed (γ) diversity in gut contents (a) and fatty acids (b) detected in round goby and yellow perch across six sites in Lake Michigan. Diversity was measured at six levels of abundance weighting (q; different stacks of bars) and partitioned among levels of organization, from bottom to top: within-individual diversity (gray), among individuals within a sampling event (site/season; red), among seasons within sites (green), among sites within seasons (yellow), within species across all sites (blue), and between species (orange).

FIGURE 6 Relationship between round goby fatty acid diversity (*q* = 1, corrected for fish total length), and the first principal component of round goby gut content composition, representing a gradient between consumption of Dreissenidae mussels and non-molluscan benthic invertebrates. Points represent fish collected at six sites around Lake Michigan (FP: black points, HP: red circles, CA: green squares, SA: blue diamonds, AR: orange upward triangle, SB: pink inverted triangle; abbreviations for site names in Figure 1).



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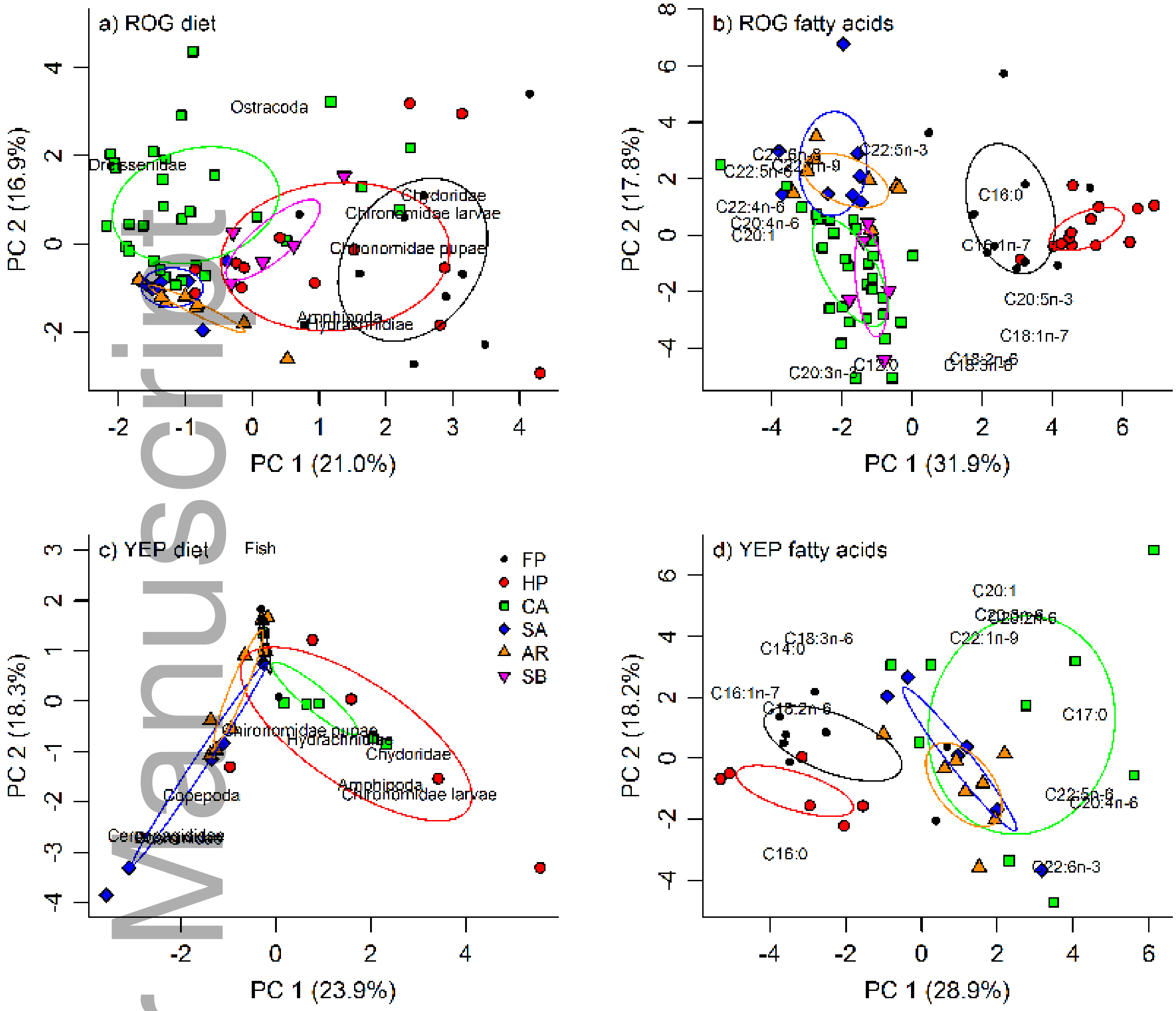

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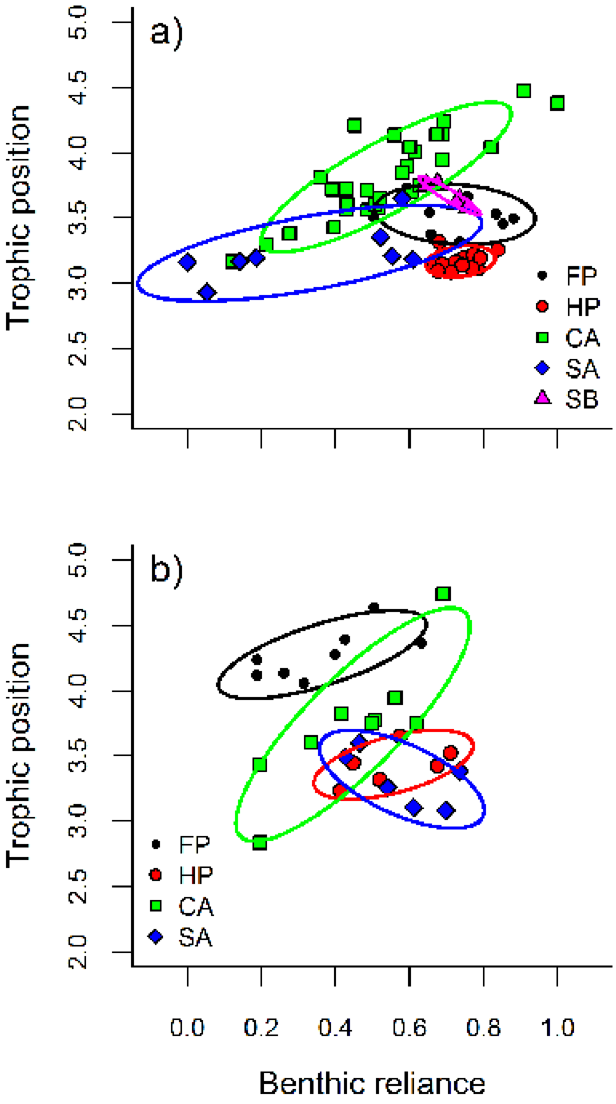

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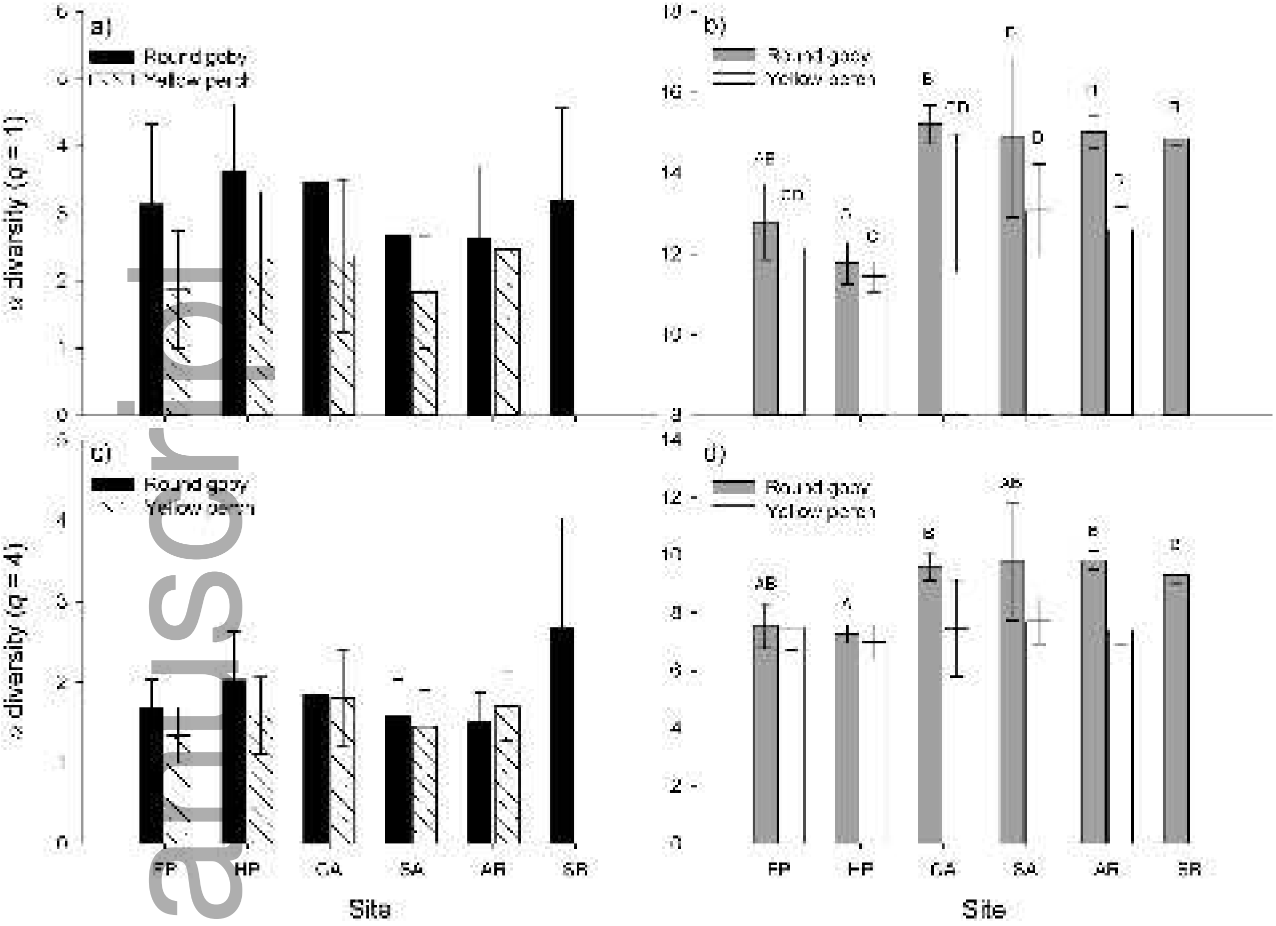

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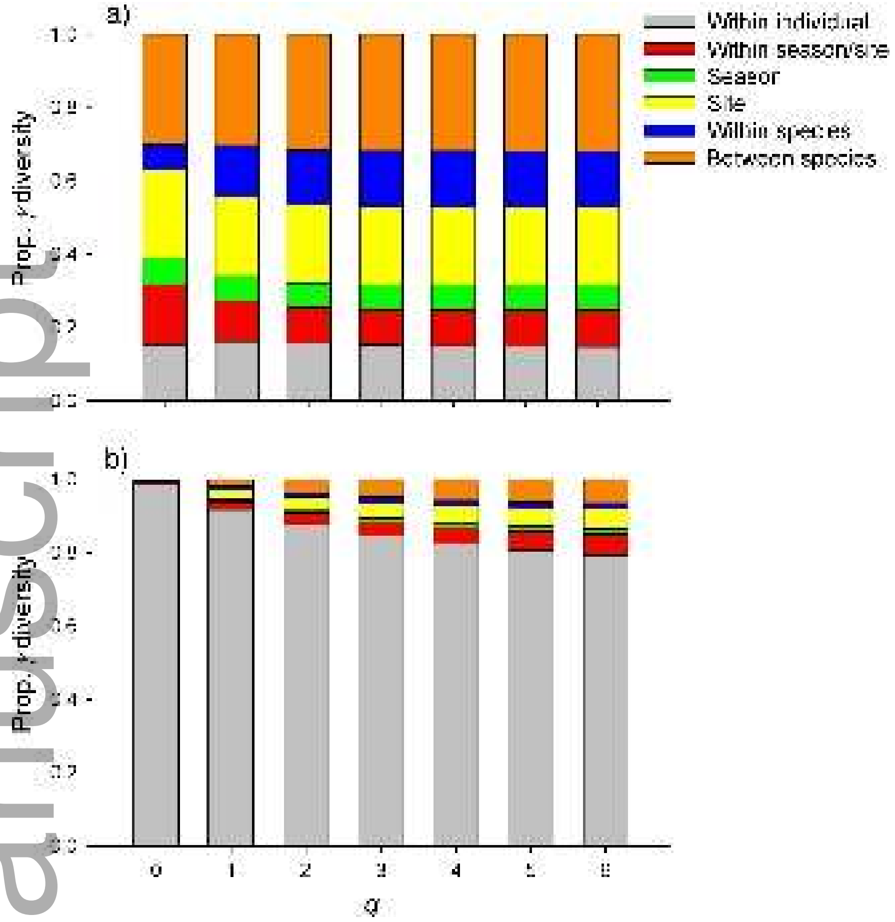

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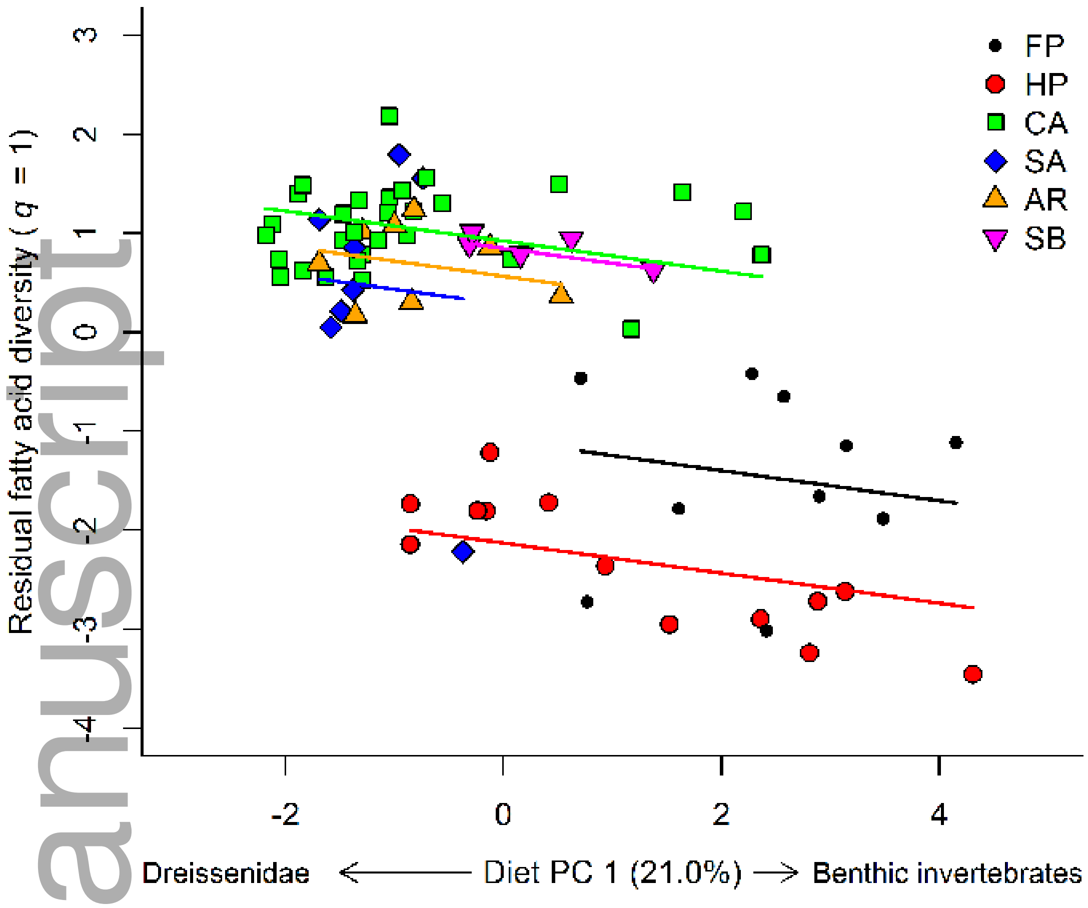

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