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Testing food web theory in a large lake: The role of body size in habitat coupling in Lake Michigan

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Abstract

The landscape theory of food web architecture (LTFWA) describes relationships among body size, trophic position, mobility, and energy channels that serve to couple heterogenous habitats, which in turn promotes long-term system stability. However, empirical tests of the LTFWA are rare and support differs among terrestrial, freshwater, and marine systems. Further, it is unclear whether the theory applies in highly altered ecosystems dominated by introduced species such as the Laurentian Great Lakes. Here, we provide an empirical test of the LTFWA by relating body size, trophic position, and the coupling of different

energy channels using stable isotope data from species throughout the Lake Michigan food web. We found that body size was positively related to trophic position, but for a given trophic position, organisms predominately supported by pelagic energy had smaller body sizes than organisms predominately supported by nearshore benthic energy. We also found a hump-shaped trophic relationship in the food web where there is a gradual increase in the coupling of pelagic and nearshore energy channels with larger body sizes as well as higher trophic positions. This highlights the important role of body size and connectivity among habitats in structuring food webs. However, important deviations from expectations are suggestive of how species introductions and other anthropogenic impacts can affect food web structure in large lakes. First, native top predators appear to be flexible couplers that may provide food web resilience, whereas introduced top predators may confer less stability when they specialize on a single energy pathway. Second, some smaller bodied prey fish and invertebrates, in addition to mobile predators, coupled energy from pelagic and nearshore energy channels, which suggests that some prey species may also be important integrators of energy pathways in the system. We conclude that patterns predicted by the LTFWA are present in the face of species introductions and other anthropogenic stressors to a degree, but time-series evaluations are needed to fully understand the mechanisms that promote stability.

KEYWORDS
Bayesian hierarchical models, benthic-pelagic coupling, consumer-resource interactions, food web structure, Laurentian Great Lakes, stable isotopes

INTRODUCTION

Food webs have become an important framework for understanding the structures and processes that impart stability in nature (Rooney et al., 2006; Yodzis, 1981). In particular, the number, strength, and relative arrangement of trophic interactions in an ecosystem (i.e., the emergent food web structure) are thought to relate to its stability or adaptive capacity—its ability to respond to perturbations without the loss of species or essential functions (Danet et al., 2021; McMeans et al., 2016). However, quantifying food web structure adequately across space and time is a monumental task, so alternative approaches are needed to map trophic interactions and their implications for stability. The landscape theory of food web architecture (LTFWA) (Rooney et al., 2008) posits that organismal traits, such as body size and foraging behavior, can be used to predict the structure of real food webs with explicit spatial and temporal components that influence how the system responds to a variable world.

Body size is a major structuring force in food webs because consumers are often constrained to feed on prey smaller than their own size, leading to positive associations between consumer size and trophic positions (Petchey et al., 2008). Larger consumers also tend to be more mobile and have larger home ranges than their prey because the cost of movement per unit of mass decreases with body size (McCann et al., 2005). They also tend to have larger brains, allowing them to quickly respond to environmental cues (Harvey & Pagel, 1988). These properties imply that large, mobile consumers may couple energy channels (i.e., sub-food webs or food chains) among habitats (Vander Zanden & Vadeboncoeur, 2020). Energy channels also show asynchronous energy flux rates due to differences in productivity (carbon influx) and turnover rates (production: biomass ratios) of organisms in different habitats (Rooney & McCann, 2012). Turnover rate is intimately related to interaction strength (Rooney et al., 2006) and body size (Brown et al., 2004), so the emergent continuum between fast (i.e., high production: biomass ratios) and slow (i.e., low production: biomass ratios) energy channels in different habitats creates a variable trophic landscape to which consumers react. The LTFWA posits that food webs are structured such that top consumers asynchronously respond to fast and slow energy channels with asymmetric flux rates (McCann & Rooney, 2009). That is, production dynamics are driven by bottom-up and top-down forces that can both initiate and mute variability in basal energy sources, which, in turn, promotes long-term stability across the food web (Rooney et al., 2008).

While elegant in its simplicity, empirical support for the close associations among body size, trophic position, asymmetric flux rates, and trophic coupling predicted by the LTFWA varies among and within different ecosystems. For example, crocodilians in the Amazon have relatively small home ranges and specialize on distinct energy pathways related to diet and habitat preferences despite attaining large body sizes and being opportunistic predators (Villamarín et al., 2017). In Africa, large migratory herbivores, rather than top predators, couple energy channels across the Serengeti ecosystem (Fryxell et al., 2005). Although poorly studied, the strength of body size-trophic position relationships likely varies between fast-energy and slow-energy channels within food webs (Keppeler et al., 2021). In addition, the relationship between body size and trophic position varies among ecosystems and tends to be strong and positive in marine food webs, but not in freshwater or terrestrial ones (Potapov et al., 2019). Marine food webs are often efficient and size-structured in part because they are supported by unicellular phytoplankton that are digested easily and cannot be handled by larger consumers (McGarvey et al., 2016). In contrast, primary producers in terrestrial ecosystems are typically multicellular vascular plants that are less labile (i.e., high cellulose and lignin content) and variable in size. This reduces trophic efficiency and removes limitations on the size range of primary consumers, thus weakening body size–trophic position relationships (Keppeler et al., 2020). Freshwater food webs are somewhat intermediate; in rivers and small lakes, trophic position–body size relationships can be weak or even absent because food webs are supported by both unicellular (benthic algae, phytoplankton) and multicellular (riparian vegetation, aquatic macrophyte) resources (Vander Zanden & Vadeboncoeur, 2020). However, food webs in large lakes (>500 km^2) are thought to be more similar to those in marine ecosystems than those in small lakes or rivers because, like marine systems, large lakes typically have large surface areas, deep basins, and geographically distant habitats (Potapov et al., 2019).

Empirical support for the LTFWA is especially lacking from highly modified systems—those that have shifted from historical to novel states due to the effects of multiple interacting stressors such as invasive species introductions, loss of native species, habitat modifications, and altered physical conditions (Craig et al., 2017). Do the theorized relationships and stabilizing mechanisms posited by the LTFWA still hold when a whole consumer community has had only decades, not millennia, to co-evolve? This question is particularly relevant for freshwater ecosystems where population declines continue to outpace contemporaneous declines in marine or terrestrial ecosystems (Reid et al., 2019), and have likely rewired food web structures within them (Bartley

et al., 2019). The Laurentian Great Lakes, for example, contain over 80% of North America's surface freshwater and are a critical natural resource for communities across the region, but have been upended by several anthropogenically-induced environmental challenges including non-native species invasions (e.g., Ricciardi & MacIsaac, 2000), shifts in nutrient inputs from land-use changes (e.g., Han & Allan, 2012), and contaminant inputs (e.g., Lepak et al., 2019). Large freshwater lakes that have experienced major human modifications, such as the Laurentian Great Lakes, provide opportune systems to test predictions of the LTFWA. Data from Lake Michigan and Lake Huron provide preliminary evidence for adaptive benthic-pelagic coupling. Pelagic consumers have become increasingly reliant on the nearshore benthic energy channel since the invasion of dreissenid mussels. These dreissenids feed on pelagic plankton but are themselves prey for benthic consumers, and thus redirect energy from the pelagic to the nearshore benthic energy channel (Rennie et al., 2009; Turschak et al., 2014). A shift in benthic-pelagic coupling has also been documented in a suite of Fennoscandian lakes in response to the amplification of benthic food chains (Hayden et al., 2019). However, few studies have investigated the coupling of offshore pelagic and nearshore benthic energy compartments across multiple trophic positions and body sizes in large lakes. Further, the turnover rates of pelagic and benthic energy channels likely differ in Great Lakes food webs because particulate carbon represented by phytoplankton is metabolized and used quickly (Wetzel, 2001), and pelagic primary consumers (zooplankton) tend to be smaller with shorter generation times compared with their counterparts (e.g., amphipods, mollusks) in benthic habitats (Keppeler et al., 2021; Rooney et al., 2006). We are not aware of any study that has explored differences in trophic position–body size relationships between phytoplankton-based pelagic energy (fast) channels and benthic-based nearshore energy (slow) channels in large freshwater lakess.

Here, we leverage a large stable isotope dataset, containing data from 2180 samples, to test hypotheses derived from the LTFWA in Lake Michigan (Figure 1a), a Laurentian Great Lake whose food web has been highly modified over the past 150 years. First, the relationship between trophic position and body size ought to differ between the fast (offshore pelagic) and slow (nearshore benthic) energy pathway (Hypothesis 1). Therefore, we expect that body size will be positively related to trophic position, but with a stronger relationship (i.e., lower intercepts and steeper slopes) associated with the offshore pelagic channel compared with the nearshore benthic channel (Figure 1b). Second, if small consumers at lower trophic positions are more isolated in space (and thus potentially limited in the carbon source they rely on)
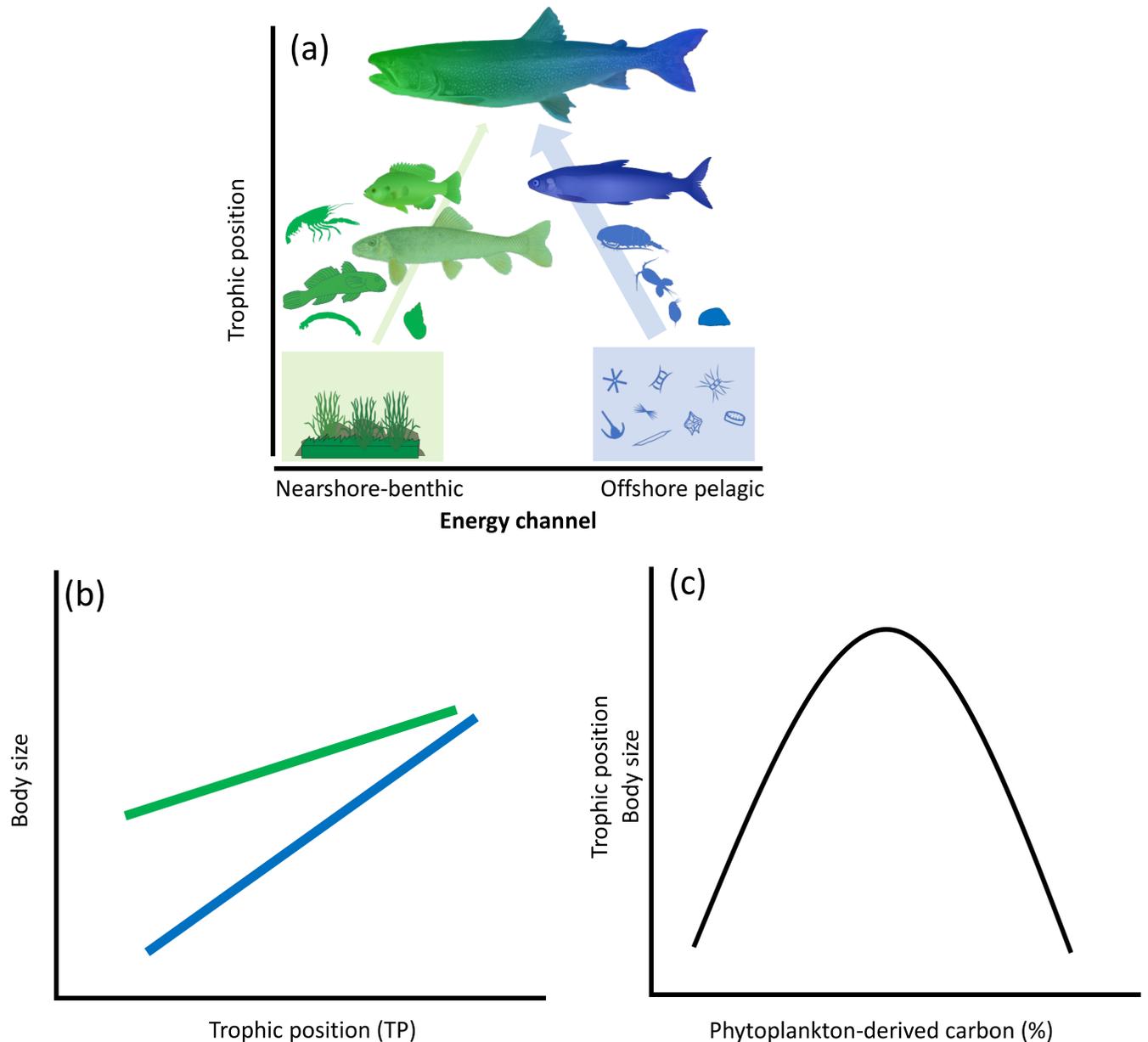
FIGURE 1 (a) Conceptual depiction of the hypothesized relationships among trophic position, body size, and the relative contribution of carbon from different energy channels or pathways in Lake Michigan. Pelagic energy pathways (thick blue arrow) are expected to be efficient and size-structured because they are supported by unicellular phytoplankton that are easy to digest and cannot be handled by larger consumers. Conversely, trophic position–body size relationships are expected to weaken in nearshore-benthic energy pathways (thin green arrow) which can be supported by both unicellular (benthic algae, phytoplankton) and multicellular (riparian vegetation, aquatic macrophyte) organisms. The landscape theory of food web architecture posits that food webs are structured such that top predators couple asynchronous energy channels from distinct habitats (nearshore and offshore). (b) An asymmetric trophic position–body size relationship where, for a given trophic position, organisms associated with the pelagic phytoplankton channel have smaller body sizes than those associated with the benthic nearshore channel, and differences diminish at higher trophic positions (Hypothesis 1). (c) Larger and higher trophic position organisms couple nearshore and offshore pelagic energy channels while smaller organisms are more restricted to single-energy channels (i.e., nearshore-benthic or offshore pelagic but not both; Hypothesis 2). Illustration attribution: University of Maryland Center for Environmental Science Integration and Application Network (http://ian.umces.edu/symbols/). Lake trout image credit: Brandon Schroeder, Michigan Sea Grant.

than large mobile consumers at higher trophic positions that may move between nearshore and pelagic habitats, then body size and trophic position should covary with the relative contribution of carbon from offshore pelagic and nearshore benthic energy channels (Hypothesis 2). Therefore, we expect a hump-shaped relationship between trophic position or body size and the percent of carbon derived through the offshore pelagic energy channel (Figure 1c).

MATERIALS AND METHODS

Study system

Lake Michigan is a temperate lake with an average depth of 85 m and maximum depth of 282 m. It is the second largest Laurentian Great Lake by volume (4,918 km^3), and third largest by surface area (57,753 km^2). Over 75% of the lake is deeper than 30 m, leaving a relatively small area (~24%) suitable for benthic algae production due to light limitation (Appendix S1: Section S1). The northern basin of the lake is generally surrounded by forested lands with relatively low population density, while the lower basin supports the Chicago Metropolitan area, the third largest metropolitan area in the United States. Historically, the lake was dominated by a highly speciated bentho-pelagic coregonine assemblage (Koelz, 1929), with other abundant species including lake trout (*Salvelinus namaycush*), burbot (*Lota lota*), three sculpin species (*Cottus* spp. and *Myoxocephalis thompsonii*), and yellow perch (*Perca flavescens*) (Wells & McLain, 1973). Non-native sea lamprey (*Petromyzon marinus*) and alewife (*Alosa pseudoharengus*) entered the system via the St. Lawrence seaway (Smith, 1972) and passed Niagara Falls to gain access to the upper four Great Lakes through the Welland Canal (Lawrie, 1970). Sea Lamprey and overfishing led to the collapse of lake trout by the 1950s (Wells & McLain, 1973) which, in turn, allowed alewife to proliferate owing to limited predation. The collapse of the diverse coregonine community occurred by the 1960s due to overfishing (Smith, 1972) and negative interactions with invasive species (Crowder, 1980). Chinook and Coho salmon (*Oncorhynchus tshawytscha* and *O. kisutch*) were among several non-native salmonines successfully introduced to the Great Lakes in the 1960s, along with reintroduction of native lake trout, to capitalize on abundant alewife prey and create a strong sport fishery (Tanner & Tody, 2002; Wells & McLain, 1973). By the 1990s, a new wave of invaders had further altered the lake, including zebra and quagga mussels (*Dreissena polymorpha*, and *D. bugensis*), spiny water flea (*Bythotrephes longimanus*), fishhook water flea (*Cercopagis pengoi*), and round goby (*Neogobius melanostomus*) (Madenjian et al., 2002). Since their introduction, dreissenids have likely had the greatest impact on the food web by redirecting nutrients and energy away from pelagic production and depositing nutrients and energy in the nearshore zone and offshore profundal zone (e.g., Cuhel & Aguilar, 2013). In the nearshore zone, mussel grazing has greatly increased water clarity and benthic nutrient sequestration, causing large blooms of nearshore benthic algae, including *Cladophora* and epiphytic diatoms (Bootsma et al., 2004). Round gobies have also contributed to nearshore benthic energy pathways by serving as a conduit of energy from dreissenid mussels, their predominant prey, to piscivorous secondary consumers (Foley et al., 2017; Kornis et al., 2012).

Data

We analyzed data (Maitland et al., 2024) collected from 40 ports throughout the main basin of Lake Michigan collected in the spring, summer, and fall of 2015 (Figure 2; see Appendix S1: Section S1 for details on sample collections). Data were compiled from two primary sources: (1) the Cooperative Science and Monitoring Initiative lake-wide survey in 2015 (Foley & Collingsworth, 2018), and (2) the U.S. Fish and Wildlife Service Great Lakes Mass Marking Program (Bronte et al., 2012; Kornis et al., 2020). The data consisted of 2,180 samples from 29 groups (Figure 3), including basal resources, invertebrates, and fishes, where each sample is from an individual organism (fishes) or pooled groups of organisms from a common taxonomic group (invertebrates; Appendix S1: Table S1). Each sample has been analyzed for stable carbon (ratios of ^{13}C:^{12}C relative to the Vienna PeeDee Belemnite carbonate international standard; $\delta^{13}C$, hereafter) and nitrogen (ratios of ^{15}N:^{14}N, relative to atmospheric N; $\delta^{15}N$, hereafter) isotope values. Full details of stable isotope analyses are given Appendix S1: Section S2 and in Sierszen et al. (2014), Hoffman, Kelly, et al. (2015), and Kornis et al. (2020).

$\delta^{15}N$ is correlated with trophic position due to fractionation during trophic transfers that typically increases by 3–4‰ at each trophic step (Vander Zanden & Rasmussen, 1999). $\delta^{13}C$ values are typically distinct among primary producers due to differences in photosynthetic pathways and inorganic sources of assimilated carbon (Peterson & Fry, 1987). In temperate lakes such as the Laurentian Great Lakes, variation in $\delta^{13}C$ is primarily driven by differences in fractionation during photosynthesis such that primary producers in nearshore habitats (e.g., benthic algae) are ^{13}C-enriched, while offshore producers (e.g., phytoplankton) are ^{13}C-depleted (Hoffman, Kelly, et al., 2015; Hoffman, Sierszen, et al., 2015). This creates a nearshore-offshore gradient in $\delta^{13}C$ values at the base of the food web with only slight enrichment (0–1‰) following each trophic transfer (Vander Zanden & Rasmussen, 1999). Because lipids are depleted in ^{13}C relative to muscle tissues (Post et al., 2007), we normalized $\delta^{13}C$ values for lipid content using equations specific to functional groups: fishes (Hoffman, Sierszen, et al., 2015), zooplankton (Smyntek et al., 2007), and benthic invertebrates (general aquatic organism correction) (Logan et al., 2008).
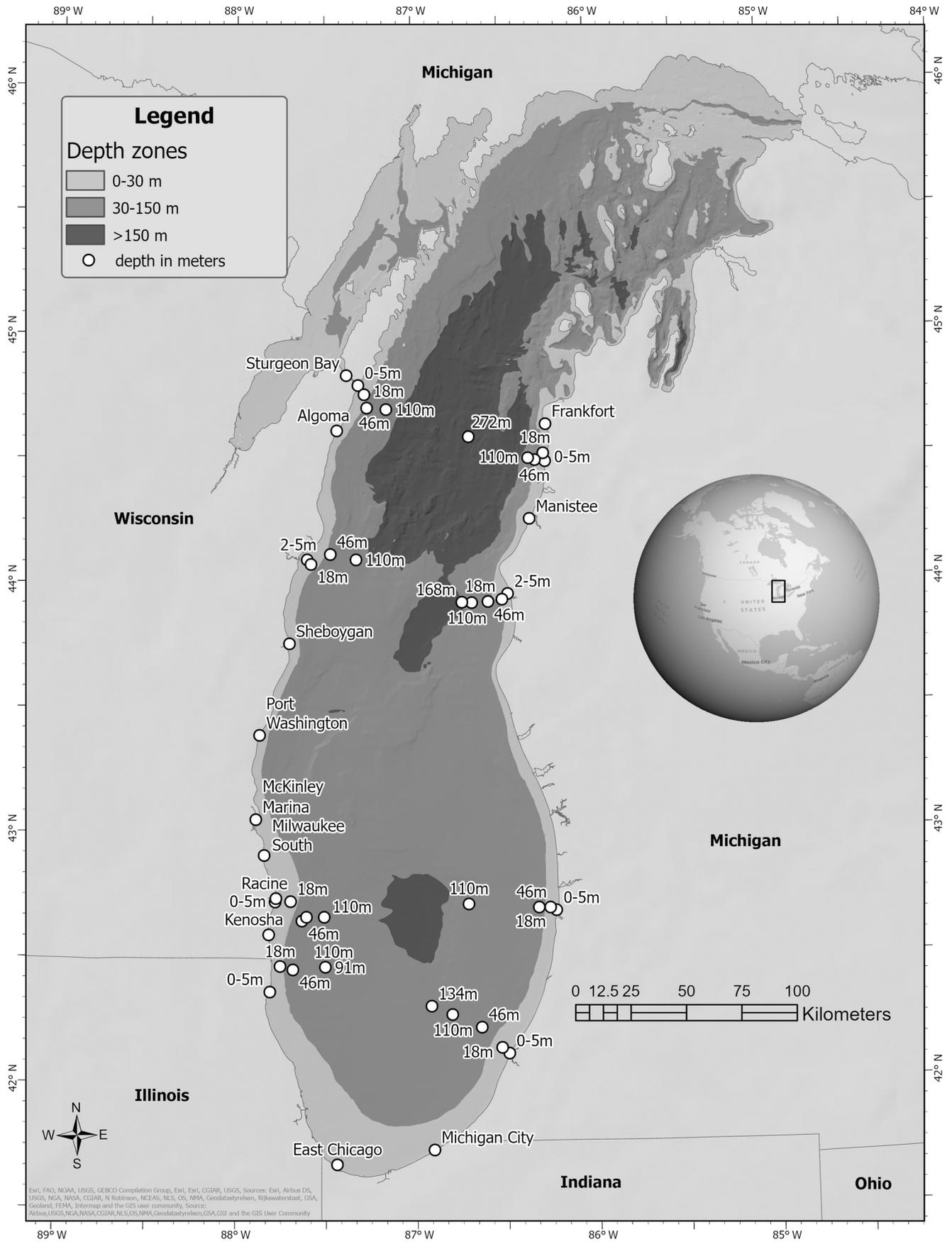
FIGURE 2 Map of Lake Michigan showing the ports of landing and open water locations for data used in this study.
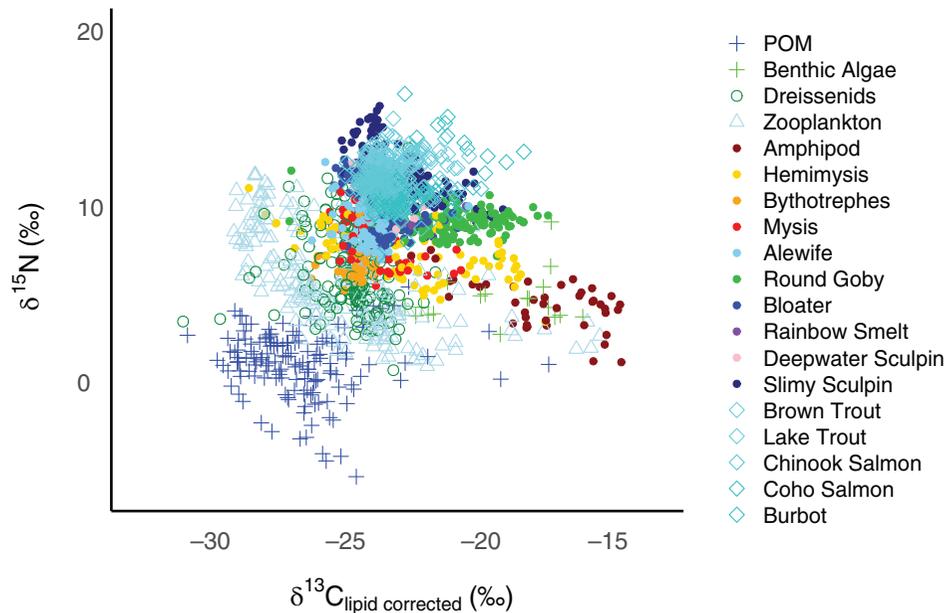
FIGURE 3 Bi-plot showing stable isotope values for trophic baselines (POM = particulate organic matter, a proxy for phytoplankton and thus offshore, pelagic energy, and benthic algae, a proxy for nearshore benthic energy) and consumer organisms used in this study.

Body size measurements were available for 57% of all animal samples. To standardize body size measurements, we converted length to body mass for all measured organisms. Fishes' total length (in millimeters) measures were converted to body mass (in grams) using an allometric formula. For organisms without body size measurements, which encompassed mostly invertebrates and zooplankton, we characterized body mass using mean body size data from a literature survey (Appendix S1: Section S3).

Data analysis

TP and alpha estimation

We used Two Baselines Full Bayesian models (TBF models) in the R package tRophicPosition (Quezada-Romegialli et al., 2018) to estimate relative trophic position and the relative contribution of energy pathways to consumers using $\delta^{15}N$ and $\delta^{13}C$ values. In TBF models, coupling is inferred by the parameter alpha, which varies from 0 (supported only by nearshore benthic production) to 1 (supported only by offshore pelagic production). The TBF model also includes a mixing model to discriminate among different sources of $\delta^{15}N$ and $\delta^{13}C$ and is described in detail in Appendix S1: Section S4. We specifically choose to use the best proxy available for primary production sources in the system so we could incorporate benthic and pelagic primary consumers into our full analysis. Average isotope ratio values for the nearshore benthic endmember

(benthic algae and associated periphyton, $n = 22$) were $\delta^{13}C = -19.9‰ \pm 2.75$ SD and $\delta^{15}N = 5.16‰ \pm 1.69$ SD, and for the offshore pelagic endmember (particulate organic matter [seston], $n = 147$) were $\delta^{13}C = -26.8‰ \pm 2.07$ SD and $\delta^{15}N = 1.09‰ \pm 1.89$ SD. We assumed fixed trophic discrimination factor values ($\Delta N = 3.4‰$, $\Delta C = 0.4‰$) with some level of uncertainty (SD of 0.98 and 1.3, respectively) because this has been shown to be a valid approximation when averaged over multiple trophic pathways (Post, 2002). It is important to note that TBF models generate relative trophic positions that may be lower than 2 for some species as a result of using primary producer baselines (Quezada-Romegialli et al., 2018).

We grouped data from the various ports into four major regions of the lake (i.e., northwest, northeast, southwest, southeast) given expected spatial variability observed in previous studies (e.g., Foley et al., 2017; Kornis et al., 2020; Turschak et al., 2019). Given that $\delta^{15}N$ and $\delta^{13}C$ values vary in space and time, and that there is uncertainty in consumers' space use, trophic position and alpha were estimated at different scales: (1) lake-wide: for each species across all seasons and regions; (2) regional: for each species in each region; and (3) regional/seasonal: for each species in each region and season. Further, because it is unlikely that some species reach isotopic equilibrium with region- or season-specific isotopic baselines (Turschak et al., 2019, 2022), we estimated trophic position and alpha for scales 2 and 3 using region-specific (scale 2) and region- and season-specific (scale 3) baselines, as well as lake-wide pooled baselines, to ensure results were robust. For the

analysis at scale 3 using specific baselines, data from the northeast in spring and southeast in spring were removed because no benthic algae samples were available.

We also calculated averages of species body mass for each lake region and season depending on the scale being analyzed. In addition, we used TBF models to estimate trophic position and alpha values for each individual sample in our dataset (individual level analysis, hereafter). This was necessary to investigate whether the patterns at the interspecific level were still consistent after accounting for intraspecific variation.

Hypothesis testing

We used Bayesian generalized linear multilevel models to explore the relationships between body size, trophic position, and alpha. To test predictions from Hypothesis 1 (Figure 1b), body size was the response variable, and trophic position, alpha, and the interaction between alpha and trophic position were the predictors. To test Hypothesis 2, trophic position and body size were the response variables, and the quadratic term of alpha was the predictor. The quadratic term implies a dome-shaped relationship among the variables, which is in line with our predictions. Lake region (northwest, northeast, southwest, southeast) and season (spring, summer, fall) were included as random slopes and intercepts in models conducted at regional and regional/seasonal scales to incorporate the hierarchical structure of the data. All hypotheses were tested at the species or taxonomic group level, but only the relationships between trophic position and alpha was tested with individual estimates as body size was not available for all samples. For models using individual sample data, we weighted the contribution of each individual sample in the analysis according to the sample size of its respective species (i.e., 1/species sample size) to ensure that all species contribute equally to the analysis. We fit models to the data in Stan using the R package brms (Bürkner, 2017). See Appendix S1: Section S5 for details of Bayesian generalized linear multilevel model fitting and diagnostics.

For each hypothesis, we compared the global model (with all variables) against a model without either the interaction term (Hypothesis 1) or quadratic effect (Hypothesis 2), and against a null model without any predictors (i.e., intercept-only model). Models were ranked according to their out-of-sample pointwise predictive accuracy, which was estimated through approximate leave-one-out (LOO) cross-validation (Vehtari et al., 2017) using posterior simulations.

We inferred the weight of evidence for a downward-facing hump-shape association between alpha and either trophic position or body mass by calculating the posterior probability that estimated quadratic coefficients were less than zero using the hypothesis() function in the brms package. Quadratic alpha parameters with posterior probabilities closer to 1 indicate stronger certainty of the downward-facing relationship. We used a similar procedure to assess weight of evidence for all other fixed parameter estimates. In these cases, posterior probabilities closer to 1 indicate stronger certainty of association (either positive or negative, depending on the direction of the estimated coefficient) with either body mass or trophic position.

Finally, we estimated the alpha value at which the vertex occurs (alpha*) in each model containing a quadratic term. We did this by setting the derivative of the regression equation to zero and solving for the corresponding alpha value. For each model, we repeated this for 1000 samples from the joint posterior distribution of the regression parameters to generate a distribution of alpha*.

RESULTS

Trophic position values generated by the TBF models using specific (region, scale 2; region/season, scale 3) and lake-wide pooled baselines were strongly correlated (scale 2: $r = 0.98$; scale 3: $r = 0.86$). Alpha values generated by the TBF models at the intermediate scale 2 (region) using specific and lake-wide pooled baselines were also similar ($r = 0.91$), though at the finest scale 3 (region/season), TBF models using specific baselines compared with lake-wide pooled baselines were less correlated ($r = 0.63$). Nonetheless, regression analyses testing our predictions at different scales and using specific versus lake-wide pooled baselines led to similar results (see Appendix S2: Sections S1–S5 for results from all analyses). Therefore, although we provide results associated with analyses at scale 3 (because this scale is most resolved in terms of spatial and temporal variation in resource use), results were largely insensitive to this decision. Hereafter, we provide results for analyses at scale 3 that used both specific baselines (for each season and region), and using lake-wide pooled baselines, given the difficulty in selecting appropriate baselines for organisms that use resources over vastly different spatial scales.

Hypothesis 1: TP–body size relationship

Body size was positively related to trophic position (Figure 4a,e), and both the interaction models and additive models had consistently higher predictive power than the null models using both specific and pooled
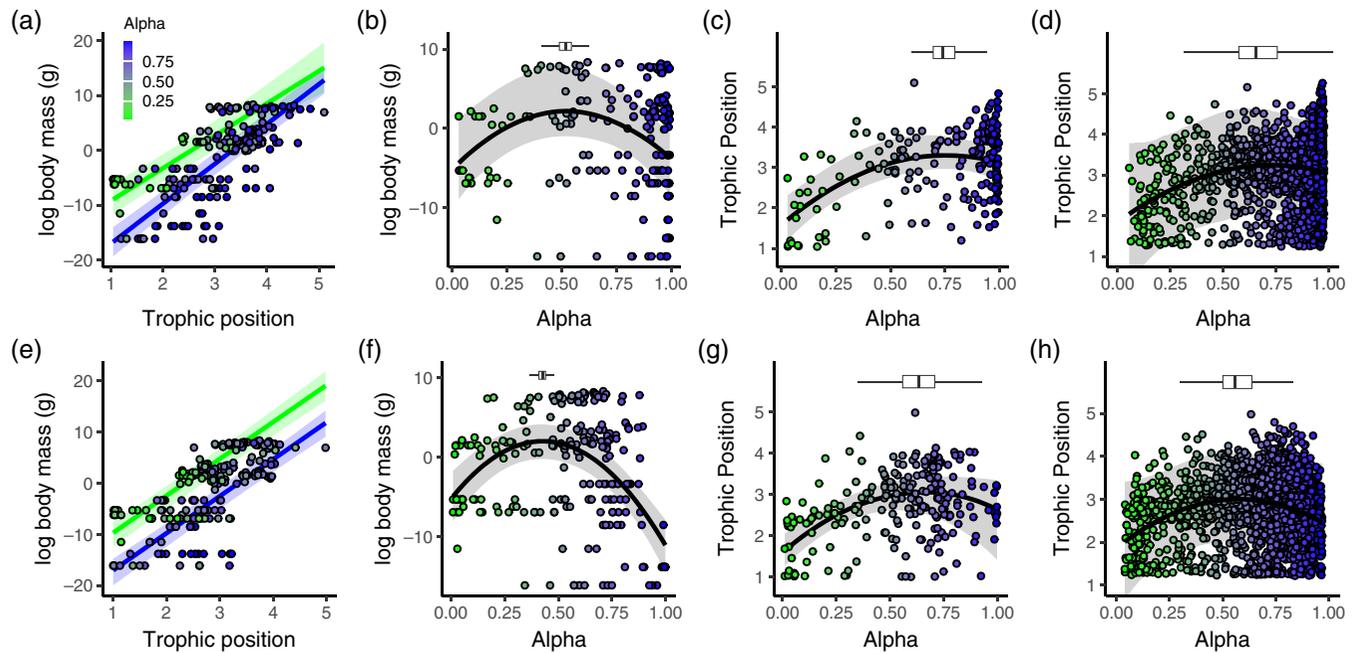
FIGURE 4 Modeled relationships among trophic position, body size, and alpha values for food web members in Lake Michigan at scale 3 using region- and season-specific baselines (a–d) and lake-wide pooled baselines (e–h). In each panel, points are colored according to their alpha value, which varies from 0 to 1 and indicates the importance of pelagic phytoplankton energy to the consumers. Panels (a, e) show the relationship between body mass and trophic position. The blue trend line represents the predicted effect of trophic position on body mass when alpha is equal to 0.8 (i.e., consumers associated with the pelagic phytoplankton channel), while the green trend line represents the predicted effect of trophic position on body mass when alpha is equal to 0.2 (consumers associated with the nearshore benthic channel). Panels (b, f) show the relationship between alpha and body mass. Panels (c, g) show the relationships between alpha and trophic position at the taxa level, and panels (d, h) show the relationships between alpha and trophic position at the individual sample level. Body mass values are averages of individuals of the same species/taxa collected at each season and lake region. Ribbons around the trend lines indicate uncertainty intervals (i.e., 95% CI) associated with each model. Predictions in each panel are based on the best Bayesian regression model (see Tables 1 and 2). Horizontal boxplots in panels (b–d) and (f–h) show the distribution of alpha* values at the vertex calculated from 1000 samples from the joint posterior distribution of the regression parameters.

baselines (Tables 1 and 2). We found minor differences between models containing the interaction terms (body mass × alpha) or only the main effects (body mass + alpha) in all analyses using either specific baselines or lake-wide baselines (range of LOO-R^2 values from 0.62 to 0.64 across models; Tables 1 and 2). For a given trophic position, consumers more associated with the pelagic phytoplankton pathway had smaller body sizes than consumers more strongly associated with the nearshore benthic pathway (Figure 4a,e, Tables 3 and 4), indicating additive effects of trophic position and pelagic reliance on body size. As measured by out-of-sample pointwise predictive accuracy, the interaction model performed only marginally better than the additive model when using specific baselines, while the additive model performed only marginally better than the interaction model when using pooled baselines (Tables 1 and 2), suggesting negligible interaction effects of trophic position and pelagic reliance on body size.

Hypothesis 2: Coupling of different pathways

Both body size and trophic position formed asymmetric hump-shaped relationships with alpha (Figure 4b–d, f–h). Models containing the quadratic term of alpha performed consistently better than models with only the linear term or null (intercept only) models (Tables 1 and 2). Of the six models with quadratic terms, four provide strong evidence for a downward-facing hump-shaped relationship (CIs for the quadratic alpha term are less than zero), while the remaining two (the individual-level models with a high degree of variability) provide marginal support (Tables 3 and 4). The best fit quadratic models indicate that the highest trophic position and largest body sizes occur at intermediate values of alpha (Figure 4b–d, f–h, Tables 3 and 4). Median values for alpha* (alpha at the vertex) for the six models with the quadratic term ranged from 0.43 to 0.74 (horizontal boxplots in Figure 4b–d, f–h). However, we also found high dispersion in residuals at

TABLE 1 List of Bayesian regression models used to estimate the association among trophic position (TP), body size, and alpha values using specific baselines at scale 3.

Model	ELPD diff.	ELPD	LOOIC	LOO-R^2	R^2 marginal	R^2 conditional
Asymmetric TP–body size relationship						
Mass ~ TP × alpha [a]	0 (0)	−550.9 (10.11)	1101.79 (20.23)	0.63	0.64 (0.02)	0.65 (0.02)
Mass ~ TP × alpha [b]	−0.43 (0.68)	−551.33 (10.08)	1102.65 (20.17)	0.63	0.64 (0.04)	0.65 (0.02)
Mass ~ TP + alpha [a]	−1.38 (1.54)	−552.27 (9.67)	1104.55 (19.33)	0.63	0.63 (0.02)	0.65 (0.02)
Mass ~ TP + alpha [b]	−1.75 (1.52)	−552.65 (9.64)	1105.3 (19.28)	0.62	0.64 (0.04)	0.65 (0.02)
Mass ~ 1	−97.26 (10.45)	−648.16 (8.03)	1296.31 (16.07)	−0.02	0 (0)	0.01 (0.01)
Coupling of different energy pathways—TP						
TP ~ alpha + alpha^2 [a]	0 (0)	−226.37 (9.11)	452.74 (18.22)	0.2	0.2 (0.05)	0.25 (0.05)
TP ~ alpha + alpha^2 [b]	−0.08 (1.01)	−226.45 (9.24)	452.91 (18.47)	0.2	0.21 (0.08)	0.27 (0.05)
TP ~ alpha [a]	−6.4 (3.58)	−232.77 (8.47)	465.53 (16.94)	0.15	0.17 (0.05)	0.19 (0.05)
TP ~ alpha [b]	−7.65 (3.6)	−234.02 (8.48)	468.03 (16.95)	0.13	0.17 (0.08)	0.2 (0.04)
TP ~ 1	−17.27 (6.7)	−243.64 (8.84)	487.28 (17.69)	0.05	0 (0)	0.08 (0.04)
Coupling of different energy pathways—TP (individual level)						
TP ~ alpha + alpha^2 [a]	0 (0.14)	−34.34 (0.88)	68.68 (1.76)	0.09	0.1 (0.07)	0.17 (0.08)
TP ~ alpha [a]	0 (0)	−34.34 (0.9)	68.68 (1.79)	0.06	0.05 (0.06)	0.13 (0.08)
TP ~ 1	−0.2 (0.21)	−34.54 (0.91)	69.07 (1.82)	0.06	0 (0)	0.08 (0.07)
TP ~ alpha + alpha^2 [b]	−0.85 (0.16)	−35.19 (0.89)	70.38 (1.78)	0.11	0.13 (0.1)	0.21 (0.08)
TP ~ alpha [b]	−0.9 (0.05)	−35.24 (0.9)	70.48 (1.8)	0.07	0.06 (0.08)	0.18 (0.09)
Coupling of different energy pathways—body size						
Mass ~ alpha + alpha^2 [a]	0 (0)	−642.67 (8.82)	1285.35 (17.64)	0.04	0.11 (0.05)	0.1 (0.04)
Mass ~ alpha + alpha^2 [b]	−0.9 (0.5)	−643.57 (8.9)	1287.15 (17.79)	0.03	0.12 (0.06)	0.11 (0.04)
Mass ~ 1	−5.48 (3.65)	−648.16 (8.03)	1296.31 (16.07)	−0.02	0 (0)	0.01 (0.01)
Mass ~ alpha [a]	−6.26 (3.48)	−648.93 (7.87)	1297.87 (15.74)	−0.03	0 (0.01)	0.02 (0.02)
Mass ~ alpha [b]	−7.6 (3.48)	−650.27 (7.9)	1300.54 (15.8)	−0.04	0.01 (0.01)	0.03 (0.02)

Note: Models were ranked according to their prediction accuracy. [a] Random Intercept model, [b] Random Intercept Random Slope model. ×, Interaction between the left- and right-side variables; ~, indicates that the variable on the left side is modeled by the variable on the right side; ~1, indicates the null model (without explanatory variables); +, addition of a new explanatory variable.

Abbreviations: ELPD, expected log pointwise predictive density; LOOIC, leave-one-out information criterion; LOO-R^2, R^2 for leave-one-out cross-validation.

intermediate values of alpha (pooled baseline models) and high values of alpha (specific baseline models; Appendix S2: Figure S22), suggesting that for a subset of taxonomic groups both small and large organisms are simultaneously assimilating energy from the nearshore benthic and offshore pelagic channels.

DISCUSSION

Consistent with the LTFWA, and despite major modifications to the ecosystem, we found a gradual increase in the coupling of pelagic phytoplankton and nearshore benthic energy channels with larger body sizes and higher trophic positions in Lake Michigan. Our findings were also nuanced—highly mobile predators coupled

energy from the distinct energy channels (which also exhibited variability among species) as expected, but smaller bodied prey fish and some invertebrates also appeared to couple benthic and pelagic energy pathways. Further, while we did find evidence for positive trophic position–body size relationships, we found weak evidence for steeper trophic position–body size relationships in food chains supported by the putative fast energy channel (offshore pelagic) compared with the slow energy channel (nearshore benthic). Our results are notable in this highly disturbed ecosystem and are suggestive of how species introductions and other anthropogenic impacts can affect food web structure.

Positive trophic position–body size relationships among organisms in Lake Michigan support results from studies in estuaries (Akin & Winemiller, 2008; Keppeler et al., 2021)

TABLE 2 List of Bayesian regression models used to estimate the association among trophic position (TP), body size, and alpha values using lake-wide pooled baselines at scale 3.

Model	ELPD diff.	ELPD	LOOIC	LOO-R^2	R^2 marginal	R^2 conditional
Asymmetric TP–body size relationship						
TP ~ mass + alpha [a]	0 (0)	−637.91 (11.28)	1275.81 (22.56)	0.64	0.65 (0.02)	0.65 (0.02)
TP ~ mass + alpha [b]	−0.02 (1.01)	−637.93 (11.38)	1275.86 (22.76)	0.64	0.65 (0.04)	0.66 (0.02)
TP ~ mass × alpha [a]	−0.15 (0.93)	−638.06 (11.37)	1276.12 (22.73)	0.64	0.65 (0.02)	0.66 (0.02)
TP ~ mass × alpha [b]	−0.27 (1.32)	−638.18 (11.49)	1276.36 (22.97)	0.64	0.65 (0.04)	0.66 (0.02)
TP ~ 1	−114.55 (11.1)	−752.46 (8.73)	1504.92 (17.47)	−0.02	0 (0)	0.01 (0.01)
Coupling of different energy pathways—TP						
TP ~ alpha + alpha^2 [b]	0 (0)	−245.12 (10.95)	490.24 (21.89)	0.23	0.21 (0.07)	0.28 (0.04)
TP ~ alpha + alpha^2 [a]	−2 (2.15)	−247.12 (10.91)	494.25 (21.81)	0.21	0.19 (0.04)	0.25 (0.04)
TP ~ alpha [a]	−13.21 (5.05)	−258.33 (9.68)	516.65 (19.36)	0.13	0.11 (0.04)	0.17 (0.04)
TP ~ alpha [b]	−13.78 (4.84)	−258.9 (9.52)	517.79 (19.05)	0.13	0.11 (0.08)	0.18 (0.04)
TP ~ 1	−24.79 (7.02)	−269.91 (9.73)	539.82 (19.47)	0.04	0 (0)	0.07 (0.03)
Coupling of different energy pathways—TP (individual level)						
TP ~ alpha + alpha^2 [a]	0 (0)	−33 (0.88)	66.01 (1.76)	0.11	0.12 (0.09)	0.18 (0.1)
TP ~ 1	−0.26 (0.28)	−33.27 (0.87)	66.53 (1.75)	0.02	0 (0)	0.07 (0.06)
TP ~ alpha [a]	−0.37 (0.21)	−33.37 (0.87)	66.75 (1.73)	0.03	0.03 (0.04)	0.11 (0.08)
TP ~ alpha + alpha^2 [b]	−0.76 (0.06)	−33.76 (0.88)	67.52 (1.75)	0.13	0.15 (0.11)	0.23 (0.09)
TP ~ alpha [b]	−1.25 (0.21)	−34.25 (0.86)	68.5 (1.71)	0.04	0.05 (0.07)	0.17 (0.09)
Coupling of different energy pathways—body size						
Mass ~ alpha + alpha^2 [a]	0 (0)	−728.82 (11.37)	1457.63 (22.75)	0.18	0.21 (0.04)	0.22 (0.04)
Mass ~ alpha + alpha^2 [b]	−0.36 (0.94)	−729.18 (11.36)	1458.36 (22.72)	0.18	0.21 (0.06)	0.23 (0.04)
Mass ~ alpha [a]	−21.35 (7.01)	−750.16 (8.18)	1500.32 (16.36)	0	0.03 (0.02)	0.04 (0.03)
Mass ~ alpha [b]	−22.72 (7.08)	−751.53 (8.18)	1503.06 (16.35)	−0.01	0.03 (0.03)	0.06 (0.03)
Mass ~ 1	−23.65 (8.2)	−752.46 (8.73)	1504.92 (17.47)	−0.02	0 (0)	0.01 (0.01)

Note: Models were ranked according to their prediction accuracy. [a] Random Intercept model, [b] Random Intercept Random Slope model. ×, Interaction between the left- and right-side variables; ~, indicates that the variable on the left side is modeled by the variable on the right side; ~1, indicates the null model (without explanatory variables); +, addition of a new explanatory variable.

Abbreviations: ELPD, expected log pointwise predictive density; LOOIC, leave-one-out information criterion; LOO-R^2, R^2 for leave-one-out cross-validation.

and marine ecosystems (Romero-Romero et al., 2016). For a given trophic position, organisms mostly associated with the presumed fast energy channel (offshore pelagic) had smaller body sizes than those associated with the slower energy channel (nearshore benthic). The differences were mainly driven by dissimilarities in trophic positions at small body sizes in the nearshore benthic pathway. However, the differences in slopes between energy channels were muted compared with those observed in marine or estuarine ecosystems where phytoplankton-based pathways have much steeper slopes than benthic energy pathways (Keppeler et al., 2021; Rooney et al., 2006). One explanation for the lack of differing slopes in this study may relate to a weakening of the pelagic energy channel and strengthening of the nearshore benthic channel through nearshore invasive mussel grazing that has

reduced offshore transport of nutrients and energy (Hecky et al., 2004; Vanderploeg et al., 2010). If fishes and invertebrates have compensated for reduced availability of phytoplankton-based pelagic energy by deriving more energy from alternative nearshore benthic energy channels (e.g., Rennie et al., 2009; Turschak et al., 2014), this may diminish differences in trophic position–body size relationships between energy channels.

Trophic position and body size relationships with alpha formed asymmetrical humped-shaped curves where larger body sizes and higher trophic position values were found at intermediate alpha values (0.43–0.74). This corroborates the hypothesis that organisms lower in the food web are energetically compartmentalized, whereas higher-order consumers progressively couple pelagic phytoplankton and

TABLE 3 Parameter estimates for the Bayesian regression models used to estimate the association among trophic position (TP), body size, and alpha values with specific baselines at scale 3.

Fixed parameter	Estimate	Est. error	l-95% CI	u-95% CI	Posterior probability
Asymmetric TP–body size relationship					
Intercept	−11.912	2.826	−17.293	−6.189	1.00*
TP	5.452	0.868	3.757	7.171	1.00*
Alpha	−15.302	3.033	−21.21	−9.341	1.00*
TP × alpha	2.267	1.137	0.004	4.48	0.98*
Coupling of different energy pathways—TP					
Intercept	1.571	0.384	0.837	2.32	1.00*
Alpha	4.726	0.958	2.833	6.615	1.00*
Alpha^2	−3.208	0.877	−4.938	−1.51	1.00*
Coupling of different energy pathways—TP (individual level)					
Intercept	1.82	1.018	−0.182	3.814	0.96*
Alpha	4.039	3.571	−2.881	11.134	0.88
Alpha^2	−2.824	3.055	−8.878	3.062	0.83
Coupling of different energy pathways—body size					
Intercept	−4.977	2.945	−10.617	1.071	0.95*
Alpha	29.578	8.497	12.763	45.959	1.00*
Alpha^2	−28.68	7.885	−43.883	−13.3	1.00*

Note: Only results from best fit models are given. In the posterior probability column, * denotes that the posterior probability exceeds 95% for a one-sided hypothesis test; the direction of the test was determined by the direction (either positive or negative) of the parameter estimate.
Abbreviations: CI, credible interval; l-95% CI, lower bound of the 95% CI; u-95% CI, upper bound of the 95% CI.

TABLE 4 Parameter estimates for the Bayesian regression models used to estimate the association among trophic position (TP), body size, and alpha values with lake-wide pooled baselines at scale 3.

Fixed parameter	Estimate	Est error	l-95% CI	u-95% CI	Posterior probability
Asymmetric TP–body size relationship					
Intercept	−14.59	2.346	−19.323	−9.559	1.00*
TP	7.328	1.041	5.274	9.548	1.00*
Alpha	−12.119	1.171	−14.453	−9.801	1.00*
Coupling of different energy pathways—TP					
Intercept	1.599	0.366	0.916	2.287	1.00*
Alpha	4.506	0.676	3.151	5.821	1.00*
Alpha^2	−3.616	1.135	−5.876	−1.454	1.00*
Coupling of different energy pathways—TP (individual level)					
Intercept	1.865	0.756	0.387	3.375	0.99*
Alpha	4.007	2.789	−1.417	9.514	0.93
Alpha^2	−3.48	2.735	−8.871	1.842	0.90
Coupling of different energy pathways—body size					
Intercept	−5.133	2.356	−9.44	−0.385	0.98*
Alpha	34.1	5.85	22.496	45.312	1.00*
Alpha^2	−40.027	5.804	−51.25	−28.594	1.00*

Note: Only results from best-fit models are given. In the posterior probability column, a * denotes that the posterior probability exceeds 95% for a one-sided hypothesis test; the direction of the test was determined by the direction (either positive or negative) of the parameter estimate.
Abbreviations: CI, credible interval; l-95% CI, lower bound of the 95% CI; u-95% CI, upper bound of the 95% CI.

nearshore benthic energy pathways. The main couplers in Lake Michigan were the largest predatory animals—salmonines and burbot—which have larger home ranges, forage across larger areas (and thus potentially distinct energy channels) than their smaller bodied counterparts, and which are expected to be important stabilizers in spatially expansive ecosystems, such as Lake Michigan, by responding to asynchronous production in space and time (McCann et al., 2005).

We did observe important deviations from our coupling expectations, however, which likely relate to differences in species identities and life history traits. First, introduced predators may be more limited in their ability to couple pelagic and benthic energy pathways than native predators. Nonnative Chinook salmon, one of the dominant piscivores in the system, were relatively poor couplers as they had high alpha values among top predators (mean of $Alpha_{mode} = 0.69$) that did not differ among lake regions and seasons (range of $Alpha_{mode} = 0.05$). This notion is corroborated by diet studies in Lake Michigan that find Chinook salmon feed almost exclusively on planktivorous alewife (Leonhardt et al., 2020), and undergo lake-wide movements to search for and consume this prey (Adlerstein et al., 2008; Benjamin & Bence, 2003; Kornis et al., 2019). In contrast, mean Alpha values for the native lake trout ($Alpha_{mode} = 0.61$) and burbot ($Alpha_{mode} = 0.39$) were relatively lower than for Chinook salmon, and in particular, exhibited a large degree of seasonal and spatial variation in alpha values (range = 0.43 and 0.45, respectively) that correspond with seasonal and spatial diet variation (Happel et al., 2018; Leonhardt et al., 2020; Luo et al., 2019). Further, both species show large movement patterns across vertical and horizontal planes (Gorman et al., 2012; Harrison et al., 2016; Hrabik et al., 2006), and their diets have been found to be relatively plastic among populations in the Great Lakes and elsewhere, including both benthic- and pelagic-oriented prey (Fratt et al., 1997; Happel et al., 2018; Harrison et al., 2017), thereby allowing them to respond to food variation in both space and time (Vinson et al., 2021).

Somewhat unexpected in this study was the degree to which smaller bodied organisms at low-to-intermediate trophic positions also appeared to couple energy from both the offshore pelagic and nearshore benthic channels. One explanation is that physical processes can act to couple otherwise distinct habitats through the exchange of materials between nearshore and pelagic zones. Upwellings, for example, occur in the Great Lakes following several days of sustained and directional winds (Plattner et al., 2006), and have been shown to transfer nutrients from profundal to nearshore waters

(Haffner et al., 1984) as well as boost algal productivity in nearshore waters of southern Lake Michigan for a limited amount of time (Yaguchi, 1977). However, evidence for cascading ecological effects of upwelling in the Great Lakes is equivocal (Haffner et al., 1984). More likely, the large-quantity transport of nearshore benthic algae to the pelagic zone during the late summer and fall (Bootsma et al., 2004) could deliver nearshore production to offshore energy pools with resulting increases in $\delta^{13}C$ (lower alpha) in invertebrates and fishes (Turschak et al., 2014). Epiphytic diatom frustules (that likely grow on *Cladophora*) have been found in offshore sediment cores, indicating that nearshore benthic energy is transported and stored in the profundal zone (Edlund et al., 2021).

This deviation from expectations may also arise from responses to species invasions, particularly in the use of alternative food resources or seasonal movement patterns in small-bodied fishes. For example, there is evidence that pelagic and planktivorous alewife are increasingly consuming benthic-oriented chironomids during their emergent pupal stage (Janssen & Luebke, 2004; Kornis & Janssen, 2011) or mysids (Bunnell et al., 2015) since the dreissenid invasion. Mysids, themselves, are a key coupler of benthic and pelagic habitats through diel vertical migration and consumption of prey in both areas (O'Malley & Bunnell, 2014; Sierszen et al., 2011). Simultaneously, benthically oriented round goby make seasonal migrations between nearshore and offshore habitats (Carlson et al., 2021). They are also co-evolved predators of dreissenids—and in fact have thrived in the Great Lakes in part due to high dreissenid abundance—which has facilitated the transfer of energy stored in dreissenids to higher trophic levels (Kornis et al., 2012). Further, nearshore dreissenids scavenge phytoplankton that originate in the pelagic zone (Waples et al., 2017), and some of this energy is consumed by round gobies in nearshore habitats. So round gobies may impart food web resilience because they can derive energy from both the pelagic (by eating dreissenids) and the nearshore benthos (by eating nearshore benthic invertebrates) (Foley et al., 2017). Therefore, as dreissenid mussels have reduced the availability of phytoplankton-based pelagic energy, fishes and invertebrates could compensate by deriving more energy from alternative nearshore benthic or detrital energy channels (Turschak et al., 2014), resulting in coupling at lower trophic levels in addition to higher levels. This agrees with theoretical scaling across spatial scales implied by the LTFWA (Rooney et al., 2008), and with results from mesocosm experiments that find that greater benthic-pelagic coupling can confer greater resistance and resilience of primary producers to ecosystem perturbations (Butts et al., 2023).

We did not explicitly consider additional habitats such as wetlands, uplands, or drowned river mouths in this study. Recent work in the Laurentian Great Lakes has shown that larval fishes along coastal habitats in Lake Superior are supported by energy from several organic matter sources (Hoffman, Kelly, et al., 2015), and that mobile fish consumers can link wetland habitats to nearshore, coastal food webs (O'Reilly et al., 2023; Sierszen et al., 2019). Future analyses that consider the broader coastal nearshore are needed to fully explore food web linkages and structures in Lake Michigan that contribute to its functioning and adaptive capacity (e.g., Eglite et al., 2024). In addition, analyses that can separate pelagic and profundal detrital energy pathways, which we could not easily differentiate in our study, but that likely influence trophic position and alpha estimates (Layman et al., 2012; Vander Zanden & Vadeboncoeur, 2020), could be helpful to this end. This is especially important for both invertebrates and fishes collected from profundal habitats (e.g., deepwater sculpin, bloater), where microbial processes can alter the isotopic signature of sedimented organic matter (Sierszen et al., 2006, 2014). Furthermore, while our study encompassed a large variety of vertebrates and invertebrates, we had limited representation from some resident and transient species that occur in the Lake Michigan ecosystem, such as *Catostomus* spp., lake sturgeon (*Acipenser fulvescens*), and round whitefish (*Prosopium cylindraceum*). Therefore, additional food web analyses using a wider array of species present in Lake Michigan and additional isotope tracers, such as sulfur (Croisetière et al., 2009), may help to resolve variation observed in our study. Additional sampling and analyses will also help to determine how habitat coupling may affect the fate of contaminants, such as mercury (Lepak et al., 2019), microplastics (D'Avignon et al., 2023) or perfluoroalkyl substances (Remucal, 2019). Finally, given the difficulty in selecting appropriate baselines for isotope mixing models that are applied to multiple species using habitat and resources over vastly different scales, identifying species-specific baselines that consider the spatial and temporal scales over which energy is acquired is an important line of inquiry that will benefit stable isotope-based studies across ecosystems.

CONCLUSION

Here, we used stable isotope data from a large lake ecosystem to test predictions derived from the LTFWA (Rooney et al., 2008). We show that despite major biological and physical alterations to the system, patterns in food web structure predicted by the LTFWA are present in the relatively novel Lake Michigan food web. Body size was positively related to trophic position (although we did not find strong support for weaker relationships in nearshore benthic-based pathways), and the integration of various energy pathways increases with both body size and trophic position, forming an asymmetrical hump-shaped relationship between diversity of energy sources and trophic position. Further, our results suggest that larger species may be less affected by short-term fluctuations in food web structure than smaller species, because smaller species have fewer energy resource options to choose from when their preferred energy source becomes scarce. In addition, our study provides evidence in support of the role of body size in structuring food webs, as well as recent work examining multichannel omnivory in the Great Lakes (Matthias et al., 2021; Rennie et al., 2009; Sierszen et al., 2014; Turschak et al., 2014).

Across the Laurentian Great Lakes, large declines in biomass of many species suggest that food web stability may be decreasing (Rooney & McCann, 2012). However, many species have persisted, or even benefited, despite the proliferation of dreissenid mussels (Claramunt et al., 2019; Madenjian et al., 2015), which have muted pelagic energy channels and strengthened nearshore benthic and detrital channels (Hecky et al., 2004; Vanderploeg et al., 2010). Such persistence has been attributed to diet flexibility and a temporal shift to nearshore energy subsidies (Breaker et al., 2020; Turschak et al., 2014). Our study supports this notion, finding that both top predators and some lower-level prey species couple distinct energy channels, and thus, are being supported beyond the diminished capacity of the pelagic pathway. This may, however, pose a challenge for some species with limited diet plasticity, such as nonnative Chinook salmon and alewife. Indeed, this conclusion is supported by ecosystem models, which find that native lake trout will fare better with declining pelagic productivity than introduced Pacific salmonines (Kao et al., 2018) as they can exploit the benthic energy pathway.

More broadly, our study highlights how the LTFWA can be used to understand food web structure in large, highly modified ecosystems, and has implications for future research attempting to understand the structures and processes that impart stability in nature. We suggest that time-series evaluation of benthic-pelagic coupling in the context of the relative temporal dominance of energy pathways or consumer biomass could be useful toward understanding how food web structures predicted by the LTFWA relate to system stability over time. For example, Turschak et al. (2022) found that the isotopic niche size of salmonines varied among years as a function of the age distribution of alewife in Lake Michigan, which

suggests that isotopic metrics related to trophic position and carbon assimilation could be used to capture and understand system-level trophic variability over time. Thus, linking consumer traits such as body size, trophic position, and carbon source to ecosystem changes using the LTFWA may be a useful indicator of temporal change in food web stability.

AUTHOR CONTRIBUTIONS

Conceptualization: Bryan M. Maitland, Olaf P. Jensen, and Joel C. Hoffman. *Methodology*: Bryan M. Maitland and Friedrich W. Keppeler. *Data curation*: Bryan M. Maitland. *Formal analysis*: Bryan M. Maitland. *Visualization*: Bryan M. Maitland. *Writing—original draft*: Bryan M. Maitland. *Writing—reviewing and editing*: all authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and scripts (Maitland et al., 2024) are available in Zenodo at https://doi.org/10.5281/zenodo.12690488.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.