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ORIGINAL ARTICLE

Local resource reliance of juvenile fish in small lakes

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Abstract

Juvenile stages of fishes are frequently bottlenecks to recruitment. Habitat use of early life stages and the extent to which fish rely on local resources may affect how they respond to habitat loss and alterations, with important implications for habitat management. To investigate the potential for prolonged reliance on local resources, we quantified stable isotope ratios (δ^{13} carbon, δ^{15} nitrogen, δ^{18} oxygen and δ^{2} hydrogen) of young-of-year (YOY) largemouth bass *Micropterus salmoides* and isotope ratios of locally collected water and potential prey across three study components, a controlled pond experiment, a multi-lake survey and a detailed single-lake survey. Across study components, we observed habitat and site fidelity of YOY largemouth bass in mid-summer, demonstrated by distinct spatial differences in young bass stable isotope ratios. Additionally, we observed significant, positive correlations between δ^{13}C of YOY largemouth bass and δ^{13}C of locally collected invertebrates and small bluegill *Lepomis macrochirus* in the single lake survey, suggesting localised foraging. Later in summer, spatial differences in largemouth bass stable isotope ratios were not apparent, indicating a transition to more spatially integrated foraging. Prior to switch to piscivory, YOY largemouth bass rely on local resources indicating that they may be more susceptible, both positively and negatively, to hyper-local changes in forage availability or disturbances. This study demonstrates that stable isotope ratios allow for differentiating environmental experiences among young fish in relatively close proximity in small freshwater systems. Moreover, high spatial variation of consumer stable isotope ratios demonstrates the importance of considering spatial heterogeneity in stable isotope studies.

KEYWORDS
fish, fisheries management, invertebrates, lakes, largemouth bass, stable isotopes

1 | INTRODUCTION

Heterogeneous habitat types have the potential to affect performance of individual animals due to differential access to resources (Humston et al., 2005; Law & Dickman, 1998; Rice et al., 1983). Mobile individuals may integrate resources and conditions across multiple habitats (Armstrong et al., 2016). In contrast, relatively sedentary individuals that exhibit site fidelity will experience stronger influences of local conditions, with different individuals potentially experiencing distinct environmental conditions (Gray et al., 2004). Accurate descriptions of movement and habitat use patterns can help elucidate how groups of individuals and populations respond to

changes in habitat conditions. Understanding habitat use during critical life stages that experience highly variable survival and growth (e.g., as juveniles) may be particularly insightful, because performance during these stages has important implications for subsequent recruitment and population trajectories.

Nearshore zones of lakes are often a critical nexus of human and fish use, as they provide important recreation areas for humans, but are critical nursery and foraging grounds for many species of fishes. There are a wide range of different habitat types within nearshore zones, ranging from diverse naturally vegetated shorelines to highly developed rip-rap or armoured shorelines with minimal vegetation. As human development along the shoreline increases, the abundance of natural structures, such as large woody debris and stands of aquatic macrophytes, generally decreases (Bryan & Scarnecchia, 1992; Dustin & Vondracek, 2017; Francis & Schindler, 2006; Jennings et al., 2003; Radomski & Goeman, 2001). These decreases in natural structures have the potential to negatively impact young fishes. Juvenile game fishes have been found to congregate in areas with more complex habitat such as large woody debris (Newbrey et al., 2005) and vegetation (Middaugh et al., 2013; Savino & Stein, 1989; Weaver et al., 1997), likely because these areas offer foraging opportunities and refuge from predators. As littoral habitat is lost or modified, the survival and performance of young fish will likely depend in part on their habitat use and whether they occupy a relatively local area or move broadly throughout the system.

Largemouth bass *Micropterus salmoides* is an ecologically and economically important species across much of North America, and thus, largemouth bass can act as an umbrella species for the conservation of habitat in many lakes across its native range (Roberge & Angelstam, 2004). While largemouth bass utilise a range of habitats, nearshore environments are particularly important as they are used for nesting, nursery habitat, cover from predators and feeding grounds (Olson et al., 2003; Wagner et al., 2006; Weis & Sass, 2011). A critical bottleneck in recruitment of largemouth bass to adulthood is size-dependent survival through the first winter of life; therefore, the first summer of growth is imperative to their survival (Ludsin & DeVries, 1997). Largemouth bass hatch in nests, begin exogenous feeding while still associated with nests and remain in a school guarded by a parent up to 15 days posthatch (Davis & Lock, 1997). Past studies suggest that young-of-year (YOY) largemouth bass display varying degrees of movement throughout the littoral zone during their first summer of life ranging from individuals that are largely stationary to individuals that may move up to 500 m over the course of the summer (Copeland & Noble, 1994; Hessenauer et al., 2012; Irwin & Noble, 2000). The degree of movement may vary with ontogenetic stage, as studies of later-stage juvenile largemouth bass have documented broader movements (Hessenauer et al., 2012). In glacial lakes, local densities of YOY largemouth bass are related to local habitat features such as vegetation coverage (Middaugh et al., 2013). Moreover, habitat characteristics have been shown to lead to differences in growth rates of YOY largemouth bass, with increased growth in edge or vegetated habitats (Nohner et al., 2018). However, past studies mainly focus on short-term habitat use, and it is unknown if observed short-term preferences translate to long-term individual habitat use. Understanding long-term habitat use of individual YOY largemouth bass may elucidate whether individuals primarily occupy local habitats, essentially forming local population compartments, or if they move and forage broadly, contributing to homogeneous populations. We use the term population compartment to describe small groups of individuals within a heterogeneous population that exhibit habitat or site fidelity.

Individual animals can be physically tracked using many types of tags (e.g., physical, acoustic); however, these methods may be expensive, time and effort intensive and unsuitable for certain habitats and life stages. Alternatively, chemical analyses may provide a more suitable method of describing habitat use patterns. Stable isotopes have long been used to study migration patterns of both terrestrial and aquatic individuals based on changes in stable isotope ratios of individuals through time (e.g., McCarthy & Waldron, 2000; Soto et al., 2013). Stable isotope ratios provide a relatively long-term index of habitat occupancy and foraging history of individuals. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios reflect prey consumption and are commonly used to depict differences in production pathways and trophic position respectively (Peterson & Fry, 1987). However, given habitat differences in $\delta^{13}C$ and $\delta^{15}N$ of prey, these isotope ratios may also be applied to understand habitat usage (e.g., Syväranta et al., 2006). In fact, past studies have demonstrated intra-specific spatial variation in $\delta^{13}C$ and $\delta^{15}N$ of invertebrates and fishes within aquatic systems, such as lakes (Brauns et al., 2011; Syväranta et al., 2006). Hydrogen ($\delta^{2}H$) and oxygen ($\delta^{18}O$) isotope ratios of consumers reflect both isotopic composition of consumed prey and ambient water (Soto et al., 2013), and $\delta^{2}H$ and $\delta^{18}O$ of water have been documented to vary spatially within large lakes (Shi et al., 2017; Soto et al., 2016). Differences in various stable isotope ratios have been used in both terrestrial (Rubenstein & Hobson, 2004) and aquatic (e.g., McCarthy & Waldron, 2000) systems to infer habitat use, and measurement of stable isotope ratios may be an effective and efficient method to determine site fidelity in habitat usage of individuals.

The objective of this study was to evaluate if individual YOY largemouth bass, following emergence from the nest, move extensively among littoral habitats or if they make use of more localised resources, thereby creating population compartments. Largemouth bass are native, reproduce naturally in Indiana glacial lakes (i.e., supplemental stocking is uncommon), and are a key game species. Conservation of largemouth bass populations is of interest to resource managers and protection of suitable habitat is an important management consideration. Methodologically, we aimed to determine if measurement of stable isotope ratios allows for differentiating environmental experiences and habitat use among young fish, even if these fish inhabit areas in relatively close proximity in small lentic systems. Specifically, we used $\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$ and $\delta^{18}O$ as indices of habitat use. Our study included three components: a caging experiment and two field surveys. To determine if we could elicit site- and habitat-specific differences in YOY largemouth bass stable

isotope ratios, we caged YOY largemouth bass in discrete habitat types within two relatively controlled research ponds. To investigate whether stable isotope ratios of YOY largemouth bass differed spatially within more natural systems, we collected YOY largemouth bass across multiple locations within several glacial lakes. Finally, to more fully explore the mechanisms driving spatial differences in YOY largemouth bass stable isotope ratios, we conducted a more detailed survey of young bass and their environment in a single glacial lake and in so doing evaluated how habitat fidelity may differ with ontogeny. We expected that distinct areas of lakes would be characterised by different environmental stable isotope ratios and that YOY largemouth bass would exhibit limited movement among different habitats during the early juvenile stage. Thus, we hypothesised that YOY largemouth bass would primarily exhibit spatially distinct stable isotope ratios and that stable isotope ratios of bass would be correlated with locally-collected water and potential prey items.

2 | METHODS

2.1 | Study design

2.1.1 | Controlled pond experiments

Using the relatively controlled environments of research ponds, we examined the effects of habitat type on YOY largemouth bass stable isotope ratios. We obtained the experimental fish from a population of largemouth bass at the Indiana Department of Natural Resources Driftwood State Fish Hatchery. Upon acquisition, the juvenile fish were held at the Purdue Baker Aquaculture Research Laboratory (ARL) in a holding tank for 4 days and fed frozen Chironomidae larvae once daily. We deployed 12 cages in each of two experimental ponds (one pond at ARL, and one pond at the Purdue Palmer Research Center for Aquatic Resources, PRC). Each pond was roughly 0.1 ha with a mean depth of 1.8 m. We simulated three habitat types within the cages: vegetated, non-vegetated, and large woody debris, LWD (24 cages total, 8 of each habitat type). The experimental pond at ARL was relatively non-vegetated while the pond at PRC had extensive submerged macrophytes. We utilised 1 × 1 × 0.4 m cages with 1.27 cm PVC pipe frames and covered with 6.35 mm plastic mesh. To establish the large woody debris treatment cages, we placed wood structure (2–5 branches depending on size, such that there was structure in half the cage) in the cages 2 weeks prior to the experiment and allowed them to be colonised by invertebrates in the ponds. We established the vegetated treatments by placing two large natural slate tiles (30.48 cm × 60.96 cm) and 12 vegetation analogs (25 cm × 1.27 cm sisal rope) 2 weeks prior to the experiment and allowed this material to be colonised by invertebrates in the ponds. To anchor the cages and allow access to the benthos, we drilled holes in the PVC frame and placed 4 river rocks in each cage. We randomly arranged the cages around the ponds such that the shallowest point was less than 1 m deep, less than 2 m from the shore and approximately 3 m from each other. On 18 June 2018, we added 20 fish (31 ± 3 mm standard length, mean ± sd) to each cage. To minimise the depletion of prey items within the cages, twice per week we moved the cages a short distance to a new substrate area that had not previously had a cage (roughly 1.5 m horizontal distance for each movement), and ended the experiment after 4 weeks. A prior study using similar cages at the ARL demonstrated that young fish will survive and grow within these caged environments. Given the small size and rapid growth of YOY largemouth bass, we believed 4 weeks was sufficient to potentially elicit isotopic differentiation.

At the end of the experiment (16 July 2018), we removed individual largemouth bass, measured standard length (to the nearest mm), euthanised (rapid chilling on ice or overdose with Tricaine Methanesulfonate), wrapped animals in aluminium foil to limit drying and froze them in a −80°C freezer for subsequent analyses (see Section 2.1.4). To characterise mean water isotope ratios (δ^2H and δ^{18}O), we collected water samples at the midpoint between the penultimate location and final location of each cage. We collected these samples at the end of the experiment in 20 ml glass scintillation vials by opening and capping under water to minimise air bubbles. To minimise evaporation, we wrapped the tops of the vials with parafilm and placed the samples on ice until we returned to the lab and then refrigerated the samples until shipment for stable isotope analysis. To quantify local macroinvertebrate isotopic composition, at the end of the experiment we took dip-net samples of macroinvertebrates at the same location as water samples were collected for each cage using the bounce and sweep technique (Lowe et al., 2016) using a 305 × 254 mm dip net with 900 μm mesh. We concentrated two samples from the same location into 60 ml Whirl-Paks and placed the samples on ice until we returned to the lab and froze the samples at −80°C for subsequent analyses. Water and macroinvertebrate samples were collected at the midpoint between the penultimate cage location and the final cage location. As invertebrates could move into and out of the cages, we believe that the isotopic composition of invertebrates inside of the cages and in the immediate vicinity of cages reflected both (a) the isotopic properties inferred by the habitat treatments in the cages and (b) isotopic spatial variation within ponds independent of cage treatments.

2.1.2 | Multi-lake survey

We collected YOY largemouth bass from multiple glacial lakes in order to determine if they displayed site- and habitat-specific stable isotope ratios in a more natural environment. We selected lakes in northeast Indiana, previously studied by Middaugh et al. (2013) including Adams (Lagrange County, 120.2 ha), Big (Noble County, 87.0 ha), Dewart (Kosciusko County, 223.0 ha) and Waubee (Kosciusko County, 76.1 ha) (Figure 1a). Our intent was to examine consistency of within-lake patterns of resource use across lakes that naturally differed, and hence, we viewed these lakes as analogous to replicate study systems.

We attempted to sample the same sites as Middaugh et al. (2013), with each lake including two sites with limited macrophytes (0%–10%

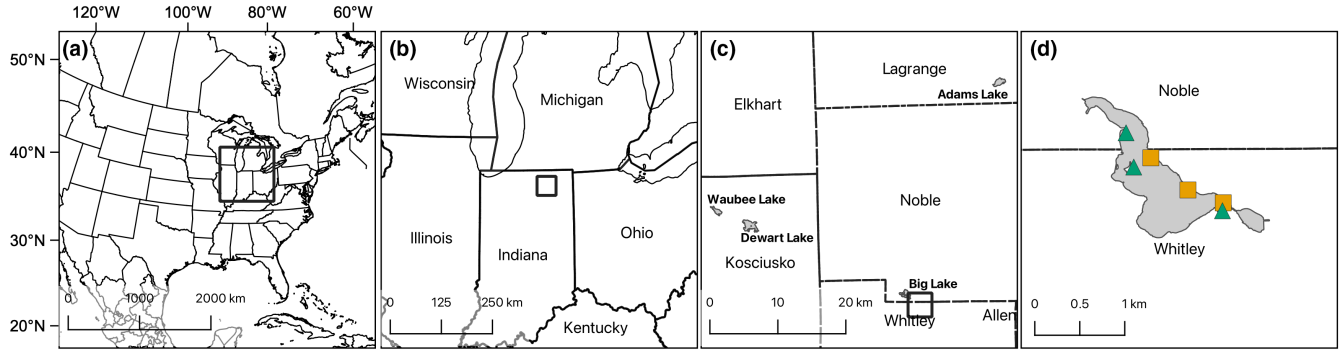

FIGURE 1 (a) Location of Indiana study region in North America. Black box represents the extent of map B. (b) Location of study lakes in northern Indiana. Black box represents the extent of map C. (c) Multi-Lake survey lakes with county names. Black box represents the extent of map D. (d) Crooked Lake with sampling points (green triangle = vegetated; gold square = non-vegetated).

coverage as measured by Middaugh et al., 2013) and two sites with high densities of macrophytes (40%–100% coverage) and a minimum distance of 50 m and a maximum distance of 1.5 km between sites. Macrophyte abundance was estimated using the same methods as Middaugh et al. (2013), in brief, abundance was estimated within 1.2 × 1.2 m quadrat at nine locations within the site and then averaged. If site conditions were deemed unsafe for sampling (e.g., unstable substrate) or if macrophyte density coverage had changed since earlier surveys (Middaugh et al., 2013), we chose a new representative site using the same methods as Middaugh et al., 2013. Sites were defined as the nearshore habitat along 25 m lengths of shoreline with relatively homogeneous vegetation abundance and shoreline structure. Due to the complexity of habitat conditions, the distance between sites was inconsistent, with alongshore distances varying from approximately 80 m to 1500 m straight line distance.

At each site, during August 2017 we sampled fish using a 3.05 m seine with a mesh size of 3 × 2 mm, following the sampling method described in Middaugh et al. (2013). We used two initial 5 m seine passes away from the site midpoint to assess largemouth bass relative abundance, based upon catch per unit effort (CPUE). If we captured fewer than 10 age-0 largemouth bass in these two passes, we performed more passes in the same area until we collected at least 10 YOY largemouth bass, or we collected no YOY largemouth bass over three additional consecutive seine passes. We euthanised, wrapped in aluminium foil and froze YOY largemouth bass (on ice & then −80°C) for subsequent analyses (see below). Additionally, at each site we recorded surface temperature, estimated the amount of vegetation present, recorded the development status of the shoreline and calculated the slope of each site (for more details on these methods see Middaugh et al., 2013).

In the laboratory, we captured an image of thawed fish and scale bar using a Panasonic LUMIX DMC-TS5 camera and measured standard length (to the nearest mm) using image analysis software (ImageJ, Schneider et al., 2012). In addition, we analysed YOY largemouth bass for stomach contents. We thawed fish, removed their stomachs and preserved the stomachs in 80% ethanol for at least 48 h. Under a dissecting microscope, we identified and enumerated distinct prey items to the lowest taxonomic level possible (typically order or family).

2.1.3 | Detailed single-lake survey

For the final component, we narrowed our scope to Crooked Lake, a relatively well-studied 83.4 ha lake in Noble and Whitley Counties, IN (e.g., Konopka, 1982; Pearson, 2000) (Figure 1c). During 2018, we examined stable isotope ratios of YOY largemouth bass across multiple sites and time periods, that is, when YOY largemouth bass are of different mean size and may differentially utilise habitats and resources (24–25 July and 23 August). In addition, we characterised the isotopic composition of prey and water at these sites. We selected three vegetated and three non-vegetated sites, defined as in the multi-lake survey (Figure 1c). We sampled these sites during both time periods using a seine in a similar manner to the multi-lake survey, additionally we used a barge electroshocker (Smith-Root Generator Power Pulsator Model 5) with one probe and two netters along 25 m of shoreline. We seined and electroshocked until a sufficient number (at least four) of YOY largemouth bass were collected, or none had been captured in 10 min of sampling. Upon collection, we measured standard lengths (to 1 mm) of largemouth bass, euthanised, wrapped individuals in aluminium foil and stored samples at −80°C.

Coincident with largemouth bass collections, we collected water and potential prey from each site in a similar manner to the caged experiment. Again, we collected and stored water samples in parafilm sealed, 20 ml glass or plastic scintillation vials, and used the bounce and sweep technique to collect invertebrates as in the controlled pond experiments (Lowe et al., 2016). Additionally, we collected a relatively large number of YOY bluegill *Lepomis macrochirus* via seining and electroshocking. We retained bluegill as potential prey, as similar to Middaugh et al. (2013) we found YOY bluegill in the stomach contents of the YOY largemouth bass in the multi-lake survey.

2.1.4 | Stable isotope analysis

In the laboratory, we thawed YOY largemouth bass, measured mass (to the nearest 0.01 g) and removed muscle fillets of largemouth bass for stable isotope analysis by using scalpel and forceps

to remove the whole side of the fish, excluding skin and scales. We dried the muscle tissue of up to 9 bass per cage or site per sampling period at 60°C for at least 48 h. We then manually homogenised the tissue using a metal spatula by scraping the tissue between two weigh papers. We packed the tissue homogenate into 3.5 × 5 mm or 5 × 9 mm tin capsules for a mass of dried fish tissue of approximately 1.0 mg for $\delta^{13}C$ and $\delta^{15}N$ analyses, and approximately 0.35 mg for $\delta^{18}O$ and $\delta^{2}H$ analyses. We thawed the concentrated invertebrate samples and sorted them into the major taxonomic orders (i.e., Amphipoda, Chironomidae, Ephemeroptera, Odonata) and, within taxonomic orders, grouped individuals as necessary to obtain sufficient biomass and dried samples at 60°C for at least 48 h. We dried whole individual YOY bluegill. We homogenised prey similar to bass tissue and packed dried material into the same size tin capsules; 0.08–1.25 mg for $\delta^{13}C$ and $\delta^{15}N$ analyses. We did not lipid wash any of the samples as YOY fish exhibited low lipid content (low C:N ratio) and because the goal of our study was to explore habitat use and not estimate diet contributions (Hrycik et al., 2018). Additionally, all largemouth bass and bluegill collected throughout the three study components were well past their yolk sack stage. They were foraging exogenously and any maternal and endogenous contributions to stable isotope ratios would have been miniscule.

We sent samples to the Cornell Stable Isotope Laboratory for analysis. C and N isotopes were measured using a Thermo Delta V isotope ratio mass spectrometer (IRMS) interfaced with a NC2500 elemental analyser. For tissue samples, O and H stable isotopes were measured using a Thermo Delta V IRMS interfaced with a Temperature Conversion Elemental Analyzer (TC/EA), while for water samples, O and H stable isotopes were measured using a Thermo Delta V IRMS interfaced with a Gas Bench II. All isotope ratios ($\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$ and $\delta^{18}O$) were expressed using delta notations which represent the ratio of the heavier isotope to the lighter isotope in the sample compared to an international reference standard measured concomitantly with standards: Vienna Pee Dee Belemnite for C, atmospheric air for N and Vienna Standard Mean Ocean Water for O and H. In addition, internal standards, Cayuga brown trout, growth chamber grown corn and whitetail deer hair were analysed with samples (for carbon and nitrogen analyses). For hydrogen and oxygen, Kudu hair, internal keratin and Caribou hair served as standards. Across all analyses, the mean standard deviation of internal standards for $\delta^{13}C$ was 0.09‰, for $\delta^{15}N$ was 0.08‰, for solid $\delta^{18}O$ was 0.40‰, for solid $\delta^{2}H$ was 2.87‰, for water $\delta^{18}O$ was 0.10‰ and for water $\delta^{2}H$ was 2.92‰.

2.1.5 | Data analysis

We analysed data using R packages cowplot, dplyr and ggplot2 (R Core Team, 2018; H Wickham, 2009; Wickham et al., 2017; Wilke, 2019). In order to balance power and the likelihood of type-I error across multiple statistical analyses, we considered two critical α-values: 0.05 and 0.001.

2.1.6 | Habitat- and site-specific variation in YOY largemouth bass stable isotope ratios

To determine if there were overall differences in stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$ and $\delta^{2}H$) of YOY largemouth bass between habitats and sites within individual systems, we used a multivariate analyses of covariance (MANCOVA) with individual length as a covariate. We then used analyses of covariance (ANCOVAs) with the same three predictor variables (habitat, site or individual length) to separately examine variation of each of the four stable isotope ratios. In so doing, we aimed to elucidate the specific stable isotope ratios contributing to overall differences in YOY largemouth bass among sites and between habitats. Across the three study components, for all YOY largemouth bass MANCOVAs and ANCOVAs, we nested site (or cage) within habitat to account for spatial variation and included standard length of the fish as a covariate. We were interested in variation within each system, and we expected that stable isotope baselines would be different across systems (individual ponds and lakes). So, we analysed each system independently. Additionally, in the detailed single-lake survey we analysed samples taken at different sampling periods separately in order to examine how isotopic variation among habitats and sites changed as the fish aged.

2.1.7 | Habitat- and site-specific variation in local macroinvertebrates and water

We used taxa-specific ANOVAs to examine habitat- and site-specific differences in $\delta^{13}C$ and $\delta^{15}N$ ratios of local macroinvertebrates collected in the controlled pond experiments and the detailed single-lake survey. Again, we used habitat and site (nested within habitat) as predictors. For the controlled pond experiments, the dominant taxa within the dip net samples were Chironomidae, Ephemeroptera and Odonata. These taxa were the only groups with sufficient biomass for stable isotope analysis across all sites and both ponds. For the detailed single-lake survey, the dominant taxa within the dip net samples were Amphipoda, Ephemeroptera and Odonata, and we compared stable isotope ratios of these taxa, along with YOY bluegill, among habitats and sites.

We used ANOVAs to determine if there were habitat- and site-specific differences in $\delta^{2}H$ and $\delta^{18}O$ of locally collected water collected in the controlled pond experiments and the detailed single-lake survey. For the controlled pond experiment, we used habitat and cage (nested within habitat) as predictors. For the detailed single-lake survey, we were unable to collect sufficient water samples to analyse separately by the two sampling periods. So, we analysed all samples collected within the lake using habitat and time as predictors.

To examine potential mechanisms leading to habitat- and site-specific differences in stable isotope ratios of YOY largemouth bass, we used linear regressions (with one-way tests of significance) to evaluate positive linear correlations between stable isotope ratio site means of YOY largemouth bass and corresponding stable isotope

ratio site (or cage) means of individual locally collected macroinvertebrates and bluegill ($\delta^{13}C$ and $\delta^{15}N$) and water ($\delta^{2}H$ and $\delta^{18}O$).

3 | RESULTS

3.1 | Controlled pond experiments

A total of 116 fish were recovered from the cages in research ponds: 55 in the ARL pond (59.4 mm ± 7.3; 4.0 g ± 1.6) (mean ± standard deviation) and 61 in the PRC pond (57.6 mm ± 10.3; 3.9 g ± 2.3). This corresponds to greater than 25 mm of mean individual growth over the four-week period of the experiment (and greater than 5× increase in mass assuming isometric length-mass relationships). We know there was some fish that escaped the cages due to finding individuals in the ponds postcaging. However, some young bass likely also died in cages, and we were unable to distinguish the numbers lost to escapement versus mortality.

Based upon MANCOVAs, there were strong habitat (empty, large woody debris and vegetated; Table 1) and cage (nested within habitat; Table 1) differences in YOY largemouth bass stable isotope ratios in both the ARL and the PRC ponds (Figure 2). Standard length was a significant positive covariate of stable isotope ratios for both ponds, though it was a stronger covariate in the PRC pond (Table 1). In both ponds, $\delta^{13}C$ of largemouth bass was significantly different among habitats (ARL: largemouth bass habitat $\delta^{13}C_{means}$: empty = −21.37, LWD = −21.47 and vegetated = −21.02; PRC: largemouth bass habitat $\delta^{13}C_{means}$: empty = −20.04, LWD = −20.77 and vegetated −21.02) and cages, with standard length as a significant covariate (Table 1). Though there were habitat differences in each pond, the effect of habitat type was inconsistent. Vegetated cages had the highest ^{13}C enrichment in the ARL pond, while in the PRC pond the empty cages were most enriched. Largemouth bass $\delta^{15}N$ differed by habitats in the ARL pond ($\delta^{15}N_{means}$: empty = 10.09, LWD = 9.85 and vegetated = 9.81; Table 1), but $\delta^{15}N$ of largemouth bass was not significantly different in the PRC pond. In contrast, $\delta^{2}H$ of largemouth bass varied only within the PRC pond and varied by habitat ($\delta^{2}H_{means}$: empty = −117.05, LWD = −116.81 and vegetated = −122.21) and cage with standard length as a significant covariate (Table 1). Relative enrichment of ^{18}O varied in both ponds across habitats (ARL: $\delta^{18}O_{means}$: empty = 10.38, LWD = 11.17 and vegetated = 11.05; PRC: $\delta^{18}O_{means}$: empty = 13.44, LWD = 12.29 and vegetated = 12.19), and cages, but standard length was only a significant covariate in the PRC pond (Table 1). Largemouth bass from the vegetated and large woody debris cages again had similar $\delta^{18}O$ values, while bass from empty cages had distinct $\delta^{18}O$ values. However, the relative enrichment of the fish from the empty cages was inconsistent between the ponds, with relatively high and low $\delta^{18}O$ values in PRC and ARL respectively. All statistics can be found in Table 1, Tables A.1 and A.2 in Appendix S1.

We compared spatial variation (habitat and site nested within habitat) of $\delta^{13}C$ and $\delta^{15}N$ values for three locally collected macroinvertebrates (Chironomidae, Ephemeroptera and Odonata) within the two research ponds (PRC and ARL). There were no significant differences between habitat or sites for either $\delta^{13}C$ or $\delta^{15}N$ in any of the potential prey items within the ARL pond. However, there was spatial variation evident for macroinvertebrate stable isotope ratios within the PRC pond. $\delta^{13}C$ of Chironomidae, Ephemeroptera and Odonata were not significantly different by habitats, but all three were significantly different among cage sites (Table A.3, Figure A.1: Appendix S1). Mean $\delta^{15}N$ of Ephemeroptera was significantly different among both habitats and cage sites ($\delta^{15}N_{habitat\ means}$: empty = 0.68, LWD = 0.41 and vegetated = 0.58; Figure A.1: Appendix S1). The stable isotope ratios of $\delta^{18}O$ and $\delta^{2}H$ of the locally collected water were never significantly different among habitats or cage sites in either the ARL or the PRC pond (Figure A.2: Appendix S1).

PRC pond mean cage site $\delta^{13}C$ of Ephemeroptera and Odonata was significantly, positively correlated to mean cage site $\delta^{13}C$ of YOY largemouth bass (adjusted $R^2 = .50$, $p = .01$; $R^2 = .45$, $p = .01$ respectively; Figure 4a). Similarly, $\delta^{13}C$ of Odonata and $\delta^{13}C$ of YOY largemouth bass within the ARL pond were positively, significantly correlated ($R^2 = .24$, $p = .04$; Figure 3a). In addition, $\delta^{15}N$ of Odonata and $\delta^{15}N$ of YOY largemouth bass within the PRC pond were positively, significantly correlated ($R^2 = .26$, $p = .046$; Figure 3b). None of the relationships between $\delta^{18}O$ or $\delta^{2}H$ of locally collected water and corresponding values of YOY largemouth bass $\delta^{18}O$ or $\delta^{2}H$ in either pond were significant (Figures 3 and 4).

3.2 | Multi-lake survey

A total of 65 YOY largemouth bass were collected from four lakes in August 2017: Adams, Big, Dewart, and Waubee (Figure 1b). Catch per unit effort was variable among both sites and lakes (Table 2). The largest fish were caught at Big Lake (49.4 mm ± 8.0), followed by Dewart (47.3 mm ± 6.5), Adams (45.9 mm ± 5.3) and lastly Waubee (43.7 mm ± 5.0; Table 2) There was a wide variety of diet items consumed by the largemouth bass, with zooplankton and benthic invertebrates being the most consumed items, but fish, in particular bluegill, were found in several diets, especially in Dewart Lake (Nease, 2019). Vegetation abundance varied within and among lakes, ranging from 5% to 100% vegetated (Table 2).

Stable isotope ratios of YOY largemouth bass varied between habitat types in Adams, Big and Dewart Lakes but based upon MANCOVA there were only significant differences between sites (nested within habitat) in Dewart and standard length was a significant covariate in Big and Dewart (Table 1; Figure 5).

$\delta^{13}C$ and $\delta^{2}H$ appeared to be the main drivers of overall differences in largemouth bass stable isotope ratios among habitats and sites within lakes. There were differences in largemouth bass $\delta^{13}C$ between habitats in Adams and Big Lakes (Adams: $\delta^{13}C_{mean}$: vegetated = −22.57, non-vegetated = −21.18; Big: $\delta^{13}C_{means}$: vegetated = −26.84, non-vegetated = −29.88; Table 1). Largemouth bass $\delta^{2}H$ varied between habitats in Adams, Big and Dewart Lakes (Adams: $\delta^{2}H_{means}$: vegetated = −138.77, non-vegetated = −133.67;

TABLE 1 Results of multivariate analyses of covariance (MANCOVA) and individual element analyses of covariance ($\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$ and $\delta^{18}O$) of differences in YOY largemouth bass stable isotope ratios.

	Controlled pond experiments		Multi-lake survey				Detailed single-lake survey	
Response	ARL	PRC	Adams	Big	Dewart	Waubee	Early	Late
MANCOVA								
Habitat	$F_{2, 44} = \mathbf{7.98}$, $p < \mathbf{.001}$	$F_{2, 51} = \mathbf{10.11}$, $p < \mathbf{.001}$	$F_{1, 19} = \mathbf{8.74}$, $p = \mathbf{<.001}$	$F_{1, 6} = \mathit{24.48}$, $p = \mathit{.01}$	$F_{1, 8} = \mathit{11.72}$, $p = \mathit{.01}$	$F_{1, 13} = 2.43$, $p = .12$	$F_{1, 37} = \mathit{4.91}$, $p = \mathit{.003}$	$F_{1, 14} = 0.91$, $p = .49$
Habitat (site)	$F_{7, 44} = \mathbf{2.35}$, $p < \mathbf{.001}$	$F_{6, 51} = \mathbf{6.64}$, $p < \mathbf{.001}$	$F_{2, 19} = 1.32$, $p = .27$	$F_{2, 6} = 2.42$, $p = .12$	$F_{1, 8} = \mathbf{31.33}$, $p < \mathbf{.001}$	$F_{2, 13} = 1.45$, $p = .23$	$F_{4, 37} = \mathbf{3.47}$, $p < \mathbf{.001}$	$F_{2,14} = 0.91$, $p = .52$
Standard length	$F_{1, 44} = \mathit{2.67}$, $p = \mathit{.045}$	$F_{1, 51} = \mathbf{62.82}$, $p < \mathbf{.001}$	$F_{1,19} = 1.28$, $p = .32$	$F_{1, 6} = \mathit{11.07}$, $p = \mathit{.04}$	$F_{1, 8} = \mathit{9.67}$, $p = \mathit{.01}$	$F_{1, 13} = 1.80$, $p = .21$	$F_{1, 37} = \mathbf{16.19}$, $p < \mathbf{.001}$	$F_{1, 14} = 2.71$, $p = .09$
$\delta^{13}C$								
Habitat	$F_{2, 44} = \mathit{4.97}$, $p = \mathit{.01}$	$F_{2, 51} = \mathbf{23.33}$, $p < \mathbf{.001}$	$F_{1, 19} = \mathbf{33.29}$, $p = \mathbf{<.001}$	$F_{1, 6} = \mathit{18.04}$, $p = \mathit{.005}$	$F_{1, 8} = 4.28$, $p = .07$	$F_{1, 13} = 3.03$, $p = .11$	$F_{1, 37} = .46$, $p = .50$	$F_{1, 14} = .42$, $p = .53$
Habitat (site)	$F_{7, 44} = \mathit{3.58}$, $p = \mathit{.004}$	$F_{6, 51} = \mathbf{30.69}$, $p < \mathbf{.001}$	$F_{2, 19} = 1.98$, $p = .17$	$F_{2, 6} = 2.72$, $p = .14$	$F_{1, 8} = 0.53$, $p = .49$	$F_{2, 13} = 2.91$, $p = .09$	$F_{4, 37} = \mathbf{8.14}$, $p < \mathbf{.001}$	$F_{2,14} = 0.22$, $p = .81$
Standard length	$F_{1, 44} = \mathit{5.76}$, $p = \mathit{.02}$	$F_{1, 51} = \mathbf{132.35}$, $p < \mathbf{.001}$	$F_{1, 19} = 0.63$, $p = .44$	$F_{1, 6} = 5.23$, $p = .06$	$F_{1, 8} = 2.21$, $p = .18$	$F_{1, 13} = 0.41$, $p = .53$	$F_{1, 37} = \mathit{7.92}$, $p = \mathit{.01}$	$F_{1, 14} = 0.40$, $p = .54$
$\delta^{15}N$								
Habitat	$F_{2, 44} = \mathit{5.98}$, $p = \mathit{.005}$	$F_{2, 51} = 1.87$, $p = .16$	$F_{1, 19} = \mathbf{19.76}$, $p < \mathbf{.001}$	$F_{1, 6} = 5.86$, $p = .05$	$F_{1, 8} = 1.99$, $p = .20$	$F_{1, 13} = 2.42$, $p = .14$	$F_{1, 37} = \mathit{5.13}$, $p = \mathit{.03}$	$F_{1, 14} = 0.55$, $p = .47$
Habitat (site)	$F_{7, 44} = 1.29$, $p = .28$	$F_{6, 51} = 1.35$, $p = .25$	$F_{2, 19} = 2.93$, $p = .08$	$F_{2, 6} = 0.28$, $p = .76$	$F_{1, 8} = 0.89$, $p = .37$	$F_{2, 13} = 1.87$, $p = .19$	$F_{4, 37} = 1.06$, $p = .39$	$F_{2,14} = 0.94$, $p = .41$
Standard length	$F_{1, 44} = 0.00$, $p = .99$	$F_{1, 51} = 0.25$, $p = .62$	$F_{1, 19} = 3.56$, $p = .07$	$F_{1, 6} = 0.25$, $p = .63$	$F_{1, 8} = 5.23$, $p = .05$	$F_{1, 13} = 1.28$, $p = .06$	$F_{1, 37} = \mathbf{20.40}$, $p < \mathbf{.001}$	$F_{1, 14} = 0.33$, $p = .58$
$\delta^{2}H$								
Habitat	$F_{2, 44} = 0.59$, $p = .59$	$F_{2, 51} = \mathit{4.26}$, $p = \mathit{.02}$	$F_{1, 19} = \mathit{7.36}$, $p = \mathit{.01}$	$F_{1, 6} = \mathit{10.18}$, $p = \mathit{.02}$	$F_{1, 8} = \mathit{10.12}$, $p = \mathit{.01}$	$F_{1, 13} = 0.18$, $p = .68$	$F_{1, 37} = \mathit{5.42}$, $p = \mathit{.02}$	$F_{1, 14} = 0.57$, $p = .46$
Habitat (site)	$F_{7, 44} = 0.37$, $p = .91$	$F_{6, 51} = \mathbf{6.54}$, $p < \mathbf{.001}$	$F_{2, 19} = 2.27$, $p = .13$	$F_{2, 6} = 4.10$, $p = .08$	$F_{1, 8} = \mathbf{61.77}$, $p < \mathbf{.001}$	$F_{2, 13} = 0.15$, $p = .87$	$F_{4, 37} = 2.42$, $p = .07$	$F_{2,14} = 2.77$, $p = .10$
Standard length	$F_{1, 44} = 0.01$, $p = .91$	$F_{1, 51} = \mathbf{15.55}$, $p < \mathbf{.001}$	$F_{1, 19} = 0.004$, $p = .95$	$F_{1, 6} = 0.07$, $p = .80$	$F_{1, 8} = \mathit{11.33}$, $p = \mathit{.01}$	$F_{1, 13} = 0.28$, $p = .61$	$F_{1, 37} = 0.88$, $p = .36$	$F_{1, 14} = \mathit{8.71}$, $p = \mathit{.01}$
$\delta^{18}O$								
Habitat	$F_{2, 44} = \mathbf{13.54}$, $p < \mathbf{.001}$	$F_{2, 51} = \mathbf{19.87}$, $p < \mathbf{.001}$	$F_{1, 19} = 0.12$, $p = .73$	$F_{1, 6} = \mathit{9.63}$, $p = \mathit{.02}$	$F_{1, 8} = 1.32$, $p = .28$	$F_{1, 13} = 0.48$, $p = .63$	$F_{1, 37} = \mathit{4.69}$, $p = \mathit{.04}$	$F_{1, 14} = 0.83$, $p = .38$
Habitat (site)	$F_{7, 44} = \mathit{3.97}$, p .002	$F_{6, 51} = \mathbf{19.64}$, $p < \mathbf{.001}$	$F_{1, 19} = 0.09$, $p = .91$	$F_{1, 6} = 1.36$, $p = .33$	$F_{1, 8} = 1.80$, $p = .22$	$F_{2, 13} = 0.48$, $p = .63$	$F_{4, 37} = 1.90$, $p = .13$	$F_{2,14} = 0.25$, $p = .78$
Standard length	$F_{7, 44} = 0.26$, p .61	$F_{1, 51} = \mathbf{19.51}$, $p < \mathbf{.001}$	$F_{1, 19} = 0.13$, $p = .73$	$F_{1, 6} = 2.04$, $p = .20$	$F_{1, 8} = 2.78$, $p = .13$	$F_{1, 13} = 1.31$, $p = .27$	$F_{1, 37} = 0.02$, $p = .89$	$F_{1, 14} = 0.19$, $p = .67$

Note: Habitat and site (nested within habitat) were predictors for each analysis, with standard length (mm) as a covariate. *F*-values, degrees of freedom and *p*-values are reported for each analysis. Bold results represent significance below .001, italicised results represent significance below .05.

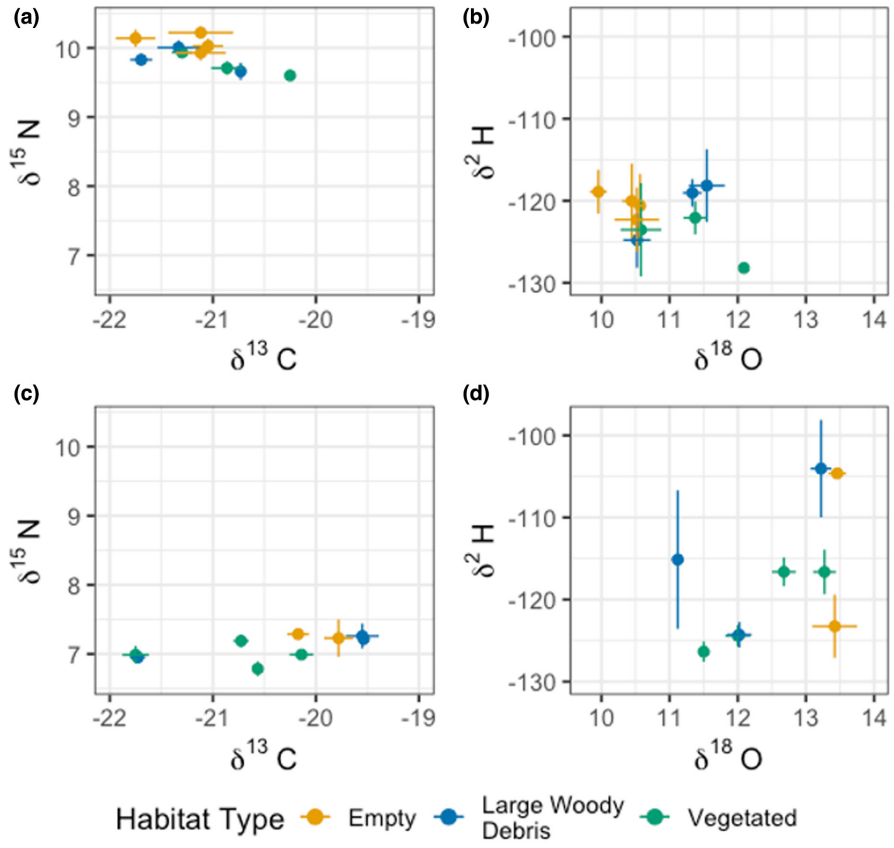

FIGURE 2 Mean stable isotope values by cage ± standard error of YOY largemouth bass in the controlled pond experiments. Colour indicates habitat-type (gold = empty, blue = large woody debris, green = vegetated). Plots a and b are from the Aquaculture Research Laboratory (ARL) cages, and plot c and d are from the Palmer Research Center (PRC) cages.

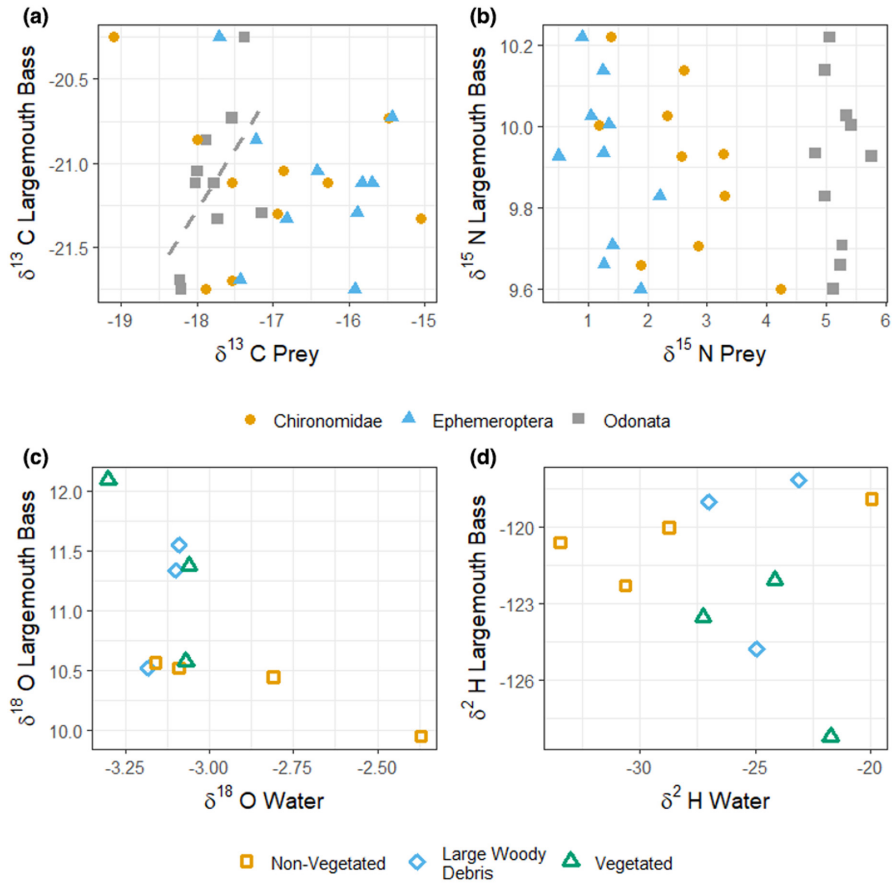

FIGURE 3 (a, b) Relationships of $\delta^{13}C$ (a) and $\delta^{15}N$ (b) site means of locally collected invertebrates and largemouth bass collected in the Aquaculture Research Laboratory (ARL). Shape and colour indicate prey item, gold circle = Chironomidae, blue triangle = Ephemeroptera, and Grey square = Odonata. Grey dashed line represents a significant relationship between $\delta^{13}C$ of Odonata and $\delta^{13}C$ of YOY largemouth bass (adjusted $R^2 = 0.24$, one-tailed $p = .04$). (c, d) Relationships of $\delta^{18}O$ (c) and $\delta^{2}H$ (d) site means of locally collected water and largemouth bass collected in the Aquaculture Research Laboratory (ARL). Shape and colour indicate habitat type, gold square = non-vegetated, blue diamond = large woody debris and green triangle = vegetated.

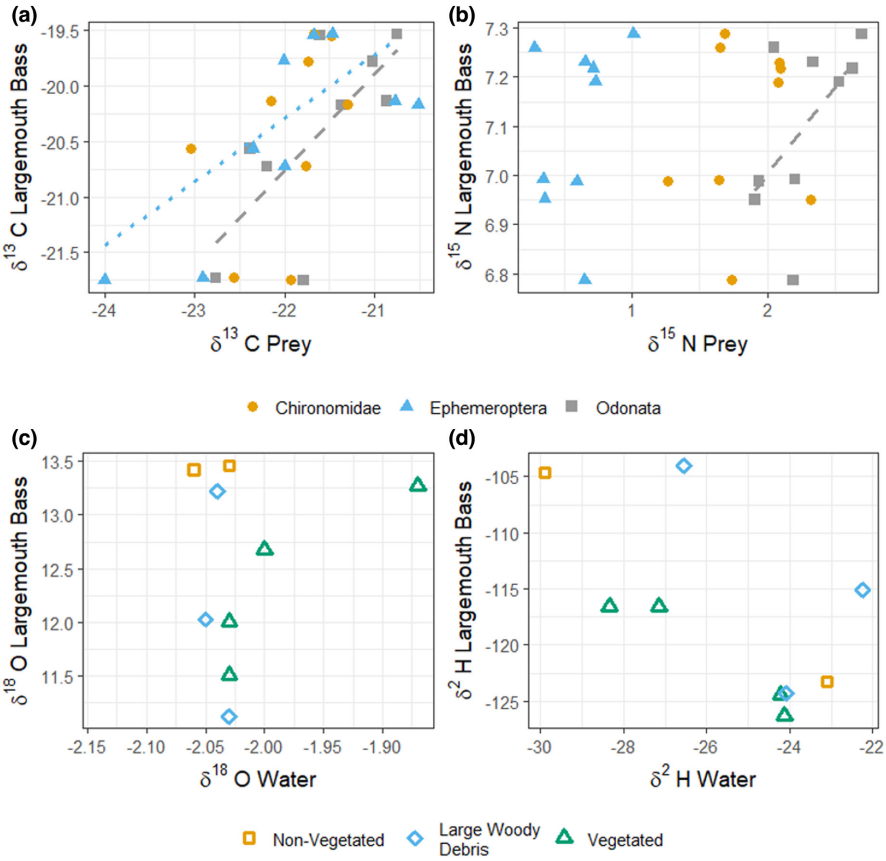

FIGURE 4 (a, b) Relationships of $\delta^{13}C$ (a) and $\delta^{15}N$ (b) site means of locally collected invertebrates and largemouth bass collected in the Palmer Research Center for Aquatic Resources (PRC). Blue dotted line indicates a significant linear relationship between $\delta^{13}C$ of Ephemeroptera and $\delta^{13}C$ of YOY largemouth bass (adjusted $R^2 = .56$, one-tailed $p = .01$). Grey dashed line indicates a significant linear relationship between $\delta^{13}C$ of Odonata and $\delta^{13}C$ of YOY largemouth bass ($R^2 = .45$, p-value = .01) or a significant linear relationship between $\delta^{15}N$ of Odonata and $\delta^{15}N$ of YOY largemouth bass ($R^2 = .26$, p-value = .046). Shape and colour indicate prey item, gold circle = Chironomidae, blue triangle = Ephemeroptera, and grey square = Odonata. (c, d) Relationships of $\delta^{18}O$ (c) and $\delta^{2}H$ (d) site means of locally collected water and largemouth bass collected in the Palmer Research Center for Aquatic Resources (PRC). Shape and colour indicate habitat type, gold square = non-vegetated, blue diamond = large woody debris and green triangle = vegetated.

Big; δ^2H_{means}: vegetated = −146.23, non-vegetated = −152.86; Dewart: δ^2H_{means}: vegetated = −128.61, non-vegetated = −133.07; Table 1), and among sites in Dewart. Standard length was only a significant covariate for δ^2H in Dewart Lake. $\delta^{15}N$ and $\delta^{18}O$ stable isotope ratios were only significantly different between habitats in Adams Lake ($\delta^{15}N_{means}$: vegetated = 14.71, non-vegetated = 15.55) and Big Lake ($\delta^{18}O_{means}$: vegetated = 10.38, non-vegetated = 11.60) respectively (Figure 5).

3.3 | Detailed single-lake survey

We collected 63 YOY largemouth bass in Crooked Lake during two sampling occasions in 2018, 44 in July (44.2 mm ± 6.2; 1.5 g ± 0.8) and 19 in August (66.1 mm ± 12.9; 4.5 g ± 3.0). During July, stable isotope ratios of YOY largemouth bass varied strongly by site, weakly by habitat, and standard length was a significant covariate (Table 1; Figure 6). While there were weak habitat-specific differences for largemouth bass $\delta^{15}N$, $\delta^{18}O$ and $\delta^{2}H$ ($\delta^{15}N_{means}$: vegetated = 8.03, non-vegetated = 8.60; $\delta^{18}O_{means}$: vegetated = 12.32, non-vegetated = 11.94; δ^2H_{means}: vegetated = −132.92, non-vegetated = −127.79 respectively), $\delta^{13}C$ of largemouth bass did not vary by habitat. Rather, $\delta^{13}C$ of YOY largemouth bass varied strongly by site, with a weak effect of individual standard length. Standard length was also a strongly significant covariate of $\delta^{15}N$. In August, there were no significant differences in stable isotope ratios of YOY largemouth bass between habitats or sites, and standard length was not a significant covariate (Figure 6).

For the two separate sampling periods (July and August), we compared spatial variation (habitat and site nested within habitat) of $\delta^{13}C$ and $\delta^{15}N$ of three locally collected macroinvertebrates (Amphipoda, Ephemeroptera and Odonata) and fish (YOY bluegill) (Figure A.3: Appendix S1). In general, spatial differences were far more apparent for $\delta^{13}C$ as compared to $\delta^{15}N$ (Figure A.3: Appendix S1). During July collections, $\delta^{13}C$ of Amphipoda and Odonata varied by habitat (Amphipoda: $\delta^{13}C_{means}$: vegetated = −21.96, non-vegetated = −24.21; Odonata: $\delta^{13}C_{means}$: vegetated = −23.01, non-vegetated = −25.47; Table A.4: Appendix S1), $\delta^{13}C$ varied strongly by site for Amphipoda,

TABLE 2 Multi-Lake survey site information based on sampling during 2017.

Lake	Date	Site	Vegetation class	Surface temperature (°C)	Mean slope (m/m)	CPUE	Total number caught	Mean standard length	Standard deviation of length
Adams	8 Aug	1	Non-vegetated	22.8	0.97	4	10	48.1	4.6
		2	Non-vegetated	25	0.80	0	7	46.7	7.2
		3	Vegetated	23.3	3.31	0.5	5	45.8	4.7
		5	Vegetated		0.97	2	9	43.0	4.1
Big	4 Aug	1	Vegetated	18.1	2.38	1	4	43.4	2.9
		2	Vegetated	25.1	2.78	0.5	1	36.0	
		4	Non-vegetated	24.8	7.24	9.5	19	51.1	7.8
		5	Non-vegetated	23.3	5.03	0.5	1	54.9	
Dewart	9 Aug	2	Vegetated	24	1.88	1	11	52.0	7.5
		3	Vegetated	25	1.70	1	2	45.0	12.0
		5	Non-vegetated	26.3	1.59	0	18	44.7	3.1
Waubee	10 Aug	2	Non-vegetated	25.5	1.08	0.5	1	45.5	
		3	Non-vegetated	26.7	1.53	2.5	7	43.8	4.8
		4	Vegetated	24.5	2.29	2.5	8	41.3	5.2
		5	Vegetated	26	1.51	0.5	8	45.9	4.8

Note: Site numerical codes correspond with Middaugh et al. (2013) sites or with new sites (site 5). CPUE is catch per unit effort for YOY largemouth bass per 5 m seine sweep. Total number caught includes individuals captured after CPUE sampling was completed. Standard length was measured to the hundredth of a millimetre using ImageJ software.

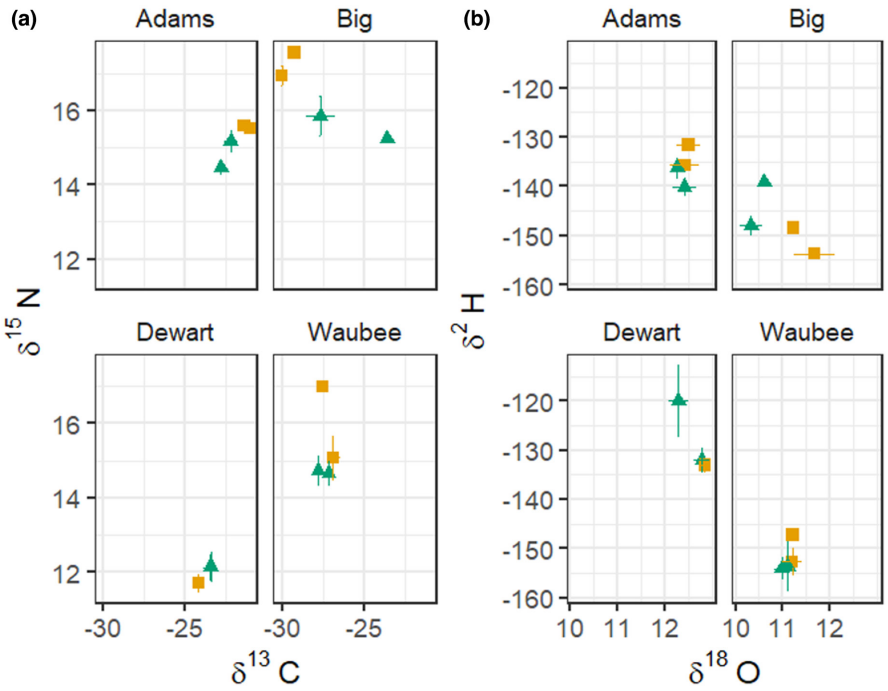

FIGURE 5 Multi-lake stable isotope ratio site means ± standard error of YOY largemouth bass. Colour and shape indicate habitat type (gold square = non-vegetated, green triangle = vegetated). (a) Carbon and nitrogen stable isotope ratios, (b) Oxygen and hydrogen stable isotope ratios.

Bluegill and Ephemeroptera and $\delta^{13}C$ of Odonata varied weakly by site. $\delta^{15}N$ was only weakly significantly different between habitat types for Amphipoda ($\delta^{15}N_{means}$: vegetated = 2.08, non-vegetated = 1.76), and never by site. Similarly, during the August collections, $\delta^{13}C$ varied by habitat and site for Amphipoda and Odonata ($\delta^{13}C_{means}$: vegetated = −22.32, non-vegetated = −24.39; $\delta^{13}C_{means}$: vegetated = −23.97, non-vegetated = −25.53, Table A.4: Appendix S1). In August, $\delta^{15}N$ was only weakly significantly different between habitats for Amphipoda and Odonata (Amphipoda: $\delta^{15}N_{means}$: vegetated = 1.86, non-vegetated = 1.76; Odonata: $\delta^{15}N_{means}$: vegetated = 3.98, non-vegetated = 3.10), and among sites for Amphipoda and Ephemeroptera (Table A.4: Appendix S1). There were no significant differences between habitats or time periods for either $\delta^{18}O$ or $\delta^{2}H$ of water.

During July, mean site $\delta^{13}C$ of all potential prey types were significantly, positively correlated to corresponding $\delta^{13}C$ of locally collected YOY largemouth bass (Amphipoda: adjusted R^2 = .67, p = .01;

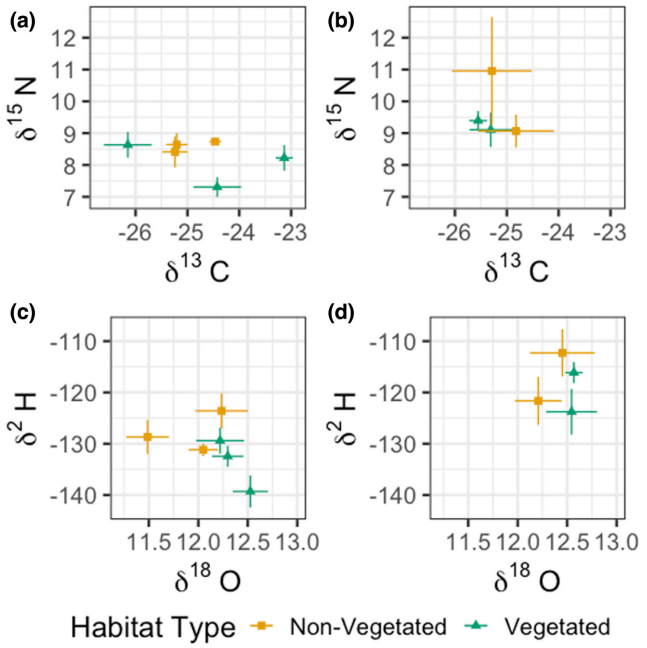

FIGURE 6 Single-Lake (crooked lake) survey largemouth site means ± standard error. (a, c) July 24–25, 2018 (b, d) August 23, 2018. Colour indicates habitat type, gold = non-vegetated and green = vegetated habitats.

Ephemeroptera: R^2 = .54, p = .048; Odonata: R^2 = .77, p = .02; Bluegill: R^2 = .47, p = .04; Figure 7a). Additionally, mean $\delta^{18}O$ of YOY largemouth bass was positively correlated with $\delta^{18}O$ values of locally-collected water (adjusted R^2 = .67, p = .01; Figure 7c). In contrast, during July site-specific mean $\delta^{15}N$ and $\delta^{2}H$ values of YOY largemouth bass were not correlated to corresponding $\delta^{15}N$ values of potential prey, nor $\delta^{2}H$ values of locally collected water (Figure 7b,d). Based on August collections, there was only one significant correlation between $\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$ or $\delta^{18}O$ of YOY largemouth bass and any of the corresponding $\delta^{13}C$ or $\delta^{15}N$ values of locally collected potential prey, or of $\delta^{2}H$ and $\delta^{18}O$ values of locally collected water ($\delta^{15}N$ of Ephemeroptera adjusted R^2 = .82, p = .03). However, of note, sample sizes for evaluating these correlations were lower during August (4 sites with sufficient data for comparison) as compared to July (6 sites).

4 | DISCUSSION

Across the three study components, we observed differences in YOY largemouth bass stable isotope ratios among habitats and sites, suggesting that young largemouth bass forage within a limited area and that the resources supporting YOY largemouth bass growth vary spatially. When confined to a specific habitat and site, as in the controlled pond experiment, YOY largemouth bass relatively rapidly develop habitat- and site-specific stable isotope values, that correlate with local environmental stable isotope ratios (e.g., $\delta^{13}C$ of local macroinvertebrates). Furthermore, in a natural environment where young largemouth bass are free to move around, their isotopic composition is related to isotope composition of local potential prey. However, the direction of habitat differences of bass stable isotope ratios was not consistent in our study, suggesting that our habitat categorisations did not affect bass stable isotope ratios in a consistent manner.

We were able to detect spatial differences in stable isotope ratios in the small, relatively homogeneous research ponds after confining YOY largemouth bass for 29 days. The majority of studies that have aimed to elicit stable isotope differences in fishes in a laboratory setting have relied on environments that are artificially different, such as tanks or mesocosms with isotopically spiked waters, or artificially enriched prey items (e.g., Coulter et al., 2017; MacNeil et al., 2006). In natural systems, several studies that have compared stable isotope differences in small fishes among habitats or sites have examined relatively large systems where distinct differences in habitat and allochthonous inputs would be expected to lead to differences in stable isotope ratios of lower trophic levels (e.g., Herzka et al., 2001; Phibbs et al., 2011). Nonetheless, even in smaller natural systems (e.g., 250–1040 hectare lakes) studies have found spatial variation of stable isotope ratios of potential fish prey items and small fish (e.g., Brauns et al., 2011; Syväranta et al., 2006). Syväranta et al. (2006) measured spatial and temporal variation in $\delta^{13}C$ and $\delta^{15}N$ in potential prey items and fishes collected in a single lake. They found significant spatial and temporal differences in macroinvertebrates, Eurasian perch *Perca fluviatilis* and roach *Rutilus rutilus*. They attributed spatial variation in stable isotope ratios to unique characteristics such as, the presence of a harbour area, a major river inlet and migratory fish, and cautioned that spatial variation of fish stable isotope ratios should be considered if a system has similar unique characteristics. In the considerably smaller (0.1 ha), more homogeneous research ponds, we were able to elicit and detect habitat (treatment) and spatial (cage) variation in stable isotope ratios of fish and relate this to spatial variation in stable isotope ratios of macroinvertebrates. We believe that these differences reflect a combination of (a) the isotopic properties of invertebrate prey related to the habitat treatments in the cages and (b) isotopic spatial variation of invertebrates within ponds independent of cage treatments. The strength of the differences between habitat types and sites was somewhat surprising given the uniformity of water-stable isotope ratios and the size of the research ponds. Nonetheless, note that the magnitude of spatial differences of stable isotope ratios generally exceed measurement variation (see variation of internal standards reported above). These results reinforce the potential for relatively sedentary individuals to develop stable isotope ratios that reflect highly localised prey utilisation. Additionally, the intraspecific variation in stable isotope ratios underscores the importance of considering spatial heterogeneity when comparing within systems.

In addition to within lake and pond variation, the mean stable isotope ratios of YOY largemouth bass varied among lakes. Patterns were generally consistent with the ratio of lake area to total catchment area (LA:CA). We found that lakes that had a larger catchment relative to lake size (e.g., Big and Waubee LA:CA 0.04 and

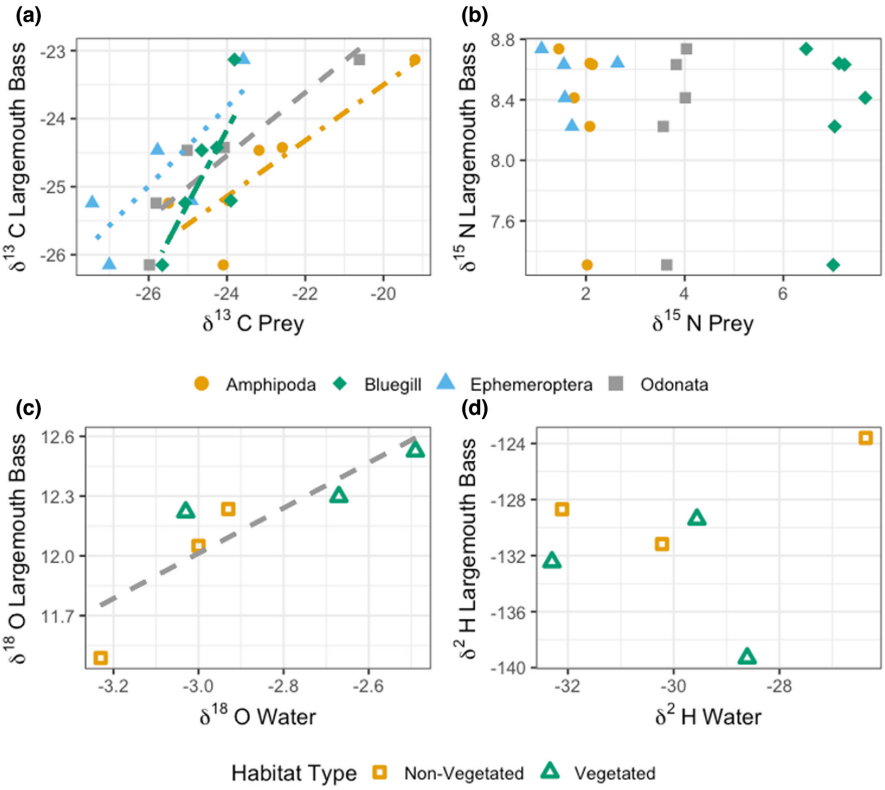

FIGURE 7 (a, b) Correlations of $\delta^{13}C$ (a) and $\delta^{15}N$ (b) site means of locally collected invertebrates and largemouth bass collected in July of the single-Lake survey of crooked lake. Shape and colour indicate prey item, gold circle = Amphipoda, green diamond = young of year bluegill, blue triangle = Ephemeroptera, and Grey square = Odonata. Gold dot-dash line indicates a significant linear relationship between $\delta^{13}C$ of Amphipoda and $\delta^{13}C$ of YOY largemouth bass (adjusted $R^2 = .68$, one-tailed $p = .03$). Green dashed line indicates a significant linear correlation between $\delta^{13}C$ of YOY bluegill and $\delta^{13}C$ of YOY largemouth bass ($R^2 = .47$, $p = .04$). Blue dotted line indicates a significant linear correlation between $\delta^{13}C$ of Ephemeroptera and $\delta^{13}C$ of YOY largemouth bass ($R^2 = .54$, $p = .048$). Grey dashed line indicates a significant linear correlation between $\delta^{13}C$ of Odonata and $\delta^{13}C$ of YOY largemouth bass ($R^2 = .77$, $p = .03$). (c, d) Correlations of $\delta^{18}O$ (c) and $\delta^{2}H$ (d) site means of water and largemouth collected in July. Grey dashed line indicates a significant linear correlation between $\delta^{18}O$ of YOY largemouth bass and $\delta^{18}O$ of locally collected water ($R^2 = .67$, $p = .028$). Shape and colour indicate habitat type, gold square = non-vegetated and green triangle = vegetated.

0.03 respectively) had lower $\delta^{13}C$ and $\delta^{2}H$ ($\delta^{13}C_{means}$: Big = −28.50, Waubee = −27.26; $\delta^{2}H_{means}$: Big = −149.85, Waubee = −153.18) relative to lakes that had smaller catchments relative to lake size (e.g., Adams and Dewart LA:CA 0.12 and 0.13 respectively; $\delta^{13}C_{means}$: Adams = −21.99, Dewart: −23.72; $\delta^{2}H_{means}$: Adams = −136.64, Dewart: −130.47). This is consistent with measured allochthonous and autochthonous sources of $\delta^{13}C$ and $\delta^{2}H$ (Karlsson et al., 2012), suggesting that young bass in lakes that have a relatively large catchment area may be supported more by allochthonous sources. However, inherent differences in catchment sizes, lake morphologies, taxonomic composition and thus baseline stable isotope ratios make direct comparisons of inter-habitat differences among lakes less straightforward.

There were some consistencies in the specific stable isotope ratios that varied across habitats and sites. Specifically, there were more marked differences in largemouth bass carbon and hydrogen stable isotope ratios than nitrogen and oxygen stable isotope ratios. This is consistent with the pathways of enrichment of stable isotopes within aquatic systems (e.g., Post et al., 2000; Soto et al., 2013). Carbon stable isotope ratios reflect the source of carbon at the base of the food web; and may vary spatially, potentially as a product of variation in dominant primary production sources and allochthonous inputs across habitat types (Brauns et al., 2011; McMahon et al., 2005). Hydrogen stable isotope ratios of consumers are influenced by both the $\delta^{2}H$ of their diet, as well as ambient water. However, up to 70% of consumer $\delta^{2}H$ is related to diet (Soto et al., 2013), and thus, spatial variation in $\delta^{2}H$ of largemouth bass likely primarily reflects differences in prey and not water $\delta^{2}H$ (which did not display much spatial variation). Brauns et al. (2011) found that macroinvertebrate food webs were shorter and less complex at developed shorelines as compared to natural shorelines. They also found that the bases of food webs were supported differently, with natural shoreline food webs deriving more of their carbon and nitrogen from terrestrial inputs, while developed shorelines relied on fine particulate organic matter. Such spatial variation could affect higher trophic levels, leading to intra-taxa spatial variation in $\delta^{13}C$ of macroinvertebrates. Significant positive association between $\delta^{13}C$ of potential prey items and young largemouth bass at the same collection site suggest that invertebrates, YOY bluegill and YOY largemouth bass are similarly responding to spatial variation in basal carbon stable isotope ratios.

The potential prey items collected generally are not as mobile as the YOY largemouth bass studied (Marklund et al., 2001), suggesting that the young bass were foraging within a smaller area, and not foraging homogeneously across nearshore habitats. We collected and analysed YOY largemouth bass across a range of sizes (see Table A.2: Appendix S1). However, they were consistently much larger than the reported sizes when young largemouth bass leave their nest (Davis & Lock, 1997; Kramer & Smith, 1960). Thus, we believe that local foraging is maintained after young bass leave their nest.

Though δ^2H and δ^{13}C of largemouth bass tended to vary more among locations than δ^{15}N and δ^{18}O, the directions of differences of stable isotope ratios among habitat types were not consistent. For example, the mean stable isotope ratio values of largemouth bass from empty cages did not vary consistently with respect to the vegetated and large woody debris cages (i.e., in the ARL pond bass from empty cages had a lower mean δ^{13}C than bass from vegetated cages, but in the PRC pond bass from empty cages displayed higher mean δ^{13}C than the other two habitat types). We observed, but did not quantify, differences in the availability of macroinvertebrate potential prey items within the two ponds, with greater availability in the PRC pond. In the ARL pond, zooplankton may have been a more important food source for young bass. This is consistent with δ^{13}C values of YOY largemouth bass relative to macroinvertebrate δ^{13}C values in the ARL pond, as they do not align as closely as expected for consumers and prey items. Among lake surveys, there was also limited consistency in how bass stable isotope ratio values varied by habitat type. At more developed sites and sites with less structure (i.e., non-vegetated sites), we expected to observe less reliance on terrestrial sources of carbon (Brauns et al., 2011), which would be indicated by lower δ^{13}C and δ^2H values at non-vegetated sites as compared to vegetated sites (Doucett et al., 2007). Consistent with this expectation, macroinvertebrates within Crooked Lake exhibited habitat differences, with vegetated sites having higher δ^{13}C values. Across the multi-lake survey, YOY largemouth bass from non-vegetated sites were consistently distinct, and bass from vegetated sites tended to group together. However, we did not consistently observe the pattern of lower δ^{13}C and δ^2H values of largemouth bass at non-vegetated relative to vegetated sites.

Across all three study components, there were very few habitat or site differences in δ^{15}N of YOY largemouth bass. While δ^{15}N of producers may vary somewhat with different allochthonous inputs into different areas of a system, δ^{15}N of consumers is also reflective of trophic level (given ~3.4‰ fractionation per trophic level; Post, 2002). While δ^{15}N varied across potential prey types, there was limited spatial variation in δ^{15}N. We may have expected to see a decrease in δ^{15}N with decreasing habitat complexity, as it has been found that less complex habitats have less diverse food webs, and shorter food chains (Brauns et al., 2011). However, we did not consistently observe this pattern. Variation of individual largemouth bass δ^{15}N values would likely reflect feeding at different trophic levels. To this point, we did observe a positive relationship between individual largemouth bass length and δ^{15}N values in Crooked Lake. Further, δ^{15}N of largemouth bass increased in Crooked Lake from the early sampling period to the later sampling period, consistent with feeding at higher a trophic level as the bass increased in size across the season.

While differences in prey isotopic composition likely had strongest influence on YOY largemouth bass stable isotope ratios, spatial differences in water-stable isotope ratios likely also contributed to differences in bass stable isotope ratios. Again, hydrogen stable isotope ratios of consumers are influenced by both diet and water-stable isotope ratios, with greater contributions from diet (Soto et al., 2013). While observed spatial differences in largemouth bass δ^2H were likely primarily influenced by prey, we cannot rule out an effect related to spatial variation of water δ^2H. Largemouth bass δ^{18}O is expected to be primarily a reflection of oxygen isotopic composition of ambient water (Soto et al., 2013), and we observed very few habitat or site-specific differences in YOY largemouth bass δ^{18}O across components. This again suggests that water-stable isotope variation was less influential than prey. However, in Crooked Lake in July we did observe a positive relationship between δ^{18}O of largemouth bass and δ^{18}O of locally-collected water (see Figure 7), suggesting that locally foraging young largemouth bass may develop a stable isotope composition reflective of local water composition. It is unclear what may drive spatial differences in stable isotope ratios of water in nearshore Crooked Lake. Plausibly, local differences in small tributaries influences and groundwater inputs may be contributing factors to local isotopic variation.

Later in the summer, there were limited habitat- and site-specific differences in stable isotope ratios of largemouth bass within Crooked Lake suggesting that the population of YOY largemouth bass forages in a more spatially integrated manner as they grow through the first summer. In addition, there were still significant differences in stable isotope ratios of potential prey items between both habitats and sites later in the summer, further suggesting that YOY largemouth bass are experiencing more integrated foraging conditions. Larger fish are likely less susceptible to predation and thus able to be more active foragers, and utilise more area for foraging (Ahrens et al., 2012). YOY largemouth bass switch to piscivory after reaching a certain size (Post, 2003), and there is a corresponding increase in δ^{15}N of the young bass from July to August (1.33‰ increase). This switch in prey likely led to increased movement for foraging purposes and capture of prey.

Given that we observed local habitat- and site-specific isotopic ratios, YOY largemouth bass are likely using relatively small foraging areas before the switch to piscivory. Anthropogenic alteration of nearshore areas (i.e., vegetation and large woody debris removal) may have substantial effects on YOY largemouth bass given their local resource reliance. By maintaining habitat and site preferences throughout much of their first summer, YOY largemouth bass are potentially at greater risk of being affected, both positively and negatively, by hyper-local disturbances and changes in forage availability. Hessenauer et al. (2012) relied on genetic analysis to demonstrate that YOY largemouth bass disperse beyond the nest during summer, but they did not examine the timing of dispersal or the spatial scale of foraging by young bass after dispersing from the nest. Our results

suggest that regardless of dispersal beyond the nest, YOY largemouth bass spend a portion of time foraging locally before expanding their foraging grounds. These results underscore the importance of maintaining high-quality habitat patches throughout both spatial and temporal scales. Maintaining access to foraging and refuge areas within smaller ranges potentially allows the lake-wide population to act as a portfolio with many compartments contributing to the recruitment success of the population.

The portfolio effect has been widely studied in other fish species, in particular populations occupying much larger systems, (e.g., Schindler et al., 2010; Waldman et al., 2016; Worm et al., 2006) and has been suggested to temper recruitment variability at the population level. The first year of life is a critical period for largemouth bass, with many individuals not surviving through the winter (Ludsin & DeVries, 1997). The growing period prior to the shift to piscivory is crucial as without adequate size and gape individuals will be unable to shift to larger prey, ultimately limiting their growth and decreasing the likelihood of survival. The areas of a lake allowing for better survival and growth may vary from year to year. Maintaining or restoring natural shorelines with complex habitats may provide the diversity of habitats necessary for juvenile fishes and ultimately may facilitate differential habitat-specific recruitment and temper overall recruitment variation (e.g., Höök et al., 2008).

We observed the presence of habitat and site fidelity in our study and the shift from local trophic reliance within populations to more spatially uniform trophic reliance as largemouth bass developed. Thereby, we demonstrated that the measurement of stable isotope ratios allows for differentiating habitat use among young fish, even when young fish inhabit areas in relatively close proximity within small lentic systems. This approach is suitable to asses spatial foraging patterns by early life stages of a variety of species. Several young fish species forage on similar macroinvertebrates during early life and may reveal similar local trophic reliance based on isotopic analyses, such as observed for YOY yellow perch (Senegal et al., 2020). Further, observed intraspecific spatial variation in stable isotope ratios among both young fish and macroinvertebrates suggests the need to consider stable isotope heterogeneity within small systems, as failure to do so can confound whole-system interpretation of trophic interactions. Finally, understanding habitat use during the juvenile stage provides an important insight into the benefit of heterogeneous habitats and has implications for the spatial scale of habitat conservation efforts.

AUTHOR CONTRIBUTIONS

PN carried out the majority of field and laboratory analysis. PN and TH both contributed to the conception and design of the study and analysis of data. Both were involved in drafting and revising the intellectual content of the manuscript, are accountable for all aspects of the study and give approval for publication.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

Upon acceptance of the manuscript for publication, data will be made available through Purdue University's Research Repository (https://purr.purdue.edu/).

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SUPPORTING INFORMATION

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

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