NEARSHORE HABITAT AND LAND-USE EFFECTS ON TROPHIC INTERACTIONS AND GROWTH OF LARGEMOUTH BASS AND BLUEGILL IN INDIANA'S GLACIAL LAKES

by

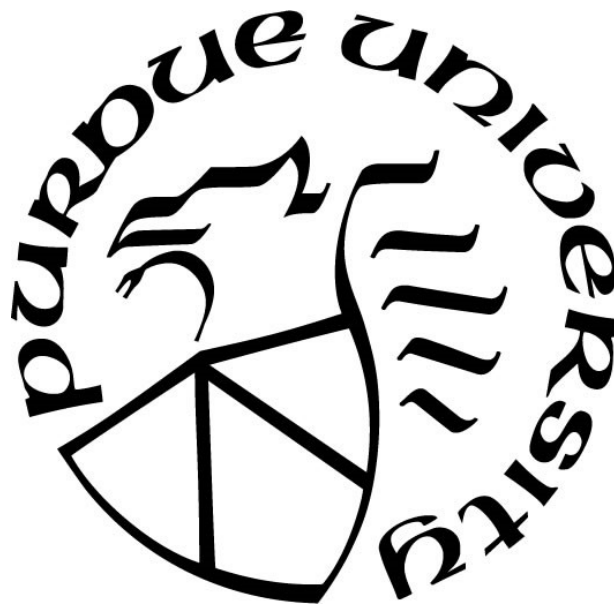**Patricia A. Nease**

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So Long and Thanks for all the Fish

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ABSTRACT

Glacial lakes, such as those in the Midwest region of the United States, are ecologically and economically important, and they provide a wide range of ecosystem services, such as habitat for wildlife and fishes, flood control and recreational boating. Glacial lakes often support locally important sport fisheries, such as largemouth bass *Micropterus salmoides* and bluegill *Lepomis macrochirus*, which are partially dependent on suitable habitat within lakes. Nearshore vegetation is often removed by lakeshore landowners for perceived aesthetics and boat access, or by area managers as a form of indirect fisheries management and invasive species control. The connection between nearshore vegetation and fish population health, though widely studied is somewhat unclear. In the two research chapters of this thesis we attempted to further understanding of the environmental factors that influence vegetation abundance and distribution, how vegetation abundance and distribution influences fish population abundance and size structure, and how young-of-year (YOY) largemouth bass utilize habitats within the nearshore environment. In the first research chapter, we used structural equation modeling (SEM) and data collected by the Indiana Department of Natural Resources to quantify the complexity of relationships among catchment characteristics (e.g., catchment size), lake morphology, water quality, vegetation abundance and distribution, and fish population abundance and size structure. Across multiple lakes, lake productivity was more influential in explaining cross-lake variation of largemouth bass and bluegill proportional stock density (PSD) and largemouth bass catch per unit effort (CPUE) than vegetation. This may be a result of the feedback between phytoplankton production and rooted vegetation production. The models we constructed provide insights into the complexity of environmental variables that influence nearshore vegetation and fish populations. In the second research chapter we used stable isotopes (δ^{13} Carbon, δ^{15} Nitrogen, δ^{18} Oxygen and δ^2 Hydrogen)

to examine the consistency of habitat use and foraging of YOY largemouth bass within Indiana glacial lakes. We observed spatial variation in stable isotope ratios of YOY largemouth bass between habitat types and sites. Additionally, there were significant, positive relationships between $\delta^{13}C$ of locally collected potential prey items and $\delta^{13}C$ of YOY largemouth bass suggesting localized foraging patterns. Later in the summer, as young bass grew in size and likely switched to piscivory, we did not observe similar spatial variation in young bass stable isotopes or spatial relationships between prey and the young bass suggesting more homogeneous foraging patterns. Understanding the habitat use patterns of young bass may allow for more efficient and effective management of the nearshore environment. Overall, a greater consideration for the complexity of relationships between nearshore habitat and fish populations may facilitate more effective management.

CHAPTER 1.   INTRODUCTION

Midwestern glacial lakes provide a wide range of ecosystem services including recreational opportunities for boaters, anglers and swimmers; flood mitigation during extreme weather events; wildlife and fish habitat; and increased value of local real estate. Indiana glacial lakes are the furthest southern extent of Midwestern glacial lakes and tend to have relatively high agriculture and residential development within their watersheds. The relatively warm and productive glacial lakes support a variety of fish species, in particular warmwater fishes, such as bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides).* Nearshore zones within these lakes provide important ecosystem services for humans, but they also provide critical nursery habitats for fishes. These areas are especially important environments during early-life of fishes due to warmer, shallow waters with abundant three-dimensional structure that can serve as a refuge.

Anthropogenic disturbances in nearshore areas include, but are not limited to, shoreline armoring, dredging, downed tree and vegetation removal, and dock and pier construction. Construction of shoreline structures (e.g., shoreline armoring, docks) and dredging to facilitate boat passage alter nearshore physical characteristics and can dramatically limit the establishment of nearshore macrophytes (Asplund and Cook 1997). Similarly, boating can affect macrophyte beds through propeller damage and wave generation, which prevent plant establishment. Most directly, physical, chemical and biological removal of macrophytes (for swimming, boating or perceived aesthetics) significantly alter nearshore habitats, and the associated fish community (Weaver et al. 1997). As a result of these disturbances nearshore complexity decreases with increasing shoreline development (e.g. Jennings et al. 1999; Radomski and Goeman 2001; Sass et al. 2010). Additionally, with reductions in nearshore complexity there are subsequent alterations

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of fish communities and decreased abundance of some populations (Sass et al. 2006a, 2006b). For example, following a significant removal of large woody debris in a lake Sass et al. (2006b) observed a rapid decrease in yellow perch (*Perca flavescens*) abundance, and a shift in the diets of largemouth bass.

Fish populations within inland lakes are important contributors to ecosystem services, adult fishes are often popular with anglers and top predators can be critical for top-down control of the lake food web, which may prevent undesirable algal blooms (Eby et al. 2006). Due to the ubiquity and popularity of largemouth bass and bluegill, and their predator-prey dynamic, several studies have focused on the influence of vegetation on the performance of these two species (e.g., Savino and Stein 1982; Valley and Bremigan 2002). As largemouth bass are top predators (Shoup et al. 2003), preferred fish by anglers, and use nearshore areas throughout their life (Wagner et al. 2006) they may act as an umbrella species for conservation of habitat and other less popular fishes (Roberge and Angelstam 2004).

Vegetation is a critical form of three-dimensional structure and habitat complexity within the nearshore area. Patches of vegetation provide important foraging and refuge areas for both juvenile and adult fishes (e.g., Savino and Stein 1989a; Stahr and Shoup 2016). There are many studies across a wide range of scales that have examined the influence of nearshore vegetation on fish behavior, growth and population size (e.g., Unmuth et al. 1999; Smokorowski and Pratt 2007; Middaugh et al. 2013). Generally, these studies are motivated as a form of indirect management (Trebitz et al. 1997; Smith 2002) to increase the abundance and size of sport fishes (Olson et al. 1998; Unmuth et al. 1999). In many Midwestern glacial lakes, warmwater game fishes, such as largemouth bass or bluegill, are supported by naturally reproducing populations, with little to no stocking. Therefore, indirect management approaches, including managing for suitable habitat,

can be important tools for improving populations. Additionally, there is widespread removal of nearshore vegetation for perceived aesthetics, boat access or invasive species control. Little is known about the specific impacts of changes in aquatic vegetation on fish population responses in inland lakes (Radomski et al. 2019). Therefore, our studies aimed to better understand the drivers of plant abundance and distribution, the impact on two target fish species and the nearshore habitat use of young-of-year (YOY) largemouth bass.

There are many potential approaches to examine the environmental factors that influence nearshore vegetation, the relationship between vegetation and fish, and habitat use of young fishes. Several studies have studied vegetation's impact on fish habitat use, growth and predation (e.g., Crowder and Cooper 1982; Olson et al. 2003), while other studies have examined patterns *in situ* (e.g., Nohner et al. 2018). Within natural systems past studies have ranged from patterns within a single lake (e.g., Bryan and Scarnecchia 1992) to studies that have examined lake-wide patterns across multiple lakes (e.g., Cheruvelil et al. 2005). We used structural equation modeling to quantitatively study the complexity of environmental factors that influence lake-wide vegetation abundance and fish population size structure and abundance across 106 lakes. In our second study, we used stable isotopes to determine if YOY largemouth bass exhibit habitat or site fidelity.

Ecological data are inherently related through networks of complex relationships, as such structural equation models (SEMs), originally developed for social sciences, are a technique to facilitate description and understanding of these complex data and relationships (Grace et al. 2010). In a recent paper Radomski et al. (2019) called for work that connects environmental variables to vegetation abundance and subsequently vegetation to fish populations in north temperate lakes. Our models provide insights to factors structuring lake-wide vegetation within Indiana glacial lakes, and how vegetation interacts with other environmental variables to influence fish population

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abundance and size structure. While our models are not necessarily predictive, they do provide insight into potential 'intervention points' that may help prevent approaching tipping points of ecosystem change. We found that lake productivity is more often a direct predictor of fish population size structure and abundance than vegetation. There is a positive feedback between water clarity and nearshore vegetation (Scheffer et al. 1993) suggesting that the effects of vegetation on fish population that have previously been observed may result from this feedback instead of just vegetation. Being able to quantitatively examine the complexity of relationships that structure within lake processes provides a clearer picture and shows that holistic management strategies may be more effective.

For our second study we used stable isotopes to investigate YOY largemouth bass habitat use within Indiana glacial lakes. This study included three study components, a controlled pond experiment, a multi-lake survey and a detailed single lake survey, and we used stable isotope ratio differences to measure habitat and site use of YOY largemouth bass across all components. Stable isotope ratios have been used in migration studies for many years (McCarthy and Waldron 2000; Soto et al. 2013), and it has been shown that there is spatial and temporal variability in stable isotope ratios of potential fish prey items and small fishes within lakes (Syväranta et al. 2006; Brauns et al. 2011). Stable isotope ratios are a relatively long-term index of the habitat occupancy and foraging history of an individual. Due to their wide usage in aquatic systems it is generally understood how each elemental ratio becomes enriched or depleted. Carbon ratios (^{13}C : ^{12}C) are indicative of differences in the carbon source at the base of the food web (e.g., allochthonous vs. autochthonous sources), while nitrogen stable isotope ratios (^{15}N : ^{14}N) indicate trophic position, but the base position can be affected by anthropogenic disturbances (i.e., fertilizer runoff; Peterson and Fry 2003). Hydrogen (^{2}H : ^{1}H) and oxygen (^{18}O : ^{16}O) stable isotope ratios have been less

frequently used om ecological studies, but have important implications for aquatic systems as they reflect ambient water conditions in addition to the isotopic composition of consumed prey items (Soto et al. 2013). Because stable isotopes integrate in fish tissue over time, we are able to examine the consistency of habitat occupancy and foraging patterns of YOY largemouth bass over a period of time instead of a only during a very recent period.

Across our three study components, we observed differences in YOY largemouth bass stable isotope signatures among habitat types and sites. This suggests that individuals are foraging in local areas, and that the resources supporting growth vary among habitats and sites. This variation in resources is corroborated by differences in stable isotope ratios of potential prey items between habitats and sites, and the relationships between site means of $\delta^{13}C$ of potential prey items and $\delta^{13}C$ of YOY largemouth bass. Generally, there were more consistent spatial differences in largemouth bass $\delta^{13}C$ and δ^2H, but there were also limited spatial differences in $\delta^{15}N$ or $\delta^{18}O$. Much of the variation in young bass stable isotope signatures is as a result of different production sources, further suggesting localized foraging. There were no differences in YOY largemouth bass stable isotope ratios later in the season suggesting that as individuals grow they forage within the nearshore area more homogeneously. Larger fish are potentially able to forage more actively because they are less susceptible to predation (Ahrens et al. 2012), and as fish switch to piscivory they may forage over a broader area. Consistent with this expectation, we observed a corresponding increase in $\delta^{15}N$ of YOY largemouth bass from July to August in the single-lake survey. Because YOY largemouth bass forage locally during much of their first summer and then shift to more homogeneous foraging patterns the population may act as a portfolio with many compartments contributing to recruitment success.

Our two studies help to fill knowledge gaps surrounding inland lakes. We quantitatively examined the complexity of relationships between environmental variables, vegetation abundance and fish population abundance and size structure. This furthers our understanding of these systems and helps to identify intervention points where management could have the most impact. We identified long-term habitat use patterns of YOY largemouth bass and found that they forage locally through much of their first summer, but forage more extensively after switching to piscivory. Understanding habitat use of YOY largemouth bass may elucidate the importance of nearshore habitat conservation within inland lakes.

CHAPTER 2.   STRUCTURAL EQUATION MODELING AS A TOOL TO UNDERSTAND RELATIONSHIPS BETWEEN VEGETATION AND FISH POPULATIONS

2.1   Abstract

Midwest glacial lakes support locally important sport fisheries, such as bluegill *Lepomis macrochirus* and largemouth bass *Micropterus salmoides*. A large component of managing these fish populations and the fisheries that depend upon them involves indirect management of habitat. For example vegetation removal is often desired by lakeshore landowners for recreation and perceived aesthetic benefits, but the connections between these removals and fish population performance are poorly understood. Using data collected by the Indiana Department of Natural Resources (INDNR), we calculated average littoral biovolume from hydroacoustic survey within 4.6 m depth. Additionally, we calculated largemouth bass and bluegill catch per unit effort (CPUE) and proportional stock density (PSD) from the same lakes within the INDNR collection program. We used structural equation models to examine the complex relationships between multiple scales of environmentally relevant lake characteristics; catchment characteristics, lake morphology, water quality measures, vegetation data and standardized fish population metrics from 106 Indiana glacial lakes. Structural equation models allowed us to examine indirect and direct effects of these data, and separate the effect of vegetation from other lake characteristics. Structural equation models generally suggested that association between vegetation coverage and fish metrics may be a result of variation in lake productivity and other factors influencing both vegetation and fish metrics. We only observed a direct relationship with vegetation for a single fish metric, largemouth bass catch per unit effort. The most influential variable on fish metrics varied across models, but included an index of lake productivity (for modeling bluegill PSD), water clarity (for modeling

largemouth bass PSD), amount of land development near each lake (negatively influencing bluegill CPUE), and vegetation coverage (negatively influencing largemouth bass CPUE). Our models show the importance of considering broader contexts when examining direct cause and effect relationships in natural systems.

2.2   Introduction

Ecosystems have complex networks of abiotic and biotic factors and processes influencing each other. In these complex systems, it is difficult to elucidate individual cause and effect relationships between two factors without considering the context within which these take place, and without considering the potential impact of multiple factors. Due to the inherent interrelatedness of environmental variables, traditional statistical methods, such as linear regressions, are often unlikely to capture the entire suite of relationships and the strength of individual relationships. Consider for instance, the relationship between nearshore vegetation and fish. This relationship has often been studied as a cause and effect relationship with vegetation effecting fish populations by influencing an individual's behavior or growth (e.g., Savino and Stein 1989; Valley et al. 2004). However, such an apparent bivariate relationship may actually reflect the influence of additional co-varying factors.

Management of vegetation in lakes is frequently used as an indirect strategy for managing sport fish, such as largemouth bass *Micropterus salmoides* and bluegill *Lepomis macrochirus* (Cross et al. 1992; Trebitz et al. 1997; Smith 2002). Species such as largemouth bass and bluegill reproduce naturally in most lakes they occupy and are not typically stocked. While harvest regulations may somewhat affect population abundances and size structures, manipulating habitat represents a potentially important mechanism to manage these populations (Trebitz et al. 1997;

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Unmuth et al. 1999). With the increasing presence of invasive species of aquatic vegetation, management of vegetation has become popular as a technique to improve sportfish habitat (Valley and Bremigan 2002; Valley et al. 2004). However, a challenge with this approach is that the direct relationship of vegetation and fish population abundance and size is generally not fully described and difficult to measure.

Studies examining interactions between vegetation and fish span a wide range, from controlled experimental systems, to multi-lake surveys or analyses. Experimental studies have shown that intermediate densities of vegetation are most conducive to efficient foraging and increased growth of young largemouth bass and bluegill, especially along the edge of vegetation stands (Crowder and Cooper 1982; Savino and Stein 1989a; Nohner et al. 2018). However, the effects of vegetation may vary by species and life stage. In a study comparing vegetation effects on two piscivores, increasing densities of macrophytes had no effect on the ambush predator northern pike *Esox lucius*, but the more active forager largemouth bass had reduced foraging success (Savino and Stein 1989b). Experimental studies have the benefit of greater control of the conditions experienced by an individual, however, it is difficult to extrapolate experimental results to population success, or whole lake effects. The environmental context within which a study is conducted has implications on the results, especially in whole lake studies, and results from a single whole lake manipulation may not be indicative of how all other systems will be expected to respond. Due to the cost of whole lake studies typically only one lake is manipulated, which affects the power of the results. Olson et al. (1998) and Unmuth et al. (1999) showed that removals of approximately 20% of lake vegetation positively increases growth of certain age-classes of both largemouth bass and bluegill. Both these studies were conducted in heavily vegetated lakes, so it is unclear how similar removals would affect fish populations in less-densely vegetated lakes.

Controlling for the inherent relationships between environmental factors that influence vegetation is complicated, however multi-lake analyses and modeling approaches begin to tease out these relationships. In a study of 45 lakes in Michigan, Cheruvelil et al. (2005) found results similar to Olson et al. (1998) and Unmuth et al. (1999) in that growth rates of specific age classes of bluegill and largemouth bass were related to measures of vegetation density, however, there was no consistency across age classes. Furthermore, Cheruvelil et al. (2005) noted that though the relationships were significant, they did not explain much of the variation in fish responses, and many other variables such as lake morphology and productivity likely also contributed to variation in fish population abundance and growth. Trebitz et al. (1997) built an individual based model to examine the dynamics of predator prey interactions between bluegill and largemouth bass under different levels and distributions of simulated vegetation in a model lake. While largemouth bass growth increased with decreasing vegetation, bluegill were less responsive. Furthermore, the distribution of vegetation was important for determining the bluegill response, with increasing edge habitat increasing the growth rates of bluegill. Even in the controlled modeling environment the authors noted the complexity of relationships that impact both vegetation and fish and the importance of considering the context of environmental variables.

Structural equation models (SEMs) were originally developed for social science studies in which many factors may be correlated and interactive. Recently SEMs have become more popular in ecological studies due to potential interactions of diverse variables in nature and because they can capture more variability than traditional univariate or multivariate statistical analyses (Grace et al. 2010). Structural equation models depict complex, related systems, and may elucidate how different environmental variables affect response variables. SEMs assume that there are mechanisms leading to a theoretical structure among variables. In building a SEM, a proposed

structure is compared to the theoretical structure of the data. Good model fit means there is little difference between the proposed structure and the theoretical structure. SEMs have been applied to address relationships in aquatic systems and the potentially interactive effects of external stressors on biotic responses (e.g., fish or macroinvertebrate communities in streams; Malaeb et al. 2000; Schmidt et al. 2019). There are two primary approaches for developing of SEMs, a) model building where all possible relationships between variables are evaluated, or b) hypothetical model evaluation whereby an initially-proposed model is compared to data patterns. Model building is more of an exploratory technique used when relationships are not well understood. Hypothetical model evaluation is more appropriate when multiple individual relationships of interest have been proposed and described through previous studies.

The aim of this study was to develop structural equation models to understand how a variety of environmental factors influence lake-wide vegetation biomass and fish population abundance and size structure. Because multiple individual relationships of interest have previously studied (e.g., Swingle and Smith 1942; Scheffer et al. 1993; Radomski et al. 2019) we developed a hypothesis model based on these known relationships. Then, we used data from 106 glacial lakes in Indiana, systematically sampled for vegetation abundance and distribution and fish populations by the Indiana Department of Natural Resources, to test the hypothesized model structure. We developed individual structural equation models with lake catchment characteristics, morphology, water quality and lake-wide littoral vegetation biomass as potential explanatory variables with largemouth bass or bluegill relative abundance and size structure as response variables. We anticipate that our hypothesis model will explain some of the variation in the data, however, model fit will be improved through model trimming and evaluation. Furthermore, we expect that vegetation abundance will be a main predictor of fish population size and structure.

2.3 Methods

2.3.1 Data

We used data collected by the Indiana Department of Natural Resources (INDNR) as a part of their Status and Trends (S&T) program which assesses abiotic (i.e. temperature and dissolved oxygen) and biotic (i.e. fish populations and vegetation abundance) conditions in Indiana glacial lakes annually. In 2009, INDNR revised their S&T program so that it is more standardized and comprehensive and thus, we analyzed data collected from 2010 - 2018. Approximately twelve lakes were sampled annually based on a stratified random selection of glacial lakes and we ultimately included data from 106 lakes. If a lake was sampled more than once during this period we only included data from the most recent sampling effort.

As a component of annual S&T sampling, fish community surveys were conducted during the month of June using three methods. Two experimental gillnets (consisting of 1.9 cm, 2.54 cm, 3.175 cm, 3.81 cm, and 5.08 cm square mesh) were set overnight in habitats intended to be reflective of the entire lake. Overnight sets of two trap nets with double 1.83 m * 0.91 m front frames, 1.27 cm mesh, and a 15.24 m * 0.91 m lead were used to collect fish in shallow water habitats. Two 15-minute nighttime boat electrofishing transects (with 5-6 amp DC electrofishing units) were used to sample the nearshore areas of the lake. All fish caught were identified to species, and measured to nearest 0.1 in (2.5 mm). To index fish population relative abundance and size structure, we calculated catch per unit effort (CPUE) of stock size or greater bluegill ($\geq$ 3 in, 7.6 cm) and largemouth bass ($\geq$ 8 in, 20.3 cm) using only the gear with the largest catch of the target species (electrofishing for each species). We limited CPUE to stock size and greater fish in part to limit potential influence of large numbers of recently emerged age-0 fish in some lakes. We calculated proportional stock density (PSD) using the following equation:

$$\frac{\text{\# of fish above quality length}}{\text{\# of fish above stock length}}$$

Quality is defined as $\geq$ 6 in (15.2 cm) for bluegill and $\geq$ 12 in (30.5 cm) for largemouth bass) we calculated PSD using length measures from individuals collected in all three methods (Neumann et al. 2012).

Acoustic bathymetric and aquatic habitat data were collected between July 15 and August 15 using a BioBase EcoSound system (C-MAP, Inc.). These acoustic surveys provided a measure of vegetation biovolume and location, as well as depth and bottom hardness along boat transects. Vegetation biovolume was calculated as a percent of the water column occupied by vegetation. We calculated average littoral biovolume by taking an average of all points within the defined littoral zone, lake area with a depth of 15 ft (4.6 m) or less (Radomski et al. 2010). To corroborate our measure of average littoral biovolume, we compared our calculated value to the percent of sites with vegetation collected as part of INDNR sampling efforts targeting vegetation species composition (from point-based rake grab samples in some lakes; Indiana Department of Natural Resources 2014). We found a positive and significant relationship between the percent of sites with vegetation and average littoral biovolume ($p < 0.001$, $R^2 = 0.32$, Figure A.1).

Indiana DNR gathered water quality measurements in June immediately prior to the S&T fish sampling. Secchi depth (to the nearest 0.5 ft, 0.15 m), temperature and dissolved oxygen profiles (measurements every 2 ft, 0.61 m) were collected at the deepest point of the lake. In addition to the INDNR S&T data, we considered water quality data collected by the Indiana Clean Lakes Program (CLP). The Indiana CLP collects a wide suite of water quality measures, including nutrient concentration (e.g., total phosphorus), and lake productivity measures (e.g., chlorophyll-a concentrations). The CLP sampling regime is inconsistent with the INDNR S&T sampling

program so data were not available for all the included lakes. Additionally, sample collection time was often inconsistent leading to long periods of time between CLP and S&T samples if a lake was sampled by both programs. Ultimately, we did not include data collected through the CLP, however, we examined relationships between CLP Secchi depth, dissolved oxygen and other measures of lake productivity to better understand what Secchi depth and dissolved oxygen variability may index (Figure A.2 & Figure A.3). We calculated dissolved oxygen difference using the following equation:

$$DO \ at \ 0 \ ft \ (0 \ m; mg/L) - DO \ at \ 10 \ ft \ (3.05 \ m; mg/L)$$

This is an approximation of net primary productivity as we see a positive relationship of surface dissolved oxygen and chlorophyll-a concentration (indicative of productivity), and a negative relationship of dissolved oxygen at depth and chlorophyll-a concentration (indicative of respiration). This index of dissolved oxygen difference was positively associated with concentrations of chlorophyll a, total Kjeldahl nitrogen and total phosphorus. Secchi depth was negatively associated with concentrations of chlorophyll a, total phosphorus and total Kjeldahl nitrogen.

To describe catchment characteristics and lake morphology, we used data extracted from INDNR lake morphology databases, United States Geological Survey geospatial databases and the National Land Cover Database (Perry 2011; Feiner et al. 2016; Table A.1). We included the percent of the total catchment area that was agricultural or developed, as well as the percent development within a 100 m buffer of the lake perimeter. We also calculated the ratio of lake area to catchment area, a proxy of potential nutrient loading for a lake (Honsey et al. 2016). We considered many possible morphology and catchment characteristics, however, to minimize redundancy of variables (i.e., mean depth vs. maximum depth) and maximize degrees of freedom,

we selected lake surface area as it had broad coverage across the study lakes and was associated with several other measures of lake morphology including maximum depth ($R^2 = 0.07$, P = 0.01) and shoreline development index (a measure of the circularity of a lake; $R^2 = 0.13$, P < 0.001).

The variables considered in our models were: area of developed and agricultural land in total catchment (%), lake surface area (m^2), ratio of lake area to total catchment (a proxy for the potential nutrient loading to a lake; Honsey et al. 2016), dissolved oxygen difference (a proxy for lake productivity), Secchi depth, average littoral biovolume, largemouth bass PSD and CPUE, and bluegill PSD and CPUE (Table A.1).

2.3.2 Structural Equation Model Development

We used structural equation modeling to examine relationships among catchment characteristics, lake morphology, water quality, vegetation and fish (largemouth bass and bluegill) population abundance and size structure metrics. Data were standardized and centered around the variable mean and standard deviation. We developed a hypothesis model based on understood relationships between individual variables (Figure 2.1). This hypothesis model was then evaluated with each individual fish metric and subsequently evaluated. All models were optimized by iterative evaluation and paths (i.e., relationships) were trimmed if they were non-significant (p-value <0.1). Once non-significant paths were removed, we evaluated the modification indices, which are suggested additional paths based on the distance between the fitted and implied covariance matrices that could improve overall model fit. If the suggested additional paths fit the model structure defined in the hypothesis model, they were iteratively added and the resulting model was evaluated as described above. Ultimately, we created three model types for all fish metrics, an initial model using the hypothesis model structure, a trimmed model that trimmed insignificant relationships, and a final model that included additional relationships.

Overall model fit was evaluated using the robust Chi-squared (χ^2) global test (good model fit = p-value > 0.05), Satorra-Bentler correction factor (near 1), Comparative Fit Index (CFI; > 0.95), Relative Non-centrality Index (RNI; > 0.95), Robust Root Mean Square Error of Approximation (RMSEA; < 0.05 and 90% confidence interval including 0), Robust Standardized Root Mean Square Residual (SRMR; < 0.08) and Incremental Fit Index (IFI; > 0.95) (Schmidt et al. 2019). These metrics represent threshold values that when examined concurrently have a low level of misspecification of model fit (Hu and Bentler 1999). The χ^2 p-value indicates the difference between the structure of the data and the expected structure based on the model design, therefore, a good model fit would have a high p-value indicating little difference between the two structures (Hu and Bentler 1999). The Satorra-Bentler correction factor is a measure of the multivariate kurtosis and degrees of freedom associated with the model, if the correction factor is high it suggests that the data modeled are not normal and may benefit from transformation (Satorra and Bentler 1994; Curran et al. 1996). A Satorra-Bentler correction factor near 1 indicates multivariate relative normality of the data. CFI, IFI and RNI are incremental fit indices, which measure the proportionate improvement of the model as compared to a null model where all the observed variables are uncorrelated. RMSEA and SRMR are absolute measures of fit, indicating how well the model reproduces the data, RMSEA is based on the non-centrality parameter (i.e., Satorra-Bentler correction factor), and SRMR is the standardized difference between the observed and predicted correlation. Once the model met these criteria it was evaluated after using Bollen-Stein bootstrapping (n = 1000) and path coefficients were again evaluated for significance. If the model was modified due to insignificant relationships it was again evaluated as described above. Variables that did not have a direct or indirect effect on the response variable were removed from

the model. Lastly, we evaluated the strength of each effect within each model based on Cohen (1988) ((±) 0.1 (weak), 0.3 (moderate), and ≥0.5 (strong)).

2.4   Results

Using the approach described above (hypothetical model to trimmed model to final model) we built three successful models based on 106 possible lakes. We were initially unable to develop a model for bluegill CPUE, however, we used a different method of model evaluation and fitting (described below) to achieve the presented final model. The standardized path coefficients from the model bootstrapping are presented in the text, tables and figures. All three model types, initial, trimmed and final are presented in Figures 2.3-2.6, however, only the final model is described in text. The overall model fit indices for all three model types can be found in Table A.3. Analyses were performed using R Studio, cowplot, dplyr, FSA, ggplot2, lavaan and semPlot (Wickham 2009; Rosseel 2012; Wickham et al. 2017; R Core Team 2018; Epskamp 2019; Ogle et al. 2019; Wilke 2019).

2.4.1   Largemouth Bass Proportional Stock Density Model

Only four of the 7 potential predictor variables influenced largemouth bass proportional stock density (Figures 2.2 and 2.3). Of those four variables Secchi depth had the greatest influence on largemouth bass PSD, accounting for 37% of the total effects. Contrary to the hypothesis model, in the final model lake area had a direct influence on both vegetation abundance and largemouth bass PSD, ultimately accounting for 26% of the total effects on largemouth bass PSD. Both Secchi depth and DO difference remained as direct influencers of largemouth bass PSD, however vegetation did not have an influence. Additionally, there was a moderate negative covariance between DO difference and Secchi depth (-0.39) which increased their total effects on largemouth

bass PSD. Moreover, there was a relatively strong indirect negative influence of lake area to catchment area ratio which influenced largemouth bass PSD by acting indirectly through Secchi depth and DO difference. The final model fit was accepted based on a robust χ^2 of 8.21 (p = 0.92, df = 17, n = 76).

2.4.2 Largemouth Bass Catch Per Unit Effort Model

The SEM describing largemouth bass CPUE included six of seven potential explanatory factors with vegetation accounting for 39% of the total effects (Figures 2.2 & 2.4). Again, the additional influence of lake area on both vegetation and largemouth bass CPUE improved model fit for the final model. The structure of the two largemouth bass models were somewhat similar, however, there was no direct influence of Secchi depth on largemouth bass CPUE. Further, importantly, there was a direct negative effect of vegetation cover on largemouth bass CPUE. The final model was relatively complex with five variables indirectly influencing largemouth bass CPUE. The final model fit was deemed good based on a robust χ^2 of 12.76 (p = 0.62, df = 15, n = 76).

2.4.3 Bluegill Proportional Stock Density Model

The final bluegill PSD model was not as complex. Over 50% of the total effects on bluegill proportional stock density were attributed to DO difference (Figures 2.2 & 2.5). There were no other direct effects on bluegill PSD. Only two other factors affected bluegill PSD indirectly through DO difference. Lake area and Lake area:catchment area ratio negatively influenced DO difference, and ultimately had a weak negative influences on bluegill PSD (-0.08 and -0.11, respectively). The model fit was acceptable based on a robust χ^2 of 14.18 (p = 0.65, df = 17, n = 78).

2.4.4   Bluegill Catch Per Unit Effort Model

When initially trimming the bluegill CPUE model all paths to bluegill CPUE were removed. Thus, to facilitate development of this model, we retained the three relationships influencing bluegill CPUE throughout the trimming process despite weak effects. Following the evaluation of modification indices, those relationships were subsequently removed. Only three of the potential explanatory variables influenced bluegill CPUE, with local development being the only direct influencer (-0.25), and having the highest percent of the total effects (56%) (Figures 2.2 and 2.6). The final model fit was acceptable based on a robust χ^2 of 10.191 (p = 0.86, df = 16, n = 78).

2.5   Discussion

Though there were many similarities between our hypothesis model and our final models, trimming and addition of variables was required to achieve acceptable model fit. This suggests that though many of the relationships included in the hypothesis model have been studied in a bivariate manner, the context within which these studies take place may have influence on perceived relationships. In particular, we were expecting to see a greater influence of littoral vegetation coverage on fish metrics, however, we only observed an influence of vegetation on largemouth bass CPUE. On average, final models described greater effects of water quality variables (i.e., Secchi depth and DO difference) on fish metrics. By examining multiple predictor variables, and accounting for associations among variables we were able to gain a more complete understanding of interactions and drivers of variation in fish populations across lakes.

Our final models are somewhat less complex than the hypothesis model, however the structure of the data required some fairly consistent additional relationships. For the three models that followed the model evaluation protocol, we added a direct influence of lake area on vegetation.

Additionally, both largemouth bass models included a direct influence of lake area on either PSD or CPUE. This would suggest that lake area was more influential on the abundance of vegetation, and on the population size structure and abundance than we anticipated in our hypothesis model, and ultimately accounted for up to 27% of the total variation in a fish metric (largemouth bass CPUE). Furthermore, with the addition of the influence of lake area on vegetation the effect of local development on fish metrics becomes insignificant, and a strong effect of lake area on local development is added. The strong influence of lake area on local development may explain why there is a weak effect of local development on vegetation in the initial model that is ultimately removed in the final model. Consistent with observations in other areas (Schnaiberg et al. 2002; Dustin and Vondracek 2017), larger glacial lakes in Indiana have more development in their immediate vicinity (unpublished data). More development and human activity will often lead to vegetation removal and more heterogeneous distributions of vegetation (Radomski and Goeman 2001). This pattern is also consistent with the negative, direct influence of percent agricultural and developed land in the catchment on littoral vegetation biovolume, however, does not explain the lack of relationship between local development and vegetation abundance.

Water quality variables (i.e., DO difference and Secchi depth) consistently explained much of the variation in fish population size structure and abundance. Combined they explained 69.2, 22.6 and 58.4 percent of largemouth bass PSD, CPUE and bluegill PSD respectively. Additionally, there was the consistent moderate covariance between the two variables. The covariance between the two variables was likely a result of their proximate measure of lake productivity. Secchi depth can be used to index the trophic state index of a lake (Carlson 1977), a measure of lake productivity. However, Secchi depth can also be influenced by turbidity resulting from suspended sediments (Scheffer et al. 1993). We calculated the difference in DO between the surface and at depth in

efforts to capture net primary productivity, however it too is likely influenced by other in lake processes. The consistent positive relationship of lake area to catchment area ratio with Secchi depth and negative relationship with DO difference is consistent with the idea that these two variables are associated with lake productivity. Lakes with a relatively small catchment area tended to be more clear, and have less of a difference between surface DO and DO at depth (i.e., less net primary productivity). This is consistent with the expectation that lakes with a high lake:catchment area ratio will receive relatively low amounts of sediment and nutrient loadings (i.e., factors potentially contributing to decreased water clarity). Moreover, these influences are consistent with the notion of feedbacks between lake productivity and vegetation in lakes. Rooted vegetation in lakes require light penetration at the substrate to establish and grow (Genkai-Kato and Carpenter 2005), and therefore require a certain level of water clarity. Nutrient uptake of phytoplankton in a system can limit nutrient availability to rooted vegetation, further leading to phytoplankton dominated systems and decreased water clarity (Scheffer et al. 1993). Contrastingly, the opposite also is true, rooted vegetation uptake of nutrients limits availability to phytoplankton leading to clearer water. Moreover, macrophytes can buffer against wave action and sediment resuspension leading to increased water clarity (Carpenter and Lodge 1986). Our models are consistent with these feedbacks, with higher nutrient input seemingly contributing to more phytoplankton production, and a lake with more turbidity and less vegetation coverage.

While we anticipated that vegetation coverage would have a greater effect on fish metric variation, vegetation did not consistently describe variation in largemouth bass or bluegill PSD and CPUE. In fact, vegetation only described variation in largemouth bass CPUE. Past studies have shown that lakes with high vegetation densities generally do not support very abundant largemouth bass populations (Trebitz et al. 1997), which is consistent with the moderate negative

influence of vegetation abundance on largemouth bass CPUE. Similarly, lakes with high vegetation variation and more vegetation edge habitat can favor more abundant largemouth bass populations with larger individuals (Trebitz et al. 1997; Nohner et al. 2018). Overall, the lack of a consistent effect of vegetation abundance on fish population size structure and abundance was surprising. The effect of vegetation on fish has often been studied on both an individual, lake wide, or multi-lake scale (e.g., Savino and Stein 1982; Unmuth et al. 1999; Cheruvelil et al. 2005), however, our models suggest that these effects may be more accurately attributed to broader environmental variation. Cheruvelil et al. (2005) found no evidence for population level effects of vegetation on largemouth bass or bluegill growth, but individual age classes were impacted by vegetation abundance. Our data did not include ages for all captured fish, but had we examined specific age increments we may have seen similar results. The effects of vegetation on individuals observed by others does not appear to translate to the population level, and lake-wide effects may be a result of environmental context.

Our two largemouth bass models are generally consistent with each other, and with observed natural systems. Both models describe a direct effect of lake area on either CPUE or PSD. A positive effect of lake area on largemouth bass PSD implies that larger lakes are better able to support more larger fish, potentially providing more access to the resources needed to support larger fish. The effect on CPUE was expected, as lake area has been shown to be a predictor for relative abundance of largemouth bass (Perry 2011), however, the direction of influence was inconsistent with the results found by Perry (2011). Again, vegetation was only a significant predictor for largemouth bass CPUE, and was the major predictor of largemouth bass CPUE accounting for 39% of the total effects. The negative effect may partially reflect gear bias of electrofishing as it can be more difficult to capture fish in heavily vegetated areas, or it may be

that largemouth bass are not able to forage as well in heavily vegetated environments. The SEMs we developed to describe fish population metrics were generally able to describe a greater proportion of variation for largemouth bass PSD and CPUE, than for bluegill PSD or CPUE.

In the bluegill PSD model, DO difference mediates the effects of all other predictor variables, meaning that there were no direct effects of other variables on bluegill PSD. Thus, the higher order factors that influenced DO difference (i.e., lake area and water clarity), indirectly also influenced bluegill PSD. The importance of lake productivity to bluegill over vegetation was surprising as field and laboratory research has indicated the importance of vegetation for refugia and foraging grounds (Crowder and Cooper 1982; Savino and Stein 1982; Pothoven et al. 1999). Typically dense vegetation has been associated with 'stunted' populations of bluegill, where there are many small fish that are unable to grow beyond a certain point (Swingle and Smith 1942; Trebitz et al. 1997). With the removal of vegetation these populations have seen rebounds in growth, potentially as a result of greater access to resources, and a reduction in intra- and inter-specific competition (Swingle and Smith 1942; Trebitz et al. 1997; Olson et al. 1998). Our models suggest that lake productivity may be more important to the size structure of bluegill rather than the vegetation. Plausibly, bluegill PSD may be more responsive to high water column productivity leading to high zooplankton prey, than they are responsive to vegetation.

Structural equation models can help to identify 'intervention points' where changes at that point may be amplified in either a positive or negative way. Radomski et al. (2019) call for research that quantifies factors, both ecological and anthropogenic, that allow for adaptive management to avoid critical tipping points. The intervention points identified by the models may provide critical insight into factors that may allow for prevention of crossing a tipping point. For the SEMs presented herein, lake productivity (as indexed by DO difference) was an important predictor of

vegetation and both directly and indirectly influenced fish metrics. Thus, lake productivity may be an intervention point where changes in the water clarity or plankton production would impact response variables. Similarly, shallow temperate lakes have been hypothesized to have two alternate stable states impacted by the relationship of water clarity and nutrient input (Scheffer et al. 1993). One state is dominated by turbid water (i.e. an abundance of phytoplankton) and has limited vegetation, the other state is dominated by littoral vegetation and has clearer water. These alternate states are mediated by nutrient inputs which are largely anthropogenically-mediated. By altering land-use practices it is possible to impact the Secchi depth and phytoplankton productivity of a lake and therefore could be an intervention point. Furthermore, there was a direct positive effect of the percent of agriculture and development within the catchment on littoral biovolume in all models. This suggests that the reduction in sediment input as a result of more natural land could increase vegetation and potentially increase water clarity as part of the feedback between vegetation and clarity.

The models presented herein provide a relatively comprehensive picture of the complexity and relatedness of factors influencing vegetation and fish metrics within glacial lakes. Obviously, we were unable to consider all potential factors influencing processes across our study systems, however inclusion of all possible variables increases the possibility of model overfitting. We selected variables in order to capture the potential influence of conditions within lakes (e.g., water clarity), as well as external drivers of these conditions (e.g., nutrient runoff from agricultural area Sass et al. 2010). Our models are a quantitative analysis of the complexity of natural systems and broaden our understanding of the indirect and direct effects on littoral vegetation and fish population size structure and relative abundance. Though our models describe a lack of direct cause and effect relationships between littoral vegetation and fish population metrics, we were able

to attribute more of the variation to other environmental predictors, and better tease apart the specific effects on fish population size structure and relative abundance.

Table 2.1: Direct, indirect and total effects (standardized path coefficients) of each predictor variable on the model response variable for Indiana glacial lakes. Variable abbreviations can be found in Table A.1.

Predictor	LMB PSD			LMB CPUE			BLG PSD			BLG CPUE		
	Direct	Indirect	Total	Direct	Indirect	Total	Direct	Indirect	Total	Direct	Indirect	Total
Lake Area	0.19	-0.07	0.12	-0.35	0.10	-0.25		-0.08	-0.08		-0.14	-0.14
LA:CA		-0.34	-0.34		0.001	0.001		-0.11	-0.11		-0.05	-0.05
Ag-Dev					0.101	0.11						
Local Dev										-0.25		-0.25
DO dif	0.28	0.15	0.43	-0.29	0.13	-0.16	0.27		0.27			
Secchi	-0.38	-0.11	-0.49		0.05	0.05						
Vegetation				-0.36		-0.36						
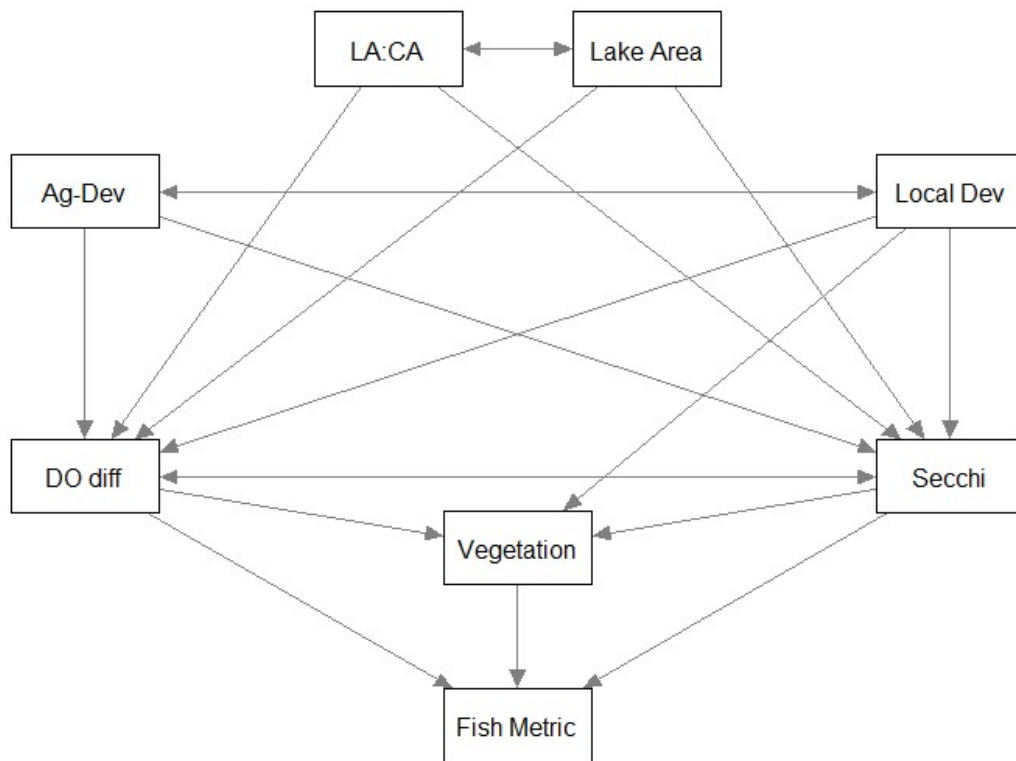
Figure 2.1: Hypothesis model depicting relationships between variables included. Double ended arrows represent a covariance between two variables, while a single ended arrow represents a direct influence between the variables in the direction of the arrow.
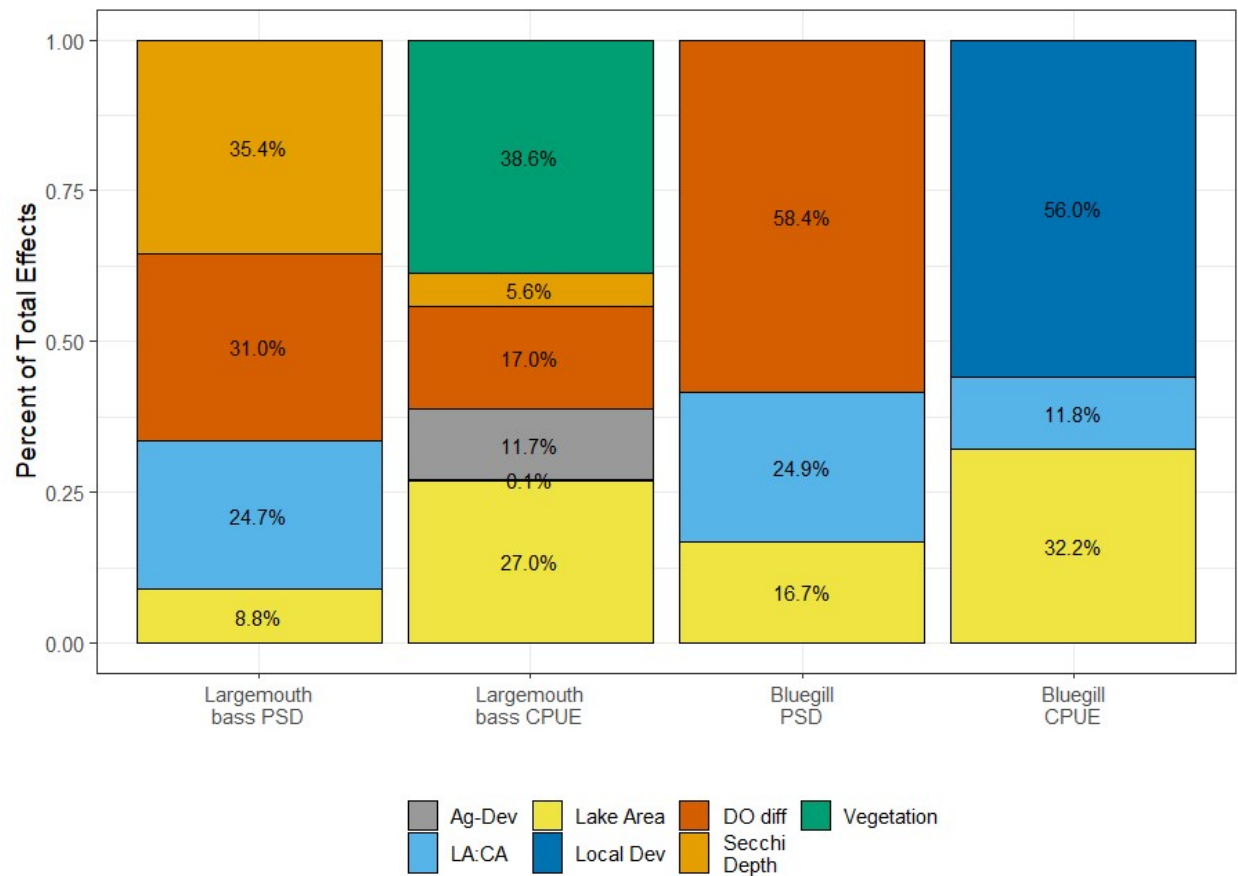
Figure 2.2: Stacked bars representing the percent of the total effects on the given response variable. See Table 1 for a breakdown of the direct and indirect effects of each variable class. Variable abbreviations can be found in Table A.1
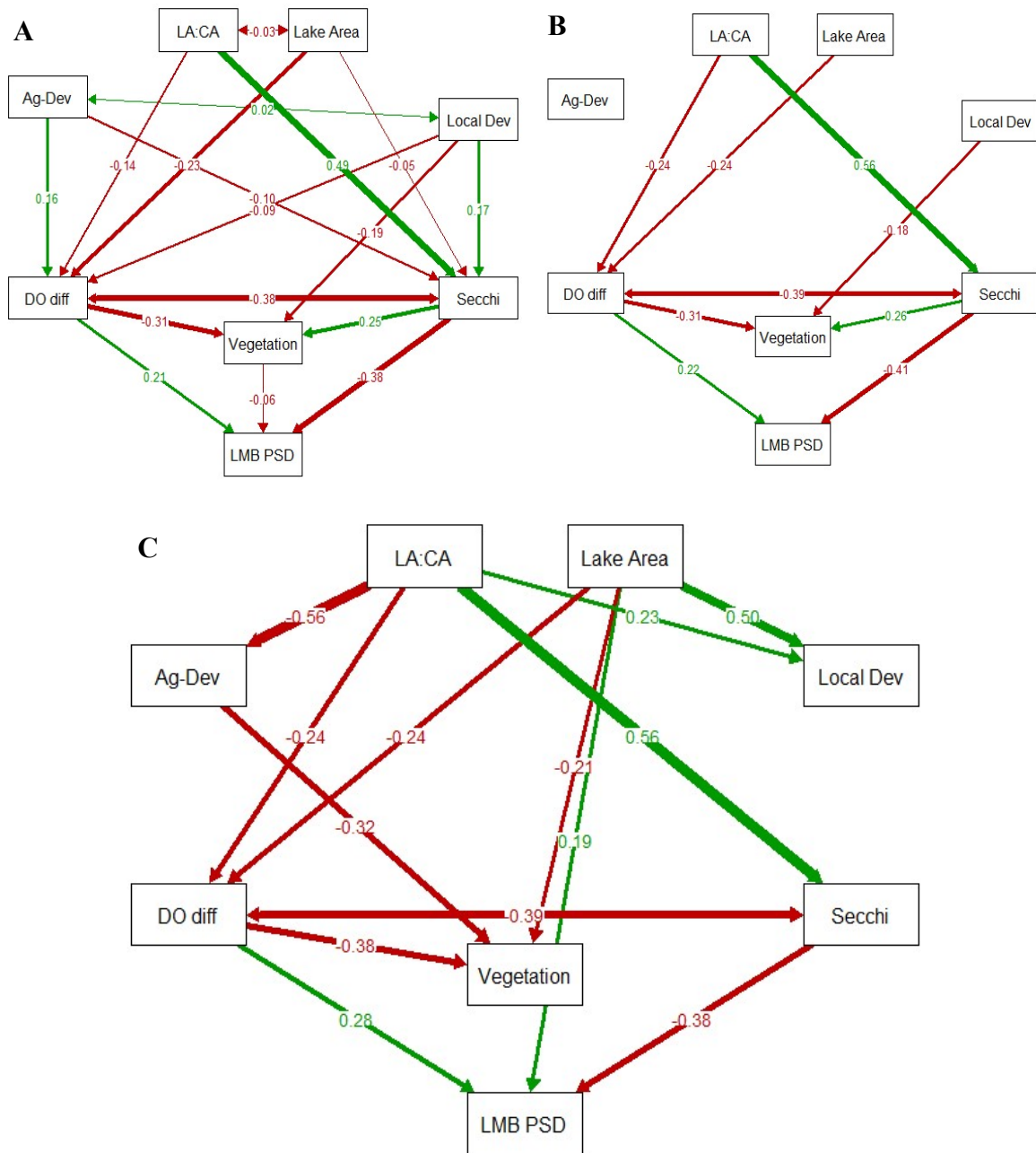
Figure 2.3: Graphical representations of A) initial, B) trimmed and C) final largemouth bass proportional stock density models. Red arrows indicate a negative relationship between the two variables, while a green arrow indicates a positive relationship between the two variables. Numbers represent standardized path coefficients, width of the arrows is scaled with the absolute value of the path coefficient. Individual model fit metrics can be found in Table A.3.
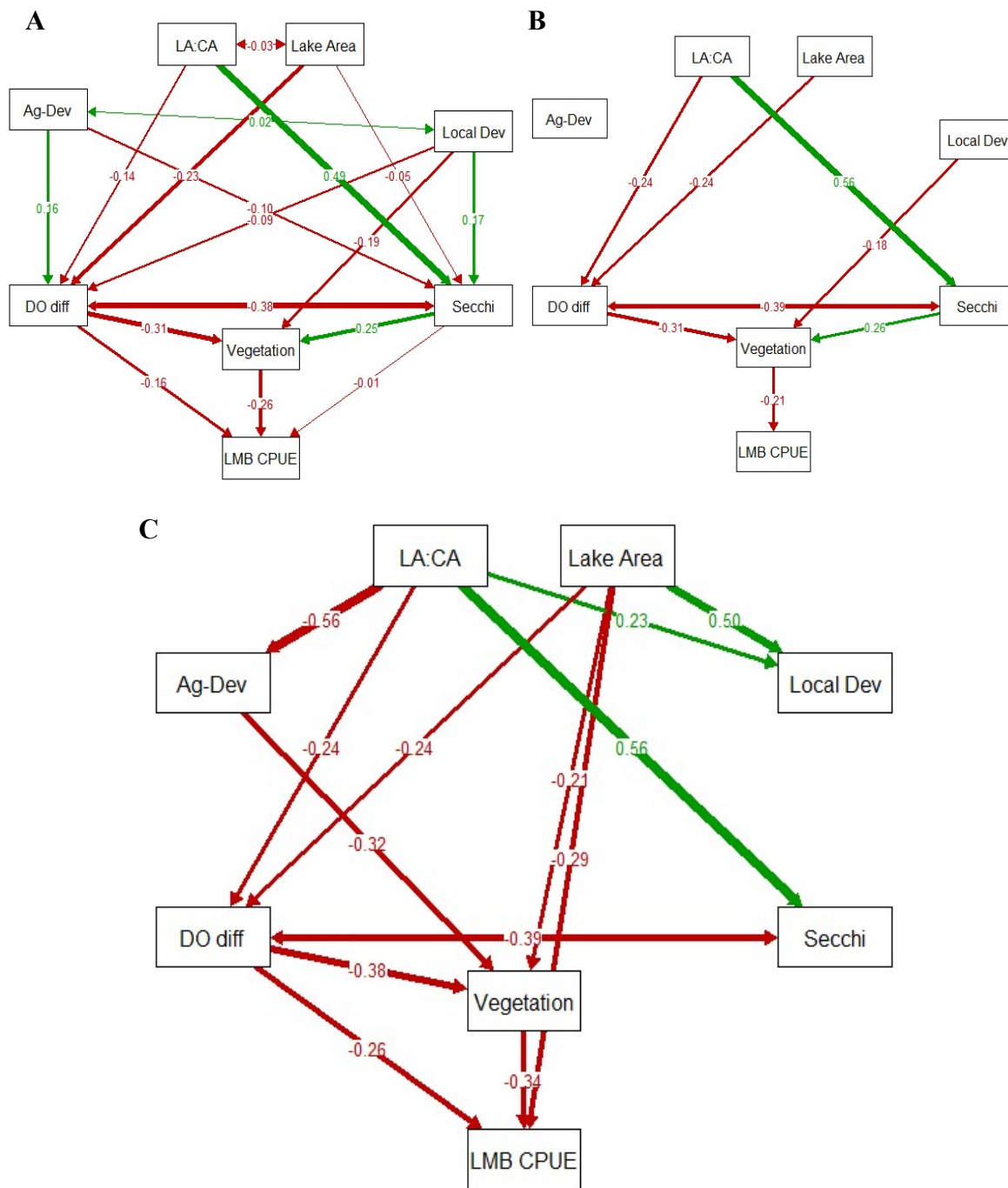
Figure 2.4: Graphical representations of A) initial, B) trimmed and C) final largemouth bass catch per unit effort models. Red arrows indicate a negative relationship between the two variables, while a green arrow indicates a positive relationship between the two variables. Numbers represent standardized path coefficients, width of the arrows is scaled with the absolute value of the path coefficient. Individual model fit metrics can be found in Table A.3.
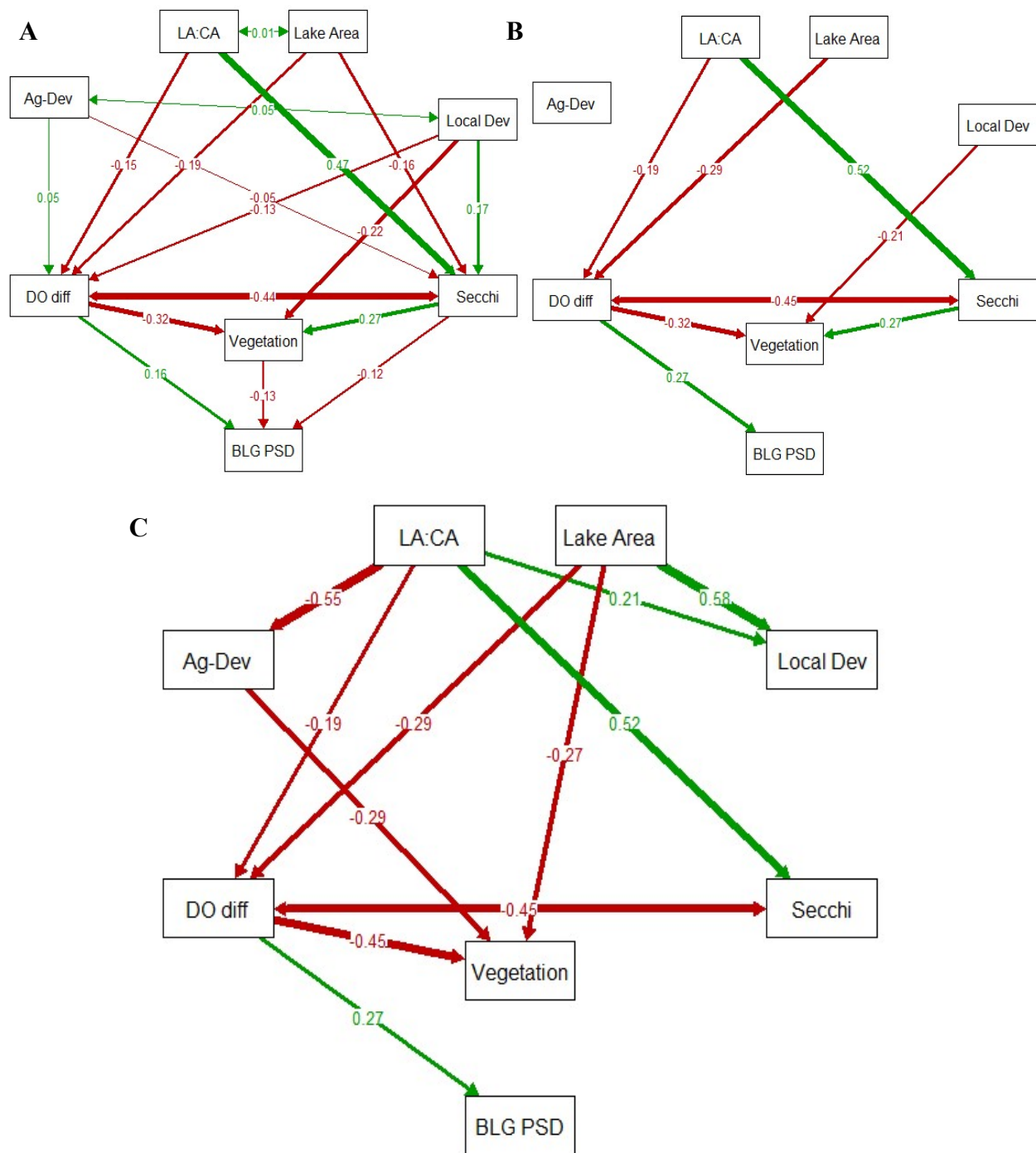
Figure 2.5: Graphical representations of A) initial, B) trimmed and C) final bluegill proportional stock density models. Red arrows indicate a negative relationship between the two variables, while a green arrow indicates a positive relationship between the two variables. Numbers represent standardized path coefficients, width of the arrows is scaled with the absolute value of the path coefficient. Individual model fit metrics can be found in Table A.3.
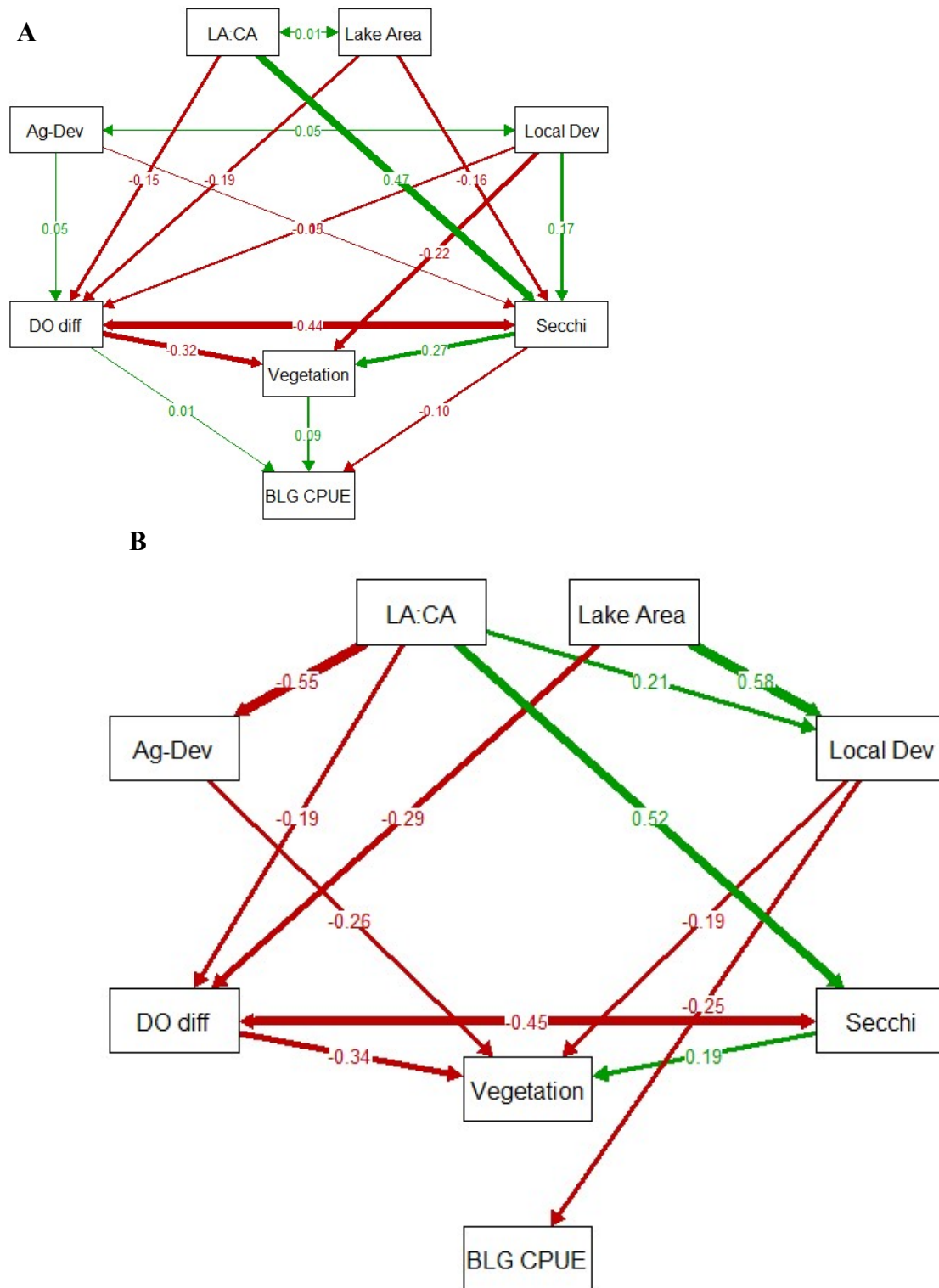
Figure 2.6: Graphical representations of A) initial, B) final bluegill proportional stock density models. Due to a different modeling style there is no trimmed model. Red arrows indicate a negative relationship between the two variables, while a green arrow indicates a positive relationship between the two variables. Numbers represent standardized path coefficients, width of the arrows is scaled with the absolute value of the path coefficient. Individual model fit metrics can be found in Table A.3.

CHAPTER 3.   LOCAL RESOURCE RELIANCE OF YOUNG-OF-YEAR LARGEMOUTH BASS *MICROPTERUS SALMOIDES* IN GLACIAL LAKES

3.1   Abstract

The degree of movement among heterogeneous habitats affects the conditions experienced by individuals, and may result in differences in performance across individuals. Often habitat use patterns change throughout the lifetime of an individual, thus conservation efforts may benefit from a better understanding of habitat use and resource reliance during critical life stages. The habitat use of juvenile fishes may have implications for overall population success as the juvenile stage is frequently a bottleneck to recruitment. Furthermore, we suggest that the extent to which fish rely on local versus lake-wide resources will have important implications for how they respond to patchy habitat alterations. 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 items across three study components, a controlled pond experiment, a multi-lake survey and a detailed single-lake survey. Across all three study components, we observed habitat- and site-fidelity of YOY largemouth bass in mid-summer, demonstrated by spatial differences in young bass stable isotope signatures. Additionally, there were significant, positive relationships between site means of δ^{13}C of YOY largemouth bass and δ^{13}C means of locally collected prey items, suggesting localized foraging. Later in the summer, spatial differences in largemouth bass stable isotope ratios and relationships with potential prey isotope ratios were non-significant, indicating more spatially-integrated foraging as the YOY largemouth bass switch to piscivory. During the critical first summer of life, prior to the 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 would suggest that conservation of habitat patches, as opposed to removal of wide swaths of vegetation, may preserve access to important foraging and refuge habitat.

3.2   Introduction

Movement among heterogeneous habitat types has the potential to affect the performance of individual fish based on the energy exerted, and access to resources (Rice et al. 1983; Law and Dickman 1998; Humston et al. 2005; Höök et al. 2008). Mobile individuals may integrate resources and conditions across multiple habitats. Alternatively, relatively sedentary individuals that exhibit site fidelity will experience stronger influences of local conditions, with different individuals potentially experiencing distinct environments. 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. 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, using chemical analyses, such as quantification of stable isotope ratios, 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

and Waldron 2000; Soto et al. 2013). Stable isotope ratios provide a relatively long-term index of the habitat occupancy and foraging history of an individual. 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 and Fry 2003). 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). 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). Differences in various stable isotope ratios have also been used in both terrestrial (Rubenstein and Hobson 2004) and aquatic (e.g., McCarthy and Waldron 2000) systems to determine habitat use. Past research has demonstrated intra-specific spatial variation in carbon and nitrogen stable isotope ratios of invertebrates and fishes within small aquatic systems, such as lakes (Syväranta et al. 2006; Brauns et al. 2011). Thus, measurement of stable isotope ratios may be an effective and efficient method to determine site fidelity and habitat usage of individuals, even in relatively small systems.

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 the nearshore area, ranging from natural to highly developed armored shorelines with minimal vegetation. As development along the shoreline increases, the abundance of natural structures, such as large woody debris and stands of aquatic macrophytes, generally decreases (Bryan and Scarnecchia 1992; Radomski and Goeman 2001; Jennings et al. 2003; Francis and Schindler 2006; Dustin and Vondracek 2017). 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 (Savino and Stein 1989a; Weaver et al. 1997; Middaugh et al. 2013), 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 (Roberge and Angelstam 2004). While largemouth bass utilize 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 and Sass 2011). A critical bottleneck in recruitment of largemouth bass to adulthood is the first winter of life; therefore, the first summer of growth is imperative to their survival (Ludsin and DeVries 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 and Noble 1994; Irwin and Noble 2000; 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, remaining in certain habitats has 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

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forming 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.

The objective of this study was to evaluate if individual YOY largemouth bass move extensively among littoral habitats or if they make use of more localized resources, thereby creating population compartments. To this end, we used $\delta^{13}C$, $\delta^{15}N$, δ^2H 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. We expected that YOY largemouth bass exhibit limited movement among different habitats and that distinct areas of lakes would be characterized by different environmental stable isotope ratios. Thus, we hypesized that YOY largemouth bass would exhibit spatially distinct stable isotope ratios, related to locally collected potential prey items and water.

3.3   Methods

The following methods were approved by the Purdue Animal Care and Use Committee under the protocol number 1803001695.

3.3.1 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 reproducing populations of largemouth bass at the Indiana Department of Natural Resources Driftwood State Fish Hatchery. Upon acquisition, the 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 1000 m^2 with a mean depth of 1.8 m. We simulated three habitat types within the cages: vegetated, non-vegetated, and large woody debris (24 cages total, 8 of each habitat type). We utilized 1 m*1 m*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 two weeks prior to the experiment and allowed them to be colonized by invertebrates in the ponds. We established the vegetated treatments by placing 2 large natural slate tiles (30.48 cm*60.96 cm) and 12 vegetation analogs (25 cm*1.27 cm sisal rope) two weeks prior to the experiment and allowing them to be colonized 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 placed the cages such that the shallowest point was less than 1 meter deep and less than 2 meters from the shore. On 18 June 2018, we added twenty fish (31 ± 3 mm standard length, mean ± sd) to each cage. To minimize the depletion of prey items within the cages, we moved the cages bi-weekly to a new substrate area that had not previously had a cage (roughly 1.5 m each movement), and ended the experiment after four weeks. A prior study using similar cages at the ARL demonstrated that YOY yellow perch *Perca flavescens* will survive and grow within a similar caged environment.

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Given the small size and rapid growth of YOY largemouth bass, we believed 4 weeks was sufficient to detect isotopic differentiation.

At the end of the experiment (16 July 2018), we removed individual largemouth bass, measured standard length (to the nearest mm), wrapped them in aluminum foil and placed the fish on ice until we returned to the lab and froze them in a -80° C freezer for subsequent analyses (see Stable Isotope Analysis). To characterize mean water isotopes, we collected water samples at the midpoint 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 minimize air bubbles. To minimize 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 prey isotope composition, at the end of the experiment we took dip-net samples of available prey items at the midpoint location for each cage using the bounce and sweep technique (Lowe et al. 2016). We concentrated two samples from the same location into 60 mL WhirlPaks and placed the samples on ice until we returned to the lab and froze the samples at -80° C for subsequent analyses.

3.3.2   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), Big (Noble County), Dewart (Kosciusko County), and Waubee (Kosciusko County) (Figure 3.1a). We sampled two additional lakes (Knapp and Robinson), however, due to insufficient catches within these two lakes they were not included in analyses. We attempted to sample the same sites as Middaugh et al. (2013), with each lake including two sites with limited

macrophytes (0-10% coverage) and two sites with high densities of macrophytes (40-100% coverage) and a minimum distance of 50 m between sites. If site conditions were deemed unsafe for sampling or if macrophyte density coverage had changed since earlier surveys (Middaugh et al. 2013), we chose a new representative site. Lakes and sites were selected based on Middaugh et al. (2013) sampling efforts to maximize potential for sufficient capture.

At each site, we sampled fish using a 3.05 meter seine, 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 ten age-0 largemouth bass in these two passes, more passes in the same area were performed until at least ten YOY largemouth bass were collected, or there were three seine passes with no YOY largemouth bass collected. We wrapped YOY largemouth bass in aluminum foil and froze them (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 measured standard length (to the nearest mm) by photographing thawed fish and a ruler using a Panasonic LUMIX DMC-TS5 camera and measured length using image analysis software (ImageJ). In addition, we analyzed YOY largemouth bass for stomach contents. We thawed fish, removed their stomachs and preserved the stomachs in 80% ethanol for at least 48 hours. Under a dissecting microscope, we identified and enumerated distinct prey items to the lowest taxonomic level possible (typically order or family).

3.3.3 Detailed Single Lake Survey

For the final component, we narrowed our scope to Crooked Lake, a relatively well-studied lake in Noble and Whitley Counties, IN (e.g., Konopka 1982; Pearson 2000) (Figure 3.1c). During 2018, we examined stable isotope ratios of YOY largemouth bass across multiple sites and time periods, i.e., when YOY largemouth bass are of different mean size and may differentially utilize habitats and resources (24-25 July and 23 August). In addition, we characterized the isotopic composition of prey and water at these sites. We selected three vegetated and three non-vegetated sites (Figure 3.1c). We sampled these sites at two time points using a seine in a similar manner to the multi-lake survey, additionally we used a barge electroshocker (Smith-Root Generator Power Puslator Model 5) with one probe and two netters. We seined and electroshocked until a sufficient number of YOY largemouth bass were collected, or none had been captured in ten minutes of sampling. Upon collection we measured standard lengths (to 1 mm) of largemouth bass, wrapped individuals in aluminum foil and stored samples at -80° C.

Coincident with largemouth bass collections, we collected prey items and water from each collection site in a similar manner to the caged experiment. Again, we used the bounce and sweep technique to collect invertebrates (Lowe et al. 2016), and collected and stored water samples in parafilm sealed, 20mL glass or plastic scintillation vials.

3.3.4 Stable Isotope Analysis

In the laboratory, we thawed YOY largemouth bass, measured mass (to the nearest 0.01 g) and removed muscle fillets 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 fish per cage or site per sampling period at 60°C for at least 48 hours. We then manually homogenized the tissue using a metal spatula by scraping the tissue between two weigh papers. We packed the

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 δ^2H analyses. We thawed the concentrated invertebrate samples and sorted them into the major taxonomic orders. Invertebrates were dried at 60°C for at least 48 hours. Within taxonomic orders, we grouped individuals as necessary to obtain sufficient biomass. These groups were homogenized similarly to the fish tissue and packed 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.

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 to a NC2500 elemental analyzer. For tissue samples, O and H stable isotopes were measured using a Thermo Delta V IRMS interfaced to 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 to a Gas Bench II. All isotope ratios ($\delta^{13}C$, $\delta^{15}N$, δ^2H 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 analyzed with samples (for carbon and nitrogen analyses). For hydrogen and oxygen, Kudu hair, internal keratin and Caribou hair served as standards. Across all jobs the mean standard deviation of internal standards for C was 0.09‰, for N was 0.08‰, for solid O was 0.4‰, for solid H was 2.865‰, for water O was 0.10‰ and for water H was 2.92‰.

3.3.5 Statistical Analyses

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

3.3.5.1 Habitat- and Site-Specific Variation in YOY largemouth bass

To determine if there were overall differences in stable isotope ratios (δ^{13}C, δ^{15}N, δ^{18}O and δ^2H) of YOY largemouth bass between habitats and sites within individual systems we used a Multivariate Analysis of Covariance (MANCOVA) with individual length as a covariate. If there were significant effects of any of the three predictor variables, we then used individual Analyses of Covariance (ANCOVAs) to better understand 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 expected that stable isotope baselines would be different across systems, so each system was analyzed independently. Additionally, in the detailed single-lake survey we analyzed samples taken at different sampling periods separately in order to examine how isotopic variation among habitats and sites changed as the fish aged.

3.3.5.2 Habitat- and Site-Specific Variation in Potential Prey Items and Water

We used taxa-specific ANOVAs to examine habitat- and site-specific differences in δ^{13}C and δ^{15}N ratios of potential prey items 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 Odonata,

Chironomidae, and Ephemeroptera. 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. Additionally, we collected a relatively large number of YOY bluegill *Lepomis macrochirus* via seining and electroshocking. We included bluegill in our stable isotope analysis as we found YOY bluegill in the stomach contents of the YOY largemouth bass in the multi-lake survey.

We used ANOVAs to determine if there were habitat- and site-specific differences in δ^2H 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 site (nested within habitat) as predictors. For the detailed single-lake survey, we were unable to analyze the samples separately by time, so we analyzed all samples collected within that lake using habitat and time (as opposed to site) 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 relationships between stable isotope ratio site means of YOY largemouth bass and corresponding stable isotope ratio site (or cage) means of individual potential prey taxa and water.

3.4   Results

3.4.1   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. We know there was some escapement due to finding individuals in the ponds post caging. However, some young bass likely also died in cages and we were unable to distinguish the numbers lost to escapement versus mortality.

There were strong habitat (empty, large woody debris and vegetated; ARL: $F_{2, 44} = 7.98$, P <0.001; PRC: $F_{2, 51} = 10.11$, P <0.001) and cage (nested within habitat; ARL: $F_{7, 44} = 2.35$, P <0.001; PRC: $F_{6, 51} = 6.64$, P <0.001) differences in YOY largemouth bass stable isotope ratios in both the ARL and the PRC ponds (Figure 3.2). Standard length was a significant positive covariate of stable isotope ratios for both ponds, though it was a stronger covariate in the PRC pond (ARL: $F_{1, 44} = 2.67$, $P = 0.045$; PRC: $F_{1, 51} = 62.82$, P <0.001). In both ponds $\delta^{13}C$ of largemouth bass was significantly different between habitats (ARL: $F_{2, 44} = 4.97$, $P = 0.01$; PRC: $F_{2, 51} = 23.33$, P <0.001) and cages (ARL: $F_{7, 44} = 3.58$, $P = 0.004$; PRC: $F_{6, 51} = 30.69$, P <0.001), with standard length as a significant covariate (ARL: $F_{1, 44} = 5.76$, $P = 0.02$; PRC: $F_{1, 51} = 132.35$, P <0.001). Though there were 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. $\delta^{15}N$ was only different by habitats in the ARL pond ($F_{2, 44} = 5.98$, $P = 0.005$), there were no significant differences in the PRC pond. In contrast, δ^2H stable isotope ratios of largemouth bass varied only within the PRC pond, and varied by habitat ($F_{2, 51} = 4.26$, $P = 0.02$) and cage ($F_{6, 51} = 6.54$, P <0.001) with standard length as a significant covariate ($F_{1, 51} = 15.55$, P <0.001). Relative enrichment of ^{18}O varied in both ponds across habitats (ARL: $F_{2, 44} = 13.54$, P <0.001; PRC: $F_{2, 51} = 19.87$, P <0.001), and cages (ARL: $F_{7, 44} = 3.97$, P 0.002; PRC: $F_{6, 51} = 19.64$, P <0.001), but standard length was only a significant covariate in the PRC pond ($F_{1, 51} = 19.51$, P <0.001). 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

δ^{18}O values in PRC and ARL, respectively. All unreported statistics can be found in Tables B.1 –

B.3.

We compared spatial variation (habitat and site nested within habitat) in δ^{13}C and δ^{15}N of

three potential invertebrate prey (Chironomidae, Ephemeroptera and Odonata) within the two

research ponds (PRC and ARL). There were no significant differences between habitat or sites for

either δ^{13}C or δ^{15}N in any of the potential prey items within the ARL pond (Figure 3.3). However,

there was spatial variation between potential prey items within the PRC pond (Figure 3.3). δ^{13}C of

Chironomidae, Ephemeroptera and Odonata were not significantly different by habitats, but all

three were significantly different among sites ($F_{9, 24} = 3.61$, $P = 0.006$; $F_{9, 23} = 6.18$, $P < 0.001$; $F_{9, 24} = 9.01$, $P < 0.001$, respectively). Mean δ^{15}N of Ephemeroptera was significantly different among

both habitats and sites ($F_{2, 23} = 4.56$, $P = 0.02$; $F_{9, 23} = 2.83$, $P = 0.02$, respectively). The stable

isotope ratios of δ^{18}O and δ^{2}H of the locally collected water were never significantly different

among habitats or sites in either the ARL or the PRC pond.

Within the PRC pond δ^{13}C of Ephemeroptera and Odonata were both significantly,

positively related to mean site δ^{13}C of YOY largemouth bass (adjusted $R^2 = 0.50$, one-tailed $P = 0.01$; $R^2 = 0.45$, $P = 0.01$, respectively; Figure 3.5a). Similarly, δ^{13}C of Ondonata and δ^{13}C of YOY

largemouth bass within the ARL pond were positively, significantly correlated ($R^2 = 0.24$, $P = 0.04$; Figure 3.4a). In addition δ^{15}N of Odonata and δ^{15}N of YOY largemouth bass within the PRC

pond were positively, significantly correlated ($R^2 = 0.26$, $P = 0.046$; Figures 3.4b). None of the

relationships between δ^{18}O or δ^{2}H of locally collected water and corresponding values of YOY

largemouth bass δ^{18}O or δ^{2}H in either pond were significant (Figures 3.4c&d and 3.5c&d).

3.4.2   Multi-lake survey

A total of 65 YOY largemouth bass were collected from four lakes in August 2017: Adams, Big, Dewart, and Waubee (Figure 3.1b). Catch per unit effort was variable among both sites and lakes (Table 3.1). 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 3.1) 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 (Figure B.1). Vegetation abundance varied within and among lakes, ranging from 5 to 100% vegetated (Table 3.2). The average slope of sites across all four lakes was 0.30 (m/m).

Stable isotope ratios of YOY largemouth bass varied between habitat types in Adams, Big and Dewart Lakes (MANCOVA: $F_{1, 19} = 8.74$, $P = <0.001$; $F_{1, 6} = 24.48$, $P = 0.01$; $F_{1, 8} = 11.72$, $P = 0.01$, respectively), but there were only significant differences between sites (nested within habitat) in Dewart ($F_{1, 8} = 31.33$, $P < 0.001$) and standard length was a significant covariate in Big and Dewart ($F_{1, 6} = 11.07$, $P = 0.04$; $F_{1, 8} = 9.67$, $P = 0.01$, respectively) (Figure 3.6).

$\delta^{13}C$ and δ^2H 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 ($F_{1, 19} = 33.29$, P $= <0.001$; $F_{1, 6} = 18.04$, P $= 0.005$, respectively). Largemouth bass δ^2H varied between habitats in Adams, Big and Dewart Lakes ($F_{1, 19} = 7.36$, P $= 0.01$; $F_{1, 6} = 10.18$, P $= 0.02$; $F_{1, 8} = 10.12$, P $= 0.01$, respectively), and among sites in Dewart ($F_{1, 8} = 61.77$, P <0.001). $\delta^{15}N$ and $\delta^{18}O$ stable isotope ratios were only significantly different between habitats in Adams Lake ($F_{1, 19} = 19.76$, P <0.001) and Big Lake ($F_{1,}$

$_6 = 9.63$, P $= 0.02$), respectively. Standard length was only a significant covariate for δ^2H in Dewart Lake.

3.4.3 Detailed Single-Lake Survey

We collected 63 YOY largemouth bass in Crooked Lake during two time points in 2018, 44 in July (44.2 mm $\pm$ 6.2; 1.5 g $\pm$ 0.8) and 19 in August (66.1 mm $\pm$ 12.9; 4.5 g $\pm$ 3.0). During July, stable isotope ratios of YOY largemouth bass varied strongly by site ($F_{4, 37} = 3.47$, $P < 0.001$), weakly by habitat ($F_{1, 37} = 4.91$, $P = 0.003$), and standard length was a significant covariate ($F_{1, 37} = 16.19$, $P < 0.001$; Figure 3.7a&b). While there were weak habitat-specific differences for largemouth bass δ^{15}N, δ^{18}O and δ^2H ($F_{1, 37} = 20.40$, 4.69 and 5.42, respectively; $P = 0.03$, 0.04 and 0.02, respectively), δ^{13}C of largemouth bass did not vary by habitat. Rather, δ^{13}C of YOY largemouth bass varied strongly by site (nested within habitat; $F_{4, 37} = 8.14$, $P < 0.001$), with a weak effect of individual standard length ($F_{1, 37} = 7.92$, $P = 0.01$). Standard length was also a strongly significant covariate of δ^{15}N ($F_{1, 37} = 20.40$, $P < 0.001$). 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 3.7c&d).

For the two separate sampling periods (July and August), we compared spatial variation (habitat and site nested within habitat) of δ^{13}C and δ^{15}N of three potential invertebrate prey (Amphipoda, Ephemeroptera and Odonata) and one fish prey (YOY bluegill). In general, spatial differences were far more apparent for δ^{13}C as compared to δ^{15}N (Figure 3.8). During July collections, δ^{13}C of Amphipoda and Odonata varied by habitat ($F_{1, 18} = 35.65$, $P < 0.001$; $F_{1, 10} = 25.81$, $P < 0.001$, respectively), δ^{13}C varied strongly by site for Amphipoda, Bluegill and Ephemeroptera ($F_{4, 18} = 17.96$, $P < 0.001$; $F_{1, 17} = 11.81$, $P < 0.001$; $F_{3, 9} = 27.19$, $P < 0.001$, respectively) and δ^{13}C of Odonata varied weakly by site ($F_{3, 10} = 12.06$, $P = 0.001$). δ^{15}N was only

weakly significantly different between habitat types for Amphipoda ($F_{1, 18}$ = 5.10, P = 0.04), and never by site. Similarly, during the August collections, $\delta^{13}C$ varied by habitat and site for Amphipoda and Odonata (Habitat: $F_{1, 18}$ = 65.43, P <0.001, $F_{1, 16}$ = 23.15, P <0.001; Site: $F_{4, 18}$= 22.02, P <0.001; $F_{4, 16}$ = 19.36, P < 0.001, respectively). $\delta^{15}N$ was only weakly significantly different between habitats for Amphipoda and Odonata ($F_{1, 18}$ = 6.31, P = 0.02; $F_{1, 16}$ = 6.40, P = 0.02, respectively), and among sites for Amphipoda and Ephemeroptera ($F_{4, 18}$ = 4.13, P = 0.02; $F_{4, 8}$ = 3.97, P = 0.046, respectively). There were no significant differences between habitats or time periods for either $\delta^{18}O$ or δ^2H of water.

During July, mean site $\delta^{13}C$ of all potential prey types were significantly, positively related to corresponding $\delta^{13}C$ of locally collected YOY largemouth bass (Amphipoda: adjusted R^2 = 0.67, P = 0.01; Ephemeroptera: R^2 = 0.54, P =0.048; Odonata: R^2 = 0.77, P =0.02; Bluegill: R^2 = 0.47, P =0.04 respectively; Figure 3.9a). In contrast, during July site-specific mean $\delta^{15}N$, δ^2H and $\delta^{18}O$ of YOY largemouth bass was not related to corresponding $\delta^{15}N$ values of potential prey, nor δ^2H and $\delta^{18}O$ values of locally-collected water (Figure 3.9 b-d). Based on August collections there was only one significant relationship between $\delta^{13}C$, $\delta^{15}N$, δ^2H 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 δ^2H and $\delta^{18}O$ values of locally-collected water ($\delta^{15}N$ of Ephemeroptera adjusted R^2 = 0.82, P = 0.03). However, of note, sample sizes for these relationships were lower during August (4 sites with sufficient data for comparison) as compared to July (6 sites).

3.5 Discussion

Across the three study components we observed differences in YOY largemouth bass stable isotope signatures among habitats and sites, suggesting that young largemouth bass forage

within a limited area and that the resources supporting YOY largemouth bass growth vary with habitat. When confined to a specific habitat, as in the controlled pond experiment, YOY largemouth bass relatively rapidly develop habitat- and site-specific stable isotope signatures, that correlate with local environmental stable isotope ratios (i.e., $\delta^{13}C$ of potential prey). 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.

We were able to detect site- and habitat-specific stable isotope differences 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 (MacNeil et al. 2006; Coulter et al. 2017). In natural systems, several studies that have examined 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 lend to differences in stable isotope ratios of lower trophic level (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., Syväranta et al. 2006; Brauns et al. 2011). 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 macroinvertebrate, perch *Perca fluviatilis* and roach *Rutilus rutilus*. They attributed spatial variation in stable isotope ratios to unique characteristics such as, the presence of a harbor 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. 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, these results reinforce the potential for relatively sedentary individuals to develop stable isotope ratios that reflect highly-localized prey utilization.

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). This ratio can be used as a proxy for the amount of allochthonous inputs from the catchment (e.g., sediments and nutrients; Honsey et al. 2016). Using catchment area presented in Perry (2011) we found that lakes that had a larger catchment relative to lake size (e.g., Big and Waubee LA:CA 0.04 and 0.03, respectively) had lower $\delta^{13}C$ and $\delta^{2}H$ relative to lakes that had smaller catchments relative to lake size (e.g., Adams and Dewart LA:CA 0.12 and 0.13, respectively), which is consistent with measured allochthonous and autochthonous sources of $\delta^{13}C$ and $\delta^{2}H$ (Karlsson et al. 2012). The inherent differences in lake morphologies, and thus baseline stable isotope ratios make direct comparisons of inter-habitat differences among lakes difficult. These across lake differences are partially why we analyzed patters in stable isotope ratios one lake at a time.

There were some consistencies in the specific stable isotopes 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; which has shown to vary spatially, potentially as a product of variation in dominant primary production sources across habitat types (McMahon et al. 2005; Brauns et al. 2011). Hydrogen stable isotope ratios are influenced up to 70% by the stable isotope ratios of diet items (Soto et al. 2013) and this spatial variation in δ^2H of largemouth bass likely primarily reflects differences in prey and not water δ^2H (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 base of the 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 linear relationships between $\delta^{13}C$ of potential prey items and young 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 are foraging within a smaller area, and not foraging homogeneously across nearshore habitats.

Though δ^2H and $\delta^{13}C$ tended to vary spatially among largemouth bass more than $\delta^{15}N$ and $\delta^{18}O$, the direction 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 the empty cage had a lower mean $\delta^{13}C$ than the large woody debris and vegetated cages, but in the PRC pond the empty cage had a higher mean $\delta^{13}C$ than the other two habitat types). Within the

multi-lake survey there was also limited consistency in how 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 $\delta^{13}C$ and δ^2H values at non-vegetated sites as compared to vegetated sites (Doucett et al. 2007). However, we did not consistently observe this pattern and there was no consistent pattern in terms of how stable isotope ratio values of largemouth bass varied across non-vegetated and vegetated sites.

Across all three study components there were very few habitat or site differences in $\delta^{15}N$ of YOY largemouth bass. While $\delta^{15}N$ of producers may vary somewhat with different allochthonous inputs into different areas of a system, $\delta^{15}N$ of consumers is also reflective of trophic level (given ~3.4‰ fractionation per trophic level; Post 2002). While $\delta^{15}N$ varied across potential prey types, there was limited spatial variation in $\delta^{15}N$. We may have expected to see a decrease in $\delta^{15}N$ 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 $\delta^{15}N$ values would likely reflect feeding at different trophic levels. To this point, we did observe a positive relationship between individual largemouth bass length and $\delta^{15}N$ values in Crooked Lake. Further, $\delta^{15}N$ of largemouth bass increased in Crooked Lake from the early sampling period to the later sampling period, consistent with feeding at a higher a trophic level.

Hydrogen stable isotope ratios of consumers, while related to the ambient water, are largely influenced by dietary sources of hydrogen, with approximately 30% and 70% contribution of ambient water and diet to fish tissue δ^2H, respectively (Soto et al. 2013). Given habitat- and site-specific differences in YOY largemouth bass stable isotope ratios were stronger and more common

for $\delta^{13}C$ and δ^2H (as opposed to $\delta^{15}N$ or $\delta^{18}O$), our data suggest that the observed spatial variation in YOY largemouth bass stable isotope ratio values primarily reflect spatial differences in prey isotopic composition. Further, we observed very few habitat or site specific differences in YOY largemouth bass $\delta^{18}O$, which is primarily a reflection of $\delta^{18}O$ of ambient water (Soto et al. 2013). This observation is consistent with limited within-system spatial variation in water stable isotope ratios.

Later in the summer there were limited habitat-, and site-specific differences in stable isotope ratios 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. Later in the summer, there were still significant differences in potential prey items between both habitats and sites, suggesting that the largemouth bass are moving more extensively between habitats and sites and thereby experiencing more integrated foraging conditions. Larger fish are likely less susceptible to predation and thus able to be more active foragers, and utilize 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 $\delta^{15}N$ 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 signatures, YOY largemouth bass are likely using small foraging areas despite being able to use more of the nearshore environment. Furthermore, the impacts of actions undertaken by individual lakeshore landowners to alter nearshore areas (i.e. vegetation 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. 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., Worm et al. 2006; Schindler et al. 2010; Waldman et al. 2016) 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 and DeVries 1997). The growing period prior to the shift to piscivory is crucial as without an 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 heterogeneous trophic reliance within populations to more homogeneous trophic reliance, suggesting the benefit of diverse habitat mosaics. The implications of habitat heterogeneity and dispersal of individuals have long been a topic of study, as very few systems are truly homogeneous (McMurtrie 1978). Heterogeneous habitats provide access to different resources within a system, which many vertebrate species require (Law and Dickman 1998). Ontogenetic shifts in habitat use have been found in a wide variety of organisms based on changing needs throughout the life of an individual (Law 1991; Lind and Welsh 1994). Often habitat requirements

of juveniles differ and are narrower than needs of adults. Understanding habitat use during the juvenile stage provides an important insight into the benefit of heterogeneous habitats.

Table 3.1: Multi-Lake survey site information based on sampling during 2017. Site 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 millimeter using Image-J software.

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
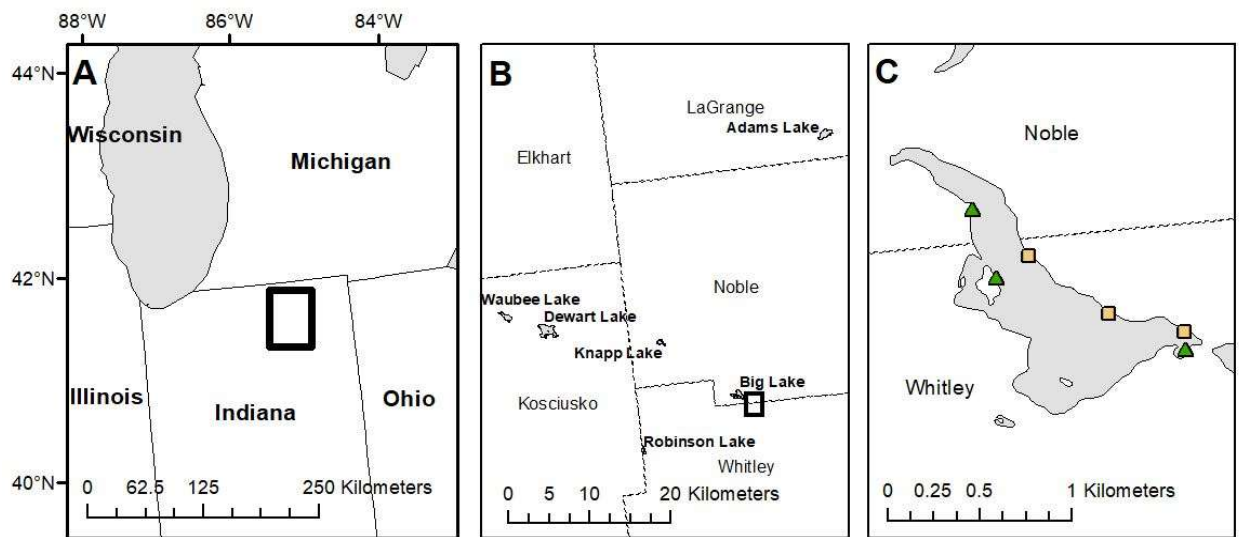
Figure 3.1: A) Location of study lakes. Black box represents the extent of map B. B) Multi-Lake survey lakes. Black box represents the extent of map C. C) Crooked Lake sampling points (green triangle = vegetated; gold square = non-vegetated).
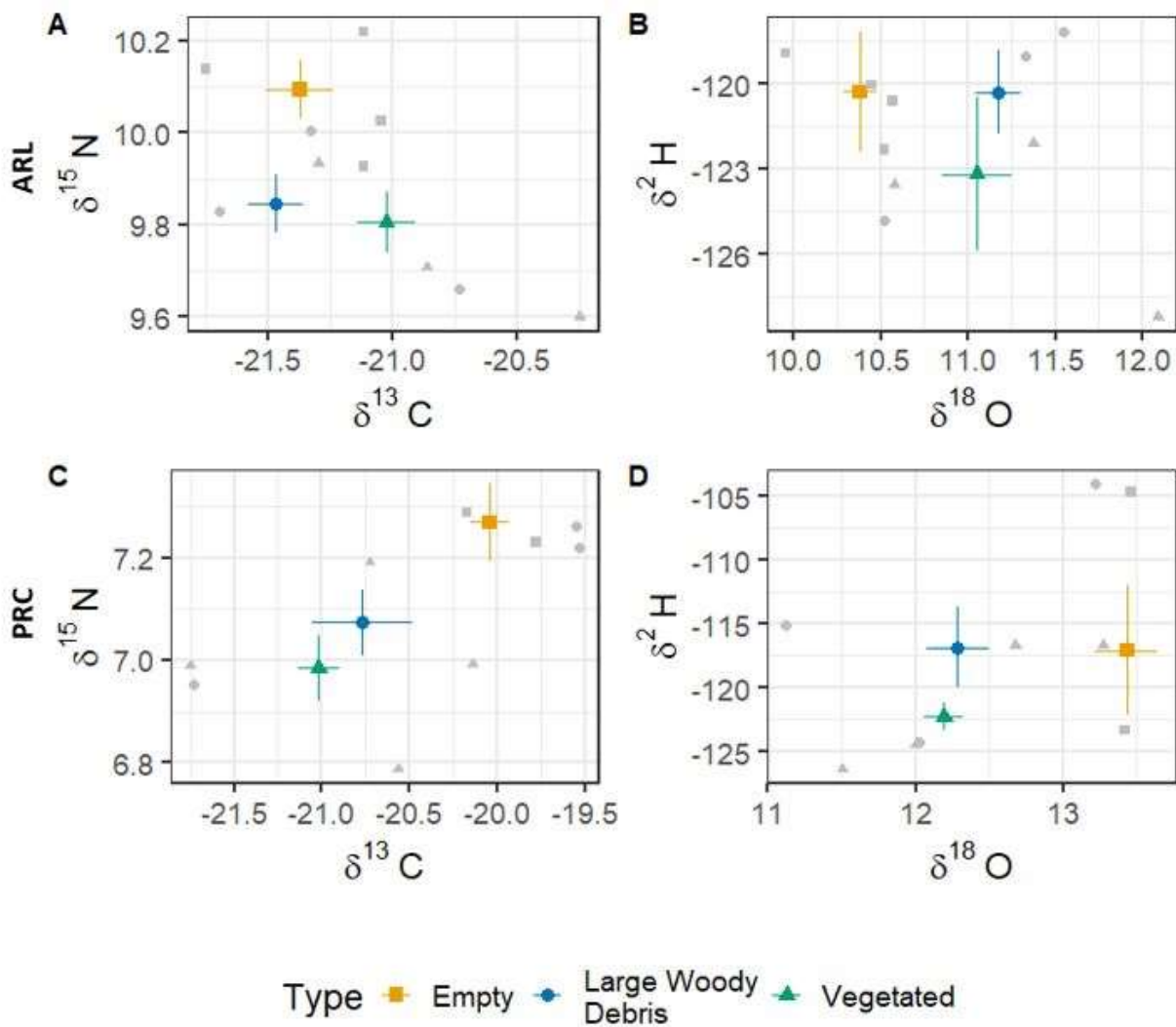
Figure 3.2: Mean stable isotope values by habitat type ± standard error of YOY largemouth bass in the controlled pond experiments. Color and shape indicate habitat-type (gold square = empty, blue circle = large woody debris, green triangle = vegetated), grey points are cage means and the shape corresponds with the colored habitat means. Plots A and B are from the Aquaculture Research Laboratory (ARL) cages, and plots C and D are from the Palmer Research Center (PRC) cages.
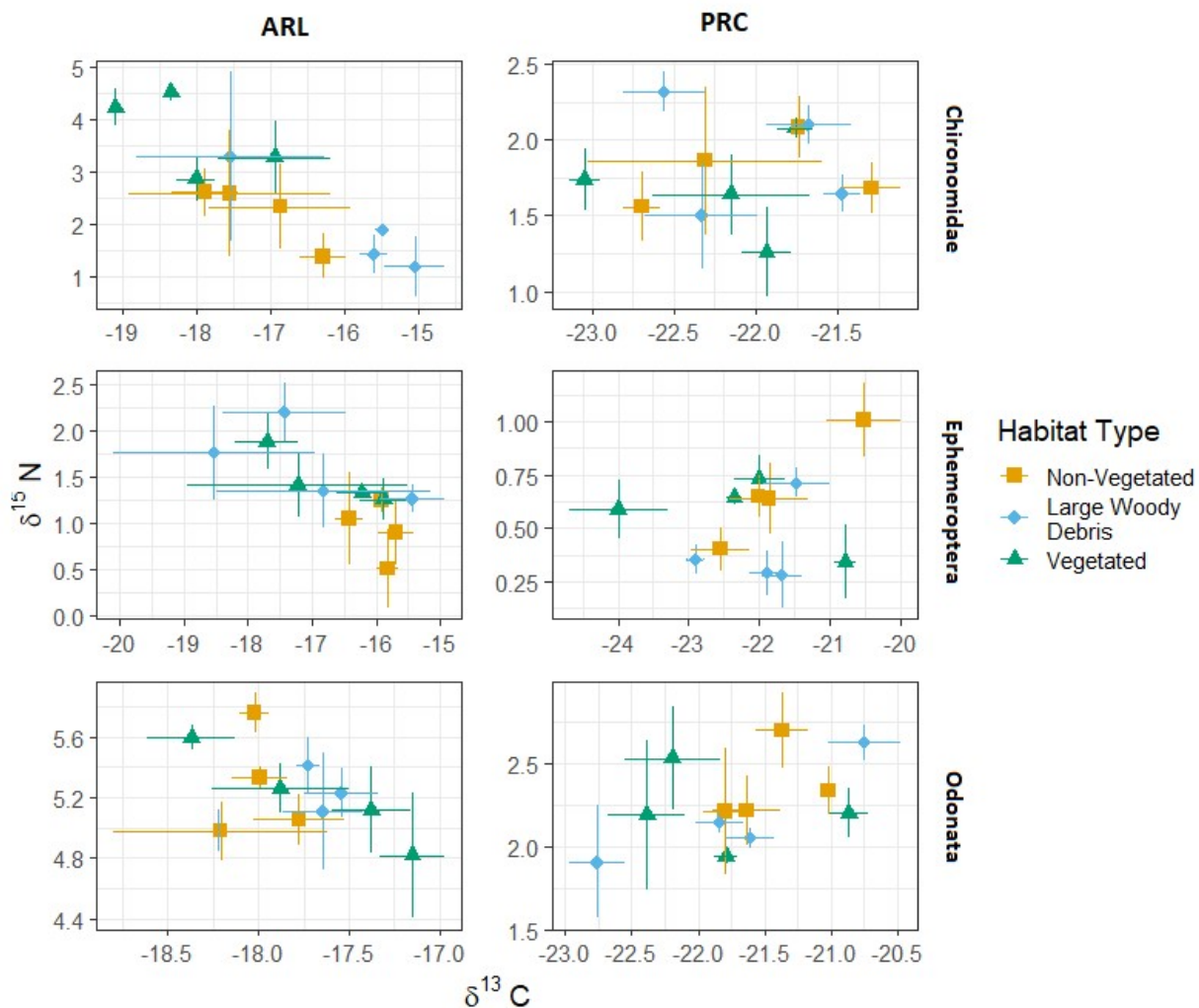
Figure 3.3: Stable isotope site means ± standard error of prey items collected at spatial midpoints of cage locations in the research ponds (Baker Aquaculture Research Laboratory (ARL) and Palmer Research Center for Aquatic Resources (PRC)). Color and shape indicate habitat type at the site; non-vegetated (gold squares), large woody debris (blue diamonds) and vegetated (green triangles).

Figure 3.4: A-B) Relationships of $\delta^{13}C$ (A) and $\delta^{15}N$ (B) site means of prey items and largemouth bass collected in the Aquaculture Research Laboratory (ARL). Shape and color 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 = 0.04). C-D) Relationships of $\delta^{18}O$ (C) and δ^2H (D) site means of locally collected water and largemouth bass collected in the Aquaculture Research Laboratory (ARL). Shape and color indicate habitat type, gold square = non-vegetated, blue diamond = large woody debris and green triangle = vegetated.
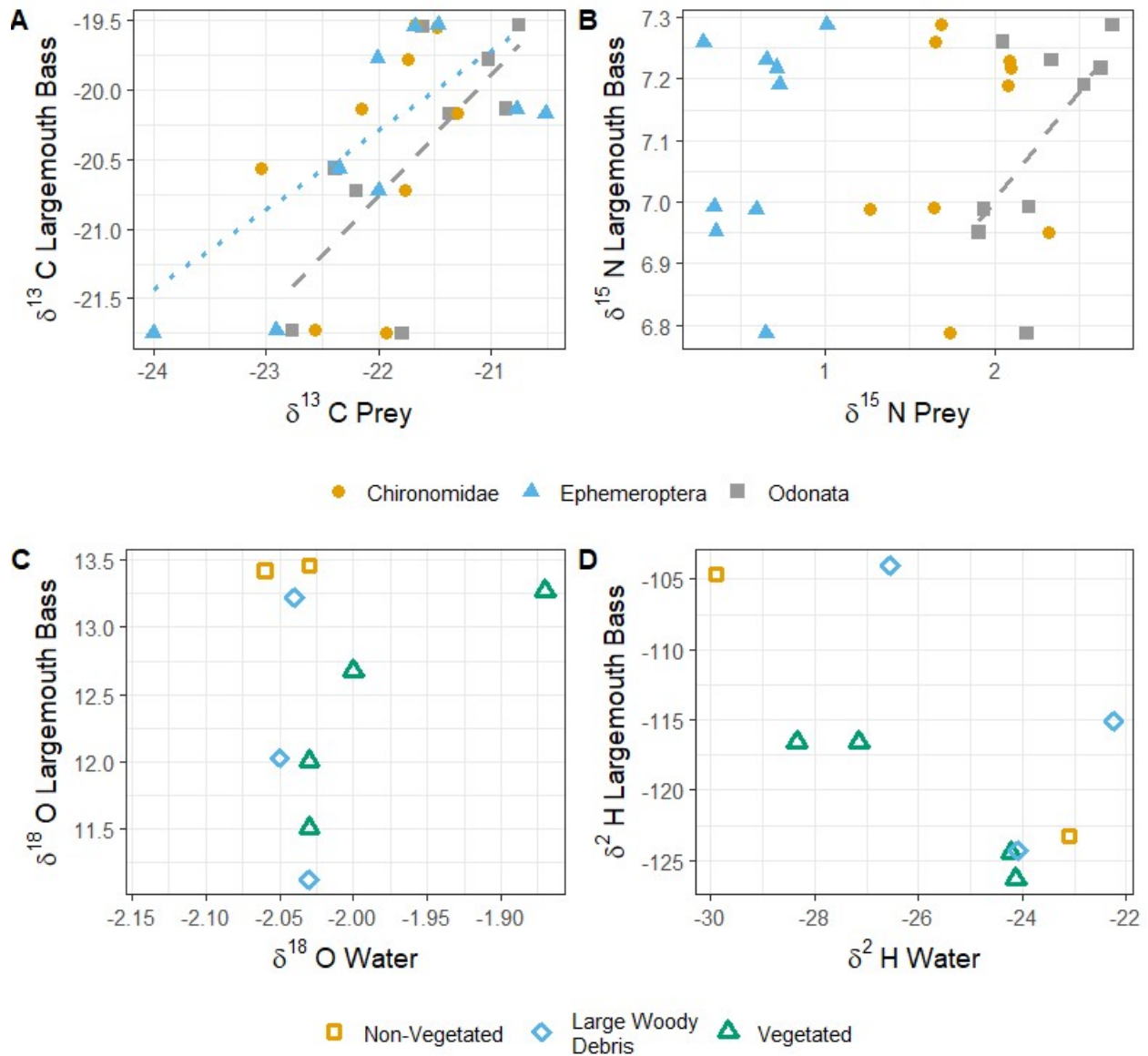
Figure 3.5: A-B) Relationships of δ^{13}C (A) and δ^{15}N (B) site means of prey items and largemouth bass collected in the Palmer Research Center for Aquatic Resources (PRC). Blue dotted line indicates a significant linear relationship between δ^{13}C of Ephemeroptera and δ^{13}C of YOY Largemouth Bass (adjusted $R^2 = 0.56$, one-tailed P = 0.01). Grey dashed line indicates a significant linear relationship between δ^{13}C of Odonata and δ^{13}C of YOY largemouth bass ($R^2 = 0.45$, p-value = 0.01) or a significant linear relationship between δ^{15}N of Odonata and δ^{15}N of YOY largemouth bass ($R^2 = 0.26$, p-value = 0.046). Shape and color indicate prey item, gold circle = Chironomidae, blue triangle = Ephemeroptera, and grey square = Odonata. C-D) Relationships of δ^{18}O (C) and δ^2H (D) site means of locally collected water and largemouth bass collected in the Palmer Research Center for Aquatic Resources (PRC). Shape and color indicate habitat type, gold square = non-vegetated, blue diamond = large woody debris and green triangle = vegetated.
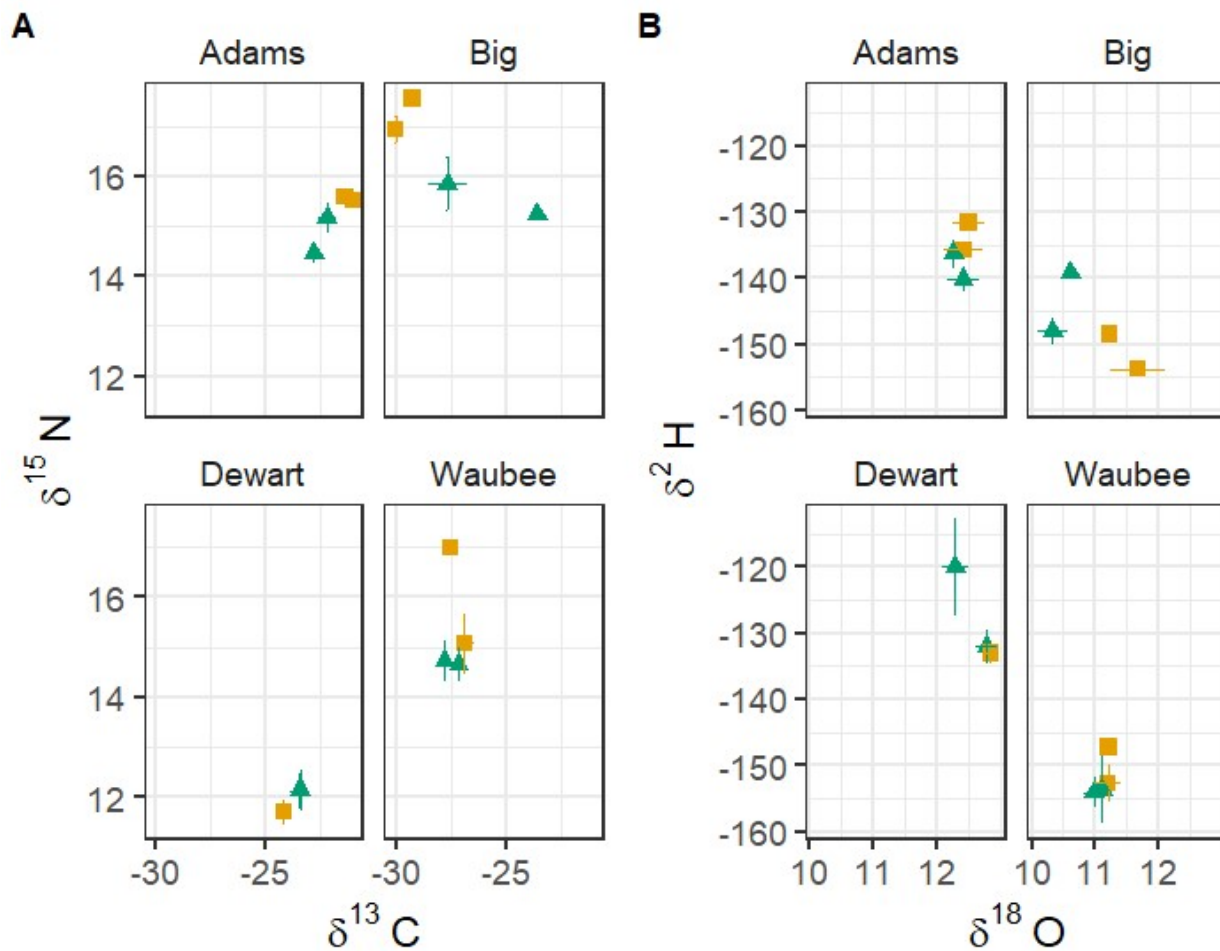
Figure 3.6: Multi-lake stable isotope ratio site means ± standard error of YOY largemouth bass. Color and shape indicate habitat type (gold square = non-vegetated, green triangle = vegetated). A: Carbon and Nitrogen stable isotope ratios, B: Oxygen and Hydrogen stable isotope ratios.
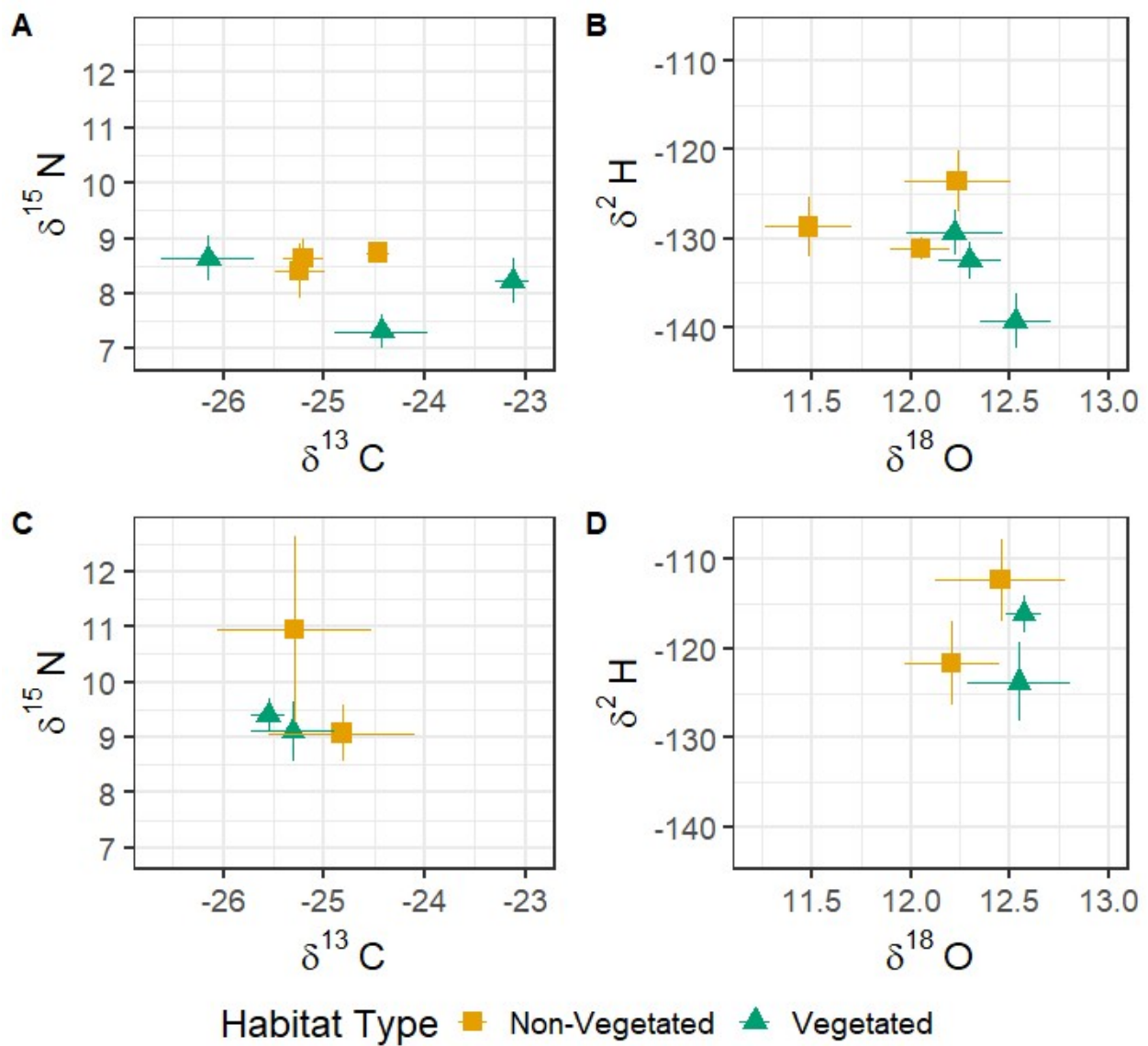
Figure 3.7: Single-lake (Crooked Lake) survey largemouth bass stable isotope ratio site means ± standard error. A-B) July 24-25, 2018 C-D) August 23, 2018. Color and shape indicate habitat type, gold squares = non-vegetated and green triangles = vegetated habitats.
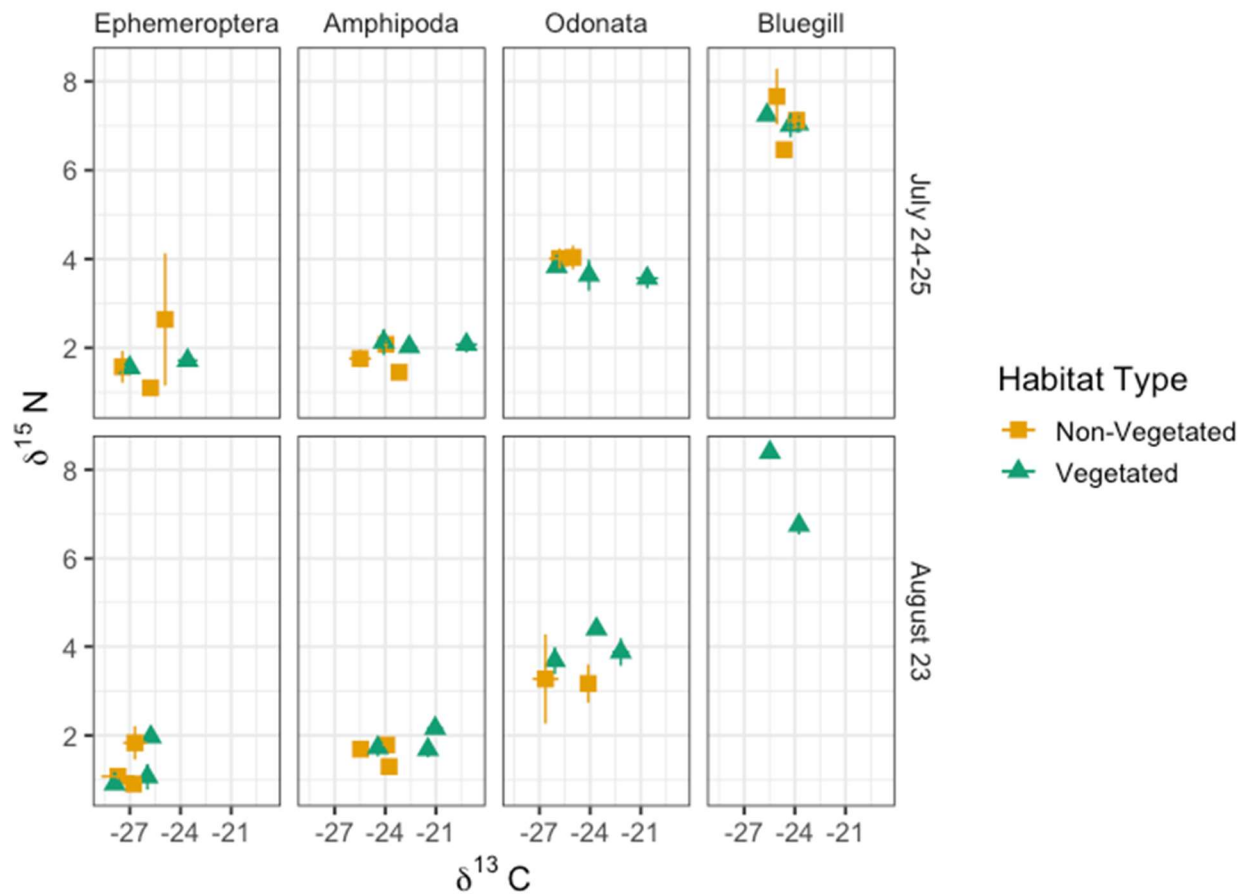
Figure 3.8: Stable isotope ratio ($\delta^{13}C$ and $\delta^{15}N$) site means ± standard error of prey items collected at largemouth bass collection sites during the single-lake survey of Crooked lake. Color and shape indicates habitat type at the site; non-vegetated (gold squares) and vegetated (green triangles).
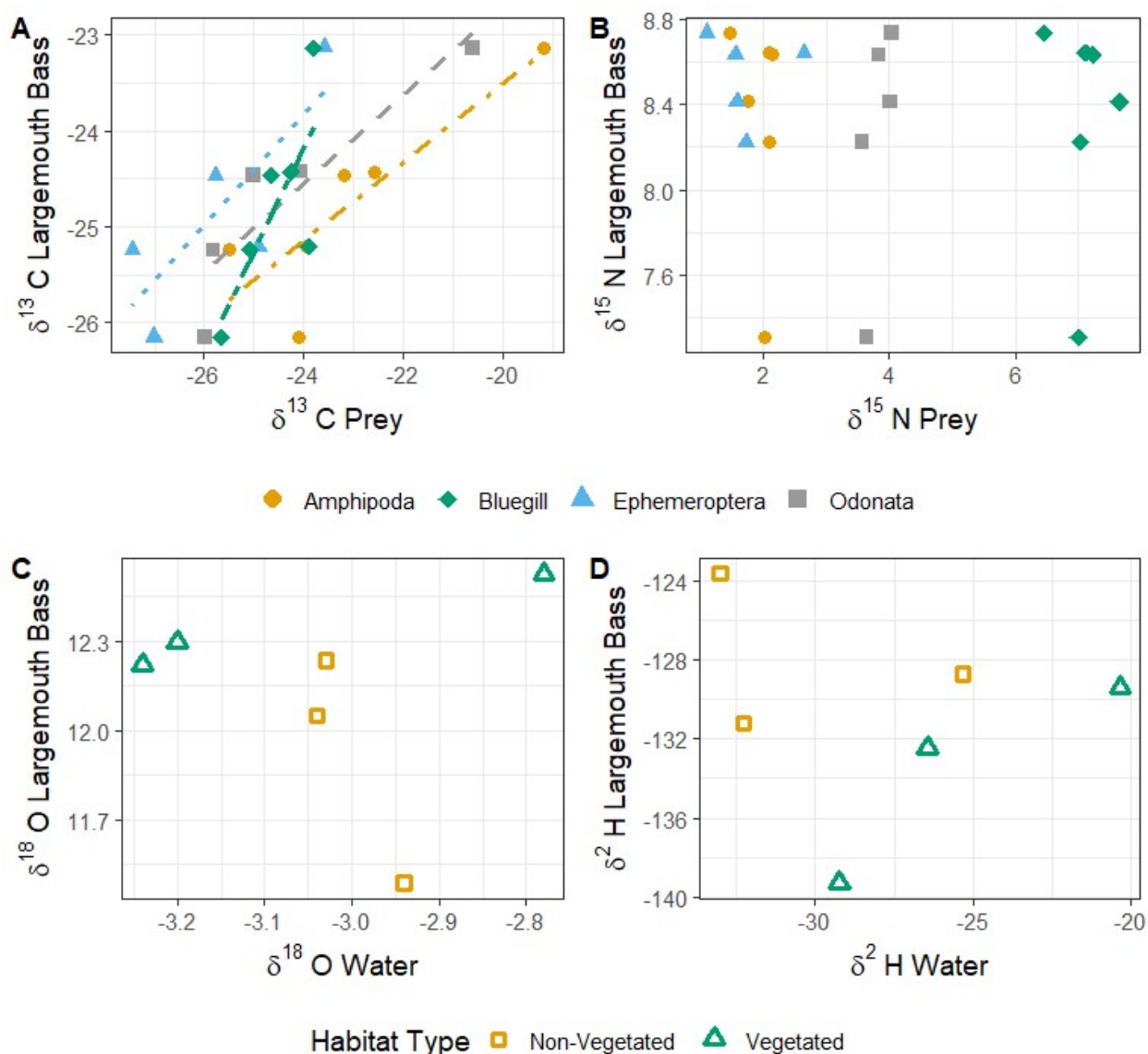
Figure 3.9: A-B) Relationships of δ^{13}C (A) and δ^{15}N (B) site means of prey items and largemouth bass collected in July of the single-lake survey of Crooked Lake. Shape and color indicate prey item, gold circle = Amphipoda, green diamond = young of year bluegill, blue triangle = Ephemeroptera, and grey square = Odonata. Gold dot-dash line indicates a significant linear relationship between δ^{13}C of Amphipoda and δ^{13}C of YOY largemouth bass (adjusted R^2 = 0.68, one-tailed P = 0.03). Green dashed line indicates a significant linear relationship between δ^{13}C of YOY bluegill and δ^{13}C of YOY largemouth bass (R^2 = 0.47, P = 0.04). Blue dotted line indicates a significant linear relationship between δ^{13}C of Ephemeroptera and δ^{13}C of YOY largemouth bass (R^2 = 0.54, P = 0.048). Grey dashed line indicates a significant linear relationship between δ^{13}C of Odonata and δ^{13}C of YOY largemouth bass (R^2 = 0.77, P = 0.03). C-D) Relationships of δ^{18}O (C) and δ^2H (D) site means of water and largemouth collected in July. Shape and color indicate habitat type, gold square = non-vegetated and green triangle = vegetated.
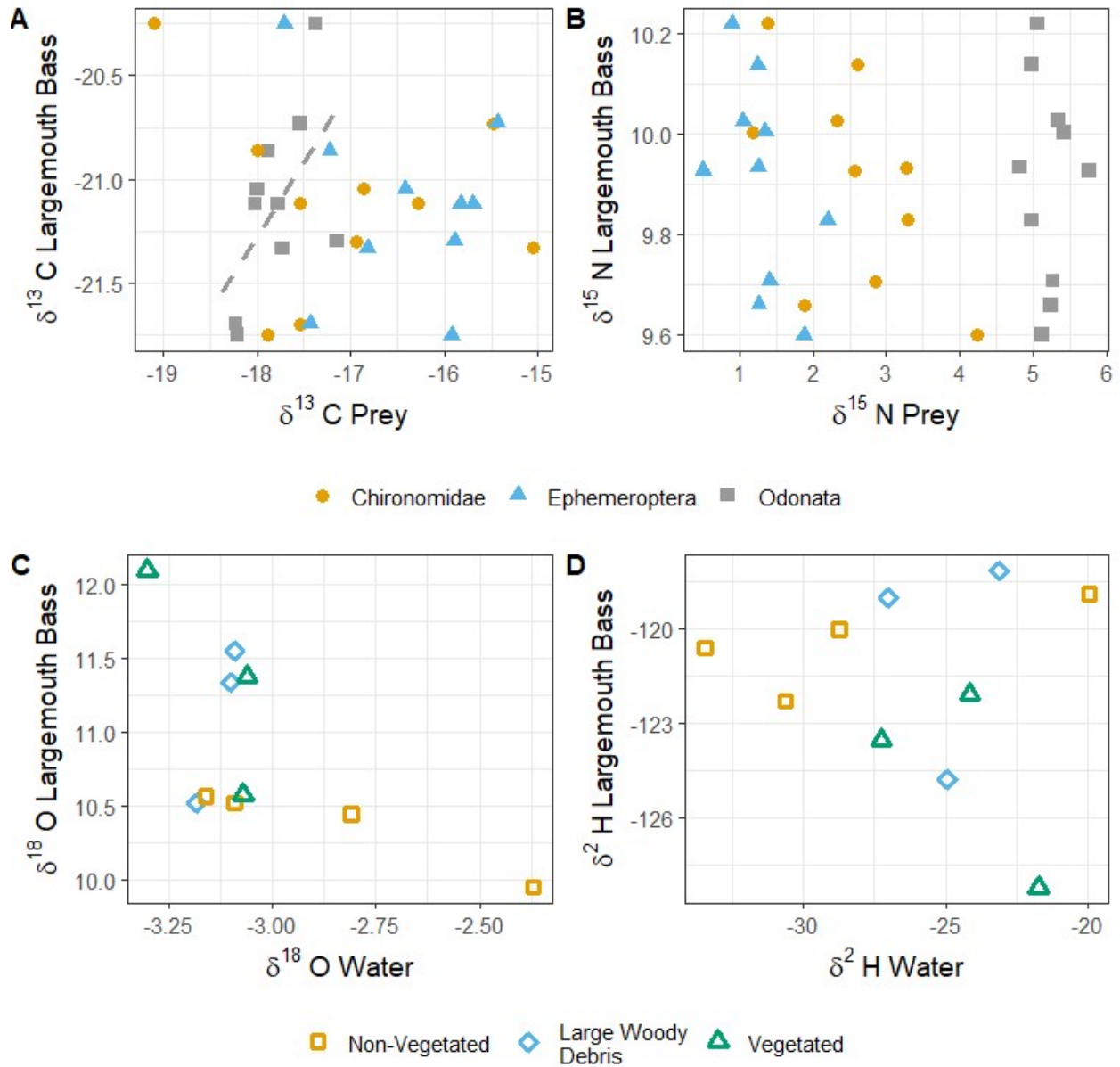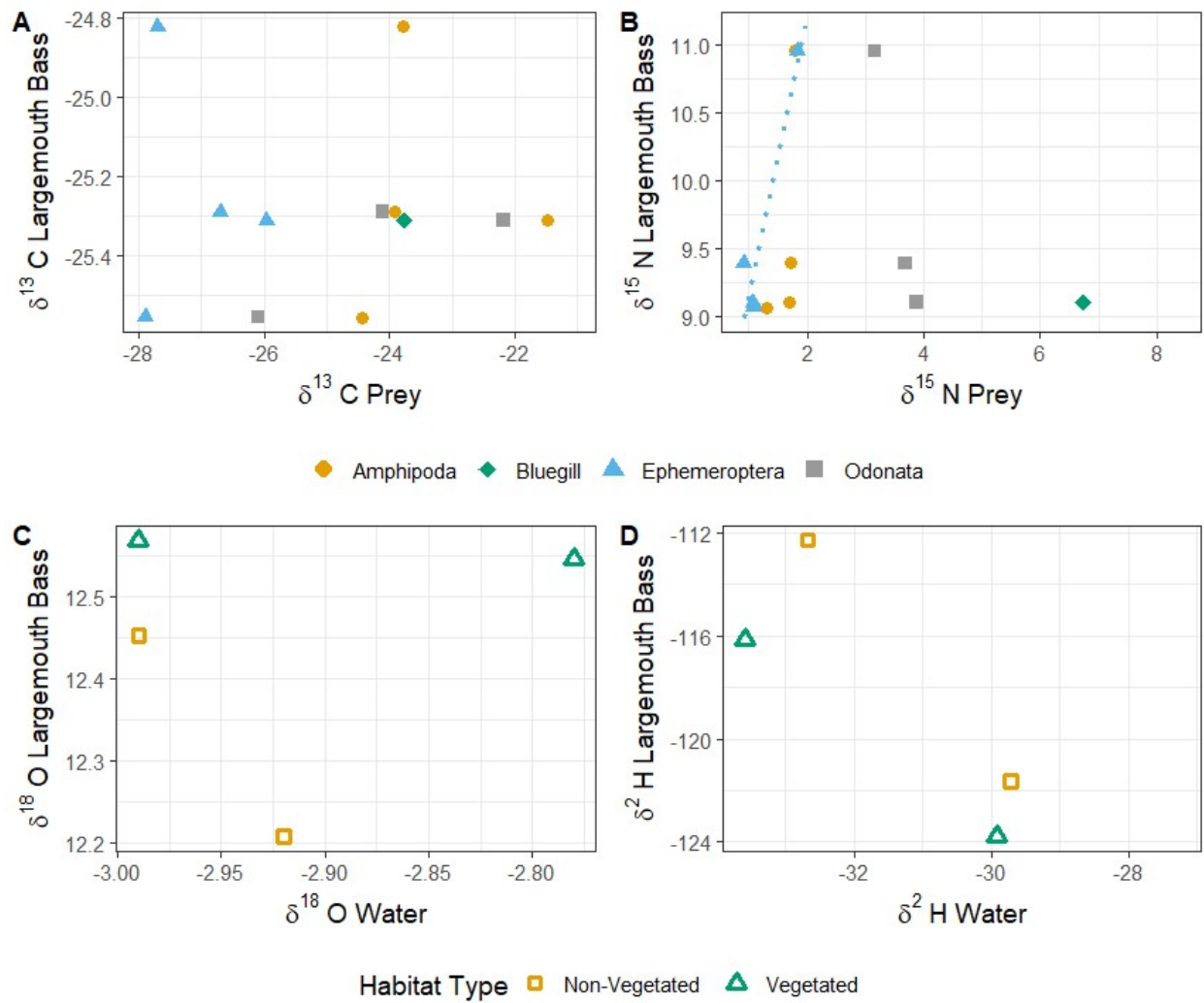
Figure 3.10: A-B) Relationships of δ^{13}C (A) and δ^{15}N (B) site means of prey items and largemouth bass collected in August of the single-lake survey of Crooked Lake. Shape and color indicate prey item, gold circle = Amphipoda, green diamond = young of year bluegill, blue triangle = Ephemeroptera, and grey square = Odonata. Blue dotted line indicates a significant linear relationship between δ^{15}N of Ephemeroptera and δ^{15}N of YOY largemouth bass (Adjusted R^2 = 0.82, one-tailed P = 0.03). C-D) Relationships of δ^{18}O (C) and δ^2H (D) site means of water and largemouth collected in July. Shape and color indicate habitat type, gold square = non-vegetated and green triangle = vegetated.

APPENDIX A. CHAPTER 2 SUPPLEMENTAL MATERIALS

Table A.1: Table of all variables considered, abbreviation, units of measure, equation used to calculate the variable, their classification and the source of the data.

Variable	Abbreviation	Unit	Equation	Source
Agricultural and Developed Area in Total Catchment	Ag-Dev	%		NLCD
Developed Area within 100 m buffer of Lake	Local Dev	%		NLCD
Lake Surface Area	Lake Area	m^2		USGS geospatial database
Ratio of Lake Area to Catchment Area	LA:CA		$\dfrac{\text{Lake Surface Area}}{\text{Total Catchment Area}}$	USGS geospatial database
Secchi Depth		m		INDNR S&T
Average Littoral Biovolume	Vegetation			INDNR S&T
Largemouth Bass Proportional Stock Density	LMB PSD		$\dfrac{\#\ \text{LMB}\ \geq\ 30.5\ \text{cm}}{\#\ \text{LMB}\ \geq\ 20.3\ \text{cm}}$	INDNR S&T
Largemouth Bass Catch Per Unit Effort	LMB CPUE		$\dfrac{\#\ \text{fish caught}}{2}$	INDNR S&T
Bluegill Proportional Stock Density	BLG PSD		$\dfrac{\#\ \text{BLG}\ \geq\ 15.2\ \text{cm}}{\#\ \text{BLG}\ \geq\ 7.6\ \text{cm}}$	INDNR S&T
Bluegill Catch Per Unit Effort	BLG CPUE		$\dfrac{\#\ \text{fish caught}}{2}$	INDNR S&T

Table A.2: Covariance matrix of variables used to estimate the structural equation model relationships among variables for all 4 fish metrics in Indiana glacial lakes. Variable definitions can be found in Table A.3.

	Vegetation	Secchi Depth	Lake Area	BLG CPUE	BLG PSD	LMB CPUE	LMB PSD	LA:CA	Ag-Dev	Local Dev	DO diff
Vegetation	1.046536										
Secchi Depth	0.29515	0.981405									
Lake Area	-0.15797	-0.00108	0.904798								
BLG CPUE	-0.05742	-0.14892	-0.14179	1.096802							
BLG PSD	-0.24534	-0.21804	0.037102	-0.48085	1.098687						
LMB CPUE	-0.20472	-0.11433	-0.24174	0.426414	-0.15009	1.162726					
LMB PSD	-0.33366	-0.54175	0.143213	-0.03878	0.15546	-0.14848	0.993966				
LA:CA	0.178199	0.565294	0.000229	-0.12466	-0.0925	-0.16229	-0.32022	0.790671			
Ag-Dev	-0.35223	-0.32104	0.103632	-0.0556	0.131832	0.131583	0.220248	-0.39077	0.750223		
Local Dev	-0.02588	0.265578	0.464543	-0.20478	0.206461	-0.2772	-0.02826	0.249478	-0.0149	0.931168	
DO diff	-0.41371	-0.40236	-0.21921	0.096605	0.262528	0.032312	0.381228	-0.22399	0.176712	-0.22347	0.999753

Table A.3: Model fit statistics for each model. Sartorra-Bentler correction factor (near 1), CFI = comparative fit index (> 0.95), RNI = relative non-centrality index (> 0.95), RMSEA = robust root mean square error of approximation (< 0.05, 90% confidence interval including 0), SRMR = robust standardized root mean square residual (< 0.08) and IFI = incremental fit index (> 0.95).

Fish Metric	Model Version	Robust χ^2	N	Robust p-value	Sartorra-Bentler	CFI	RNI	RMSEA	SRMR	IFI
LMB PSD	Initial	73.439	76	0	0.961	0.585	0.585	0.267	0.164	0.629
	Trimmed	77.66	76	0	0.958	0.614	0.614	0.196	0.184	0.637
	Final	8.21	76	0.915	0.951	1	1.05	0	0.05	1.046
LMB CPUE	Initial	78.581	76	0	0.99	0.481	0.481	0.283	0.172	0.542
	Trimmed	82.694	76	0	1.005	0.51	0.51	0.204	0.189	0.539
	Final	12.759	76	0.621	0.956	1	1.022	0	0.058	1.02
BLG PSD	Initial	68.587	78	0	1.208	0.486	0.486	0.289	0.168	0.542
	Trimmed	76.71	78	0	1.152	0.511	0.511	0.209	0.184	0.537
	Final	14.181	78	0.654	1.049	1	1.015	0	0.062	1.014
BLG CPUE	Initial	70.143	78	0	1.205	0.451	0.451	0.293	0.173	0.513
	Final	10.191	78	0.856	1.077	1	1.037	0	0.054	1.034

Table A.4: Linear regression statistics between response variables (columns) and predictor variables (rows).

	0m [DO] (mg/L)	3m [DO] (mg/L)	[Difference btwn 0&3m]
Log(chlorophyll-a concentration)	$R^2 = 0.01$, $p = 0.18$	$R^2 = 0.10$, $p = 0.002$	$R^2 = 0.18$, $p < 0.001$
Sqrt(Secchi Depth)	$R^2 = 0.02$, $p = 0.12$	$R^2 = 0.12$, $p = 0.001$	$R^2 = 0.21$, $p < 0.001$
Log(Total Kjeldahl Nitrogen)	$R^2 = 0.002$, $p = 0.29$	$R^2 = 0.06$, $p = 0.02$	$R^2 = 0.11$, $p = 0.002$
Sqrt(Total Phosphorus)	$R^2 = -0.013$, $p = 0.98$	$R^2 = 0.04$, $p = 0.04$	$R^2 = 0.04$, $p = 0.04$
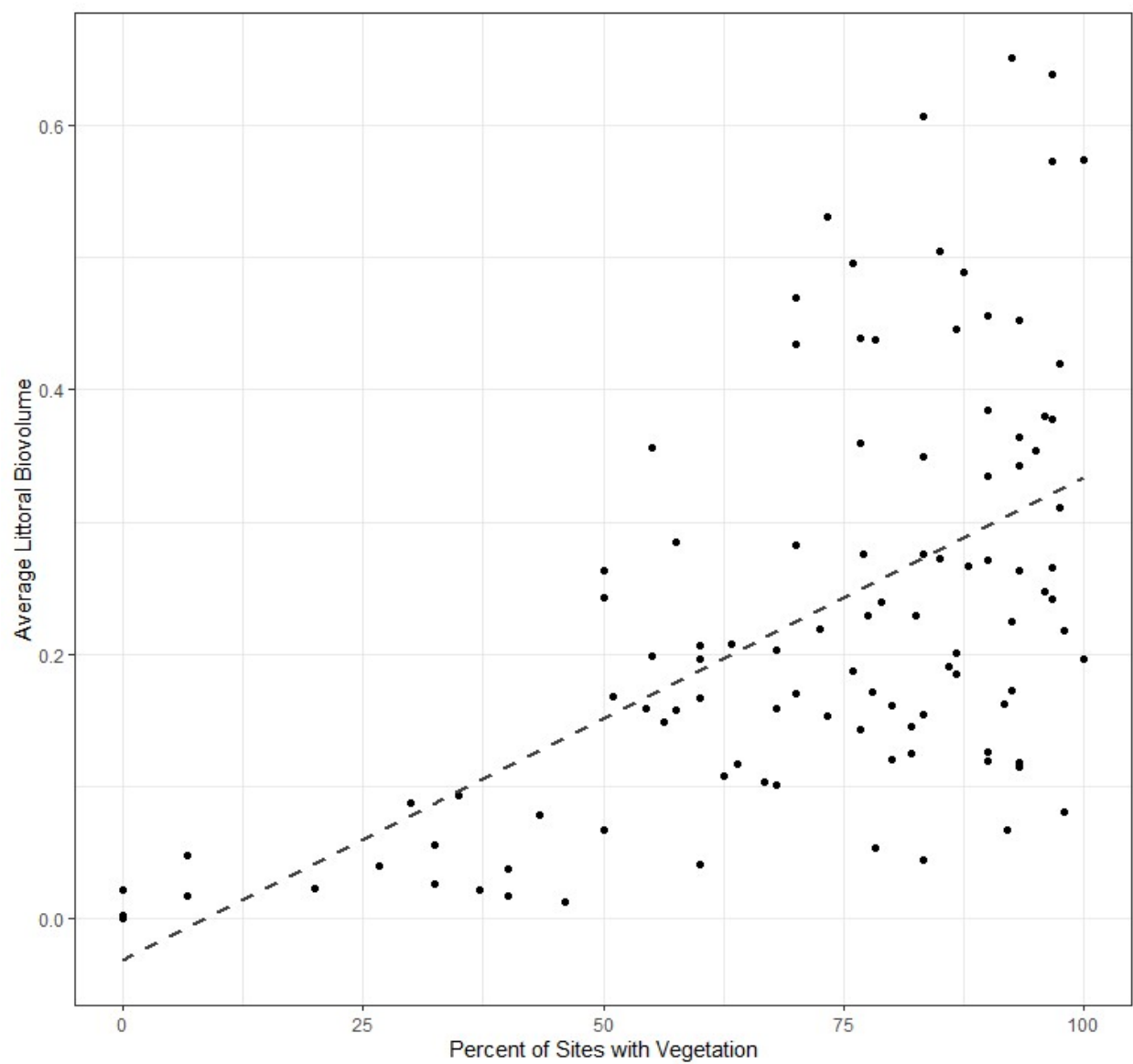
Figure A.1: Relationship between the percent of vegetated sites during the Tier-2 sampling effort and the average littoral biovolume.
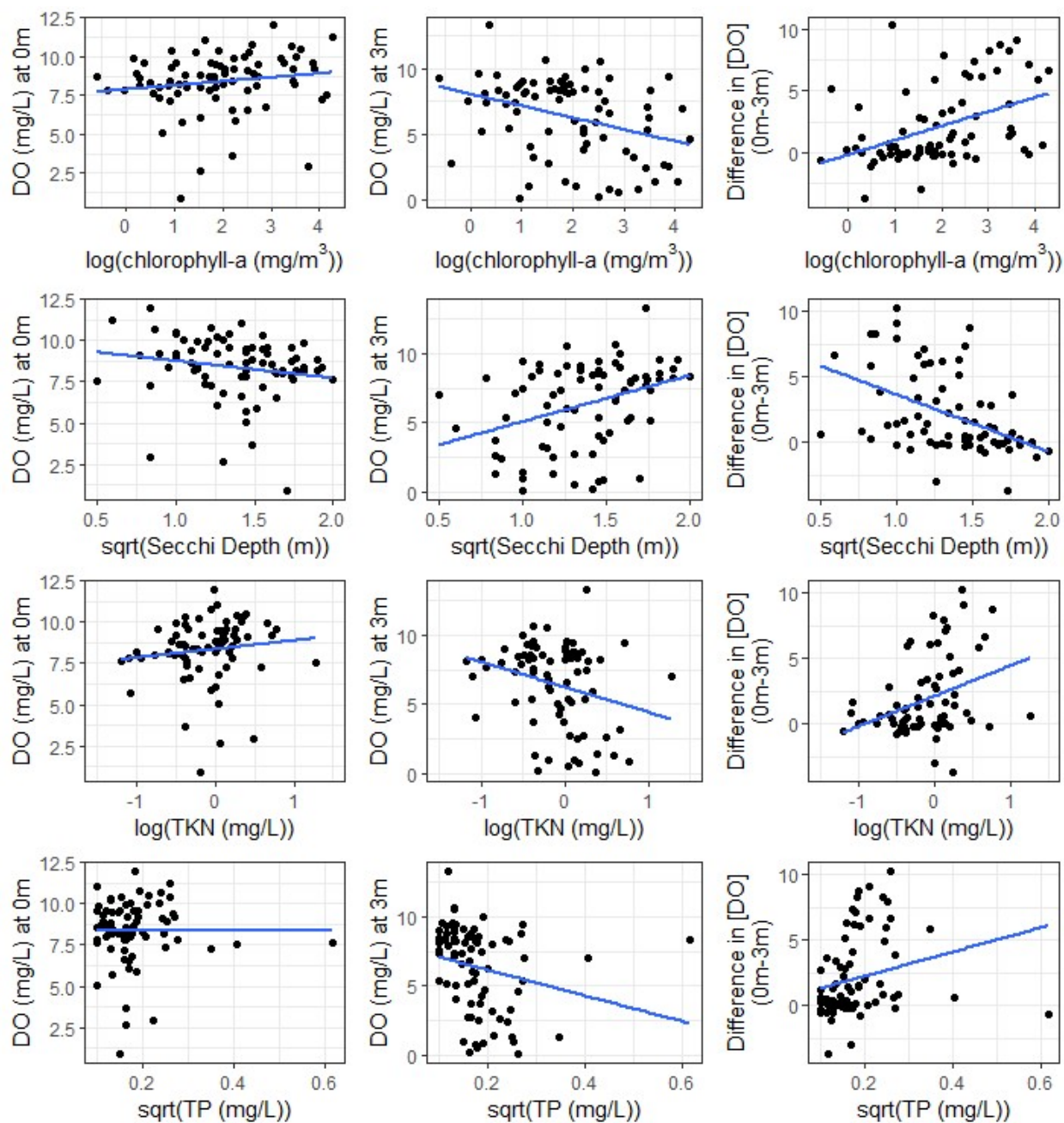
Figure A.2: Relationships between Indiana Clean Lakes Program collected dissolved oxygen (mg/L) at two depths (0 m and 3 m), the difference between dissolved oxygen concentration at those two depths and four measures of productivity or nutrient loading. TKN is total Kjeldahl nitrogen, and TP is total phosphorus. Linear regression statistics can be found in Table A.4.
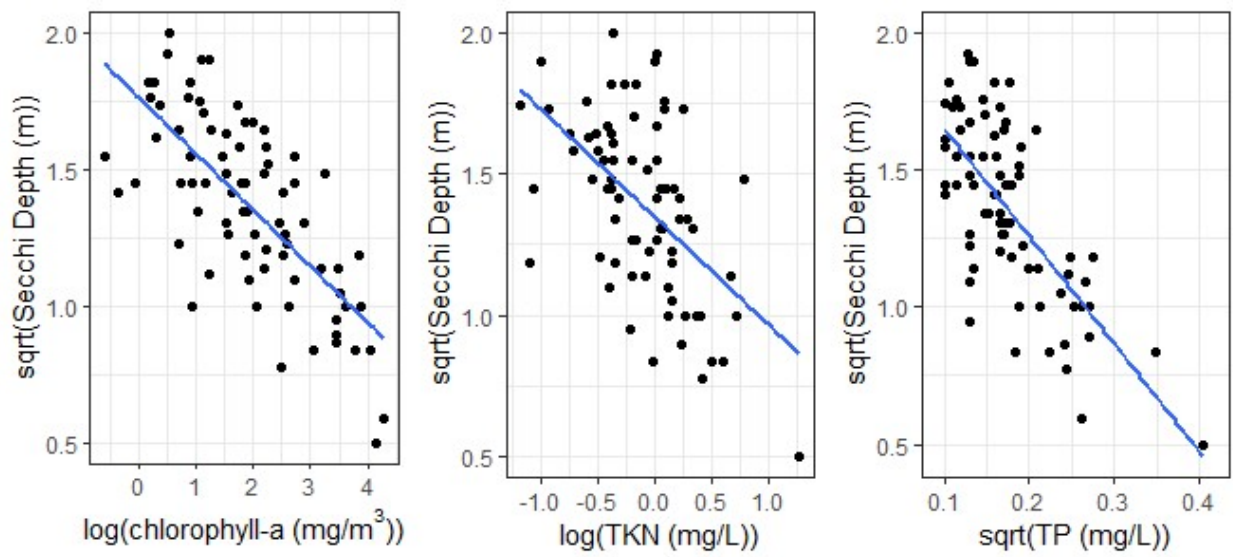
Figure A.3: Relationships between Indiana Clean Lakes Program sqrt(Secchi Depth (m)) and log(chlorophyll-a) ($R^2 = 0.50$, $P < 0.001$), log(total Kjeldahl nitrogen) ($R^2 = 0.29$, $P < 0.001$) and sqrt(total phosphorus) ($R^2 = 0.14$, $P < 0.001$).

APPENDIX B. CHAPTER 3 SUPPLEMENTAL MATERIALS

Table B.1: Results of multivariate analyses of co-variance (MANCOVA) and individual element analyses of co-variance (Carbon, Nitrogen, Hydrogen and Oxygen) of differences in YOY largemouth bass stable isotope ratios. Habitat and site (nested within habitat) were predictors for each analysis, with standard length (mm) as a co-variate. F-values, degrees of freedom and p-values are reported for each analysis. **Bold** results represent significance below 0.001, *italicized* results represent significance below 0.05.

| Response | | Controlled Pond Experiments | | | Multi-Lake Survey | | | Detailed Single-Lake Survey | |
		ARL	PRC	Adams	Big	Dewart	Waubee	Early	Late
MANCOVA	Habitat	**$F_{2,44} = 7.98$, P <0.001**	**$F_{2,51} = 10.11$, P <0.001**	**$F_{1,19} = 8.74$, P = <0.001**	*$F_{1,6} = 24.48$, P = 0.01*	*$F_{1,8} = 11.72$, P = 0.01*	$F_{1,13} = 2.43$, P = 0.12	*$F_{1,37} = 4.91$, P = 0.003*	$F_{1,14} = 0.91$, P = 0.49
	Habitat (Site)	**$F_{7,44} = 2.35$, P <0.001**	**$F_{6,51} = 6.64$, P <0.001**	$F_{2,19} = 1.32$, P = 0.27	$F_{2,6} = 2.42$, P = 0.12	**$F_{1,8} = 31.33$, P <0.001**	$F_{2,13} = 1.45$, P = 0.23	**$F_{4,37} = 3.47$, P <0.001**	$F_{2,14} = 0.91$, P = 0.52
	Standard Length	*$F_{1,44} = 2.67$, P = 0.045*	**$F_{1,51} = 62.82$, P <0.001**	$F_{1,19} = 1.28$, P = 0.32	*$F_{1,6} = 11.07$, P = 0.04*	*$F_{1,8} = 9.67$, P = 0.01*	$F_{1,13} = 1.80$, P = 0.21	**$F_{1,37} = 16.19$, P <0.001**	$F_{1,14} = 2.71$, P = 0.09
Carbon	Habitat	*$F_{2,44} = 4.97$, P = 0.01*	***$F_{2,51} = 23.33$, P <0.001***	**$F_{1,19} = 33.29$, P = <0.001**	*$F_{1,6} = 18.04$, P = 0.005*	$F_{1,8} = 4.28$, P = 0.07	$F_{1,13} = 3.03$, P = 0.11	$F_{1,37} = 0.46$, P = 0.50	$F_{1,14} = 0.42$, P = 0.53
	Habitat (Site)	*$F_{7,44} = 3.58$, P = 0.004*	***$F_{6,51} = 30.69$, P <0.001***	$F_{2,19} = 1.98$, P = 0.17	$F_{2,6} = 2.72$, P = 0.14	$F_{1,8} = 0.53$, P = 0.49	$F_{2,13} = 2.91$, P = 0.09	**$F_{4,37} = 8.14$, P <0.001**	$F_{2,14} = 0.22$, P = 0.81
	Standard Length	*$F_{1,44} = 5.76$, P = 0.02*	**$F_{1,51} = 132.35$, P <0.001**	$F_{1,19} = 0.63$, P = 0.44	$F_{1,6} = 5.23$, P = 0.06	$F_{1,8} = 2.21$, P = 0.18	$F_{1,13} = 0.41$, P = 0.53	*$F_{1,37} = 7.92$, P = 0.01*	$F_{1,14} = 0.40$, P = 0.54
Nitrogen	Habitat	*$F_{2,44} = 5.98$, P = 0.005*	$F_{2,51} = 1.87$, P = 0.16	**$F_{1,19} = 19.76$, P <0.001**	$F_{1,6} = 5.86$, P = 0.05	$F_{1,8} = 1.99$, P = 0.20	$F_{1,13} = 2.42$, P = 0.14	*$F_{1,37} = 5.13$, P = 0.03*	$F_{1,14} = 0.55$, P = 0.47
	Habitat (Site)	$F_{7,44} = 1.29$, P = 0.28	*$F_{6,51} = 1.35$, P = 0.25*	$F_{2,19} = 2.93$, P = 0.08	$F_{2,6} = 0.28$, P = 0.76	$F_{1,8} = 0.89$, P = 0.37	$F_{2,13} = 1.87$, P = 0.19	$F_{4,37} = 1.06$, P = 0.39	$F_{2,14} = 0.94$, P = 0.41

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	Standard Length	$F_{1,44}=0.00$, P = 0.99	$F_{1,51}=0.25$, P = 0.62	$F_{1,19}=3.56$, P = 0.07	$F_{1,6}=0.25$, P = 0.63	$F_{1,8}=5.23$, P = 0.05	$F_{1,13}=1.28$, P = 0.06	**$F_{1,37}=20.40$, P <0.001**	$F_{1,14}=0.33$, P = 0.58
Hydrogen	Habitat	$F_{2,44}=0.59$, P = 0.59	*$F_{2,51}=4.26$, P = 0.02*	*$F_{1,19}=7.36$, P = 0.01*	*$F_{1,6}=10.18$, P = 0.02*	*$F_{1,8}=10.12$, P = 0.01*	$F_{1,13}=0.18$, P = 0.68	*$F_{1,37}=5.42$, P = 0.02*	$F_{1,14}=0.57$, P = 0.46
	Habitat (Site)	$F_{7,44}=0.37$, P = 0.91	**$F_{6,51}=6.54$, *P* <0.001**	$F_{2,19}=2.27$, P = 0.13	$F_{2,6}=4.10$, P = 0.08	**$F_{1,8}=61.77$, P <0.001**	$F_{2,13}=0.15$, P = 0.87	$F_{4,37}=2.42$, P = 0.07	$F_{2,14}=2.77$, P = 0.10
	Standard Length	$F_{1,44}=0.01$, P = 0.91	**$F_{1,51}=15.55$, P <0.001**	$F_{1,19}=0.004$, P = 0.95	$F_{1,6}=0.07$, P = 0.80	*$F_{1,8}=11.33$, P = 0.01*	$F_{1,13}=0.28$, P = 0.61	$F_{1,37}=0.88$, P = 0.36	*$F_{1,14}=8.71$, P = 0.01*
Oxygen	Habitat	**$F_{2,44}=13.54$, P <0.001**	**$F_{2,51}=19.87$, P <0.001**	$F_{1,19}=0.12$, P = 0.73	*$F_{1,6}=9.63$, P = 0.02*	$F_{1,8}=1.32$, P = 0.28	$F_{1,13}=0.48$, P = 0.63	*$F_{1,37}=4.69$, P = 0.04*	$F_{1,14}=0.83$, P = 0.38
	Habitat (Site)	*$F_{7,44}=3.97$, P 0.002*	**$F_{6,51}=19.64$, *P* <0.001**	$F_{1,19}=0.09$, P = 0.91	$F_{1,6}=1.36$, P = 0.33	$F_{1,8}=1.80$, P = 0.22	$F_{2,13}=0.48$, P = 0.63	$F_{4,37}=1.90$, P = 0.13	$F_{2,14}=0.25$, P = 0.78
	Standard Length	$F_{7,44}=0.26$, P 0.61	**$F_{1,51}=19.51$, P <0.001**	$F_{1,19}=0.13$, P = 0.73	$F_{1,6}=2.04$, P = 0.20	$F_{1,8}=2.78$, P = 0.13	$F_{1,13}=1.31$, P = 0.27	$F_{1,37}=0.02$, P = 0.89	$F_{1,14}=0.19$, P = 0.67

Table B.2: Results of individual element analyses of co-variance (Carbon, Nitrogen, Hydrogen and Oxygen) of differences in locally collected potential prey items and water stable isotope ratios from the controlled pond experiments. Habitat and site (nested within habitat) were predictors for each analysis. F-values, degrees of freedom and p-values are reported for each analysis. **Bold** results represent significance below 0.001, *italicized* results represent significance below 0.05.

Response		ARL				PRC			
		Chironomidae	Ephemeroptera	Odonata	Water	Chironomidae	Ephemeroptera	Odonata	Water
Carbon	Habitat	**$F_{2,\ 17} = 12.95$, $P < 0.001$**	$F_{2,\ 22} = 1.31$, $P = 0.29$	$F_{2,\ 24} = 1.05$, $P = 0.36$		$F_{2,\ 24} = 0.67$, $P = 0.52$	$F_{2,\ 23} = 2.00$, $P = 0.16$	$F_{2,\ 24} = 3.00$, $P = 0.07$	
	Habitat(Site)	$F_{9,\ 17} = 1.88$, $P = 0.13$	$F_{9,\ 22} = 0.89$, $P = 0.55$	$F_{9,\ 24} = 1.49$, $P = 0.21$		*$F_{9,\ 24} = 3.61$, $P = 0.006$*	**$F_{9,\ 23} = 6.18$, $P < 0.001$**	**$F_{9,\ 24} = 9.01$, $P < 0.001$**	
Nitrogen	Habitat	**$F_{2,\ 17} = 7.40$, $P = 0.005$**	*$F_{2,\ 22} = 4.61$, $P = 0.02$*	$F_{2,\ 24} = 0.22$, $P = 0.80$		$F_{2,\ 24} = 0.73$, $P = 0.49$	$F_{2,\ 23} = 4.56$, $P = 0.02$	$F_{2,\ 24} = 0.65$, $P = 0.53$	
	Habitat(Site)	$F_{9,\ 17} = 1.25$, $P = 0.33$	$F_{9,\ 22} = 1.14$, $P = 0.38$	$F_{9,\ 24} = 1.76$, $P = 0.13$		$F_{9,\ 24} = 1.67$, $P = 0.15$	*$F_{9,\ 23} = 2.83$, $P = 0.02$*	$F_{9,\ 24} = 1.17$, $P = 0.36$	
Oxygen	Habitat				$F_{2,\ 6} = 1.66$, $P = 0.27$				$F_{2,\ 6} = 2.98$, $P = 0.13$
	Habitat(Site)				$F_{3,\ 6} = 0.48$, $P = 0.70$				$F_{3,\ 6} = 0.75$, $P = 0.56$
Hydrogen	Habitat				$F_{2,\ 6} = 0.95$, $P = 0.44$				$F_{2,\ 6} = 1.26$, $P = 0.35$
	Habitat(Site)				$F_{3,\ 6} = 0.99$ $P = 0.46$				$F_{3,\ 6} = 3.83$, $P = 0.08$

Table B.3: Results of individual element analyses of co-variance (Carbon, Nitrogen, Hydrogen and Oxygen) of differences in locally collected potential prey items and water stable isotope ratios from the detailed single-lake survey. Habitat and site (nested within habitat) were predictors for each analysis. F-values, degrees of freedom and p-values are reported for each analysis. **Bold** results represent significance below 0.001, *italicized* results represent significance below 0.05. We were unable to analyze differences in locally collected water due to a limited number of degrees of freedom.

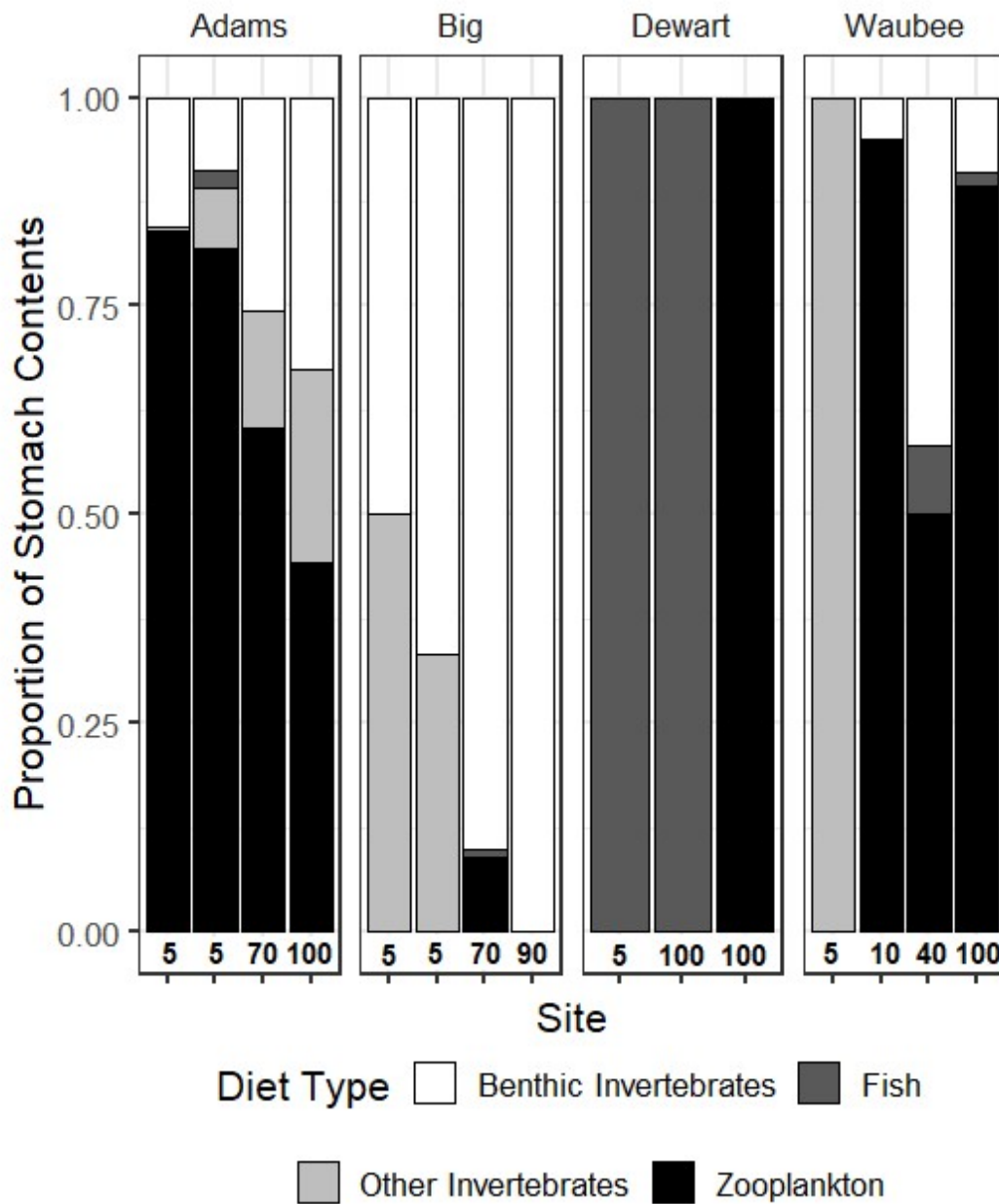| Response		Early				Late			Water
		Amphipoda	Ephemeroptera	Odonata	YOY Bluegill	Amphipoda	Ephemeroptera	Odonata	Water
Carbon	Habitat	**$F_{1, 18} = 35.65$, $P < 0.001$**	$F_{1, 9} = 4.96$, $P = 0.05$	**$F_{1, 10} = 25.81$, $P < 0.001$**	$F_{1,17} = 0.19$, $P = 0.67$	**$F_{1,18} = 65.43$, $P < 0.001$**	$F_{1, 8} = 4.94$, $P = 0.06$	**$F_{1, 16} = 23.15$, $P < 0.001$**	
	Habitat (Site)	**$F_{4, 18} = 17.96$, $P < 0.001$**	**$F_{3, 9} = 27.19$, $P < 0.001$**	*$F_{3, 10} = 12.06$, $P = 0.001$*	**$F_{4, 17} = 11.81$, $P < 0.001$**	**$F_{4,18} = 22.02$, $P < 0.001$**	$F_{4, 8} = 1.78$, $P = 0.23$	**$F_{4, 16} = 0.53$, $P < 0.001$**	
Nitrogen	Habitat	*$F_{1, 18} = 5.10$, $P = 0.03$*	$F_{1, 9} = 0.08$, $P = 0.78$	$F_{1, 10} = 2.00$, $P = 0.19$	$F_{1,17} = 0.10$, $P = 0.75$	*$F_{1,18} = 6.31$, $P = 0.02$*	$F_{1, 8} = 0.20$, $P = 0.67$	*$F_{1, 16} = 6.40$, $P = 0.02$*	
	Habitat (Site)	$F_{4, 18} = 1.76$, $P = 0.18$	$F_{3, 9} = 1.40$, $P = 0.30$	$F_{3, 10} = 0.06$, $P = 0.98$	$F_{4, 17} = 2.70$, $P = 0.07$	*$F_{4,18} = 4.13$, $P = 0.02$*	*$F_{4, 8} = 3.97$, $P = 0.046$*	$F_{4, 16} = 0.53$, $P = 0.72$	
Oxygen	Habitat								$F_{1, 14} = 0.06$, $P = 0.21$
	Time								$F_{2, 14} = 0.07$, $P = 0.37$
Hydrogen	Habitat								$F_{1, 14} = 12.15$, $P = 0.31$
	Time								$F_{2, 14} = 25.50$, $P = 0.34$

Figure B.1: Mean diet proportions (relative prey abundance) by site of the multi-lake survey. Labels beneath bars represent percent vegetation cover. Non-vegetated sites had percent vegetation cover less than 40%.

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