The roles of spatial scale and landscape change in mediating predator effects on stream fish communities

by

Lindsey Ann Bruckerhoff

B.S., Missouri State University, 2012
M.S., University of Arkansas, 2016

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

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Abstract

The role of predators in ecosystems has not only intrigued and puzzled ecologists over time, but predators are charismatic icons of conservation whose status indicates threats of global change. Through habitat alteration and fragmentation, climate change, and species introductions, predation pressure has been altered globally through the loss of apex predators, introduction of predators, and changes in predator distributions and abundance. While we know predators can influence ecosystems through top-down processes, managing changes in predation pressure requires quantifying effects of predators at scales relevant to management and conservation. In lotic systems, scales relevant to management often span across drainage basins, so predator effects must be quantified across stream networks. Because lotic communities also respond to landscape change, understanding the role of predators across stream networks requires careful consideration of local and broad scale abiotic factors influencing both predators and prey. I combined simulated, experimental, and observational data to 1) assess sampling strategies to determine effects of landscape change on stream fish communities, 2) measure changes in predator consumption rates across spatial scales and the role of prey behavior in driving scaling relationships, and 3) quantify the relationship between the presence of predators and stream fish community structure while controlling for abiotic variability across stream networks. In chapter 2, I compared how the distribution of sample sites (completely random, highly skewed, or uniform distributions) across landscape gradients influenced variability in measured responses of stream fish community metrics. Strong responses (species richness) to environmental gradients were robust to sample distributions, but large sample size and uniform distributions of samples across gradients were necessary to quantify more complex ecological responses (community composition). In chapter 3, I conducted a mesocosm study to quantify differences in per capita

consumption across different arena sizes and measured three aspects of prey behavior hypothesized to be important in driving consumption rates: aggregation, movement, and spatial overlap with predators. Per capita consumption was highest in the largest arena relative to the smallest. I hypothesize the positive relationship between consumption and spatial scale was driven by lower group vigilance because prey aggregated less in large arenas. In chapter 4, I compared fish community structure, including richness and abundance of species, at sites in which a predatory fish, largemouth bass (*Micropterus salmoides*), were present or absent. I first identified which abiotic factors, including both natural stream attributes and anthropogenic landscape changes, drove the presence of largemouth bass and stream fish community structure. I then controlled for important abiotic factors to determine relationships between largemouth bass and stream fish community structure. Richness was higher than predicted based on abiotic factors at sites where bass were present. Several species associated with small impoundments exhibited significant co-occurrence patterns with largemouth bass, likely driving the heightened richness at sites with bass. Complex ecological phenomena such as community responses to predators are difficult to measures, especially in the context of landscape change. These studies highlight the importance of thoughtful study design, the scale-dependence of biotic interactions, and challenges of quantifying responses to predators at scales relevant to conservation and management.

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Acknowledgements

Dedication

I dedicate this dissertation to my grandfather, Norm Sucher, who passed away during my time as a PhD student. Thank you for providing so many opportunities for me to get interested in conservation and fish. The time I spent with you, grandma, mom and dad fishing at the farm truly shaped my interest in freshwater fish. You are greatly missed by all of us.

Preface

Chapters 2 - 4 of this dissertation were prepared in submission format and include co-authors. Chapter 2 is published in the American Fisheries Society Symposium book entitled *Advances in Understanding Landscape Influences on Freshwater Habitats and Biological Assemblages* and has been adapted with permission from the American Fisheries Society. Chapter 3 is formatted for submission to *Freshwater Biology* and Chapter 4 is formatted for submission to *Ecology Letters* and both include appendices in the chapter that will be included in the submissions. Chapters 3 and 4 will be submitted for publication following the defense.

Chapter 1 - The role of predators across riverscapes: spatial scale and interactions between abiotic and biotic factors

The role of predators in ecosystems has long been debated by ecologists (Hairston et al. 1960, Paine 1966, Polis 1999). The relative importance of top-down versus bottom-up controls of ecosystems (Hunter and Price 1992, Power 1992), the role of predation in maintaining biodiversity (Ives et al. 2004, Ritchie and Johnson 2009) and the vulnerability of apex predators to global change (Estes et al. 2011, Wallach et al. 2015) highlight the need to understand, conserve and manage predator-prey interactions in natural systems. Some predators have disproportional effects on ecosystem structure and function ("keystone predators"; Paine 1980) and many predators have been introduced into systems beyond their native range (Eby et al. 2006). Introduced predators can replace native predators (Nakano et al. 1998, Simon and Townsend 2003), increase predator richness (Vander Zanden et al. 1999, Eby et al. 2006), and sometime have profound negative consequences on native prey (Sharpe et al. 2017). Ecosystem consequences of losing native predators and introducing nonnative predators are further amplified by climate and landscape change driving changes in predator distributions (Wisz et al. 2013). Further, predators are often considered charismatic fauna and are often public figures of conservation efforts (Estes 1996, Sergio et al. 2005). In short, most ecologist would agree predators play important roles in ecosystems and there is a need to understand these roles to conserve biodiversity in the face of global change.

In streams, fishes are typically among top predators with birds, reptiles, mammals, and amphibians. Although terrestrial and semi-aquatic predators can play important roles in structuring stream communities (Angermeier and Karr 1983, Power et al. 1985), this dissertation will focus on stream fish predators and prey because stream fishes are highly diverse and

threatened relative to other vertebrate groups (Darwall and Freyhof 2016). To begin exploring the importance of predators in driving stream fish community structure, it is useful to consider evidence supporting nonrandom structure and the interacting effects of abiotic and biotic factors in driving community structure. The relative importance of stochastic (random) and deterministic (nonrandom) processes, including both abiotic and biotic interactions, as drivers of stream fish community structure have been largely debated (Grossman et al. 1982, Yant et al. 1984, Winston 1995, Gotelli and McCabe 2002, Peres-Neto 2004, Giam and Olden 2016). While there is evidence of randomly structured stream fish communities (Matthews 1982, Gotelli and McCabe 2002), many freshwater fish communities are organized in response to abiotic, biotic, and spatial factors (reviewed in Jackson et al. 2001). Due to the temporal and spatial heterogeneity of abiotic conditions in streams, some argue abiotic factors and disturbance events dominate as drivers of stream community structure (Grossman et al. 1998), and biotic interactions are more important in begin environments relative to harsh environments (Peckarsky 1983). Despite debate over the importance of biotic interactions relative to abiotic factors, there is evidence of biotic interactions playing a role in structuring freshwater communities (Holomuzki et al. 2010), including fish communities (Jackson et al. 2001). The relative importance of any factor is context and spatial scale dependent (Zorn and Wiley 2010), so that processes may be viewed as influencing communities through a series of hierarchical filters (Smith and Powell 1971, Jackson and Harvey 1989, Tonn 1990, Poff 1997). Abiotic, biotic, historic, and stochastic process likely interact at multiple spatial scales to produce observed patterns of stream fish community structure.

Stream fish predator-prey interactions started receiving more attention in the 1980s. Research conducted in the 1980-1990s focused on experimental studies (mesocosm and stream enclosure experiments) of a few single predator species (*Micropterus, Semotilus, Esox, Hoplias*)

and single prey species, with a focus on localized effects of predators on prey behavior, predominately through changes in habitat use and activity levels, as well as direct effects on mortality (reviewed in Matthews 1998 and in Hoeinghaus and Pelicice 2010). Matthews (1998) summarized experimental evidence of one or a few piscivores effects on one or a few prey species, as well as several case studies of introduced predator effects on natural stream systems (Garman and Nielsen 1982, Rincón et al. 1990, Ruppert et al. 1993) and pointed out the lack of studies investigating community level responses of stream fish to predators. Despite Matthews (1998) call for the "marriage of empirical and theoretical work" to assess predator effects on entire fish assemblages, studies conducted over the subsequent decade continued to remained focused on single predator-prey interactions and were largely experimental and local in scale. In their review of fish predator-prey interactions in streams, Hoeinghaus and Pelicice (2010) restricted their review to small scale experiments due to the lack of studies at broad spatial scales or in natural systems.

Experimental work in streams suggest predators can have a wide array of consumptive and non-consumptive effects on stream fishes at fine spatial scales (reviewed in Hoeinghaus and Pelicice 2010; see Chapter 3 introduction) and evidence from natural systems suggest predator effects in streams, especially from introduced predators, can be variable (Townsend 2003, Billam et al. 2010, Turschwell et al. 2018) and/or weak relative to other factors (Giam and Olden 2016). The mixed effects of predators on stream fish communities is likely influenced by variation introduced by increasing spatial scale, measuring responses across environmental gradients, stochastic processes, and context dependency of responses. In this dissertation, I explore two of these sources of variation, spatial scale and environmental variability, to assess the role of a

widely introduced and voracious predator, largemouth bass (*Micropterus salmoides*) in driving stream fish community structure in Flint Hills streams.

A critical step in understanding predator effects across environmental gradients is accurately quantifying community responses to abiotic variability across stream networks. In Chapter 2, I compared site-selection strategies, or the distribution of sample sites across landscape gradients, for modeling effects of landscape factors on stream fish community structure. I used randomization tests to compare responses of stream fish species richness and community composition in response to catchment agriculture and catchment area of sites distributed randomly, highly skewed, or uniformly across these landscape gradients. I compared variability in responses to these manipulated distributions for three difference sample sizes. In this chapter, I conclude that detecting ecological responses to subtle or complex environmental gradients can be difficult, but careful consideration of study design can help elucidate responses.

In Chapter 3, I build off Chapter 2 and not only quantify stream fish community responses to landscape gradients, but also quantify how the presence of a predator, largemouth bass (*Micropterus salmoides*), vary across these gradients as well. Identifying important abiotic drivers of both stream fish community structure and the presence of predators allowed me to measure responses to predator presence mediated by abiotic factors. Field data collected in the summers of 2017 and 2018 was used for structural equation modeling (SEM) and a multi-scale modeling approach to measure effects of largemouth bass presence on stream fish assemblage richness, species relative abundances, and co-occurrence patterns. I hypothesized the prevalence of impoundments in the study area would play an important role in supplementing largemouth bass occurrences. Natural attributes of the stream network were important mediators of predator relationships with fish community structure and I observed positive relationships between bass

presence and richness and presence of several species. I discuss the challenges of quantifying landscape gradients, such as impoundments, in ecologically meaningful ways and the complex and often context depend effects of predators in driving community structure.

I wrap up Chapter 3 discussing challenges associated with quantifying the effects of predators at broad spatial scales. We know predators can have strong local effects in experimental studies, but predicting how predators influence natural systems at broad spatial scales requires understanding how scale biases measurements of responses to predators. In Chapter 4, I present results of a mesocosm study in which I compared consumption and prey behavior across a gradient of experimental stream sizes. I predicted per capita consumption would vary across arena sizes driven by changes in prey behavior associated with prey vigilance and encounter rates between predators and prey. I measured prey behavior and consumption by largemouth bass for two minnows occupying different habitat guilds. I observed unexpected changes in consumption with increasing arena size and hypothesize group vigilance plays an important role in driving consumption rates in Flint Hill stream fish communities

Collectively, these studies contribute to our understanding of predator-prey interactions across scales and environmental gradients to ultimately aide in the conservation of native fish. Conserving native fish is challenging due to the widespread effects of riverscape changes paired with the overwhelming number of introduced and often predatory fishes. I hope that this research contributes guidance for future studies to use more thoughtful experimental designs when developing sampling schemes to assess landscape change and urges others to continue to consider to impact of scale when interpreting biological interactions. My work highlights the challenges with identifying effects of predators in stream systems, and developing creative ways

to quantify predator-prey relationships across riverscapes is needed to help guide prioritized decision making regarding management of predators.

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Chapter 2 - Assessing site-selection strategies for modeling the influence of landscape factors on stream fish assemblages

Lindsey A. Bruckerhoff and Keith B. Gido

Abstract

Linking landscape features, both natural and human-altered, to aquatic ecosystem structure and function is a fundamental objective in landscape ecology and freshwater science, but this process is data- and resource-intensive. Quantifying how landscape stressors influence aquatic communities requires balancing logistic and financial constraints with effectively sampling the landscape to capture gradients of interest. There is a variety of ways to balance these constraints, such as using existing data, handpicked site selection, or a statistical site selection scheme. Poor sampling design reduces statistical power; however, we do not know how differences in site-selection designs influence our ability to measure ecological responses to landscape gradients. We quantified how the distribution of sample sites across landscape gradients affected the measured responses of stream fish assemblages to these gradients at different sample sizes. Specifically, we used randomization tests to compare the variability in the responses of fish assemblage structure (species richness and composition) to catchment area and land use (agricultural land) with manipulated distributions (random, highly skewed, and uniform) of sites across these landscape gradients. Assemblage composition was more sensitive than species richness to sampling design, and we observed less variability in the detected response of assemblage composition when samples were distributed uniformly across landscape gradients, especially when sample sizes were small. Although strong responses to environmental gradients,

such as species richness to catchment area, are robust to sampling distributions, large sample size and a uniform distribution of samples might help elucidate more subtle responses to environmental gradients.

Introduction

Lotic communities face multiple stressors as humans continue to modify landscapes (Roth et al. 1996, Allan et al. 1997, Allan 2004). Land-use change is one of the primary drivers of biodiversity loss in freshwater systems (Sala et al. 2000), so determining how landscapes influence the structure and function of riverine systems is a top goal in freshwater ecology and management. Landscape alterations influence freshwater systems through a variety of mechanisms at multiple spatial scales (Schlosser 1991, Townsend et al. 2003, Allan 2004). For example, land-use changes alter physiochemical attributes of stream habitats through sedimentation, nutrient enrichment, contaminant pollution, hydrologic alteration, riparian modification, and loss of woody debris (summarized in Allan 2004). These impacts may be the result of landscape change at multiple spatial scales, including changes in areas directly connected to the river channel, areas within the floodplain and riparian zones, and areas with indirect contact through surface-water, groundwater, and sediment flows into the river channel (Wang et al. 2006). Landscape alterations interact with natural characteristics across these spatial scales, as well as with stochastic (such as precipitation or temperature) and historic (biogeography) factors, to produce ecological patterns across river networks.

Because multiple environmental gradients interact at multiple spatial scales to drive patterns of lotic community structure, quantifying ecological responses to even a single landscape factor is a data intensive task. Capturing coarse-scale gradients of environmental features requires sampling large areas and collecting many samples. In addition to the intensive

sampling required to capture terrestrial landscape features, researchers must also consider the hierarchical structure of riverine systems. Broad scale landscape features may interact with properties of the stream network (e.g., stream size or location in the network). For example, in one study, insects unique to headwaters were at greater risk of extirpation from urbanization than species common throughout the stream network (Smith and Lamp 2008). To capture these types of interactive effects, stream network features must also be adequately sampled. As a result, researchers are often constrained in their ability to sample enough sites to capture complex responses across multiple environmental gradients, and it is critical to develop efficient sampling strategies to optimize allocation of effort.

There are many biomonitoring datasets collected by a variety of institutions (e.g. local, state, and federal governments, citizen science, universities, and museums) available to study impacts of landscape change on various ecological responses (see Buss et al. 2015 for summary of national datasets). To save time and money, many studies have used these existing datasets to assess how landscape patterns influence stream systems. We performed a cursory review of papers written since 2002 assessing the effects of land-use on stream fish assemblages. Our review included the first 50 papers found from major freshwater science and landscape journals. From this review, we found 18 out of 50 papers used pre-existing datasets (Table 2.1). Although few people may criticize scientists for being resourceful, there is potential bias associated with using existing landscape-stream datasets because data were likely collected with different objectives, sampling designs, and sampling methods (Deweber et al. 2014, Maas-Hebner et al. 2015). For example, the U.S. Environmental Protection Agency (USEPA) collects biological, chemical, and physical data at stream sites throughout the country through the National Aquatic Resource Survey (NARS). Stream sites in this program are randomly selected based on stream

size, spatial distribution (interspersed across the U.S.), and accessibility (USEPA 2012). Thus, they may not be ideal for studying, for example, the influence of impervious surfaces on aquatic communities within a state, because they were not collected with this intention. The NARS data likely cover a full gradient of stream sizes in the study area, but may not capture the full gradient of impervious surfaces. In addition to using pre-existing data, many studies also used what we classified as hand-picked sites (Table 2.1). In those studies, authors provided little to no rationale for choosing sample sites. For example, an author investigating the influence of impervious surfaces on fish assemblages may indicate sites were sampled along a gradient of urbanization intensity, but not provide any information about how that gradient was quantified or how sites were chosen.

Our observation that many broad-scale analyses quantifying impacts of landscape features on stream biota used existing data or provided little rationale for site selection led us to ask, how does sample-site selection across environmental gradients influence the measured response of ecological metrics? Specifically, we tested how the measured relationships between stream fish assemblage structure (species richness and composition) and landscape factors (both natural and human land-use changes) varied with different sampling designs (random, highly skewed, or uniformly distributed) of sample sites (stream segments) across landscape gradients. We also compared variation in measured responses across different sample sizes to evaluate the importance of sample designs at different levels of effort. This study provides insight into the importance of study design when conducting landscape studies and may serve as a resource to those designing studies to quantify the relationship between landscape change and stream biotic responses.

Methods

General Framework

We combined two datasets to quantify how the distribution of sample sites across environmental gradients influenced measured ecological responses. Our two response variables were fish species richness (hereafter richness) and assemblage composition, and the predictors were catchment area and the proportion of agricultural lands in the catchment of each site. We calculated catchment areas based on data included in the National Hydrography Dataset (USGS 2016) using Arc Hydro Tools in ArcMap 10.4 (ESRI 2011). Use of the term "catchment" in this paper refers to true upstream catchments delineated from the downstream point of all sites (Omernik et al. 2017). We then calculated the proportion of agricultural land within each catchment using Landsat raster data from the Kansas Satellite Image Database (KARS 2005). Agricultural land in this dataset was classified as cropland planted with corn, soybeans, sorghum, winter wheat, or alfalfa, or land used as fallow or planted with multiple crops, but did not include land classified as pasture (Peterson et al. 2010). We defined a site as a stream segment, or the portion of stream between two confluences. Our general framework consisted of grouping similar sites based on each predictor (e.g. small catchment area, low proportion of agriculture), randomly drawing sites from each group to fit different sample designs (random, right-skewed, and uniform) and modeling the relationship between the ecological responses (richness or composition) and gradients of interest (e.g., linear regression of richness versus catchment area). We repeated draws of sites for each relationship at varying sample sizes (25, 50, 75, and 100) 1,000 times (without replacement), developed models for each draw, and assessed the distribution of estimated coefficients across those 1,000 draws. We were interested in the

variability in our ability to detect a response (the proportion of times we detected a non-zero slope or significant relationship). All analyses were completed in R 3.4.2 (R Core Team 2017).

Fish Assemblage Datasets

We combined fish assemblage data for streams in the Flint Hills Ecoregion of Kansas (Figure 2.1) using existing records from the Kansas Department of Wildlife, Parks, and Tourism (KDWPT) and Kansas State University (KSU). KDWPT conducts streams surveys to monitor distributions of native fish throughout different parts of Kansas each year; this dataset contains data from different sites collected between 1995 and 2012. The KDWPT sites are selected using a variety of methods depending on the goals of sampling for each particular year. The KSU data were collected in the summer of 2017 to determine the influence of multiple stressors on stream fish assemblages. These sites were selected using a random stratified design across a range of stream sizes and gradient of agricultural land-use. All sites in the KSU dataset were wadeable and sampled using backpack electroshocking and seining. We combined these two datasets to increase the pool of sites used to create manipulated sampling distributions. All results in this study are constrained by the ecological responses apparent in the global pool of sites. In other words, the largest effect sizes produced by combinations of sample sizes and sampling distributions were constrained by the effect sizes observed in the global dataset. In addition, our random samples actually represent random samples of the sites in this combined dataset, not random samples of the environmental gradients. For the sake of this study, we consider patterns observed in the global pool of sites to represent the "true" relationships. We then compared how our ability to detect these relationships changed with different combinations of sample sizes and site-selection designs.

Sample Distributions

We chose to test fish assemblage responses across environmental gradients with random, right-skewed, and uniform distributions (Figure 2.2). We chose these distributions because they are (based on the authors' experience) commonly encountered by researchers conducting landscape studies. Completely random and random stratified designs are commonly used to designate samples across space (Manly 2001, Quinn and Keough 2002). Because completely random sampling does not account for probabilities of encountering different environmental gradients, more samples are likely needed to capture a full range of variability across gradients. Random-stratified designs distribute sites across strata representing different levels of gradients of interest, but samples are randomly designated within each stratum. If samples are allocated equally across strata, (i.e. equal-random-stratified), this design gives rise to uniform distributions of predictor variables, whereas random designs will produce distributions that mirror the proportional distribution of gradients across the landscape. Because samples are allocated equally across strata, fewer samples are needed to capture variability of environmental gradients of interest. However, the choice of strata may be inappropriate for other studies or other inferences. Highly skewed distributions may arise from a combination of the natural distribution of the gradient across the landscape and bias associated with sampling. For example, within a drainage basin, stream networks are dominated by small streams (regardless of how you measure stream size). Within a given area, a histogram of stream sizes will likely be right-skewed, so a randomly sampled stream network will produce right-skewed distributions of stream size. In addition, stream size bias may also arise from sampling bias. Smaller streams are typically easier to access and sample relative to larger streams, potentially adding further bias toward a right-skewed distribution of sample sites. We therefore distributed our samples randomly, right-

skewed, and uniformly (using an equal-random-stratified design) to capture those common sampling distributions.

Landscape Predictors and Ecological Responses

We chose catchment area and the proportion of agricultural lands in upstream catchments as predictor variables because we expected to see differences in our ability to detect a response between those variables. The influence of catchment area on fish assemblage structure is well documented for stream fishes (Matthews 1998). Although this pattern may not be considered an ecological response in the same way communities respond to land-use change, this known pattern allowed us to confidently explore the influence of sample design. Because we expected a strong effect, we predicted the influence of sample design on detecting a relationship between catchment area and fish assemblages would be less important. Land-use effects on fish assemblages, however, were expected to be harder to detect because of multiple indirect influences on instream physical and chemical conditions that influence fish (Berkman et al. 1986, Schlosser 1991, Hering et al. 2006), therefore we expected the importance of study design to be more conspicuous when assessing the influence of agricultural lands.

We chose richness and assemblage composition (Jaccard dissimilarity) as response variables because they are basic descriptors of assemblage structure. Jaccard dissimilarity was used rather than other distance matrices because it is based on presence/absence data, and abundance data from these datasets was unreliable due to the variety of methods and range of years included. Species richness and Jaccard dissimilarity capture both univariate (richness) and multivariate (composition) responses so that we could compare the influence of sample design on response variables with different statistical properties.

Randomization Tests

To quantify the influence of sample design on the response of richness to landscape factors, we developed ordinary least squares linear regression models for 1,000 random draws of sites with varying sample sizes (N=25, 50, 75, and 100) across the three sample distributions (random, right-skewed, and uniform) of catchment area and the proportion of catchment agricultural lands. Before drawing, we removed sites with catchment areas greater than 1,000 km2 or less than 2.7 km2 because those few outlier sites influenced the classification scheme used to draw samples. From this final dataset, we classified sites into five strata (Table 2.2) for each predictor (catchment area and proportion of agricultural lands) using the Jenks natural breaks classification method (Jenks 1977). The Jenks algorithm finds natural groups inherent in the dataset and maximizes differences between classes. We used these groups to draw samples with uniform (equal number of samples in each group) and highly right-skewed (dominated by low values) distributions for both landscape predictors. Catchment area was log transformed in regression models to improve linearity. Across each sample size and distribution combination, we calculated the mean slope and 95% confidence intervals in the predicted slopes across the 1,000 draws. We also calculated the proportion of draws that produced slopes of zero (indicating no relationship). We tested for positive slopes for the relationship between richness and catchment area because we expected richness to increase with increasing stream size. We also tested for negative relationships between the proportion of agricultural lands and richness because we expected decreases in richness with increasing upstream area converted for agricultural use.

To evaluate the relationship between fish assemblage composition and landscape features, we used Mantel tests to quantify the concordance of fish assemblage dissimilarity and

landscape features across sites. We started with the same global pool of sites used in richness

regressions (outlier sites based on catchment area removed) and then removed rare species (those

not present across at least 5% of the sites). We used the same strata used in regression models to

draw sites exhibiting the three sampling distributions. For each draw, a Jaccard dissimilarity

index representing the proportion of unique taxa between samples was computed for each pair of

sites. We also calculated the differences between catchment areas or proportion of agricultural

land between these same pairs of sites. Two matrices, one of Jaccard dissimilarity and one of

differences in environmental gradients, were generated to represent all pair-wise comparisons for

each set of samples. We then completed a permutational (N=1,000) Mantel test to determine if

the correlation between assemblage distance and difference in catchment area or proportion of

agricultural lands between all pairs of sites was significant. We calculated the proportion of tests

with non-significant Mantel tests and assessed the distribution of p-values across all draws and

sample distributions.

We tested for correlations between the distance between sites, differences in richness, and

assemblage dissimilarity to test for potential issues regarding spatial autocorrelation. Richness

was not correlated with distance between sites (Pearson's r=0.04) and assemblage dissimilarity

was only moderately correlated with distance between sites (Pearson's r=0.32), so we did not

correct for spatial proximity in our analysis. We also tested for correlations between the two

predictor variables, catchment area and proportion of agriculture, which were also not correlated

(Pearson's r=0.08, Figure 2.3).

Results

Our combined fish assemblage dataset had 279 sites after removing outliers. For richness

regressions, 72 species were included in the global species pool. After removing rare species,

there were 33 in the global pool for composition comparisons. Strata classifications allowed us to produce a gradient of skewness in the distribution of sites across landscape gradients (Table 2.3). Sites in the combined dataset were evenly distributed across the gradient of catchment size, but most sites had low catchment agriculture regardless of catchment size (Figure 2.3).

Fish Species Richness

Richness had a significant, positive relationship (p <0.001, m= 2.35, Adjusted r2 =0.29) with catchment area in the global dataset (Figure 2.4a). This positive relationship was detected across all combinations of sample sizes and sampling distributions (Figure 2.5a).

Richness also had a significant, negative relationship (p=0.005, m=-3.93, Adjusted r2=0.03) with the proportion of agricultural land in the catchment of each site (Figure 2.4b). Mean slopes derived from randomization tests varied between -5.02 and -3.48 across all sample sizes and sampling distributions, with lower, steeper slope means for uniform distributions across all sample sizes (Figure 2.5b). Confidence intervals did not overlap zero for uniform distributions at samples sizes of 50, 75, or 100 (Figure 2.5b), suggesting robust analyses at those levels of effort. The proportion of draws that produced non-negative slopes for the relationship between richness and the proportion of agricultural lands decreased with increased sample size and was consistently lowest for uniform sampling distributions (Figure 2.6).

Assemblage Composition

Jaccard dissimilarity was significantly correlated with difference in catchment area (p <0.001) and the proportion of agricultural lands (p < 0.001) in the global dataset. Mantel tests evaluating the correlation between Jaccard dissimilarity and catchment area were significant across all sampling distributions at sample sizes greater than 50 and for all sample sizes with a

uniform distribution (Figure 2.7a). When the sample size was 25, 6% and 4% of the draws produced non-significant Mantel test for random and right-skewed distributions (Figure 2.7a).

There was more variability, however, in the distribution of p-values when testing for associations between assemblage composition and catchment agriculture (Figure 2.7b). There were at least some non-significant Mantel tests across all combinations of sample sizes and sampling distributions except uniform distributions with sample sizes of 100 (Figure 2.7b). The proportion of non-significant Mantel tests decreased with sample size and was consistently the lowest for uniform distributions (Figure 2.8). Over 50% of draws produced non-significant Mantel tests at sample sizes of 25 with random and right-skewed distributions, whereas less than 2% of draws were not significant with uniform distributions and sample sizes greater than 25 (Figure 2.8).

Discussion

Study design, as indicated by differing predictor variable distributions, influenced the variability in our ability to detect fish assemblage responses. We observed less variability in the response of both fish species richness and assemblage composition to catchment area versus the proportion of catchment agriculture. This fit our prediction that land-use effects on fish assemblages would be weaker than the influence of catchment area. Similarly, we observed more variation in our ability to detect these relationships using Jaccard dissimilarity than species richness. However, we consistently observed less variation with uniform distributions and large sample sizes for both Jaccard index and species richness responses to catchment agriculture. This indicates sample design is especially important to consider when investigating relatively weak or multivariate ecological relationships. We expect this result to be consistent across different

regions, although the strength of the relationship between fish community structure (species richness and composition) and environmental gradients may vary.

We observed more variability in assemblage responses when samples sizes were small, but sample design could offset those differences. For example, our ability to detect correlations between assemblage dissimilarity and differences in catchment area or catchment agriculture declined with fewer samples, but was improved when those samples were from a uniform variable distribution. This is an important consideration because factors such as study objectives, timelines, funding, personnel, and other logistic constraints (e.g. access, distance between sites) limit the number of sample sites included in a study (Hughes and Peck 2008). Although statistical power is always a consideration when determining how many sites to sample (Toft and Shea 1983, Fairweather 1992, Quinn and Keough 2002), our study and others (Albert et al. 2010) suggest poor sample design can reduce statistical power by incorporating unnecessary variability. Further, if a response is tested across multiple environmental gradients, power will further be limited, as more samples are needed to capture multiple gradients. Thus, efficient sample design across multiple gradients may help optimize the designation of sample units to improve statistical power (see Additional Research and Management Needs).

We observed less variation in our ability to detect relationships between fish assemblage structure and environmental gradients when sites were drawn across uniform gradients. Uniform designation of sites incorporates prior knowledge about the system by requiring identification of important environmental gradients before sampling. These designations are achieved using equal-random-stratified sampling designs (Figure 2.2), in which an equal number of samples are allocated to each stratum, but samples are randomly allocated within strata. Equal-random-stratified designs are ideal, as gradients can be sampled efficiently without wasting effort

oversampling any part of the gradient. Similar to the current study, Hirzel and Guisan (2002) observed equal-stratified designs were the most accurate and robust when predicting habitat suitability and the presence/absence of virtual species in simulated terrestrial landscapes relative to random, regular, or proportional-stratified designs. However, other studies comparing ecological responses across different sample designs produced mixed results and do not always suggest the use of uniform gradient distributions. For example, Albert et al. (2010) used similar methods as those used in this study and discovered the efficiency of different sample designs were dependent on the types of parameters being estimated. Mean values of biological variables were best estimated by simple-random sampling designs, whereas optima were best predicted using model-based designs (iterative learning methods that incorporate prior knowledge; Albert et al. 2010). Mohler (1983) used simulations to recommend sampling designs that favor the extremes of gradients to best quantify abundance patterns of multiple species. Alternatively, sample design did not influence the prediction accuracy of species distribution models (SDMs) because the extent of individual species distributions had more influence on SDM predictions than sample design (Tessarolo et al. 2014). These studies suggest sample design is (usually) important and influences the ability to detect a response, but different designs may be better suited for different response variables. Similarly, the importance of sample design may also vary with different modeling approaches, with some statistical models being more robust to sampling distributions. More work is needed to determine which type of designs are ideal for different ecological responses (presence/ absence, abundance, diversity metrics, disturbance indices, etc.) and different types of statistical models.

Comparisons of sample designs are primarily studied using either real or simulated data. We drew samples from existing data to maintain some realism in our ecological relationships.

Our dataset included some of the biases that are apparent in true sample schemes (such as issues with accessibility or sampling close to roads) and provide realistic estimates of variability that would be detected in the study system. Albert et al. (2010) called this approach a "semi-virtual simulation". Whereas the decision to use a semi-virtual approach allowed us to capture realism, it did not allow us to account for some potential bias. For example, we did not account for differences in detection probabilities of species across environmental gradients. In addition, our observed ecological responses may also be biased due to the different methods of site selection used by our two data sources. Although we potentially could have avoided some of this bias by utilizing a larger dataset, such as one of the publically available datasets mentioned in the Introduction, we would have to alter the geographic extent of our study. Alternatively, we could have simulated data to compare different gradient distributions. Simulated datasets are useful because the true correlation structure between the response and predictor is known (Olden et al. 2004), making them useful in assessing the performance of different statistical tests used in ecology (Jackson 1993, Olden and Jackson 2000, Olden et al. 2004). Although we did not use simulated data in this study, other comparisons of sample designs that did use simulated data (Hirzel and Guisan 2002) produced similar results.

Additional Research and Management Needs

Our study is a first step in assessing the influence of sample design on the ability to detect ecological responses in stream systems. More work is needed to determine how unique properties of stream systems can be incorporated into sampling designs. The structure and function of streams is driven by heterogeneity at multiple spatial scales (hierarchical filters; Poff 1997), and stochastic events (disturbance; Townsend 1989). Although these processes have been integrated and studied in terrestrial systems using classic landscape principles like hierarchical

patch dynamics (Wu and Loucks 1995), unique properties of dendritic networks challenge direct application of these ideas in streams (Benda et al. 2004). For example, confluences have unique geomorphological properties (Poole 2002), and the placement and number of confluences within a network may create uneven patterns of heterogeneity within and between networks (Benda et al. 2004). These unique properties of confluences and the spatial position of sites within stream networks are known to influence relationships between fish community metrics and local environmental conditions (Hitt and Angermeier 2008). The age of geomorphic landforms might also vary from headwaters to main-stems (Benda et al. 2004) and other attributes of stream ecosystems (e.g. sediment size, functional trait composition, primary production, allochthonous inputs) vary longitudinally in stream networks (Vannote et al. 1980). Heterogeneity is also inherent in studies with extents that include multiple ecoregions or cross biogeographic boundaries (Pinto et al. 2009). Those sources of heterogeneity are common in broad scale studies across stream networks and should be considered when designing studies to measure effects of landscape change of stream ecosystems. Further work is needed to assess the effect of these attributes (location in the network, proximity to a confluence, differences in drainage density between networks, ecoregion, etc.) on the ability to detect ecological responses to landscape changes. One promising method proposed to account for spatially structured patterns of heterogeneity are spatial stream network (SSN) models that capture spatial auto-correlation in stream networks due to confluences, network connectivity, and the direction of stream flow (Ver Hoef et al. 2006, Ver Hoef and Peterson 2010).

Controlling for these sources of variability while simultaneously comparing the effects of multiple landscape stressors requires many samples and it is likely difficult to efficiently capture multiple landscape gradients (both natural and altered). Although we did not investigate multiple

gradients in the current study, we know statistical power will decline as more strata are included in a statistical model, and more samples are needed to capture multiple gradients. Obtaining a representative sample of multiple stressors across stream networks is complicated by both difficulties in calculating a priori landscape metrics for streams and the lack of sampling schemes based on multiple gradients. Typically, variables describing upstream catchments (e.g. catchment area, proportion of catchment land-cover classes) are calculated post hoc for sample sites (reach or segments). This makes stratifying across these types of variables a priori difficult, as one would have to compute catchment-based metrics for every possible site within a study area. Estimates of catchment-based metrics can be made at coarser spatial scales (e.g. using HUCs or ecoregions), but these estimates may not accurately reflect the true upstream conditions for an individual sample unit, complicating the use of stratified designs for catchment-based predictors. In addition, current sampling strategies are largely based on single predictor variables. Stratified sampling requires classifying gradients into multilevel strata, and capturing multiple gradients requires sampling all factorial combinations of strata levels. This is difficult to do when the natural gradient distribution is skewed because all factorial combinations of strata may not exist. For example, in the current study, it would be difficult to find sites with both intermediate sized catchments areas and intermediate levels of agriculture, or both large catchment areas and high catchment agriculture, but there are many sites with low catchment agriculture at a variety of catchment areas (Figure 2.3). Response surface methodology, a sequential process involving several designed experiments (Box and Wilson 1951),has been suggested as a method to incorporate multiple predictor variables when trying to estimate the optimal value of a response (e.g. peak abundance of species), and its application to ecology has been explored in terrestrial systems (Albert et al. 2010). Other options for capturing multiple gradients may include

compressing variability in multi-dimensional environmental space using ordination techniques (such as Principal Coordinate Analysis) and stratifying samples in lower dimensional space (across a few axes; Stevens and Olsen 2004). Overall, a methodological framework for capturing multiple strata in stream networks is needed.

Policy Implications

Understanding the effect of study design on our ability to detect ecological responses can help inform the management of riverine systems by improving the interpretation of studies and by helping managers effectively allocate sampling effort to detect ecological relationships. Inefficient study designs may run the risk of producing Type II errors (false negative), and researchers may conclude environmental gradients are not important when in reality they are. For example, if policy makers were interested in the impact of agriculture on fish community structure, they should be aware that a lack of pattern might be due to low statistical power, as observed in our results. Thus, management recommendations should consider the nature of the data, including the spatial distribution of sample sites, prior to any decision-making process. Thorough descriptions of study design and the use of post hoc power analysis may help provide clarity on how much confidence can be placed in results so policy makers and managers can make decisions based on studies with robust designs. Beyond robust study designs, the biological significance is also an important consideration when translating science into policy and management decisions. While this paper was mainly focused on the influence of study design on detecting statistical relationships, detected statistical relationships may not always translate into biologically significant responses. Detailed investigation into individual species responses, for example, might be more relevant to specific management goals.

Conclusions

Overall, sample design influences our ability to detect ecological responses to environmental gradients, especially when sample sizes are low. This point has already been developed as a main component of study design theory, but we would like to emphasize that sample design is particularly important when assessing subtle or complex ecological phenomena. The unique attributes of stream networks and the interactions between terrestrial and aquatic environments likely make most landscape-stream ecology relationships complex. Stream ecologists should strive to develop new ways to overcome these inconveniences to maximize the probability of detecting complex but ecologically important relationships. Implementation of improved study designs is needed to help us uncover environment-ecological relationships, especially as humans continue to modify many landscape attributes.

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Tables

Table 2.1 Site selection methods used in 50 papers investigating the influence of landscape factors on fish assemblage data. These papers were compiled by conducting a cursory review of papers written since 2002 assessing the effects of land-use on stream fish assemblages, and included the first 50 papers found from major freshwater science and landscape journals. Hand-picked designs were those with vague description indicating sites were distributed across environmental gradients, but no formal method for the allocation of sample units across these gradients was provided. Studies were classified as using existing data if they indicated the use of data from a publicly available dataset from a public or private institution or used data collected in another study for a different purpose. Designed studies were those in which a clear description of the sample unit allocation (random, systematic, etc.) was provided. SDM and historic occurrences represents samples that were allocated based on species distribution models or historic occurrence data.

Site Selection Method	Number of Papers
Hand-picked	20
Existing Data	18
Not Provided	6
Designed	5
SDM and Historic Occurrences	1

Table 2.2 Predictor variables were classified into five strata using the natural Jenks algorithm to

produce distributions with right-skewed and uniform distribution.

| | Range | | | | |
Variable	Stratum 1	Stratum 2	Stratum 3	Stratum 4	Stratum 5
Proportion of agricultural land	0.00-10.20	10.30-25.40	25.50-48.20	48.30-67.60	67.70-89.00
Catchment area (km^2)	2.85-10.27	10.28-27.67	27.68-79.64	79.65-246.23	246.24-864.19

Table 2.3 Mean skewness values of the distribution of agricultural land across draws with different sample sizes and random, right-skewed, and uniform distributions. Distributions of catchment area across the three distributions exhibited similar skewness values as these.

Gradient Distribution	Sample Size	Skewness
Random	25	0.91
	50	0.91
	75	0.91
	100	0.92
Right-Skewed	25	1.27
	50	1.24
	75	1.16
	100	1.17
Uniform	25	0.16
	50	0.16
	75	0.16
	100	0.16

Figures
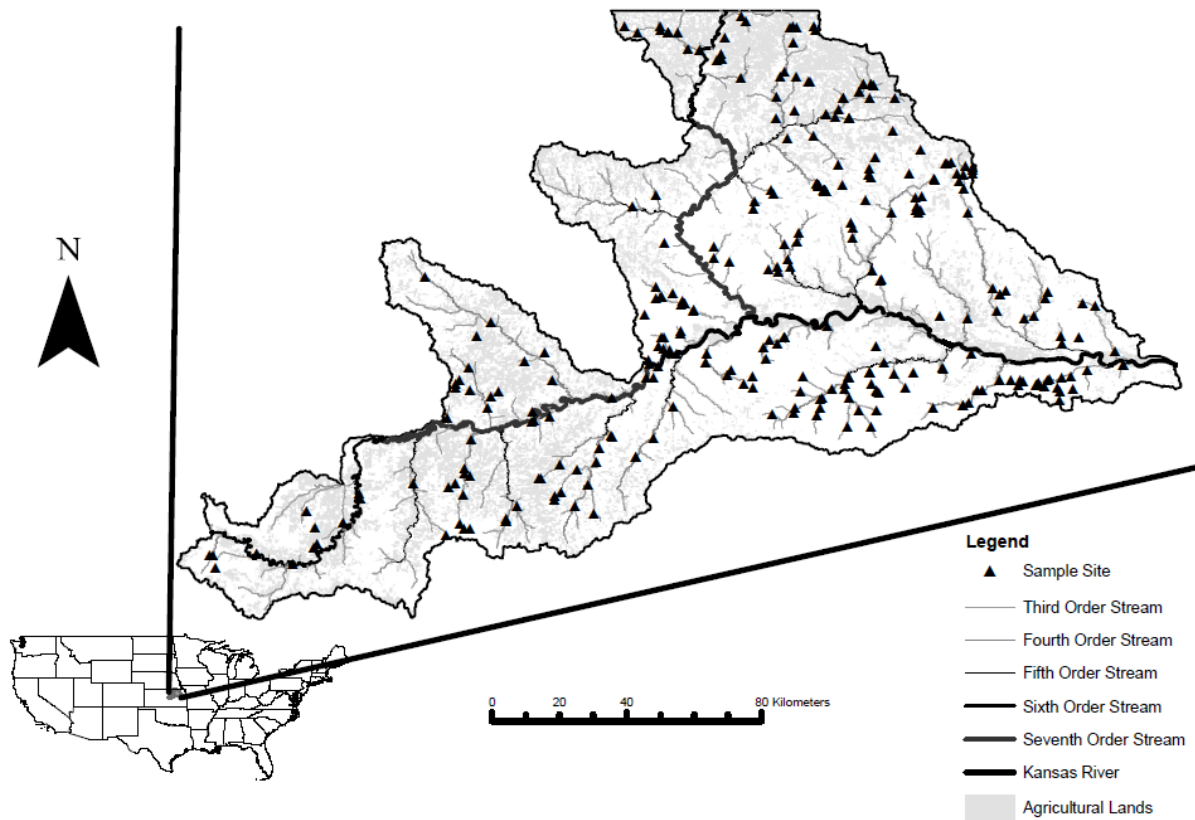
Figure 2.1 Locations of sites included in the combined fish assemblage dataset sampled by Kansas Department of Wildlife, Parks, and Tourism (KDWPT; black) and Kansas State University (KSU; grey). All sites were located in the Kansas River Basin and the Flint Hills ecoregion of Kansas, USA.

Gradient Distribution	Frequency Distribution	Produced By	Strengths	Weaknesses
Random	Mirrors landscape composition	Completely random sampling	Sample units independent Do not need *a priori* knowledge about the system	May not capture gradients of interest Wasted effort in common habitats
Highly Skewed	# of Samples: 23, 18, 13, 8, 3, -2 — Gradient 1 2 3 4 5	Biased sampling	Convenient, may be able to achieve high sample size	Not enough samples across entire gradient Wasted effort around some value of gradient Sample units may not be independent
Uniform	# of Samples: 10, 8, 6, 4, 2, 0 — Gradient 1 2 3 4 5	Equal-random-stratified sampling	No wasted effort Entire gradient sampled	Need *a priori* knowledge about the systems Potential spatial clumping

Figure 2.2 Random, highly skewed, and uniform gradient distributions are produced by different sampling distributions, and there are different strengths and weaknesses associated with each distribution.
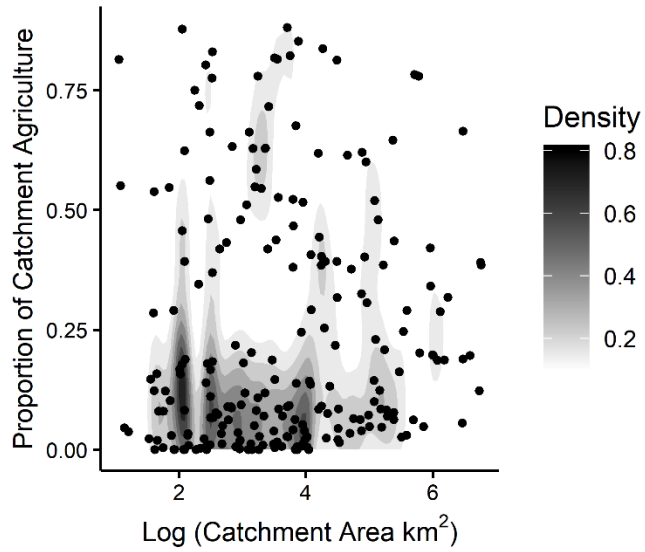
Figure 2.3 The density of sites across log transformed catchment area (km^2) and the proportion of catchment agriculture. Shading represent kernel density estimates of sites, with darker values representing a higher density of sites.
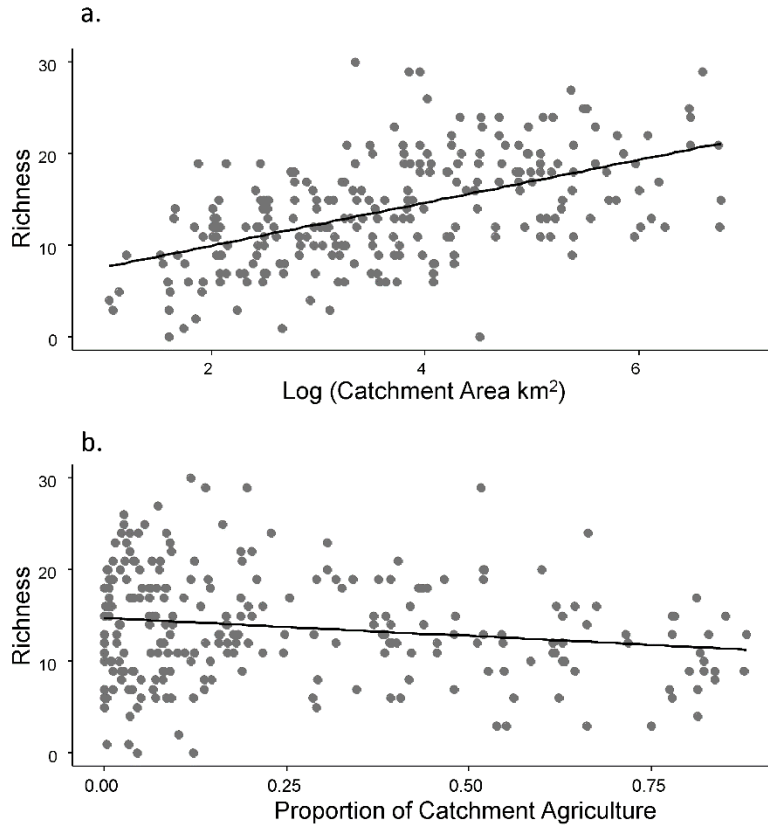
Figure 2.4 Fish species richness increased ($p < 0.001$, $m = 2.35$, Adjusted $r^2 = 0.29$; a.) with increased catchment area and decreased ($p = 0.005$, $m = -3.93$, Adjusted $r^2 = 0.03$; b.) with increased proportion of agricultural land in each catchment across the global pool of sites.
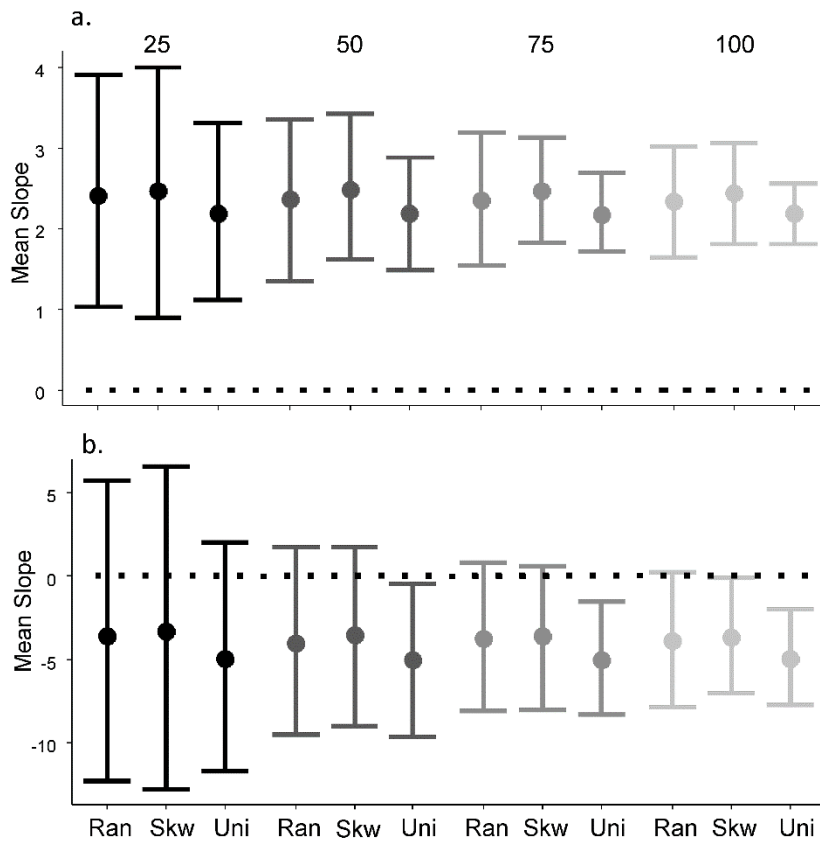
Figure 2.5 Mean slope and confidence intervals derived from 1,000 iterations of regressions of stream fish species richness against catchment area (a) and the proportion of agricultural land in the catchment (b) for N= 25, 50, 75, and 100 samples. Samples were drawn randomly (Ran), right-skewed (Skw), and uniformly (Uni) from an existing dataset. The dotted line at mean slope = 0 indicates when no relationship was observed between richness and catchment area or proportion catchment agriculture.
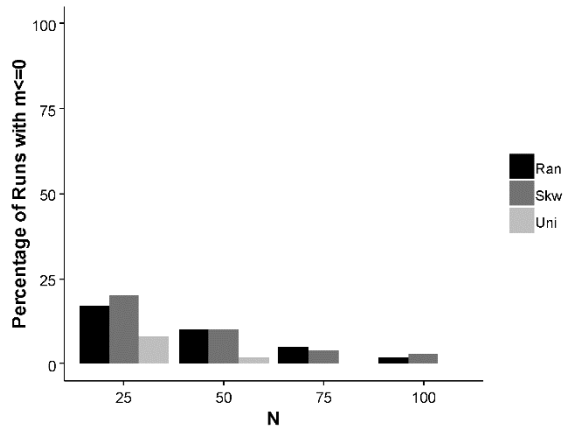
Figure 2.6 The proportion of runs (N=1,000) with slopes less than or equal to zero indicating no relationship between catchment land-use and fish species richness for sample sizes of 25, 40, 75, and 100 for random (Ran), right-skewed (Skw), and uniform (Uni) distributions.
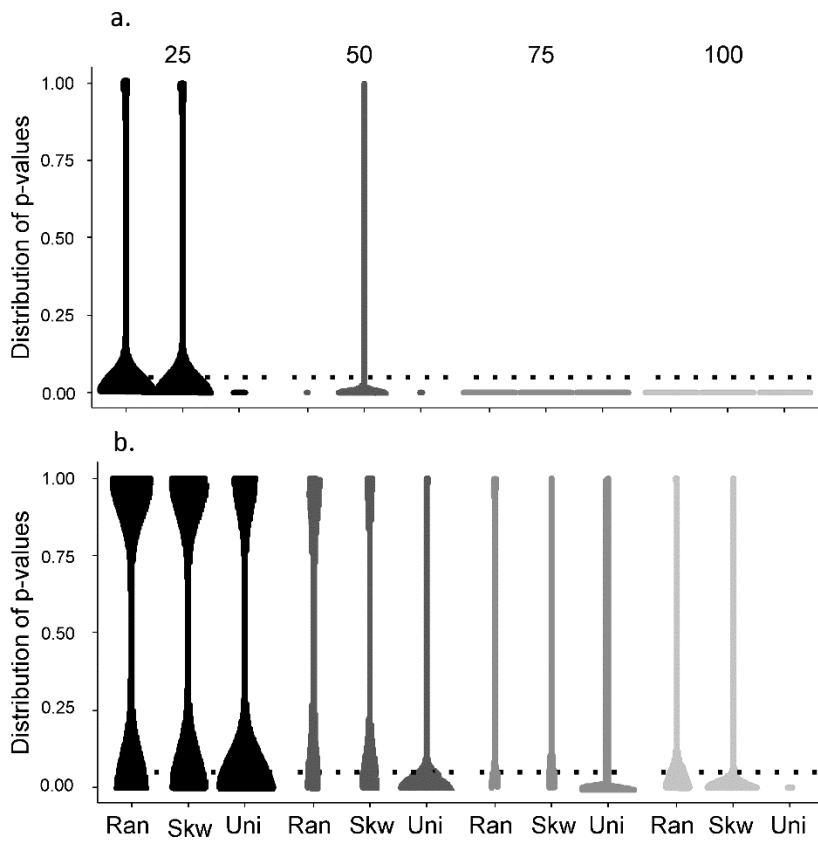
Figure 2.7 Distribution of p-values obtained from Mantel tests of difference in catchment area (a) and the proportion of agricultural land in the catchment (b) versus fish assemblage Jaccard dissimilarity for sample sizes of 25, 50, 75 and 100. Samples were drawn randomly (Ran), highly right-skewed (Skw), and uniformly (Uni) from an existing dataset.
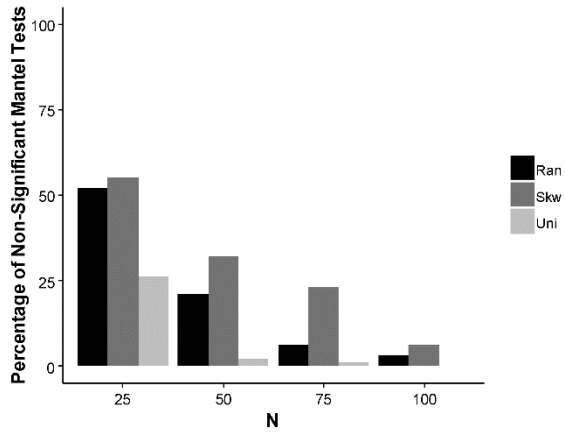
Figure 2.8 The proportion of runs (N=1,000) with non-significant Mantel tests indicating no relationship between upstream land-use and fish assemblage composition for sample sizes of 25, 40, 75, and 100 for random (Ran), right-skewed (Skw), and uniform (Uni) distributions.

Chapter 3 - Disentangling effects of predators and landscape factors as drivers of stream fish community structure

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Summary

1. Experimental and fine-scale studies indicate predators can have strong effects on stream fishes. It is unclear, however, how these responses scale up to influence stream fish communities at coarse spatial scales relevant to management and conservation. Because predators and prey respond to environmental variability, measuring community responses to predators requires resolving the effects of abiotic factors on both predators and prey.

2. We collected fish community data in the summers of 2017 and 2018 and used a multi-scale modeling approach paired with structural equation modeling to test whether factors measured at the watershed and reach spatial scales influence the distribution of a predatory fish, largemouth bass (*Micropterus salmoides*). We then compared how fish species richness and community composition responded to the presence of bass mediated by environmental factors.

3. Probability of occurrence of bass increased with catchment area, while richness responded to both natural stream variation and anthropogenic modifications in the watershed. Richness was greater at sites with bass, likely driven by co-occurrence between bass and several species associated with impoundments.

4. As stream habitats and predation pressure continue to change through species introductions and landscape change, it is necessary to understand the effects of predators and environmental variation as drivers of community structure to inform management of stream biota. We outline

several challenges and the need for creative solutions to understanding effects of predators in natural systems.

Introduction

Do predators influence stream fish communities? This question is not only a fundamental aspect of basic community ecology, but also has implications regarding the conservation of freshwater fishes. Although stream fishes participate in all types of biotic interactions, understanding predator-prey interactions in streams is of particular interest because predatory fishes can produce strong effects across all levels of biological organization in freshwater systems (Cucherousset & Olden, 2011). Further, predatory fishes have been both introduced to (Welcomme, 1988) and lost from (Estes et al., 2011; Winemiller, Humphries, & Pusey, 2016) freshwater systems globally. Negative effects of introduced predators in lake systems are well known, including reduced abundance of small-bodied fishes (MacRae & Jackson, 2001; Jackson, 2002), homogenization of freshwater fauna (Rahel, 2002), species extinctions (Kaufman, 1992; Ligtvoet, Goldschmidt, Van Oijen, Wanink, & Goudswaard, 1991), and changes in food web structure (Vander Zanden, Olden, Thorne, & Mandarak, 2004). Most of what we know about predator effects in streams has been observed at relatively fine spatial scales (mesocosm experiments or within a stream reach). Direct consumption by piscivores increases mortality rates and decreases densities of prey, mediated by predator and prey identity (Schlosser 1987, Marsh-Matthews et al. 2013), body size (Schlosser, 1988; Magoulick, 2004; Layman & Winemiller, 2004), habitat characteristics (Harvey & Stewart, 1991; Angermeier, 1992; White & Harvey, 2001), and predator density (Gilliam & Fraser, 1987; Harvey, 1991). Non-consumptive effects are wide ranging, including well-documented shifts in habitat use (Power, Matthews, & Stewart, 1985; Schlosser, 1987; Schlosser, 1988; Harvey, 1991; Fraser & Gilliam, 1992;

Greenberg, 1994; Magoulick, 2004) and changes in prey activity levels, foraging behavior,

growth, life history, reproduction, and movement/dispersal patterns (reviewed in Hoeinghaus &

Pelicice, 2010). Predators can increase emigration rates (Power et al., 1985; Fraser & Gilliam,

1992; Schaefer, 2001) or act as both barriers and promoters of dispersal (Fraser, Gilliam, & Hip-

Hoi, 1995). While experimental studies provide evidence for several mechanisms that may elicit

a variety of prey responses to predators at fine spatial scales (within a stream reach or segment),

we do not yet understand the role of these mechanisms in structuring stream fish communities in

natural stream systems or how predators interact with landscape factors to produce patterns of

fish assemblage structure at coarse spatial scales (across stream networks).

Several studies have documented effects of predators on prey fishes in natural streams.

Much of this literature documents relationships between a nonindigenous predator with one or

several prey species. Nonindigenous predators can lower prey abundance at local sites (Gilliam,

Fraser, Alkins-Koo, 1993; Labbe and Fausch, 2000), create source-sink dynamics (Woodford &

McIntosh, 2010), and influence genetic diversity (Vanhaecke, Garcia de Leanix, Gajardo,

Dunham, Giannico, & Consuegra, 2015). Negative associations between predator-prey pairs

have been observed across drainage basins, revealed through both taxonomic and functional

group analysis (Hoeinghaus, Winemiller, & Birnbaum., 2007; Giam & Olden, 2016). Nonnative

predation pressure may be uneven throughout stream networks (Hedden, Gido, & Whiteny,

2016), and nonnative predators may feed disproportionately on native prey fishes relative to

nonnative prey (Pilger, Franssen, & Gido, 2008). For example, nonnative *Ictalurus punctatus*,

Ameiurus melas, and *Lepomis cyanellus* lowered the abundance of several native prey species

and altered food web networks in the San Rafael River (Walsworth, Budy, & Thiede, 2013).

These studies highlight the potential for nonnative predators to influence fish community

structure, and we predict predators interact with abiotic factors to produce patterns of stream fish community structure across stream networks.

Understanding how community structure responds to predators in stream systems requires isolating predation effects from abiotic drivers of community structure. Natural landscape features, including both terrestrial and stream network attributes, influence fish communities, and anthropogenic landscape modifications can significantly alter population and community dynamics of stream fishes (Schlosser, 1991; Allan, 2004). Attributes throughout a watershed interact at hierarchical spatial scales to influence the ecological integrity of streams by driving habitat characteristics, water quality, connectivity, flow regime, and biotic processes (Poff, 1997; Labbe & Fausch, 2000). Landscape context may therefore not only influence the distributions of predators and prey, and therefore where they overlap in space and time, but also influence the magnitude of predation impacts. For example, densities of native small-bodied cyprinids in the Gila River watershed of New Mexico declined during low-flow years but were lowest at sites that also had nonnative *Micropterus dolomieu* (Stefferud, Gido, & Propst., 2011). Ecologists recognize the complex interactions of landscape factors at multiple spatial scales and strive to conserve stream fish communities using a "riverscape" perspective (Fausch, Torgersen, Baxter, & Li., 2002). To conserve fishes across riverscapes, we need to understand how biotic processes, such as predation, interact with abiotic factors across spatial scales to produce patterns of community assembly.

Objectives

We used a multi-scale modeling approach and structural equation modeling to assess the effect of a predator on stream fish community structure (richness and composition) mediated by abiotic factors. Our goal was to identify abiotic drivers of fish community structure and the

presence of predators, then control for abiotic drivers to assess how fish community structure responded to the presence of a voracious and widely introduced predator, largemouth bass (*Micropterus salmoides,* Centrarchidae). Predation pressure in streams has likely changed and will continue to change over time in response to stocking programs, accidental introductions, impounding waterways, overfishing, habitat fragmentation and alteration, and changing temperature and flow regimes. Stream fish communities already face challenges responding directly to these same alterations, so we need to understand how alterations in predation pressure influence fish communities to manage and conserve this threatened fauna.

Methods

Study Area

This study was conducted in Great Plains prairie streams in the Neosho and Kansas River basins in the Flint Hills ecoregion of eastern Kansas (Figure 1). Great Plains prairie streams are characterized by a large proportion of intermittent streams with highly variable hydrographs and watersheds historically dominated by grasslands (Dodds, Gido, Whiles., 2004). Small impoundments are a major landscape modification in and around the Flint Hills (Perkin et al., 2015). Impoundments are often stocked with sportfish species (especially *M. salmoides*) that may increase predation in nearby streams by expanding the distribution of predators across the landscape or if stocked fish act as more voracious predators than other potentially less aggressive piscivores commonly found in Great Plains prairie streams (e.g., creek chub *Semotilus atromaculatus,* Cyprinidae; green sunfish *Lepomis cyanellus,* Centrarchidae; black bullhead *Ameiurus melas,* Ictaluridae; and spotted bass *Micropterus puntulatus,* Centrarchidae). Our study is in the western edge of what is considered the native range of largemouth bass, but because bass have been moved around and stocked since the late 1800s (Long, Allen, Porak, & Suski

2015), it is unclear if the largemouth bass in the study area are predominately from native or nonnative stocks. While the nonnative status of largemouth bass in our study area is unclear, this system provided the opportunity to investigate the relationships between altered predation pressure, abiotic factors, and stream fish assemblage structure.

Site Selection

Sites were selected using a random-stratified design (Bruckerhoff & Gido, 2019) with the goal of capturing both the hierarchy of stream networks (drainage basin and stream order) and land use. Major anthropogenic land use gradients in the region used for stratification included percentage of cultivated land, number of impoundments, and number of road crossings in each 10-digit Hydrologic Catalog Unit (HUC; Seaber et al., 1987) watershed within the study area. We calculated the proportion of agricultural land using Landsat raster data from the Kansas Satellite Imagery Database (KARS, 2006), the number of impoundments using both the National Wetlands Inventory (USFWS, 2018) and National Hydrography Dataset (USGS, 2016), and the number of road crossings by calculating intersections between the 2001 Topologically Integrated Geographic Encoding and Referencing (TIGER) database (US Census Bureau, 2001) and a modified stream layer based on NHD stream lines. We then classified each HUC into three classes based on 15 and 85% quantiles for the three land use variables. We randomly drew two stream segments across all combinations of stream order (1st- 4th order) and the three classifications (low, medium, high) of the three land use variables (road crossing density, percent agriculture, impoundment density). We limited our sites to 1st-4th order streams to target wadeable streams.

Our random stratification process provided us with around 200 stream segments with each iteration. We then tried to sample the randomly selected stream segments but were often

limited by landowner permission. After a round of selected streams had been successfully or unsuccessfully sampled, a new round of sites was drawn (without replacement) and targeted for sampling.

 Stream Fish and Habitat Sampling

We collected stream fish community data in the summers of 2017 and 2018 from several pools and riffles (mesohabitats) at each site. We aimed to sample at least two pools and two riffles at each site but were sometimes limited by habitat availability or landowner permission. Typically, we sampled enough mesohabitats to cover 8 times the median width at each site. Fishes were sampled using single pass backpack electroshocking (Smith-Root LR-20, Vancouver, WA) followed by multiple seine hauls (4.6 x 1.8 m, 3.2-mm mesh) in all habitat types (debris, vegetation, root wads, etc.) within each mesohabitat. Only electrofishing was used in riffle mesohabitats. All fish were identified, measured, counted, and released in the field. Small specimens difficult to identify in the field were preserved in 10% formalin solution and identified in the laboratory.

We measured habitat characteristics in all sampled mesohabitats. Width was measured at a minimum of three transects in each mesohabitat (more transects were added in pools or riffles longer than 30m). Along each transect, we documented the depth and substrate type (modified Wentworth scale; Wentworth, 1922) for five points and measured canopy cover using a densiometer at the center of each transect. We also measured the length of each mesohabitat and the dimensions of any cover habitat (root wads, overhanging vegetation, boulders, log complexes, etc.).

Geospatial Data

We delineated catchment boundaries of all sampled sites using Arc Hydro Tools in ArcMap 10.4 (ESRI, 2011) using digital elevation models from the National Elevation Dataset (USGS, 2002) and stream lines from the National Hydrography Dataset (USGS, 2016). Use of the term "catchment" or "watershed" in this paper refers to true upstream catchments delineated from the downstream point of all sites (Omernik et al., 2017). Within each catchment, we calculated the area, density of roads, the proportion of catchment surface area impounded, and proportion of cultivated land (cropland planted with corn, soybeans, sorghum, winter wheat, or alfalfa, or land used as fallow or planted with multiple crops) using the same datasets used in stratification procedures. We also calculated the linear distance to the nearest impoundment from each site.

Analysis

Our general framework included determining which abiotic factors calculated at watershed and reach scales drove the presence of bass, stream fish richness, and community composition, followed by assessing the effects of bass on stream fish community richness and composition mediated by important abiotic drivers. All abiotic factors included in analyses and any transformations used to improve linearity and minimize variability are included in Table 1. We narrowed important abiotic factors using a multi-scale modeling approach, in which we created separate models at either the reach or watershed scale and included significant predictors in final models that also included the effect of bass presence (Figure 2). All analyses were completed in Microsoft R Open 3.5.3 (Microsoft Corporation and R Core Team, 2019).

      Bass Presence and Richness

We used binomial generalized linear mixed effect models with logit link function with presence of bass as a response and Gaussian mixed effect models with rarefied richness as a response to assess abiotic factors influencing the occurrence of bass and richness at the reach and watershed scales. We used rarefied richness to control for different probabilities of detecting more species with different numbers of individuals sampled using Hurlbert's (1971) equation based on a sample size of 100 individuals. We also ran models using raw richness values and observed the same results, so only rarefied richness is presented here. Because fish community structure responses to abiotic factors are often spatially autocorrelated (Bruckerhoff, Leasure, & Magoulick, 2019), we included HUC level 10 watershed nested within major drainage basin as a random effect to control for spatial clumping of sites within watersheds. Year was also included as a main effect in all models. Correlations between predictor variables were assessed before building models and predictor variables had variance inflation factors less than 2 in all models, so multicollinearity was not considered an issue. We assessed significance of abiotic factors using likelihood ratio tests and retained significant predictors for further analysis. All mixed-effect models were developed using the package *lme4* (Bates, Maechler, Bolker, &Walker., 2015).

A structural equation model (SEM) was developed to test the relationship between presence of bass and stream fish species richness using the package *piecewiseSEM* (Lefcheck, 2016). Structural equation models allow for the simultaneous analysis of multiple predictors and response variables and the visualization of relationships using path diagrams (Shipley, 2000). The package *piecewiseSEM* allows SEM to be applied to generalized, mixed effect models and uses directed acyclic SEM, in which each equation is solved separately and goodness of fit is determined using Shipley's test of directed separation (Shipley, 2000; 2009). Relationships

between all variables identified in exploratory generalized linear models were included as predictors of either bass presence or rarefied richness, and the mediated effect of bass presence on richness was also included. We also included the random effect of HUC level 10 watershed nested within major basin across all paths to control for spatial clumping of sites within drainages. No latent variables were included in our model.

Community Composition

We used the function *manyglm* from the package *mvabund* (Wang, Naumann, Wright, & Warton2012) to identify important reach and watershed scale abiotic variables influencing fish community composition and the effect of bass on community composition. This function allows individual generalized linear models to be developed for each species, provides a global estimate of significance that controls for multiple testing and can be more powerful than distance-based multivariate methods (Wang, Naumann, Wright, & Warton2012). We used negative binomial distributions appropriate for overdispersed count data. Our fish community matrix included counts of adults collected at each stream reach (mesohabitats were pooled together). We only included fish with total lengths above 30 mm to avoid bias associated with different spawning times and sampling efficiency of small fishes. To eliminate the influence of rare species. only species present in at least 5% of samples were used. We removed largemouth bass from the community matrix because their presence was used as a predictor variable. Models were developed separately for the two drainage basins, as some species do not occur in both basins. As with bass occurrence and richness models, we included the effect of year in all models. Because random effects cannot be included in *manyglm* models, we included HUC level 10 watershed as a fixed effect. Since these models included fish raw counts, we included the total number of individuals captured at each site as a predictor variable. This allows the interpretation of results

to be similar to interpreting relative abundance of species to control for varying effort in sampling across sites but avoids the quantitative difficulties of using relative abundances (proportions) as response variables. Significant variables from this analysis were then used in proceeding *manyglm* models that also included the presence of bass as a predictor variable.

We were also interested in determining if bass presence was associated with community composition based on simple presence of species. We used permutational MANOVA of Jaccard's distance to determine if there was a global association between occurrence of bass and community composition (based on presence/absence of species). We restricted this analysis to sites in the 50th percentile for watershed area because the probability of bass occurrence was highest in these streams (49% of sites in the Kansas basin, 54% of sites in the Neosho basin). If permutational MANOVAs indicated a significant association between community composition and the presence of bass, we then used generalized linear models and permutational chi-square tests to test for associations between bass and individual species. Because watershed area captured the most variability in both bass and species occurrences, logistic regression models with species presences as a response variable and watershed area as a predictor were first used to determine whether individual species varied significantly across the restricted subset of large streams. If this relationship was not significant, we then used permutational chi-square tests to determine whether individual species co-occurred with bass more frequently than expected by chance. These analyses were completed separately for each major drainage basin.

Results

Our final dataset included abiotic and fish community data for 336 stream sites (188 sites in 2017, 148 in 2018; Figure 1), with watershed area of sites ranging 0.06 -725.74 km^2. Fifty-five

species (see Supporting Information Table S1) were captured across all sites, and mean species richness was 10.60. We collected largemouth bass at 26% of sites.

Mixed effect models suggested watershed area should be retained as a predictor of bass occurrence, and substrate size, mean depth, distance to nearest pond, catchment agriculture, road crossing density, and watershed area as predictors of richness in SEM (Table 2). We therefore only included watershed area as a predictor of bass presence, but included links of all other abiotic factors and bass as drivers of richness (Figure 3). Shipley's test of directed separation produced a Fisher's C of 9.10 and p-value of 0.52, indicating good model fit and no missing paths in the model. The estimated conditional R^2 was 0.41 for richness and 0.06 for the presence of bass. All paths were significant except for the effect of distance to the nearest pond on richness (Figure 3, Table 2). Probability of bass occurrence and richness increased with watershed area (Figure 4, Figure 5). Richness also increased in response to the proportion of large substrates and mean pool depth, but decreased with increasing catchment agriculture and density of road crossings (Figure 5). Bass presence had the strongest effect on richness, with an increase of almost three species at sites with bass mediated by environmental factors included in SEM (no bass: predicted richness = 8.0, S.E. = 0.20; bass present: predicted richness = 10.6, S.E. = 0.33).

The presence of bass was a significant predictor of community composition in the Kansas basin, but not in the Neosho. Despite significance at the community level, no individual species abundance in the Kansas basin exhibited a significant response to bass presence. Four species contributed more than 10% of deviance described by the presence of bass in the Kansas basin (redfin shiner *Lythurus umbratilus*, Cyprinidae: 19%, bluegill *Lepomis machrochirus*, Centrarchidae: 11%, yellow bullhead *Ameiurus natalis*, Ictaluridae: 11%, and black bullhead:

11%). Significant abiotic predictors of community composition (abundance of species) included year, HUC 10 level watershed, number of individuals, watershed area, and catchment agriculture for both the Kansas and Neosho river basins (Table 3). Five species had significant negative relationships with catchment area, while seven species had significant positive relationships (Figure 6). Abundance of only one species, southern redbelly dace *Chrosomus erythrogaster* (Cyprinidae), responded significantly (and negatively) to catchment agriculture (deviance = 22.92, p = 0.04; Figure 7). Abundance of spotted bass (deviance = 12.81, p = 0.03) and golden redhorse *Moxostoma erythrurum* (Catostomidae; deviance = 17.98, p = 0.01) were significantly higher in 2018 than 2017. Proportion of catchment impounded was also a significant predictor of composition in the Neosho basin, while mean depth was significant in the Kansas basin (Table 3), but no individual species had significant responses to these variables.

Permutation MANOVAs indicated a weak association between bass presence and community composition in the Kansas basin (F = 2.21, R^2 = 0.02, p = 0.01), but not in the Neosho basin (F = 1.63, R^2 = 0.03, p = 0.09). The presence of four species from the Kansas basin had nonsignificant relationships with watershed area, but positive significant associations with bass presence (Figure 8), including western mosquitofish *Gambusia affinis* (Poeciliidae; X^2 = 7.86, p < 0.01), redfin shiner (X^2 = 5.81, p = 0.03), longear sunfish *Lepomis megalotis* (Centrarchidae; X^2 = 5.33, p = 0.02), and bluegill (X^2 = 8.78, p < 0.01).

Discussion

Richness was higher than predicted based on abiotic characteristics at sites where bass were present, and this increased richness seemed to be driven by a higher probability of occurrence of several species (bluegill and western mosquitofish) associated with lentic or altered habitats. Increased richness due to co-occurrence of stream and reservoir fishes has been

documented in the study area (Falke & Gido, 2006) and likely played a role in the increased richness observed here. Two centrarchid species (bluegill and longear sunfish) had positive associations with the presence of bass when controlling for measured abiotic factors. Centrarchid species, especially bluegill and largemouth bass, are frequently stocked in impounded waters (Dauwalter & Jackson, 2005) and can become dominant in watersheds after impoundments are constructed (Taylor, Knouft, & Hiland., 2001; Hedden, unpublished data). Similarly, another species positively associated with bass, western mosquitofish, is non-native to the study area, known to be tolerant of harsh abiotic conditions (Hubbs, 2000; Hopper et al., 2020), and prefers backwater, non-flowing habitats (Casterlin & Reynolds, 1977; Matthews & Hill, 1980). The positive association between largemouth bass and western mosquitofish may have been driven stream habitats having more lentic characteristics due to landscape modifications (Sabater, 2008). Redfin shiner presence was also positively associated with the occurrence of bass. This species is a known nest associate of *Lepomis* species (Hunter & Wisby, 1961; Hunter & Hasler, 1965) and is also known to inhabit deep, slow-moving pools, which may explain observed co-occurrence patterns.

In addition to preferred habitat conditions, associations between stream fish species and bass may also be due to true effects of largemouth bass on fish communities. Largemouth bass may contribute to increased richness by disproportionately feeding on competitive species, acting as "keystone predators" (Paine, 1969). Predation can drive coexistence when consumption prevents competitive exclusion (Paine, 1966; Caswell, 1978). It is possible bass facilitate coexistence, and therefore higher richness, by reducing the intensity of competitive interactions among competitors. Predators may also maintain increased diversity and coexistence by preventing "mesopredator release" (Ritchie & Johnson, 2009), in which loss of apex predators

allows lower trophic level predators to increase in abundance, which can cause declines or local extinction of prey species (Courchamp et al., 1999). We did not, however, observe higher densities of any species at sites in which bass were absent, which is inconsistent with these mechanisms of coexistence. Although field studies across organisms and systems, including streams (Rodríguez-Lozano, Verkaik, Rieradevall, & Prat, 2015), suggest predation can facilitate coexistence (Gurevitch et al., 2000, Ritchie & Johnson, 2009), we express caution in this interpretation of our results without corresponding empirical evidence.

While predation may promote coexistence and increase richness, predators can also influence dominance patterns. We observed a significant effect of bass on community composition based on abundance of different species. Although not statistically significant, we were able to identify four species likely contributing to the significant effect of bass at the community level, including bluegill, redfin shiner, yellow bullhead, and black bullhead. All of these species had higher predicted abundance at sites with bass. Larger prey species, such as bullheads and bluegill, might not respond negatively to bass due to gape limitation. Hambright (1994) found gape-limited predation can lead to dominance by deep-bodied species when fish communities are made up of a mix of body sizes. Thus, positive associations with bluegill and bullhead species could be driven by bass consuming shallow-bodied species (Hambright, 1991), such as minnows. Although juvenile black bullhead (Rickett 1976,Phelps, Ward, Paukert, Chipps, & Willis, 2005;) and bluegill (Turner and Mittelbach, 1990; Olsen, 1996), are known prey of bass, these species are likely too large or difficult to handle (due to spines) to be consumed by bass after they reach some threshold size. Escaping predation by growing to large sizes is an evolutionary response of prey fish to predators (Reznick, Bryga, & Endler, 1990) and potentially a mechanism contributing ecosystem dynamics in reservoir systems (e.g., *Dorosoma*

cepedianum, Noble, 1981; Michaletz, 1998; Vanni et al., 2005), so it is possible similar sized-based interactions influence stream fish community structure. We recommend more work understanding the role of predators and land use (Perkin et al., 2017; Sutton & Jones 2019) in driving size distributions of stream fishes.

It is possible habitat characteristic that were not measured, and therefore not accounted for, drove observed fish community associations with predators. The only significant predictor of bass presence, watershed area, only explained 6% in the variation in bass occurrence. The large confidence intervals obtained when predicting bass presence likely indicates either high sampling error (variability in detecting bass) or relevant abiotic variables were not included in our analysis, and both of these sources of variability could have influenced observed relationships between predators and stream fishes. Hydrology, for example, can drive stream fish community structure (Poff & Allan, 1995; Mims & Olden, 2012), and local temperature can drive largemouth bass distributions (Sowa & Rabeni, 1995), but neither were considered in this analysis. Sampling variability, such as local conditions at sites also likely introduced variation in our ability to detect bass presence. Further, some environmental variables could have been measured at the wrong spatial scale (Fausch, Torgersen, Baxter, & Li, 2002). We expected to see stronger relationships between metrics capturing small impoundment distributions (upstream impounded area, distance to nearest impoundment), but these metrics were not important predictors of bass presence and only important predictors of community structure in one basin. This lack of relationship was surprising because another study within our study area indicated small impoundments are associated with declines in native and endangered fishes, presumably by supplementing bass populations in streams through emigration (Schrank, Guy, Whiles, & Brock, 2001). Densities of impoundments in a watershed also can interact with other landscape

changes to influence stream fish communities by increasing the dominance of impoundment species (Perkin, Troia, Shaw, Gerken, & Gido, 2016), and we observed co-occurrence of bass and other species associated with impoundments. It is possible our summary metrics of small impoundment distributions were measured at spatial scales weakly related to the responses measured, potentially biasing observed relationships between predators and fish community structure.

Fish community structure, including richness and composition, responded to both natural variation in stream habitats and landscape alterations. As expected, species richness increased positively with stream size, pool depth, and the proportion of large substrates (Schlosser, 1987) but decreased with increasing road crossing density and catchment agriculture (Wang, Lyons, Kanehl, & Gatti, 1997; Allan, 2004; Perkin & Gido, 2012). Road crossings can fragment stream systems, especially on smaller-order streams, leading to less accessibility and lower species richness (Perkin & Gido, 2012). Upstream agriculture can lead to lower species richness and shifts in community structure due to changes in water chemistry, altered flow regimes, and increased sediment inputs (Allan, 2004). Whereas we were able to quantify responses of stream fish richness to landscape modifications, composition responses were more difficult to detect. We detected significant responses of fish communities to catchment agriculture in both basins and upstream impoundments in one basin, but only detected a species-specific response to agriculture for one species, southern redbelly dace, which has been documented in another study (Stasiak, 2007). Overall, our targeted sampling to capture these complex environmental gradients allowed us to quantify responses of fishes to landscape alterations and natural heterogeneity, which is often difficult to detect (Bruckerhoff & Gido, 2019), but even accounting for these

known important gradients revealed complex relationships between stream fish community structure and the presence of predators.

Challenges and Future Directions

Quantifying predator effects requires disentangling complex interactions between predators, prey, and the abiotic environment, which presents several challenges. As already discussed, it is difficult to capture all sources of variability driving both predator distributions and abundance and stream fish community structure. Despite our best efforts, including a sampling protocol designed specifically to capture landscape gradients, we predict some of the associations between predator presence and community structure observed here were likely driven by unmeasured environmental variability or other factors influencing stream fish. For example, stochastic process are known to drive variability in stream fish communities across space and time (Matthews, 1982; Gotelli & McCabe, 2002). Predators likely interact with stochastic process to shape community structure and population dynamics over time. Further, predator effects are likely context dependent, interactive, and plastic, so that the effects of a predator on community structure is likely dependent on the abiotic and biotic context in which interactions take place. Predator behaviors, diets, and interactions with other species may be plastic (Chamberlain, Bronstein, & Rudgers, 2014), so that the same species effects on communities in one context may not predict effects in another (Preston, Henderson, Falke, Segui, Layden, & Novak, 2018). Last, measuring prey responses to predators is cofounded by bias associated with the scale in which measurements are made. For example, consumption rates are known to vary across different scales of measurement (Englund & Leonardsson, 2008) and are typically underestimated at fine scales (Bruckerhoff., unpublished data). In the current study, estimates of species richness, occurrences, and relative abundance may also be influenced by the

scale at which we measured these responses (reach scale), potentially biasing estimates of predator effects.

Conclusions

Predator-prey interactions are complex, but critical to understand as we try to manage complex assemblages of native and nonnative fishes. To truly understand how predators shape communities in stream systems, we need long-term studies of predator effects on community structure and ecosystem processes. Long-term, manipulated studies at coarse scales, such as replicated watersheds, are likely the best way to understand both the context dependency and long-term outcomes of predators being both lost from and introduced into systems. Long-term data is needed to distinguish between random co-occurrence or abundance relationships identified in correlative studies versus true, long-term impacts of predators. Unfortunately, decisions to remove or control predators need to be made now, so allocating time and resources to long-term studies may not be feasible. Our data help establish a baseline of expectations when quantifying predator effects in natural systems, and we hope our efforts set the path for other researchers to think creatively about how to understand the role of predators in structuring stream fish communities in the context of continued landscape modification, species introductions, and species declines to better conserve freshwater fishes.

Acknowledgments

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Tables

Table 3.1 Abiotic variables included in richness and composition models were collected at watershed and reach scales.

Scale	Variable	Description	Transformation
Watershed	Catchment area (km^2)	Total upstream catchment area from the downstream point of each sample site.	Logarithmic
	Proportion of catchment agriculture	Proportion of agricultural land in each catchment.	Square root
	Proportion of catchment impounded	Proportion of impounded area in each catchment.	Logarithmic
	Catchment road crossing density (# per km^2)	Density of road crossings (all road types) in each catchment.	Logarithmic
Reach	Distance to nearest impoundment (km)	Euclidean distance to nearest impoundment.	Logarithmic
	Proportion of large substrates	Proportion of samples containing pebble, cobble, or boulder substrates using a modified Wentworth scale (Wentworth 1922).	None
	Proportion of cover habitat	Proportion of sampled surface area providing cover habitat for fishes, including overhanging vegetation, undercut banks, root-wads, log complexes, and large boulders.	Logarithmic
	Mean Depth	Mean pool depth at each site.	Logarithmic

Table 3.2 The structural equation model (SEM) included predictor variables identified in preliminary mixed effect models and included the random effect of HUC 10 watershed level nested within major drainage basin. Shipley's test of directed separation indicated good model fit and no missing paths (Fisher's C = 9.10, p = 0.52).

Response	Predictor	Estimate	Standard Error	DF	p value	Standardized Estimate
Bass presence	Watershed area	0.24	0.09	322	0.01	--
Richness	Large substrate	2.89	0.72	281	< 0.01	0.18
Richness	Mean depth	4.51	1.47	281	< 0.01	0.14
Richness	Distance to nearest pond	0.42	0.85	281	0.62	0.02
Richness	Catchment agriculture	-1.78	0.67	281	< 0.01	-0.13
Richness	Road crossing density	-2.06	0.80	281	0.01	-0.13
Richness	Watershed area	0.70	0.12	281	< 0.01	0.28
Richness	Bass presence	2.63	0.37	281	< 0.01	0.32

Table 3.3 Final *manyglm* models (Wang, Naumann, Wright, & Warton, 2012) included predictors identified in landscape only and local models for each drainage basin; all included counts of species as predictors and year, HUC level 10 watersheds, and the total number of individuals captured at each site as predictors. This table indicates significant of variables in final models including the effect of bass presence on stream fish community composition.

Variable	Kansas Basin Deviance	p value	Neosho Basin Deviance	p value
Year	**79**	**0.001**	**107**	**0.001**
HUC 10	**1904**	**0.001**	**853**	**0.001**
Number of individuals	**900**	**0.001**	**809**	**0.001**
Landscape				
Catchment area (km^2)	**319**	**0.001**	**198**	**0.002**
Proportion of catchment agriculture	**103**	**0.022**	**74**	**0.035**
Proportion of catchment impounded	---	---	**114**	**0.03**
Catchment road crossing density (# per km^2)	---	---	---	---
Local				
Distance to nearest impoundment (km)	---	---	---	---
Proportion of large substrates	---	---	---	---
Proportion of cover habitat	---	---	---	---
Mean depth	**121**	**0.046**	61	0.307
Predators				
Bass presence	**113**	**0.023**	66	0.208

Figures
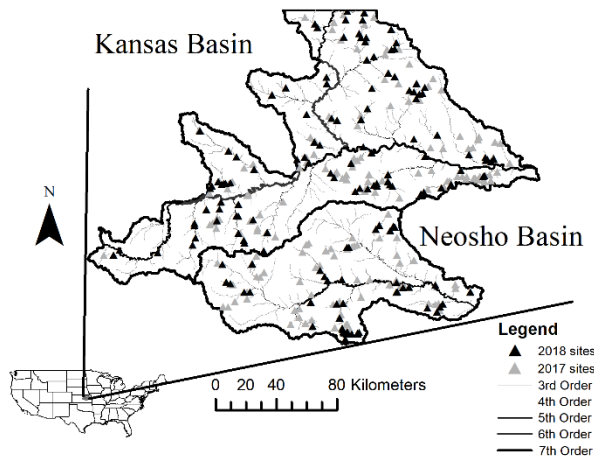
Figure 3.1 Fish communities were sampled in wadeable stream reaches throughout the Kansas and Neosho river basins in eastern Kansas, USA in 2017 (grey triangles) and 2018 (black triangles).
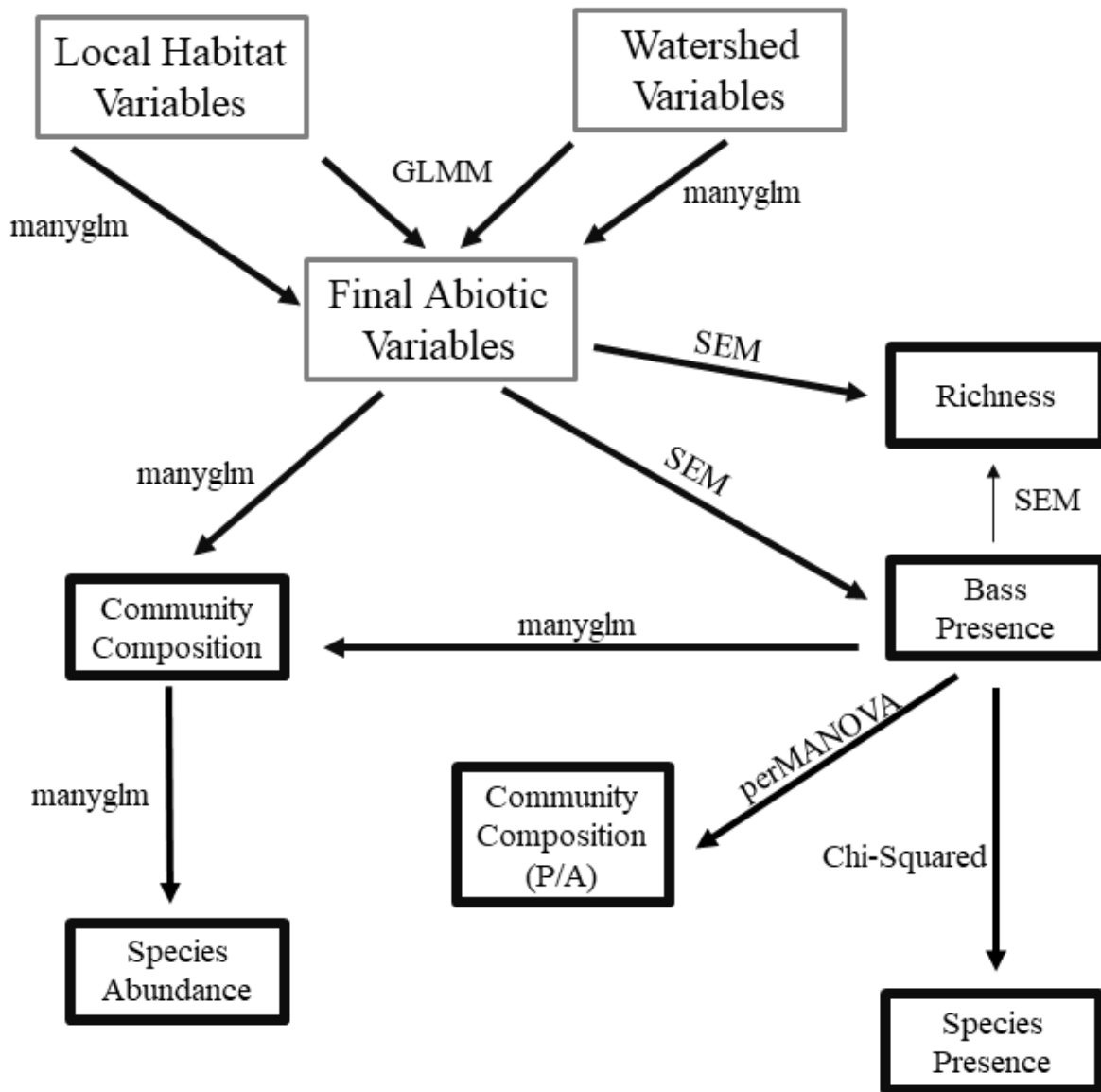
Figure 3.2 This workflow diagram displays the different analytical methods used to first identify abiotic factors predicting presence of bass, species richness, and stream fish community structure (grey) and then to account for these variables while assessing the effect of bass presence on species richness and stream fish community structure (black). GLMM= generalized linear mixed effect models; manyglm= multivariate models develop using the *manyglm* function from Wang

et al. (2012); SEM= structural equation model, perMANOVA= permutational multivariate

analysis of variance, P/A= presence absence community matrix.
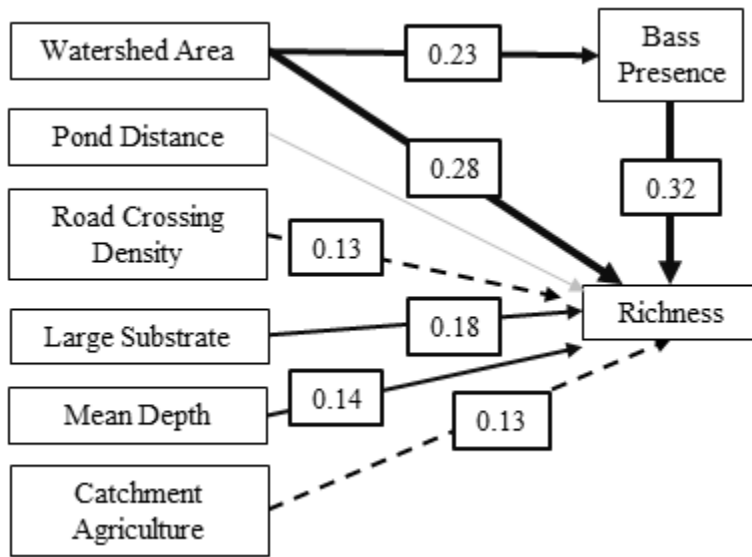
Figure 3.3 The structural equation model (SEM) included predictor variables identified in preliminary mixed effect models and included the random effect of HUC 10 watershed level nested within major drainage basin. Shipley's test of directed separation indicated good model fit and no missing paths (Fisher's C = 9.10, p = 0.52). Black lines indicate significant predictors, with solid lines representing positive and dashed lines negative relationships. The grey line indicates a non-significant predictor and the size of all lines corresponds to the weight or importance of predictors based on standardized coefficient estimates (numbers).
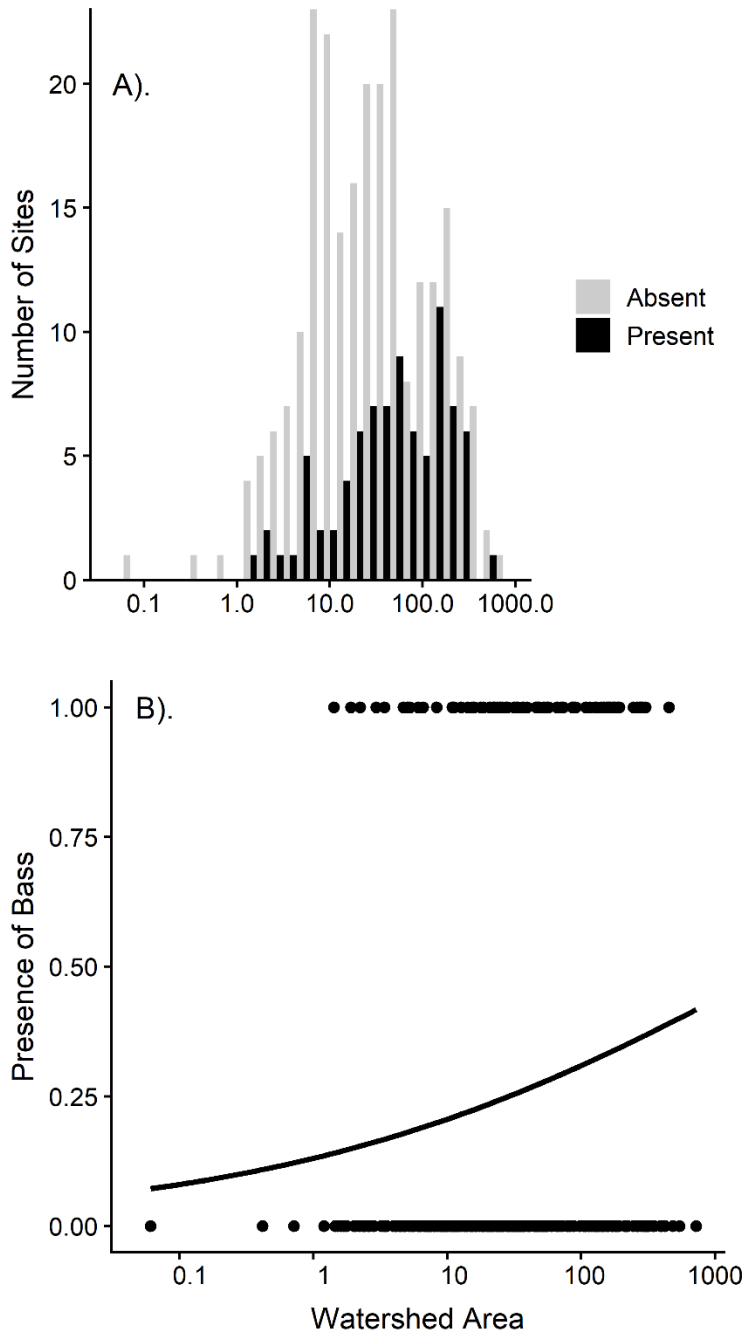
Figure 3.4 Bass were present (black) at more sites with larger watershed areas (A.), and the probability of occurrence of bass increased positively with watershed area across all sites (B.). Watershed area (km^2) is displayed on a log-transformed axis in both panels and the line displays the predicted probability of occurrence while points display raw data of bass presences and absences in panel B.
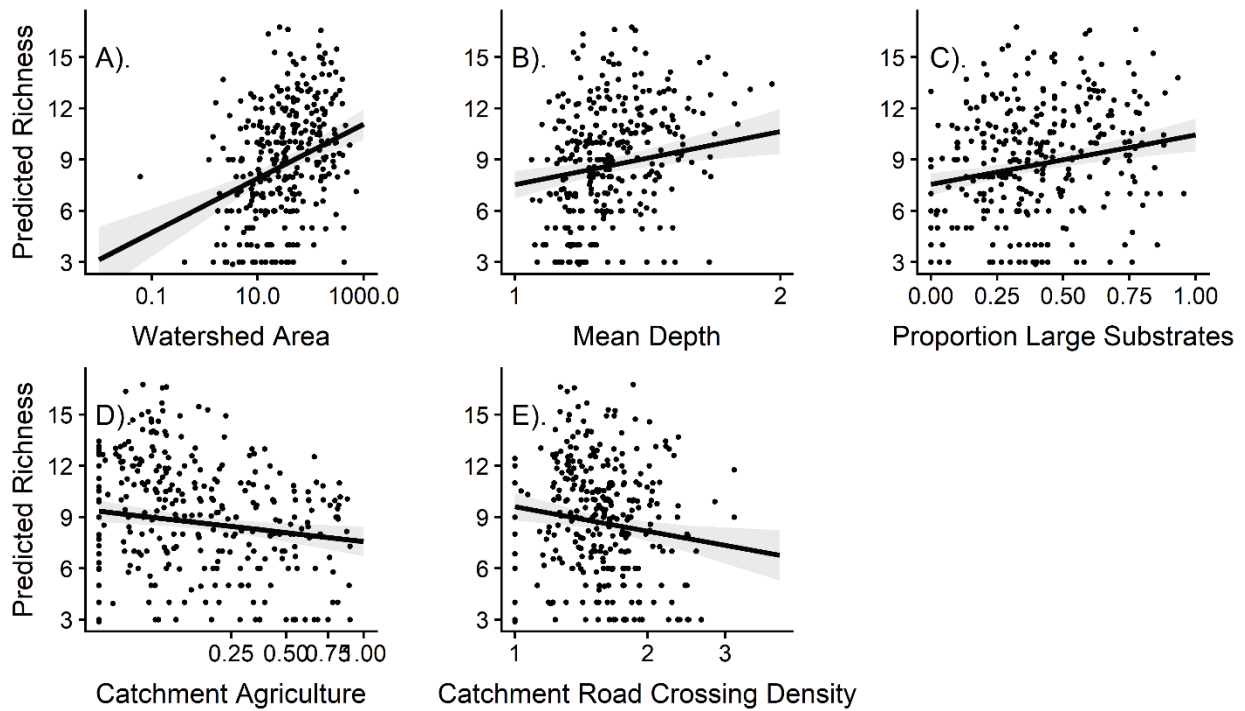
Figure 3.5 Richness increased significantly with watershed area (axis log scaled) (A), mean pool depth (axis log scaled) (B), and increased proportion of large substrates (C), but decreased with catchment agriculture (axis square root scaled) (D) and increased catchment road crossing density (axis log scaled) (E). Significance of these predictors was identified both based on preliminary hierarchical models and through a structural equation model; shading represents 95% confidence intervals.
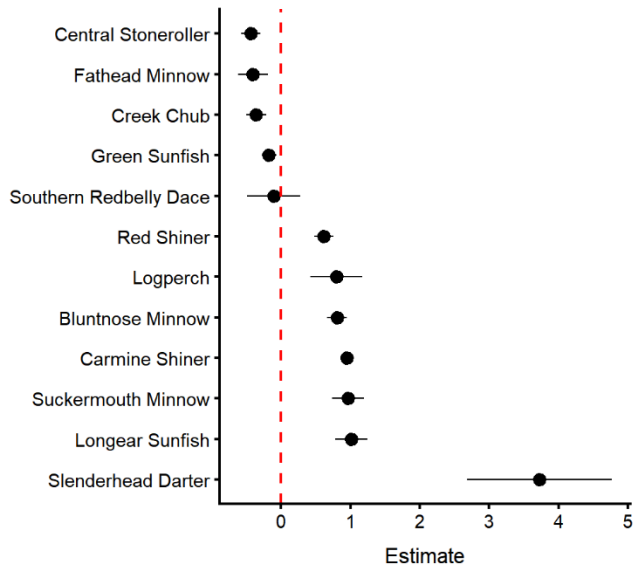
Figure 3.6 Twelve species exhibited significant responses to watershed area across both the Kansas and Neosho river basins in *manyglm* models. Slope estimates of five species were below zero, indicating a negative relationship with watershed area, while seven species exhibited significant positive relationships with watershed area. Lines represent 95% confidence intervals.
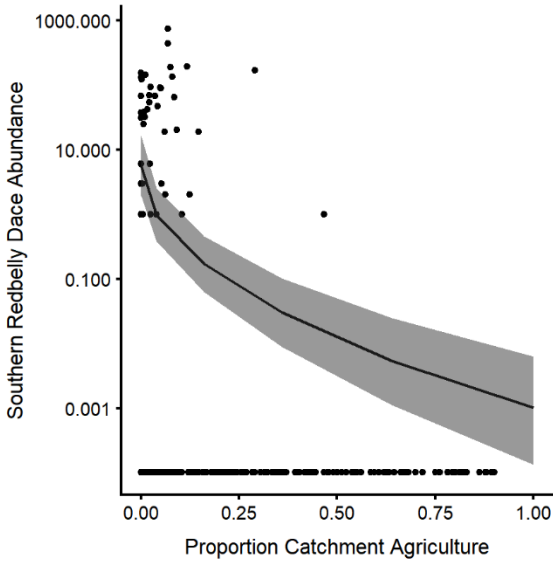
Figure 3.7 Upstream catchment agriculture was a significant predictor of fish community composition in both the Kansas and Neosho drainage basins, but abundance of only one species, southern redbelly dace, exhibited a significant response to agriculture. Abundance displayed on a log-transformed scale, and shading represents 95% confidence interval.
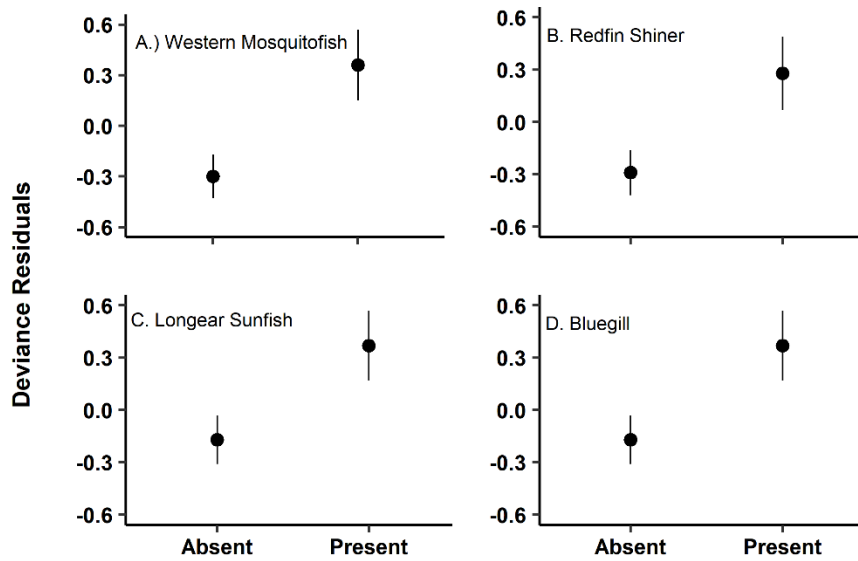
Figure 3.8 Frequency of co-occurrence between stream fish species and largemouth bass was asses using permutational chi-square tests. These plots show deviance residuals of predicted probability of occurrence of western mosquitofish (A), redfin shiner (B), longear sunfish (C), and bluegill (D) derived from a model including than main effect of watershed area from a reduced dataset including only streams in the top 50% of stream sizes in each the Kansas river basin. The mean deviance residuals are summarized for each species at sites in which bass were present and absent and lines represent standard errors.

Supporting Information

Table S1: List of species included in analyses.

Ameiurus   *melas*
Ameiurus   *natalis*
Aplodinotus   *grunniens*
Campostoma   *anomalum*
Carpiodes   *carpio*
Catostomus   *commersonii*
Chrosomus   *erythrogaster*
Cyprinella   *camura*
Cyprinus   *carpio*
Cyprinella   *lutrensis*
Dorosoma   *cepedianum*
Etheostoma   *flabellare*
Etheostoma   *nigrum*
Etheostoma   *spectabile*
Fundulus   *kansae*
Fundulus   *notatus*
Gambusia   *affinis*
Ictiobus   *bubalus*
Ictiobus   *furcatus*
Ictiobus   *niger*
Ictalurus   *punctatus*
Labidesthes   *sicculus*
Lepomis   *cyanellus*
Lepomis   *gulosus*
Lepomis   *humilis*
Lepomis   *macrochirus*
Lepomis   *megalotis*
Lepisosteus   *osseus*
Luxilus   *cardinalis*
Luxilus   *cornutus*
Lythurus   *umbratilis*
Micropterus   *punctulatus*
Micropterus   *salmoides*
Moxostoma   *erythrurum*
Moxostoma   *macrolepidotum*
Notropis   *atherinoides*
Notemigonus   *crysoleucas*
Notropis   *dorsalis*
Noturus   *exilis*
Noturus   *flavus*

Notropis   *percobromus*
Notropis   *stramineus*
Notropis   *topeka*
Notropis   *volucellus*
Percina   *caprodes*
Percina   *maculata*
Percina   *phoxocephala*
Phenacobius   *mirabilis*
Pimephales   *notatus*
Pimephales   *promelus*
Pimephales   *tenellus*
Pimephales   *vigilax*
Pylodictis   *olivaris*
Pomoxis   *annularis*
Pylodictis   *olivaris*
Semotilus   *atromaculatus*

.

Chapter 4 - Scale-dependent patterns of prey aggregation and spatial overlap with predators mediate consumption rates

Lindsey A. Bruckerhoff, Casey A. Pennock, and Keith B. Gido[1]

Abstract

Understanding ecological processes across spatial scales helps link observations and predictions from experiments to ecological patterns and processes occurring at coarser scales relevant to management and conservation. Using stream fish, we experimentally manipulated the size of arenas to measure variation in predator consumption and prey behavior (prey aggregation, spatial overlap with predators, and movement) with increasing arena size in. Variation in prey behavior across arena sizes was hypothesized to drive consumption patterns by altering prey vigilance and encounter rates with predators. Per capita consumption was highest, prey were less aggregated and overlapped less with predators in the largest arena relative to the smallest, while movement was influenced by the presence of predators but not arena size. We hypothesize low prey aggregation in large arenas lowered group vigilance, leading to more successful attacks, driving the observed increase in consumption with increasing arena size.

Introduction

Understanding ecological phenomena across spatial scales is necessary to make management and conservation decisions (Fausch et al. 2002), and important ecological processes often occur at broad, landscape scales (Dunning et al. 1992). Predator-prey interactions are typically characterized in laboratories or other fine-scale studies, but using fine-scale observations to predict processes at broader spatial scales may be difficult due to scaling effects

(Englund & Cooper 2003, Levin 1992, Wiens 1989). Different processes drive predator and prey densities across space and time, with classic functional response relationships predicting predator-prey dynamics only at the smallest spatial and temporal scales (Hunsicker et al. 2011). Phenomena measured at greater temporal or spatial scales tend to have more variability because both fine- and broad-scale effects are at play (Levin 1992). Thus, scaling up observations from experimental and fine-scale predator-prey studies requires transition corrections to account for scale-dependent variability (Englund & Leonardsson 2008, Bergström et al. 2006, Chesson 1998). A large body of theoretical work accounting for variability across spatial scales includes methods such as partitioning (Rastetter et al. 1992), calibration (Rastetter et al. 1992), or moment approximation (Bergström et al. 2006). While theoretical and computational methods provide scaling frameworks, we still need empirical measures of predator-prey responses across spatial scales to accurately account for scale transitions in ecological models.

Quantifying scale transitions requires measuring ecological responses across spatial scales and identifying mechanisms driving those transitions. Empirical and theoretical work suggests predator-prey scaling effects are often (but not always) driven by spatial covariance or movement dynamics (*i.e.*, exchange dynamics) of predators and prey (Englund 2005, Englund & Cooper 2003, Englund 1997), both of which influence the likelihood of interactions. For example, at relatively coarse spatial extents (3-300 km), bird predator and fish prey distributions are hierarchically structured into patches and overlap between predators and prey increases with spatial scale (Fauchald et al. 2000). Similarly, stream benthic invertebrate densities can vary in response to scale-dependent emigration into patches in response to fish predators (Englund 2005). However, most studies investigating scale dependent predator-prey dynamics have been conducted only at very fine scales (<1 m^2) and focus on invertebrate prey (Englund 2005,

Bergström & Englund 2004, Bergström & Englund 2002, Luckinbill 1974). This body of work suggests functional responses of invertebrate predator-prey systems vary with the size of experimental arena, with higher mortality rates in larger arenas (Bergström & Englund 2004, Bergström & Englund 2002). Increased consumption rates with increasing arena size was driven by higher attack rates due to aggregative behavior of predators and prey (Bergström & Englund 2002). In these studies, aggregative behavior was attributed to be an artifact of confinement; both predators and prey preferred perimeters of experimental arenas, biasing estimates of consumption rates (Bergström & Englund 2004, Bergström & Englund 2002). These experimental studies highlight that prey aggregation and dispersal influence the overlap of predators and prey in space and time, influencing the observed functional response.

Previous research with invertebrate prey suggests increasing arena size biases estimates of consumption due to increased prey aggregation, but many taxa might aggregate as an anti-predator defense mechanism (Blumstein & Daniel 2003, Magurran 1990, Pulliam 1973, Vine 1971). Aggregation can be beneficial if it decreases encounter rates (Ioannou et al. 2011), but increases group vigilance (Lima 1995). In species that naturally aggregate regardless of spatial scale, variation in consumption rates across scales may be lower. Further, the spatial arrangement or shape of arenas in which predators and prey interact may influence scaling effects (Dickie et al. 2017, McKenzie et al. 2012). Much research investigating scaling effects of predator-prey interactions has taken place in open arenas (circular tanks, marine systems, terrestrial systems). The interaction between prey movements, aggregative behavior, and scale might differ in linear or dendritic systems because movement is confined. For example, simulation models suggest encounter rates between wolves and their prey increases in linear systems (McKenzie et al. 2012) and movement rates of wolves is higher along linear features (Dickie et al. 2017). In dendritic

river networks, predators can interact with abiotic factors and prey traits to influence prey movement through the network (Gilliam and Fraser 2001), and landscape features such as waterfalls can act as barriers to predator movement, creating refuge for prey (Cathcart et al. 2018; Covich et al. 2009). Scaling effects on prey movement and spatial distributions (and overlap with predators) may therefore be context-dependent across taxa and spatial arrangement of arenas.

Objectives

We conducted a mesocosm experiment to quantify how predator consumption rates and prey aggregation, movement, and spatial overlap with predators vary across spatial scales (arena sizes). We chose these prey behaviors because they are related to encounter rates between predators and prey (Hatle et al. 2001, Englund & Olsson 1996, Christensen & Persson 1993) and prey vigilance, which influences whether or not an attack by a predator is successful (Krause & Godin 1996, FitzGibbon 1989). We measured these responses for fish prey in the absence of predators and in response to both consumptive and non-consumptive effects of a predator, *Micropterus salmoides* (Largemouth Bass, hereafter referred to as bass). Contrary to previous studies investigating invertebrate prey, we predicted consumption rates would decrease with arena size, driven by lower encounter rates with increased arena size. We predicted prey would spread out in larger arenas, driving lower spatial overlap between predators and prey and therefore lower encounter rates. Understanding how consumption rates, movement, aggregation, and spatial overlap between predators and prey vary with spatial scale may help inform scale transition corrections to apply ecological models to broader spatial scales more relevant to real world applications.

Methods

Mesocosm Design

This experiment was conducted at the Konza Prairie Biological Station using 18 outdoor recirculating mesocosms consisting of alternating riffle and pool habitats (see Matthews et al. 2006 for complete description). Although shallow riffles can act as movement barriers to fishes (Schaefer 2001), these riffles were deep enough (0.38 m) for both predators and prey to move freely among all habitats. Arena size was manipulated using a combination of two, four, and six riffle-pool configurations (Figure 4.1). Mesocosms were continuously supplied with local spring water and filled with rocky substrate (mean diameter approximated 25 mm). A trolling motor recirculated water within each mesocosm unit through a large polyvinyl chloride pipe from the downstream pool to the upstream riffle, creating directional flow.

Fish Collection and Stocking

Cyprinella lutrensis (Red Shiner) and *Pimephales notatus* (Bluntnose Minnow) were collected from several local streams and ponds and used as prey. These species are common and abundant in streams in the study area and represent two different feeding/habitat guilds. *C. lutrensis* are found in riffles and pools, but are known to feed on a variety of foods in open water throughout the water column (Gido & Matthews 2001, Hale 1963). *P. notatus* tend to occupy habitats closer to shore (Etnier & Starnes 1993, Moyle 1973) and feed in the benthos (Moyle 1973, Keast & Webb 1966). Prey density was held constant at 6.7 fish m^{-2} (20 fish per pool) across all arena sizes and was in the upper 95th percentile of streams containing both species in the study area (Bruckerhoff, unpubl. data). This total density was achieved using an equal number of both species. Any dead fish observed during the experiment were replaced with new individuals to keep densities constant, except during feeding treatments (see below). We aimed

to avoid density-dependent effects while predators were eating by keeping trials short (24 hours) and having initially high prey densities.

We chose bass as predators for this experiment because they are known to drive prey behavior and exert trophic cascades in streams (Power et al. 1985), share an evolutionary history with prey, and are important due to their introductions into watersheds globally (Welcomme 1988). Bass were collected from a local pond. All bass in the experiment were similar in length (mean total length=286 mm, SD=22 mm) and stocked at the same density across arena sizes (0.17 fish m^{-2}, 1 bass per pool). To minimize effects of gut fullness in trials, we collected bass using angling to capture presumably hungry fish and did not feed them for two days before introduction into experiments.

Fish Identification and Behavior

All fish were marked with passive integrated transponder (PIT) tags (8 mm x 1.44 mm; Biomark Inc., Boise, Idaho) so we could track individual movements. Small PIT tags were necessary to maximize survival and tag retention in prey fish (Pennock et al. 2016, Pennock 2017). Fish were anesthetized in a 100 mg L^{-1} concentration of buffered tricaine methanesulfonate (MS-222), and PIT tags were inserted into all fish following puncture of the peritoneal cavity with the tip of a hypodermic needle (Pennock 2017). Based on previously measured tag retention rates for small-bodied minnows, we only included prey fish larger than 45 mm total length (*P. notatus* : 45-80 mm, *C. lutrensis* : 45-72 mm; Pennock 2017; Pennock et al. 2016). Prey fish and bass were tagged one day after collection and kept in holding tanks for two days after tagging to ensure fish survived tagging and retained tags prior to introduction in the experiment.

Antenna receivers were placed in each pool habitat (Figure 1) to track movement of predators and prey among pools. Antennas were not placed in riffles due to size constraints. Antennas recorded detections of individual tags at 1-minute intervals, meaning once a tag was detected at an antenna it would not be recorded again for at least 1 minute. Two types of antennas were used: square (1 × 1 m) antennas monitored by a multiplexing reading station (QuBE-IS1001, Biomark, Boise, Idaho) and circular (1 m diameter) submersible antennas (Biomark, Boise, Idaho). Preliminary data indicated detection rates were similar between the two antenna types, and we haphazardly placed antennas in pools across trials.

Experimental Design and Schedule

Prey behavior data were collected for the three arena sizes across three experimental treatments: without predators, predators present without consumption, and predators present with consumption. This design allowed us to compare prey responses to both consumptive and non-consumptive effects. This also allowed us to track prey behavior in response to predators with no changes in prey density, as we did not restock prey fish after they were eaten in the consumption treatments. In treatments with predators present (but no consumption), bass mouths were secured shut with a cable tie (Clark & Schaefer 2016, Knight & Gido 2005), while in predator treatments with consumption, bass mouths were not secured.

Prey were introduced into mesocosms during the morning of the first day of each experiment, 48 h before predators with secured mouths were introduced ("no predators" treatment). Movement of prey in the presence of predators was then recorded for 48 h ("predators present" treatment), followed by recapture of bass from mesocosms using dip nets. Cable ties were cut and predators were reintroduced into mesocosms for 24 h ("predators eating" treatment). The same individual predators were used in both treatments within a trial based on

preliminary data suggesting bass still feed after having mouths tied shut for 48 h and to minimize the number of fish needed for the study. We only allowed predators to feed for 24 h to avoid density-dependent effects on consumption and based on preliminary data indicating bass would digest and pass prey PIT tags in time-periods longer than 24 h. At the end of each trial, we removed and euthanized bass and surveyed their full digestive tract for prey PIT tags. We ran several additional consumption trials immediately after the first 24 h trial. Prey fish were restocked to pre-consumption densities and new bass were introduced for additional consumption trials. Due to limited antenna battery life, prey behavior was not tracked during additional consumption trials.

We ran four replicates of all treatments and three additional consumption trials across each arena size from June to August 2019. One antenna malfunctioned in the middle of a six-unit trial, so that trial was dropped. Our final sample size per arena was n= 7 for consumption trials and n=4 (n=3 for six-unit) for movement, aggregation, and spatial overlap trials. Tag retention was high for all species (bluntnose minnow: 98%, red shiner: 95%, largemouth bass: 100%) and non-consumptive mortality was low (mean=2%, SD=0.02) across all replicates.

Analyses

Due to potentially low power associated with small sample sizes in this study, we *a priori* chose a significance level of 0.10 for all statistical tests. We removed all prey fish that were consumed, died, or lost tags from the analyses of prey behavior. All analyses were performed in Program R version 3.6.1 (R Core Team 2019).

Consumption

We calculated both overall differences in per capita consumption across arena sizes and differences in prey composition in diets of bass across arena sizes. Per capita consumption was

calculated as the total number of prey eaten divided by the number of predators within each replicate. Due to concerns about meeting the assumption of heteroscedasticity, we used generalized least squares regression and mixed-effects models in the package *nmle* (Pinheiro et al. 2020) to compare per capita consumption rates across arena sizes. We compared models including a modified variance structure to model heterogeneity across arena sizes, models assuming equal variance, and models with and without a random effect of trial. All models included the same fixed effect (arena size) and were compared using likelihood ratio tests. We also assessed the importance of random effects by comparing marginal R^2 (variance explained by fixed effects only) to conditional R^2 (variance explained by both fixed effects and random effects) using the *piecewiseSEM* package (Lefcheck 2016). We used Tukey's HSD for pairwise comparisons among arena sizes.

To compare composition of the two prey species in diets across arena sizes, we used the *manyglm* function from the package *mvabund* (Wang et al. 2012). This function develops generalized linear models for counts of each prey species in predator diets across arena sizes and provides a global estimate of significance, as well as significance of factors for the two prey species while controlling for multiple testing (Wang et al. 2012). We used negative binomial distributions for *manyglm* models due to the large number of zero occurrences in diets. Because replicates in this analysis were individual predators, we included the number of bass in each arena as a fixed effect to control for uneven sample sizes.

Aggregation

We used the mean distance to detected conspecifics of each prey species as an index of aggregation. For each individual fish, we calculated the number of pools between individuals of the same species so that distance equaled 0 for individuals in the same pool. We calculated the

mean distance across individuals detected in every 30 min interval of each replicate (total replicate time = 15 hrs), but dropped any fish detected in more than one pool during a 30 min interval (~20% of detections). We chose 30 min intervals to maximize the number of detections within a time interval, but to minimize the number of individuals that switched pools and because predicted responses were similar across time intervals (see Appendix S1 in Supporting Information). Higher values of average nearest conspecific represent less aggregation while lower values represent more aggregation. We only included observations between 4:30 pm and 7:30 am to capture predicted peak activity time of predators (dawn, night, and dusk) and to avoid any bias due to researcher activity during the day (predator and prey introductions and cable tie removal occurred during hours omitted from analyses). Even though treatments with no predators and those where predators were not able to consume prey were run for 48 h, we removed the first 24 h of observation to avoid bias during acclimation to mesocosms. These periods were used for all metrics and analyses.

We used *manyglm* models to compare prey species responses in aggregation to effects of arena size and predator treatment. These models allowed us to obtain a global estimate of significance for the two prey species, as well as significance tests (corrected for multiple testing) for individual species. The model is similar to the *manyglm* method described in the consumption section, but assumes a Gaussian distribution, more appropriate for continuous variables (mean distance to conspecifics within a 30 min interval). This model does not allow for the inclusion of random effects, so we included trial number as a fixed factor to control for differences between trials and time interval to control for difference in activity at different times of day. Because arena sizes had different absolute numbers of individual fish to hold densities constant, we first checked to see if there was a relationship between the number of individuals

detected within a 30 min interval and the distance between conspecifics. Because there was no significant relationship (likelihood ratio=1.34, p=0.52), we did not include the number of individuals detected in our final models.

Movements

To compare movement patterns across arena sizes and treatments, we calculated the mean number of times individuals switched pools for the entire treatment period (15 h) because most fish did not switch pools at smaller time scales. Like the aggregation index, we used the *manylm* function to compare movements across treatments and arena sizes, but did not include an effect of time interval since this metric was calculated across the entire treatment period.

Spatial Overlap

We calculated the number of pools separating each predator and all detected prey at 30 min intervals across trials during the same time periods used to calculate the aggregation index (see Appendix S1). Following the same procedure used when calculating the aggregation index, we omitted any observations in which individuals (including predator and prey fish) were detected in more than one pool. We compared the distance (number of pools) each predator was from all detected prey across arena sizes, treatments, and between prey species. We used the same model structure and method used to assess aggregation.

Results

Consumption

Per capita consumption differed across arena sizes ($F_{2,17}$= 2.99, p=0.07) and post-hoc comparisons indicated per capita consumption was higher in the largest arena relative to the smallest (Figure 4.2; t=2.44, p=0.06). The fixed-effects only model was selected over models including random effects of trial or modified variance structure based on likelihood ratio tests

(see Table S2). While overall consumption varied across arena sizes, there was no difference in prey composition across arena sizes (deviance=1.29, p=0.61). The number of predators in the arena did not significantly influence the composition of prey consumed (deviance=3.74, p=0.18).

Aggregation

The global *manylm* model indicated trial (likelihood ratio=186.10, p<0.01), arena size (likelihood ratio=761.90, p<0.01), treatment (likelihood ratio=13.50, p=0.02), and the interaction between arena size and treatment (likelihood ratio=21.20, p=0.01) were significant predictors of prey aggregation (see Table S3). The main effect of arena size was significant for *C. lutrensis* (Figure 4.3A), while the interaction between arena size and treatment was significant only for *P. notatus* (Figure 4.3B). For both species, the distance from conspecifics increased with increasing arena size, so aggregation was highest in the smallest arena (Figure 4.3).

Movement

Only trial (likelihood ratio=23.66, p<0.01) and treatment (likelihood ratio=41.09, p<0.01) were significant predictors of prey movements in the global *manylm* model (see Table S3). Both *C. lutrensis* (likelihood ratio=20.71, p<0.01) and *P. notatus* (likelihood ratio=20.39, p<0.01) movements responded significantly to treatment, with more movements occurring when predators were absent relative to when they were present or eating (Figure 4.4).

Spatial Overlap

Spatial overlap between predators and prey was significantly influenced by trial (likelihood ratio=29.21, p<0.01) and arena size (likelihood ratio=111.26, p<0.01) for both prey species (see Table S3). *C. lutrensis* and *P. notatus* both had less spatial overlap (larger distances from predators) with bass with increasing arena size (Figure 4.5). *C. lutrensis* were also further from predators than *P. notatus* in the largest arena size.

Discussion

Contrary to our prediction, we observed increased per capita consumption with increasing arena size. While this pattern has been observed in previous work (Bergström & Englund 2004, Bergström & Englund 2002, Kaiser 1983, Copper & Goldman 1982), these studies attributed this pattern to increased encounter rates between predators and prey. We hypothesize the mechanism driving increased consumption in our experiment was related to prey vigilance rather than encounter rates (Figure 4.6) and discuss how are prey behavior data support this hypothesis. Collectively, our work and others indicate predation rates are likely underestimated when measured at fine spatial scales, but the mechanisms driving this pattern may vary.

As we predicted, prey spread out and used the space provided, leading to a decline in aggregation with increasing arena size. Aggregations can provide protection from predators because more individuals have a higher probability of detecting a predator, leading to higher group vigilance (the "many eyes hypothesis"; Lima 1995, Lima & Dill 1990). We refer to group vigilance as the increased probability of prey detecting a predator before an attack due to more individuals watching for predators. If aggregative behavior leads to higher group vigilance, we hypothesize the negative relationship between aggregation and consumption observed here indicates group vigilance may be an important predator defense mechanism for *P. notatus* and *C. lutrensis*, as it is for other fishes (Pitcher 1986). In other studies investigating prey aggregation and predator consumption across arena sizes (Bergström & Englund 2004, Bergström & Englund 2002), aggregation of prey increased with increasing arena size due to changes in perimeter to area ratios because prey preferred edge habitat, resulting in increased spatial overlap between predators and prey and therefore increased consumption. In general, animals may aggregate in preferred habitats (Jeanson et al. 2005, Croft et al. 2003, Kaiser 1983), so if that habitat

availability changes with scale, so will aggregation patterns. In the current study, habitat availability (e.g., edge habitat) did not vary with scale because we increased scale linearly by attaching additional pool/riffle units. Thus, constant perimeter to area ratios across arena sizes might explain why we did not observe increases in aggregation. Our study does not shed light, however, on the potential mechanisms driving decreased aggregation with increasing spatial scale, especially if aggregation does provide strong anti-predator responses; this is an important avenue for future research

Spatial overlap between predators and prey decreased with increasing arena size. Other studies have documented hierarchical patterns of spatial overlap between predators and prey across spatial scales, but overlap typically increased with increased spatial scale (Bergström & Englund 2002, Fauchald et al. 2000, Rose & Legget 1990) and was associated with large aggregations of prey. Predators make foraging decisions based on local prey densities at multiple spatial scales (Fauchald 1999), so prey aggregation likely plays an important role for some predators to choose where to spend time and therefore how much spatial overlap there is between predators and prey. The observed negative relationship between aggregation and arena size likely drove the decrease in spatial overlap between prey and predator with arena size. Despite lowered overlap at larger arena sizes, which should be correlated with lowered encounter rates, we still observed higher consumption rates in larger arenas. It follows consumption would only be high when encounter rates are low if the proportion of successful attacks increases and/or handling times decrease. We hypothesize that low group vigilance resulting from less aggregation in large arenas potentially offset low encounter rates to drive high consumption rates in large arenas.

The presence of predators (both actively eating and not eating) reduced movement of prey, regardless of arena size. The effect of predators on prey movement is not surprising, as

predators can have strong non-consumptive effects on prey (Peckarksy et al. 2008, Lima 1998, Sih & Wooster 1994). Altering movement patterns or activity levels can be an effective defense against predation because more movement is often associated with higher encounter or consumption rates with predators (Hatle et al. 2001, Englund & Olsson 1996, Christensen & Persson 1993), so movement is likely associated with individual prey vigilance. Variation in individual prey vigilance is driven by changes in prey perception of predation threat (Brown 1999) and may vary spatially in response to habitat heterogeneity, creating a "landscape of fear" (Laundre et al. 2010). Because we did not observe a relationship between movement and arena size, we suspect individual preys' fear of predation did not vary across spatial scales, which may be an artifact of our experimental systems or a true pattern. Many fishes use chemical cues to sense nearby predators (Chivers & Smith 1998), especially fishes in the family Cyprinidae (Ferrari et al. 2010), such as the prey in this study. The strong movement response to predator treatments indicates prey were able to successfully detect predators, even in the largest arena. The lack of relationship between movement and arena size may be related to chemical cues being redistributed throughout the arenas by recirculating water. Alternatively, differences in movement associated with arena size may have occurred within pools or between pools and riffles, which we were unable to measure. Small-bodied fish are likely to make many fine-scale movements within pools rather than among pools over short temporal scales (*i.e.*, < 24 hours; Pennock et al. 2018). Overall, the lack of variation in movement across arena sizes suggests observed variation in consumption likely was not driven by movement patterns.

We observed an increase in consumption, decrease in aggregation and spatial overlap, and no change in movement with increasing spatial scale (Figure 4.6) and hypothesize the increase in consumption was due to more successful attacks and/or decreased handling times,

despite potentially lower encounter rates. Although individual fish decreased movement between pools in the presence of predators, indicating individuals were vigilant, we hypothesize small aggregations of fish had a lower probability of detecting an attack by a predator (lower group vigilance), leading to either an increase in the frequency of successful attacks and/or decreased handling times. In addition to group vigilance, predatory strategy may also explain observed increased consumption. Largemouth bass are typically considered ambush predators, which are expected to be more effective when prey are less aggregated, especially at intermediate prey densities (Taylor 1976). If this is true, we would predict largemouth bass to consume more in larger arenas where prey were less aggregated, as observed in this study. Predators are also known to vary their predation strategy with habitat complexity. For example, largemouth bass can switch from predominately using ambush techniques to stalking prey in habitats with low habitat complexity (Savion & Stein 1982). It is possible predators may also change their predation strategy in response to spatial constraints. The relative importance of pre-capture (*e.g.,* search time) versus post-capture (*e.g.,* handling time) constraints on predation is known to change with arena size (Christenson 1996), and predation strategies may do the same. We did not observe significant changes in predator activity with increases in spatial scale (number of movements, $F_{2,13}= 0.99$, p=0.40), but did not measure other aspects of predator behavior. Considering how predators adapt to spatial constraints may have important implications for scaling up predator-prey interactions and understanding how predation strategies vary in different sizes of habitat patches (Ryall & Fahrig 2006).

Our results indicated statistically robust patterns despite several potential sources of bias in our experiment. We quantified our metrics based on detections at antennas placed only in pool habitats, so we were unable to detect fish in riffles. This limited the number of total detections,

especially during treatments including bass, because movement and activity levels were low. We had the same number of riffles relative to pools across all arena sizes, so effects of movement into and out of riffles were considered minimal. Time of day is also likely an important driver of predator and prey activity levels and behavior. Pooling observations across the 15 h overnight period captured predicted peak activity times, but likely introduced variation into our indices. Finally, we did not measure the distribution of food resources, which can influence prey distributions (McMahon & Matter 2006). However, in previous studies there were minimal differences in algae or macroinvertebrate biomass among connected pools in this experimental system (Martin et al. 2016).

Measuring predator-prey response metrics across arena sizes is critical for making predictions at spatial scales relevant to higher order biological process and may also provide insight into how predator-prey interactions vary with changes in the size of natural arenas (habitat loss and fragmentation). Our study and others cited above indicate measures of predator effects are biased across different spatial scales and predict consumption may be underestimated when measured at fine spatial scales. This has important implications for predicting outcomes of predator-prey interactions in natural systems. For example, home range estimates of largemouth bass range from 100 to 37,600 m^2 in lake systems (Minns 1995, Lewis & Flickinger 1967), although estimates of home ranges in stream systems are typically smaller ($\sim$ 500 m^2; Paller et al. 2005, Minns 1995). The maximum area assessed in this study was around 24 m^2, suggesting our estimates of consumption, even in our largest arena, likely underestimated consumption by largemouth bass in natural systems. In addition to using these rates to inform predictions through scale transitions, the observed patterns of consumption and prey behavior may also help predict impacts of habitat loss and fragmentation if we assume habitat patches act as different sized

arenas for predator-prey interactions. Although we observed lower consumption rates in smaller arenas, we also observed changes in prey behavior both in response to arena size and the presence of predators. Although predators in smaller habitat patches may not consume more, non-consumptive responses can have strong negative effects on prey populations (Lima 1998, Pecarksy et al. 2008). We hypothesize prey vigilance in smaller arenas played an important role in keeping consumption rates low. Vigilance is associated with prolonged stress (Vitousek et al. 2018) and foraging costs (Balaban-Feld et al. 2019), both of which influence prey vital rates and food web structure (Ho et al. 2019). Overall, our results build on previous work suggesting predator-prey response metrics vary across spatial scales and are likely underestimated in experimental studies, and we provide testable predictions of potential mechanisms driving scaling relationships (Figure 4.6).

Acknowledgements

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Figures
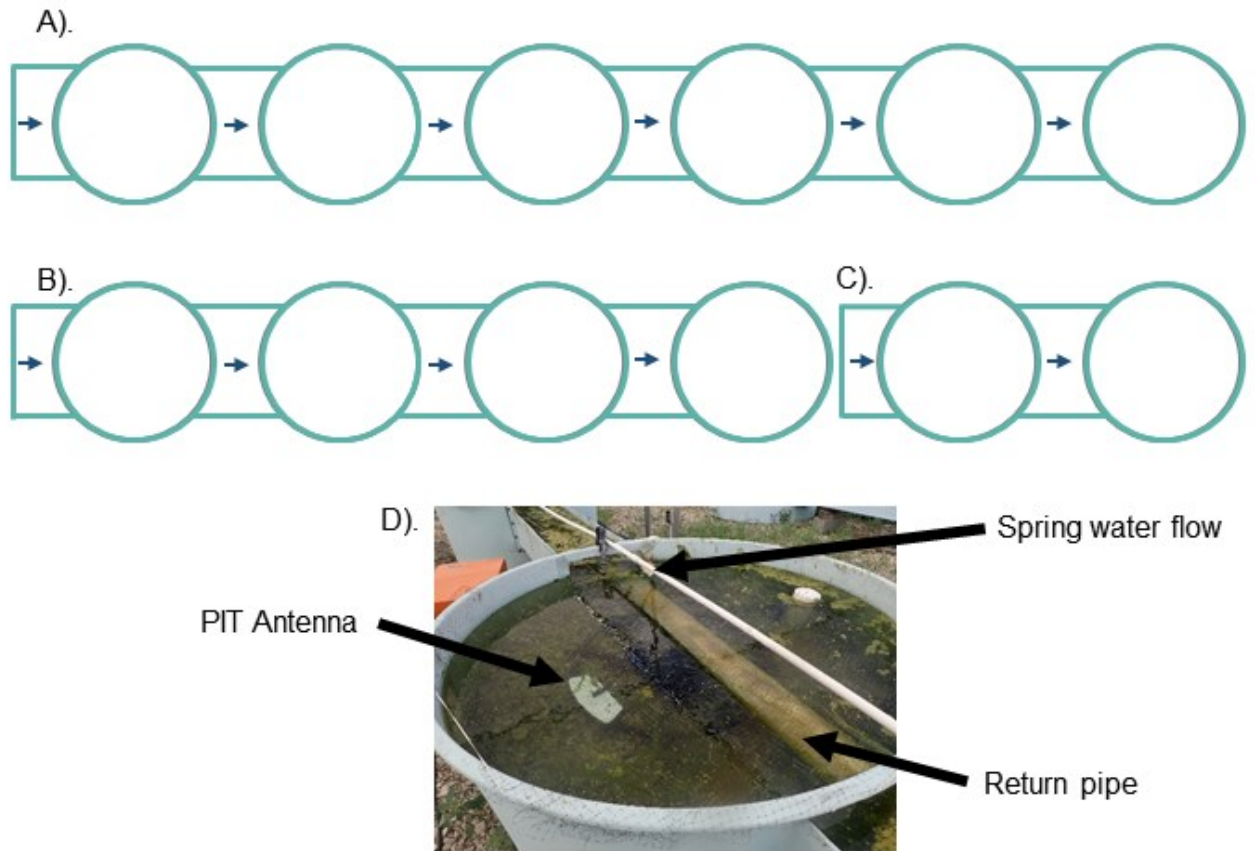
Figure 4.1Schematic of experimental mesocosms, including (A) six riffles and six pools, (B) four riffles and four pools, and (C) two riffles and two pools, with arrows indicating direction of water flow. Submersible antennas were placed under the return pipe in the center of each pool (D).
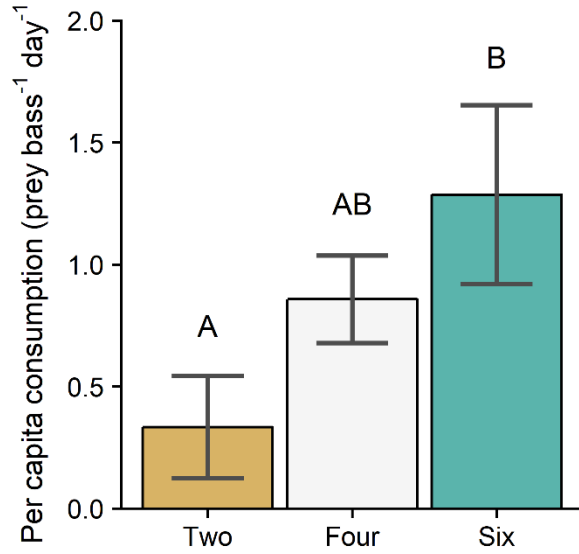
Figure 4.2 Mean per capita consumption by largemouth bass of *Cyprinella lutrensis* and *Pimephales notatus* was higher in arena with six pools and riffles relative to arena with only two pools and riffles. Error bars represent standard error around mean per capita consumption rates across arena sizes.
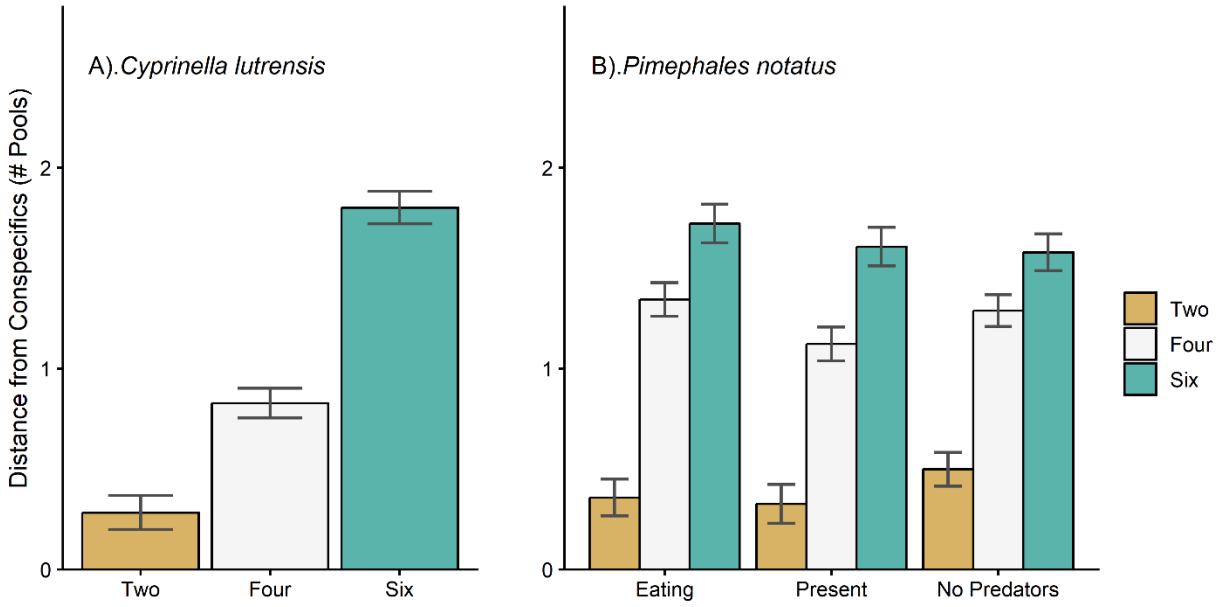
Figure 4.3 Aggregation of *Cyprinella lutrensis* (A) and *Pimephales notatus* (B) varied across

arena sizes, with less aggregation (longer distance between individuals) in larger arenas.

Treatment and arena size had interactive effects on *P. notatus*, but aggregation was still lowest in

the largest arena size. Error bars represent 90% confidence intervals of predicted distance from

conspecifics derived from *manylm* models.
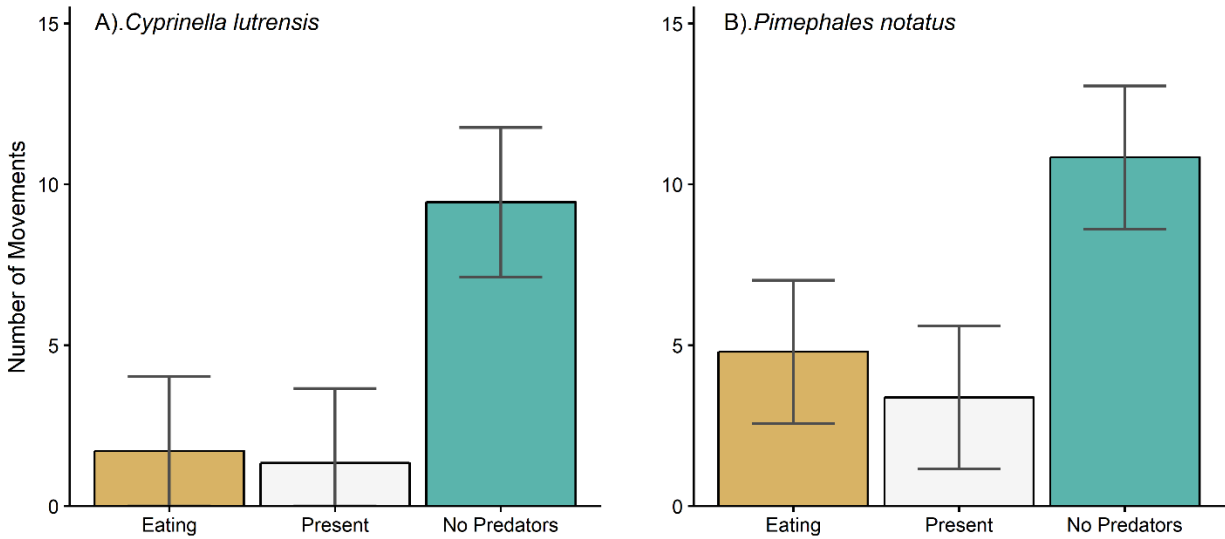
Figure 4.4 Number of movements (number of times individual fish switched pools across entire treatment period) differed across treatments, but not arena sizes. Both *Cyprinella lutrensis* (A) and *Pimephales notatus* (B) moved more when predators were not in mesocosms, but there was no difference in number of movements when predators were actively eating or just present. Error bars represent 90% confidence intervals of predicted number of movements derived from *manylm* models.
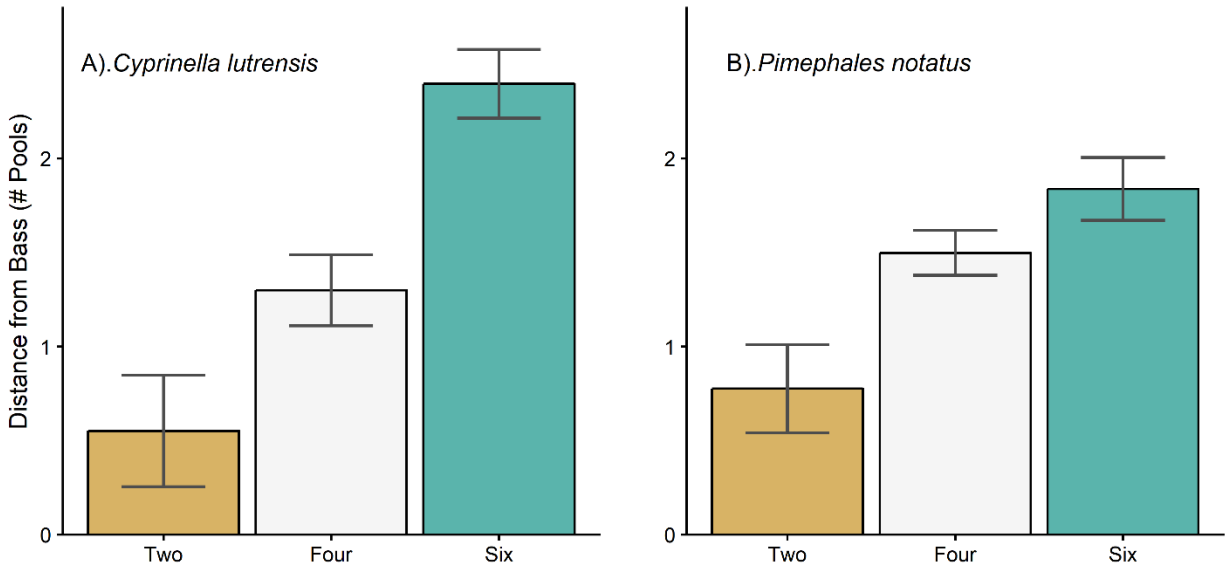
Figure 4.5 Spatial overlap (mean distance from individual prey) between bass and prey fish varied across arena size. Spatial overlap between bass and both prey species decreased with increasing arena size; differences were more profound for *Cyprinella lutrensis* (A) than *Pimephales notatus* (B). Error-bars represent 90% confidence intervals of predicted distance between bass and prey species derived from *manylm* models.
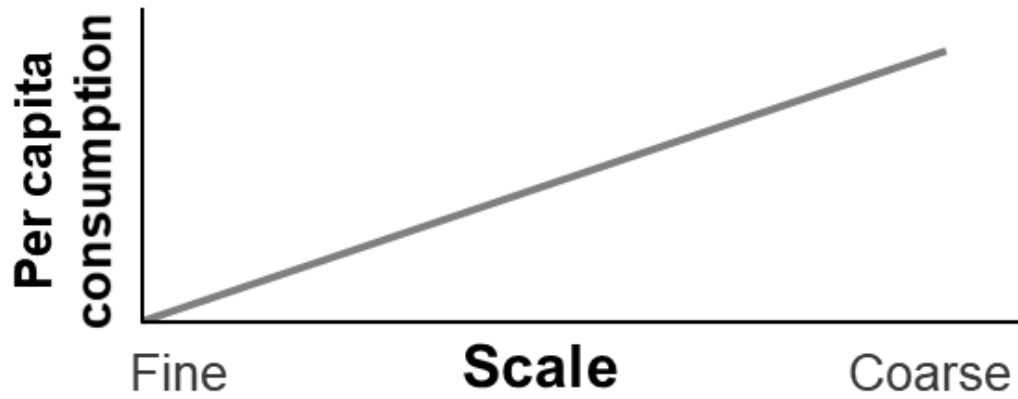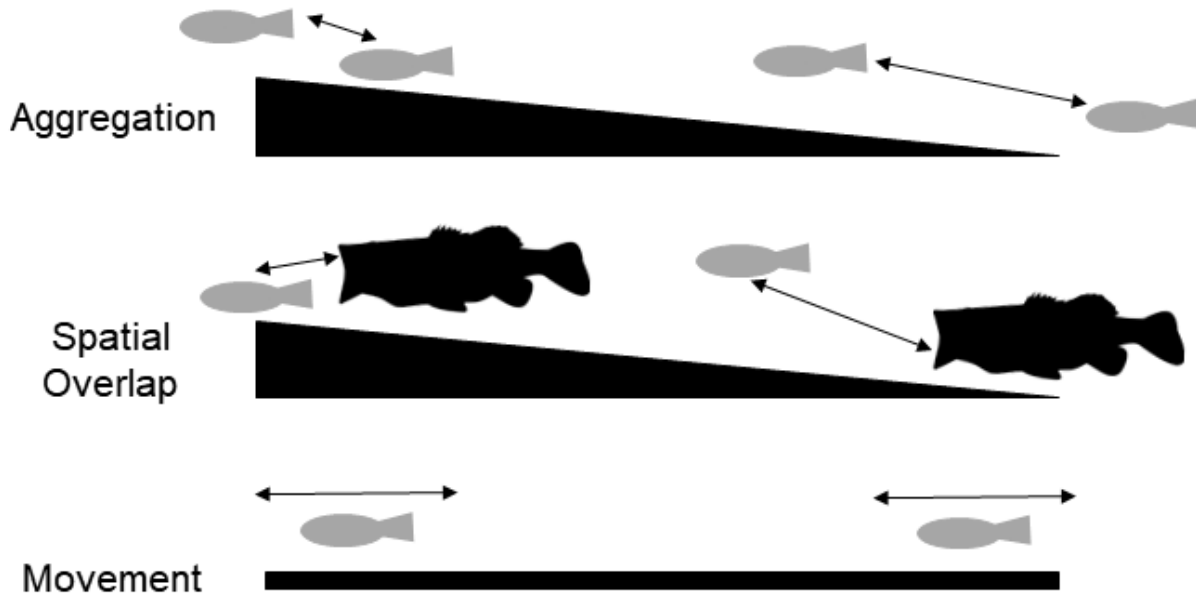
Figure 4.6 Summary of observed consumption, movement, aggregation, and spatial overlap between predators and prey across spatial scales (arena sizes), and hypothesized mechanism driving the increased consumption with spatial scale. We predict decreased aggregation of prey, and therefore decreased group vigilance, led to increased consumption rates despite decreased encounter rates.

We used 30 min time intervals to calculate aggregation and spatial overlap metrics to balance out more detections and less number of pools visited. However, differences in the estimated distance from conspecifics (aggregation) and distance from predators (spatial overlap) across arena sizes were similar across intervals greater than 5 min.
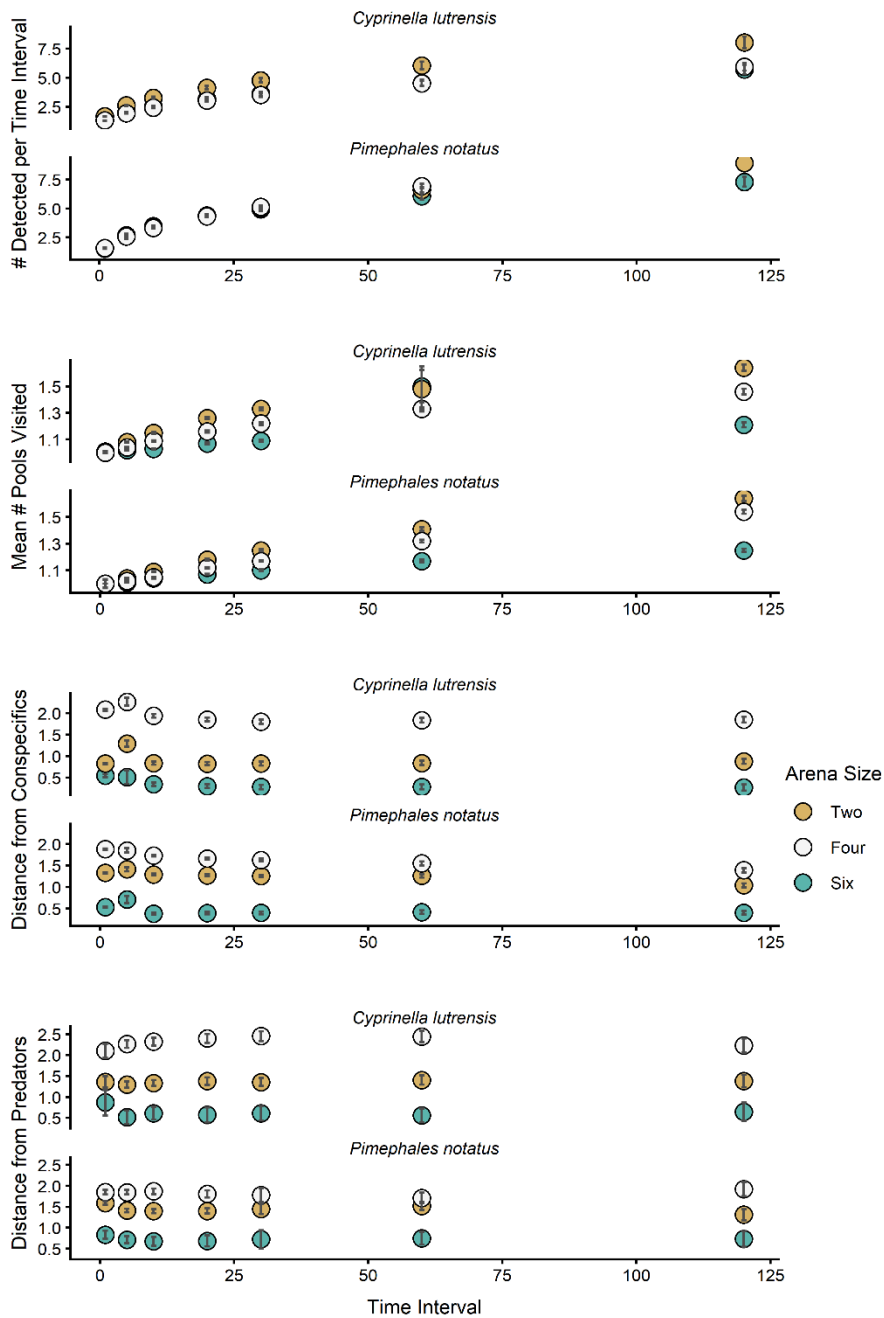
Figure S1: Number unique detections, number of pools visited, aggregation, and spatial overlap measures at different time scales (1, 5, 10, 20, 30, 60 and 120 min). Error bars are standard error around means.

Table S2

Table S2: Comparison of models assessing effect of arena size on per capita consumption by Largemouth Bass

Model	Df	AIC	Log-likelihood	Likelihood Ratio	p-value
Fixed effects only	4	49.82	-20.91		
Fixed effects + variance structure	6	50.04	-19.02	3.78	0.15
Fixed effects+ random effect of trial	5	51.82	-20.91	<0.001	0.99

Table S3

Table S3. Multivariate models of species responses of aggregation (mean distance to conspecifics), movement (number of times individual fish switched pools), and spatial overlap with predators (mean distance to largemouth bass) were assessed using the *manylm* function. Aggregation and spatial overlap of both prey species responded to arena size, while treatment effects (bass absent, present, or eating) were the only significant predictor of movement. Aggregation and spatial overlap models included a fixed effect of trial and time interval to account for pseudo-replication (repeated measures) within each trial since *manylm* models do not allow for random effects. Movement models did not include an effect of time interval because the number of movements was calculated across the entire treatment period. Significant effects (P ≤ 0.10) are shown in bold.

Predictor	Species	Aggregation			Movement			Spatial Overlap		
		DF	Likelihood Ratio	P	DF	Likelihood Ratio	P	DF	Likelihood Ratio	P
Trial		636	**186.10**	**0.002**	32	**23.66**	**0.007**	165	**29.21**	**0.003**
	Cyprinella lutrensis		**79.01**	**0.002**		5.45	0.13		**21.31**	**0.002**
	Pimephales notatus		**107.06**	**0.002**		**18.21**	**0.003**		**7.91**	**0.053**
Time Interval		606	53.00	0.763	NA	NA	NA	135	84.07	0.123
	Cyprinella lutrensis		18.72	0.959					48.87	0.128

	Pimephales notatus		34.28	0.492					35.20	0.448
Arena Size		604	**761.90**	**0.002**	30	9.14	0.139	133	**111.26**	**0.002**
	Cyprinella lutrensis		**347.91**	**0.002**		3.90	0.186		**81.49**	**0.002**
	Pimephales notatus		**413.97**	**0.002**		5.24	0.132		**29.77**	**0.002**
Treatment		602	**13.50**	**0.019**	28	**41.09**	**0.002**	132	0.95	0.688
	Cyprinella lutrensis		0.82	0.713		**20.71**	**0.002**		0.05	0.824
	Pimephales notatus		**12.70**	**0.007**		**20.39**	**0.002**		0.90	0.649
Arena Size:Treatment		598	**21.20**	**0.013**	24	7.84	0.635	130	7.86	0.214
	Cyprinella lutrensis		5.16	0.309		7.28	0.383		0.67	0.745
	Pimephales notatus		**16.09**	**0.013**		0.56	0.984		7.19	0.135

Chapter 5 - Conclusions

In this dissertation, I highlight the importance of study design and scale in quantifying complex ecological patterns. It is not surprising I concluded large sample sizes and making sure to evenly capture environmental gradients of interest is needed to measure subtle ecological responses. Proper study design is a basic principle of science, but efficiently quantifying biotic responses to abiotic gradients is significant when resources, especially time, are limited. Long-term experimental studies are ideal for understanding mechanistic drivers of population and community dynamics (Brown et al. 2001, Bruckerhoff et al. 2020), but Chapters 2 and 3 of this dissertation highlight that space for time substitutions can provide snapshots of predator-prey dynamics, such as co-occurrence of impoundment and disturbance associated fishes with largemouth bass or the underestimation of consumption rates at large scales. Our suggestions for designing landscape studies and the analytical framework used to assess predator effects mediated by environmental variability are applicable in other riverine systems. Pairing multi-scale, landscape approaches with experiments would provide a better understanding of the context dependency of predator effects on stream fish communities.

Similar to known effects of study design on quantifying ecological responses, scale is an issue when measuring most ecological phenomena (Wiens 1989, Levin 1992), but is critical to consider when making predictions (Englund and Cooper 2003). Predictive models, including those predicting outcomes of predator-prey interactions, are often parameterized with metrics measured at different scales from which the predictions are made (Chesson 1998, Bergström et al. 2006, Englund and Leonardsson 2008). This dissertation and other work (Bergström and Englund 2002, Bergström and Englund 2004, Englund 2005, Luckinbill 1974, Fauchald et al.

2000) suggest estimates of such parameters change with spatial scale. It is therefore important that researchers and managers either estimate these parameters, such as consumption rates, at scales of predictions or are able to estimate how parameters change with scale (scale transitions; Bergström et al. 2006, Englund and Leonardsson 2008). Predictive models and underlying parameters need to be developed at scales relevant to mangers and conservation actions to actually have real world applications. There is often a "mismatch" between scales in which ecological processes are measured or take place and the social scales in which decisions are made (Cumming et al. 2006). In terms of managing predators, important questions to consider include what scale is important to managers? and at what scale do populations and communities operate (Faush et al. 2002)? Predator effects in streams have often been studied at fine scales (see introduction) and are often considered to only operate at the finest spatial scales (Hunsicker et al. 2011). However, there is evidence that predators do shape ecological patterns in stream systems at coarse spatial scales (Giam and Olden 2016, Turschwell et al. 2018). While ecologists have become quite good at quantifying patterns at fine scales, we do not yet understand how to apply these observations to predict predator effects at coarse scales relevant to species distributions, abundances, and long-term population viability, and this dissertation highlights that these fine scale observations may be underestimating coarser scale processes.

Fine scale processes and biotic interactions can be important (Power et al. 1988), but more conceptual and empirical work is needed to know how to incorporate fine scale observations into conservation and management actions.

My attempt to measure predator effects across riverscapes suggest predators (largemouth bass) exhibit positive co-occurrence patterns with species, some of which are associated with disturbance or impoundments, ultimately leading to increased richness at sites with predators.

Increased richness and/or abundance of predators after introduction of stocked or non-native fishes has been documented in other studies (Eby et al. 2006). This can lead to "top-heavy" food webs, which is potentially supported in aquatic systems due to lack of resource limitation, habitat coupling (Tunney et al. 2012) and/or communities not being saturated (Gido and Brown 1999). In the Flint Hills, increased predator richness has the potential to shape stream fish communities, as many of the species associated with impoundments are predators and can consume fish and because impoundments are so numerous. Increasing predator richness has highly variable effects on ecosystems, including changes in prey density, shifts in prey assemblage structure, outperformance of single predator species in suppressing prey populations, or null effects (reviewed in Bruno and Cardinale 2008). The outcome of increased predator richness on stream fish communities is likely dependent on the combination of several processes, including resource partitioning (Ives et al. 2005), selection (Ives et al. 2005), intraguild predation (Polis and Holt 1992), and predator-predator interactions (Sih et al. 1998). In this dissertation I only considered the effects of largemouth bass, but there are other native or supplemented piscivorous fish (*i.e.* spotted bass, green sunfish) that likely interact through competition and predation of smaller life stages. Further, terrestrial predators in the system (*i.e.* Great Blue Herons, Northern Water Snakes) are severely understudied, but were often observed when collecting data for this dissertation. These contingencies make managing the effects of multiple predators difficult and outcomes of managing for predator richness will likely produce unexpected outcomes (Bruno and Cardinale 2008).

This dissertation focused on predator effects on stream fish communities, but predator effects likely extend beyond fish communities. Predator effect are known to cascade down food webs, influencing the distribution and abundance of algal biomass in streams (Townsend 2003,

Power et al 1985). In addition to these known effects on primary production, predators may influence nutrient cycling (Schindler et al. 2001, Simon et al. 2004), aquatic subsidies into terrestrial systems (Baster et al. 2004), and abundance and distribution of other taxa. As most fish are omnivores, predators likely influence macroinvertebrate communities through direct consumption and through effects on other fish species. Because intraguild predation is common (Arim and Marquet 2004, Thompson et al. 2007), roles of predators in stream food webs and ecosystem processing is complex and historic studies emphasizing linear links between predators and lower trophic levels (Pace et al. 1999, Oksanen et al. 1981) are likely to simplistic to realistically represent stream systems.

Predators can have important impacts on ecosystems, but quantifying their effects at spatial scales relevant to management and conservation can be difficult. As landscapes, riverscapes, and climate continues to change, we are faced to make conservation decisions regarding protecting apex predators and mitigating effects of non-native predators. Management actions, such as removing non-native predators or creating refugia for native predators facing habitat loss, are resource intensive. It is critical we understand and predict outcomes of predator-prey interactions to inform prioritization of limited conservation resources (Beamesderfer 2000). Non-native and predominately predatory fish have been stocked into freshwater systems globally (Gozlan 2008, Gozlan et al. 2009). Although the ecological impacts of non-native species in general are variable (Gurevitch and Padilla 2004, Didham et al 2005, Gozlan 2008), purposeful stocking of predatory species may lead to inflated negative effects of non-native species in freshwater system by replacing native predators, increasing predator richness, increasing consumption of native fish, an increasing top-down control on ecosystem structure and function (Eby et al. 2006). Deciding whether or not to remove and manage non-native species needs to be

based on evidence that these predators are having effects and whether or not those effects can actually be mitigated with action (Beamesderfer 2000). Unfortunately, some of the challenges discussed in this dissertation with quantifying predator effects make prioritizing management decisions regarding predators difficult, and often there is limited time to untangle the complex interactions between landscape change, predators, and native fish community dynamics. I hope this dissertation sheds some light in regards to study design, spatial scale, and quantitative methods to help untangle these relationships in other systems.

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