

DISSERTATION

USING POPULATION ECOLOGY TO ADVANCE STREAM COMMUNITY ASSEMBLY

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ABSTRACT

USING POPULATION ECOLOGY TO ADVANCE STREAM COMMUNITY ASSEMBLY

Biodiversity is maintained by processes operating at several hierarchical scales, including individuals making up populations of the same species, interacting individuals of different species, and whole communities and ecosystems. Key advances have been achieved in understanding communities theoretically (e.g. metacommunity theory) and analytically (e.g. state-space models). However, species within communities are often studied in isolation and researchers have called for a better integration across individuals, populations, and groups of species. The southeastern United States contains one of the most diverse freshwater fish assemblages in North America and provides a suitable system to investigate community assembly. Species' habitat and biotic interactions are still poorly understood in the southeast, and this information is important for the management and conservation of these assemblages.

Understanding how environmental conditions and population processes determine the abundance and distribution of species is a central problem of ecology and biogeography. The abiotic environment can shape species distributions and foundational studies have described the environment as a filter acting as a selective force, permitting some species to establish and persist. Species can be abundant in some habitats, whereas they are scarce or absent in others, and both occupancy and abundance can be useful measures of population status. While occupancy and abundance are potentially governed by different limiting factors operating at different scales, few studies have directly compared how factors impact both in the same study. **(Chapter 1)** My first dissertation chapter aimed to understand species occupancy and abundance

for 37 species across 203 coastal plain stream sites in relation to environmental variables such as local abiotic (e.g. velocity, turbidity) and landscape factors (e.g. landcover). Given the spatial and biological hierarchy of streams, I predicted that landscape factors would be more important to occupancy and local factors to abundance. Contrary to this hypothesis, I found that a combination of local and landscape factors was important to both occupancy and abundance.

The role of the abiotic environment in structuring community assembly has received considerable attention in the literature. However, focusing solely on abiotic variables can overstate the influence that abiotic tolerances have in structuring communities and ignore the role of biotic interactions. While environmental filters and abiotic conditions can determine which species from the regional pool occur within a local community (e.g. in Chapter 1), the influence of these variables can differ among species and sites.

Many populations of species occur in temporally dynamic environments. Demographic information is often obtained for individual species and sites, but the study of species in a community in isolation may lead to only a partial understanding of community ecology. When species are sympatric, they experience similar environmental conditions. However, a key question that remains is whether species in these communities show similar responses to environmental or seasonal variation (**Chapter 2**). For my second chapter, I investigated abiotic drivers of synchrony in survival among species within a local community, and spatial synchrony across sites for populations of the same species. I investigated synchrony in survival for two stream-fish communities in South Carolina using a mark-recapture study (lasting from November 2015 to March 2018). Specifically, I examined variation in survival and tested the impacts of abiotic drivers such as stream temperature and water-level on survival. Results showed seasonal differences in bi-monthly survival, with occasions of low survival occurring in

late summer (July-September). I observed synchrony in bi-monthly survival among species within the same stream for both sites, however I also observed spatial asynchrony in survival for populations of the same species. Spatial differences in variation in survival may be driven by climate interacting with local habitat differences between the two streams.

While abiotic drivers can structure communities, competitive interactions, particularly those that occur within species (intraspecific) are also thought to have an important role in communities. Niche differences can act as stabilizing forces to overcome fitness differences among species (e.g. interspecific competition) such that common species don't exclude others in the community (**Chapter 3**). In Chapter 3, I examined the relative strength of intra- and interspecific interactions to understand if species are limiting themselves (e.g. niche differences) versus each other. Additionally, the magnitude and direction of biotic interactions can be size dependent and influence life-history processes such as foraging, growth, and reproduction. Thus, I also investigated the presence of body size-dependent competition. I hypothesized that negative intraspecific competition would be greater than interspecific interactions, with the exception of ecologically similar species. I predicted that body size-dependent competition may be present if negative interactions (whether intraspecific or interspecific) were discovered. I found that there were a greater number of negative intraspecific interactions; however, the majority of these were not statistically significant. I also observed a significant negative interspecific interaction between two ecologically similar species (bluehead chub *Nocomis leptocephalus* and creek chub *Semotilus atromaculatus*). Overall, negative biotic interactions did not appear to be as important as abiotic factors in these communities and there was little evidence of body size dependent competition.

Collectively, these three chapters advance community theory for stream fishes. My research builds upon previous work and the metacommunity paradigm in stream fish ecology by investigating community assembly across biological, temporal, and spatial hierarchies. My dissertation research demonstrated that demographic information can be used to understand both abiotic and biotic interactions in multi-species systems. Chapter 1 demonstrated that a combination of local and landscape factors were important for occupancy and abundance, and provided needed information on what structured broad-scale distribution and local abundance for coastal plain fish species. Chapters 2 and 3 demonstrated the relative importance of abiotic and biotic factors to two focal stream communities. While species within the same community had synchronous survival, populations of the same species had asynchronous survival when comparing survival estimates between the two streams. My results contrasted with what is expected of spatial relationships of synchrony, where geographically close populations should be more likely to exhibit synchronous dynamics. This is one of the few studies that demonstrates the presence of asynchrony at finer spatial scales. Spatial differences in survival may be driven by habitat differences by the two streams and this study draws attention to the need of accounting for local habitat variation. Chapter 3 highlighted contrasting effects of intra- and interspecific density on species-specific growth rates in these fish communities. While I observed a greater proportion of negative intraspecific interactions, these were nonsignificant values. As I hypothesized, I found a greater proportion of positive interspecific interactions and found little evidence of negative interspecific interactions among species. However, the negative interspecific interaction observed between the two most ecological similar species in this study also differed spatially where this interaction was observed in one stream but not the other, which

again showed the importance of accounting for local habitat variation and potential context dependency of species interactions.

While I demonstrated that both abiotic and biotic factors are potentially important for these communities, findings from Chapter 2 demonstrated more support for abiotic drivers of temporal variation rather than biotic drivers in Chapter 3. My results suggested that while biotic interactions can be important for stream communities, they may not be the dominating factor in regulating population dynamics in these systems. This was further evidenced by the presence of positive interspecific interactions among species in Chapter 3, suggesting that when conditions were favorable all species experienced a positive growth rate. Lotic systems are very dynamic with frequent disturbances, so the fishes in these habitats may rarely reach their carrying capacity and as a result are more influenced by abiotic factors. These results suggest that more attention should be paid to accounting for context dependency in species-environment relationships, particularly since how the strength and magnitude of these relationships vary are typically not accounted for in ecological models (e.g. metacommunity theory).

Freshwater ecosystems are among the most diverse and human-altered environments on the planet, and understanding the impacts of environmental change on population recoveries is imperative given the number of threatened and declining fish species. Furthermore, nongame fishes are underrepresented in the literature for studies of demography and this has important implications for conservation of these assemblages. Methods to study multi-species relationships are needed to increase our understanding of how climate and land-use change may affect community composition, as sympatric species react in similar or different ways to changes in their environment.

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CHAPTER 1: USING HIERARCHICAL MODELS TO EVALUATE FACTORS AFFECTING OCCUPANCY AND ABUNDANCE OF FISH SPECIES IN COASTAL PLAIN STREAMS

Introduction

Evidence of global scale declines in fish populations has highlighted the need for more extensive and rigorous monitoring programs to document change in species occurrence and abundance (Burkhead 2012). As global areas devoted to urban uses grow, an increasing number of freshwater species will face imperilment due to urbanization effects (Dudgeon et al. 2006; Wenger et al. 2010). Aquatic populations must contend with increasingly human modified landscapes, which has important consequences for the connectivity and suitability of native habitats that in turn may influence occupancy, abundance and persistence of species in those habitats.

Stream fishes are ideal for studying patterns that span across scales given that streams are structured hierarchically (Hugueny et al. 2010) and are strongly influenced by the surrounding landscape (Schlosser 1991; Allan 2004; Townsend et al. 2003). Riverine systems are described as macrosystems, where regional factors (landscape, climate) can interact with local habitats to drive ecological patterns and processes (Heffernan et al 2014; McCluney et al. 2014). In a stream hierarchy, fine spatial scales are constrained by broader levels above (Frissell et al. 1986; Vannote et al. 1980) and the influence of broad landscape scales on local habitat conditions of streams has been well documented. Landscape attributes can predict patterns of fish assemblages over large spatial extents (Jackson et al. 2001) and in turn these attributes can strongly influence ecological processes such as movement and dispersal (Olden et al. 2001, Perkin and Gido 2012). Landscape level data can provide information on biogeography (Gido et

al. 2006) while smaller scale analyses provide information for the importance of local habitat characteristics and biotic interactions on fish assemblage structure.

The distribution and abundance of species may be simultaneously influenced by both local scale habitat features and broader landscape factors (Wenger et al. 2008b). Within their geographic range, species can be abundant in some habitats or areas whereas they are scarce or absent in others (Brown 1984). Factors operating at different scales may influence site occupancy and/or local abundance. Thus, studies of species occupancy and/or abundance patterns should consider how landscape as well as local factors can influence species occurrence and persistence. These niche differences among species may limit the survival and reproduction of a given species, and in turn its local density and geographic distribution.

While abundance and occupancy estimation can be useful measures of species status, both may be confounded by imperfect detection that results in false absences in data, particularly with elusive species like fish (Wenger et al. 2008b). Advancements have been made in addressing imperfect detection to estimate occupancy based on detection-nondetection data from replicated samples (MacKenzie et al. 2002), and in abundance estimation using replicated count samples (Royle 2004). Combining these approaches in a hierarchical model allows investigators to simultaneously estimate the probability of a species presence (occupancy) and local abundance, given the species is present, using a zero-inflated distribution with replicated count information (Wenger et al. 2008a). Furthermore, zero-inflated distributions can be useful in describing the spatial distribution of rare species because of their ability to account for excess zeros in the data that are common in ecological datasets (Martin et al. 2005).

Biologists often must deal with limited data to make inferences with species-specific approaches. Species-specific models have been combined into a single hierarchical model that is

useful for analyzing community-level ecology data, while accounting for imperfect detection (MacKenzie et al. 2002). Multi-species models can provide inferences for all species in the system because parameters for each species are derived from a common community-level distribution rather than if each species was fit independently (Midway et al. 2014). The data are used efficiently and fewer parameters are required (Broms et al. 2016). This borrowing strength is an advantage of random effects models (Kéry and Schaub 2012; Hobbs and Hooten 2015). Multispecies models have gained popularity to answer questions such as landscape effects on native versus non-native species (Stewart et al. 2016), impacts of land-use on biotic integrity tolerance classifications (Midway et al. 2014), and metacommunity ecology (Dorazio et al. 2010).

While occupancy and abundance may be influenced by different factors operating at different scales, few studies have directly compared both metrics for entire assemblages (Dibner et al. 2017). Much of the effects of local and landscape analyses have been focused on species distribution or occupancy. However, understanding how abundance varies among species is also important for conservation to understand how species are performing (Schindler et al. 2010). There are often data gaps in the understanding of species-habitat relationships for both abundance and occupancy.

The southeastern United States contains some of the highest aquatic biodiversity in North America, but has suffered long-term declines in native aquatic species (Warren et al. 2000). The factors affecting abundance and occupancy for southeastern fishes are still poorly understood and conservation is often limited by a lack of data (Midway et al. 2014). The North American coastal plain is a global biodiversity hotspot for many taxa and recent analyses have indicated that approximately 85% of the natural habitat has been altered or converted by humans (Noss et

al. 2015), which can have serious implications for aquatic species (Wenger et al 2010). Given the numerous imperilments that face waterways today, my objectives were to develop a modeling framework to explore the relationships between occupancy and abundance of coastal plain fishes and the relative importance of local and landscape factors on these state variables. Given the importance of habitat hierarchy in structuring fish assemblages, I predicted that landscape covariates would be more likely to drive site occupancy, and local, in-stream covariates for abundance.

Methods

Study area

Data were collected as part of statewide aquatic resources inventories conducted by the South Carolina Department of Natural Resources (SC-DNR) in 2006-2011. Sample locations were randomly selected by the SC-DNR from a list of all available stream segments that were stratified by major basin. Coastal plain wadeable streams are characterized by low flows, pH, conductivity, alkalinity, and dissolved oxygen, as well as the presence of a high proportion of endemic plant and vertebrate species (Noss et al. 2015).

Sampling methods

A total of 203 sites were sampled (Figure 1), and ranged in drainage size from 0.17 to 154-km². Three-pass depletion with backpack electrofishing (Appalachian Aquatics Model AA-24) was applied to a 100-m reach of stream, using block nets at both ends of the reach to prevent fish movement into and out of the sample area and ensure the closure assumption. Stream channel width measurements were taken every 25-m along each reach to estimate a mean wetted width. Depth and velocity were taken over a longitudinal section using a zig-zag pattern at 50

randomly selected locations, and these measurements were averaged. Physical and chemical data, which included water temperature, dissolved oxygen, conductivity, and pH were recorded prior to fish sampling using a YSI 556 MPS multiparameter probe. Turbidity was recorded using a MicroTPW turbidimeter. Local habitat was characterized by measuring velocity (m/s), depth (m), pH, dissolved oxygen (mg/l), and turbidity (NTU). Landscape habitat factors were quantified in ArcGIS 10.0, and included watershed size (km²), percent watershed land cover (forest and urban) from the 2006 National Land Cover Database (Fry et al. 2011), and elevation (m). I also ensured that covariates included in the model were not correlated by performing a Pearson's r correlation prior to including covariates in the model.

Analysis

To investigate fish occupancy and abundance jointly, I used count data for each species and each pass at a given site in a hierarchical modeling framework. I used a Bayesian multi-species hierarchical model (Appendix 2 Example JAGS Code; Kéry and Schaub 2012) implemented in Program R (R Development Core Team 2008) using the jagsUI package (Kellner 2014) and JAGS (Plummer 2003). I used 37 species that were present at >5% of sites for analysis. The model linked the occupancy and abundance in a hierarchical manner; given that a site was occupied, local abundance was modeled using an N-mixture model with zero-inflation (Wenger et al. 2008b). The ecological process model (Equations 1 and 2) used to estimate occupancy for each site i and species j included the latent state where $z_{i,j} = 1$ if a species was present and $z_{i,j} = 0$ otherwise. $z_{i,j}$ was assumed to follow a Bernoulli distribution with $z_{i,j} \sim \text{Bernoulli}(\Omega_{i,j})$ where $\Omega_{i,j}$ is the mean species occupancy for each species j at site i . Occupancy, $\Omega_{i,j}$, was modeled as a function of covariates on the logit-link scale:

$$\text{logit}(\Omega_{i,j}) = \alpha_{0j} + \boldsymbol{\alpha}_j \times \mathbf{X}_i \quad \text{Equation 1}$$

Where α_{0j} is the species-specific overall mean occupancy (intercept) that was modeled as a random effect with a normal distribution with a mean of $\mu_{\alpha 0}$ and variance ($\sigma_{\alpha 0}^2$). α_j , represents a vector of the species-specific slopes (effect sizes) for the covariates (X_i) with a normal prior distribution (Normal (0, 0.37)). Thus, α_{0j} was modelled jointly across species, but α_j was modeled independently for each species to achieve model convergence.

Species abundance, $N_{i,j}$ was assumed to follow a Poisson distribution with $N_{i,j} \sim \text{Poisson}(z_{i,j} \lambda_{i,j})$ where $\lambda_{i,j}$ is the mean abundance for species j at site i , conditional on the presence of the species at the site. Abundance was modeled as a function of covariates on the log-linear scale (Equation 2):

$$\log(\lambda_{i,j}) = \beta_{0j} + \beta_j \times X_i \quad \text{Equation 2}$$

where β_{0j} is the species-specific mean abundance (intercept) that was modeled as a normally distributed random effect with a mean of $\mu_{\beta 0}$ and variance ($\sigma^2_{\beta 0}$). Similar to occupancy, β_j , represents a vector of the slope (effect size) of the covariates X_i with a uniform prior distribution (*Uniform* (-3, 3)).

For the detection process, capture probabilities of individuals per electrofishing pass were estimated from the three-pass depletion data by assuming that fish populations were closed during surveys and capture probability ($p_{i,j}$) was constant among electrofishing passes. The observed data represented counts of individuals at site i , for each species j , and electrofishing pass k denoted as $y_{i,j,k}$ and were modelled using a binomial distribution:

$$y_{i,j,1} \sim \text{Binomial}(N_{i,j}, p_{i,j}),$$

$$y_{i,j,2} \sim \text{Binomial}(N_{i,j}, (1 - p_{i,j}) \times p_{i,j}),$$

$$y_{i,j,3} \sim \text{Binomial}(N_{i,j}, (1 - p_{i,j}) \times (1 - p_{i,j}) \times p_{i,j}),$$

Similar to the ecological process in which occupancy and abundance was modeled in relation to covariates, the capture probability was modeled as a function of turbidity and velocity covariates using a logit link:

$$\text{logit}(p_{i,j}) = \gamma_{0j} + \gamma_{1j} * (\text{turbidity}_i) + \gamma_{2j} * (\text{velocity}_i) \quad \text{Equation 3}$$

Where γ_{0j} is species-specific overall mean capture (intercept) which was modeled as a normally distributed random effect with a mean of μ_{γ_0} and a variance of $\sigma_{\gamma_0}^2$. γ_1 , and γ_2 are the normally prior distributed (Normal $\sim [0, 0.37]$) effect sizes of the covariates that I assumed important for capture. Both turbidity and velocity have been documented to be important to capture of fishes (Pregler et al. 2015).

Posterior distributions of model parameters were estimated by taking every 10th sample from 10,000 iterations of three chains after discarding 1,000 burn-in iterations. Model convergence was checked by visually examining plots of the Markov chains for good mixture and by comparing the estimated between and within chain variances for each parameter, which is referred to as the potential scale reduction factor (Gelman and Hill 2007). I ensured that the potential scale reduction factor value was less than 1.1 for all model parameters to assume model convergence (Gelman and Hill 2007). I determined the relative importance of landscape and local factors to occupancy and abundance by tallying the number of species for which each covariate was statistically significant. I defined a covariate as significant if the 95% credible interval of the posterior mean did not overlap zero. Finally, I also used Pearson's r correlation to check for model fit between predicted species abundance and observed count at each site.

Results

A total of 37 species at 203 sites were included in the analysis comprising 10 families (Table S1). The most common families included Centrarchidae (11 species), Cyprinidae (6), Ictaluridae (6), and Percidae (5). I observed low correlation among environmental covariates where the majority had Pearson's r values < 0.50 with the exception of velocity and DO ($r = 0.68$). Of the local and landscape covariates considered, the following were included in the analysis: depth, dissolved oxygen (DO), pH, turbidity, elevation, percent forest and urban cover, and watershed area (Table 1).

Mean capture probability per electrofishing pass was 0.51 with species-specific estimates ranging from 0.33 (speckled madtom) to 0.66 (lowland shiner) (Figure 2a). Mean species occupancy was 0.35 with species-specific estimates ranging from 0.06 to 0.88 (ironcolor shiner and pirate perch) (Figure 2b). Mean abundance was 6 with species-specific estimates ranging from 1 (sawcheek darter) to 62 (eastern mosquitofish) (Supplemental Table 1). While I predicted that landscape covariates would affect species occupancy and local covariates for abundance, I observed that in fact a combination of local and landscape covariates were important for both occupancy and abundance. However, I also observed species had more significant covariate effects sizes for abundance rather than occupancy (a total of 174 versus 89 significant effect sizes across species and covariates) (Figure 3). Dissolved oxygen, turbidity, and forest and urban cover were not important predictors of species occurrence for the majority of fish species in coastal plain streams. Species were more likely to occupy sites with larger watershed area (effect size range = 0.40 to 1.12) and deeper depths (effect size range = 0.57 to 1.58) (Table 2), both covariates potentially indicative of habitat volume, had higher numbers of species with significant effect sizes for covariates on for occupancy (18 and 12 respectively,

Figure 3). Distributions of species did not appear to be strongly influenced by environmental covariates (e.g. absence of habitat specialists) in South Carolina coastal plain streams.

More species had significant effect sizes for both local and landscape covariates to abundance (Table 3). A number of species (8) increased in abundance as urbanization intensified (effect size range = 0.10 to 0.48) or/in addition to a decreased in abundance with increasing forest cover (20 species; effect size range = -0.56 to -0.34). Additionally, I also observed species that had increased abundance in association with low dissolved oxygen (effect size range = -1.45 to -0.18). While some species (11) decreased in abundance with increased amounts of urban cover (effect size range = -0.616 to -0.07).

Finally, for model fit I observed a positive correlation between predicted abundance and observed count for each pass (pass 1 = 0.97; pass 2 = 0.91; pass 3 = 0.89; Figure S1) however the model tended to under-predict abundance and this difference increased from the 1st to the 3rd pass of sampling.

Discussion

Contrary to my prediction, I observed that occupancy and abundance were affected equally by local and landscape factors. A diversity of responses to the relative importance of local versus landscape has been observed in the literature and has been found to vary over large spatial extents when comparing across geographic boundaries (Kautza and Sullivan 2012). While a combination of local and landscape factors were important to occupancy and abundance, more covariates influenced species' abundance rather than occupancy. Surprisingly, land-cover covariates did not appear as important to structuring occupancy.

Studies have had similar findings in which land cover catchment-scale land cover characteristics were relatively uninfluential in explaining the occurrence of stream fish species (Wuellner et al. 2013). Stewart et al. (2016) also found that land-cover models performed poorly compared to in-stream variables in explaining fish distributions on the Great Plains. Perhaps land-cover characteristics were less important for occupancy in this study because amounts of anthropogenic land cover wasn't high, and on average, catchments had less than 10% urban cover. However, it has been noted in other studies that landscape characteristics tends to influence species occurrence more in the presence of anthropogenic disturbances (Wang et al. 2008) and urban cover as little as 2% can have deleterious effects on some species (Wenger et al. 2008b). I did observe that watershed area was positively associated with fish occurrence, a common ecological pattern where species richness increases with habitat area (Angermeier and Schlosser 1989).

A combination of local and landscape factors was also important for abundance, however all covariates affected abundance more strongly than occupancy. I identified a number of “tolerant species” that had higher densities in areas of increased urban cover, low percent forest and low dissolved oxygen. Land-use has changed extensively over time, and historically South Carolina has had a large degree of habitat loss due to de-forestation (Pinder et al. 1999). Recent research has suggested that more than 85% of all historic vegetation and 96% of savannahs and woodlands across the entire North American coastal plain have been converted to anthropogenic vegetation or are highly deviated from natural condition (Noss et al. 2015). This could create habitat suitable for species tolerant of these conditions. While I did not have data on historical coastal plain assemblages in South Carolina, studies have shown that changes in land-use resulted in more cosmopolitan species dominating the landscape (Johnston and Maceina 2009).

Furthermore, previous research in the southern Appalachians has shown that past land-use can still have influence of diversity of stream invertebrates and fish years after the stream landscape has appeared to recover where assemblages can still resemble that of an impacted stream (Harding et al. 1998). Alternatively, harsh environments have also been found to lead to community convergence due to fishes needing to have a strong tolerance to withstand environmental conditions such as those found in Great Plains fish assemblages (Ostrand and Wilde 2011). Perhaps the patterns I observed could also be attributed to community convergence in response to the harsh environment present on the coastal plain.

Although abiotic factors, together with dispersal and biotic factors, are often suggested to explain the distribution of species and their abundances, models typically focus on abiotic factors only (Boulangeat et al. 2012). To get at the underlying mechanisms of species distributions and local abundances it has been advocated to incorporate ecological traits that could directly influence species distributions. Efforts have been taken towards compiling fish trait data to describe the characteristics of a species that are linked with its fitness and performance (e.g. trophic ecology, life history, physiological tolerances) (Frimpong and Angermeier 2009; Mims et al. 2010) to facilitate conservation and management for North American freshwater fish species. Recent research in South Carolina has compared functional trait diversity (Epstein et al. 2018) as well as guild structuring (Marion et al. 2015).

Multi-species hierarchical models can aid landscape-level resource management and monitoring (Noons et al. 2012; Midway et al. 2014). Using community data can inform estimates for all observed species, and can result in increased precision in species-specific estimates. While issues in parameter identifiability have been raised with certain classes of abundance models (e.g. negative-binomial N-mixture model) (Barker et al. 2018), it has been

found that mixture models with Poisson or zero-inflated Poisson mixture are identifiable (Kéry 2018) and are an adequate method of estimating abundance of species while accounting for imperfect detection. This approach represents a single framework to simultaneously estimate occurrence and abundance.

Ultimately this study provides needed information on what structures broad-scale distribution and local abundance for coastal plain fish species. Environmental changes are expected to alter both the distribution and abundance of species (Kopf et al. 2015). Land-use change is a well-known driver of ecological change, and a leading cause of species imperilment. Human population growth is expected to be highest in the North American coastal plain regions which places biodiversity within this region at high risk (Jenkins et al. 2015). There is often a conservation mismatch between areas where land preservation occurs and areas where imperiled biodiversity is located (Jenkins et al. 2015). The majority of federal land conservation is in the western United States; however, the southeastern US also has a high proportion of imperiled species. Biologists have advocated for identifying intact habitats and communities and conserving them (Pullin et al. 2013). Given the degree of connectivity between rivers and their surrounding landscapes, additional studies have advocated to preserve ecological integrity of entire catchments as much as possible (Angermeier and Karr 1994; Fausch et al. 2002).

Tables and Figures

Table 1: Mean and range of landscape and local variables for South Carolina coastal plain sites.

Scale	Variable	Mean	Range
Local	Depth (m)	0.26	0.04-0.63
	Dissolved oxygen (mg/l)	5.72	0.08-11.37
	pH	6.64	4.86-8.33
	Turbidity (NTU)	8.34	1.01-59.29
Landscape	Elevation (m)	103.5	3-600
	Forest cover (%)	32.05	3.98-80.1
	Urban cover (%)	7.70	0-77.4
	Watershed area (km ²)	31.14	0.17-154.13

Table 2: Occupancy covariate effect size estimates for each species included in the analysis; posterior mean and (95% credible interval).

Species	Depth	Dissolved Oxygen	pH	Turbidity	Elevation	Forest Cover	Urban Cover	Watershed Area
American eel <i>(Anguilla rostrata)</i>							-0.83 (-1.48, -0.29)	0.87 (0.43, 1.35)
Blackbanded darter <i>(Percina nigrofasciata)</i>					1.21 (0.59, 1.96)	-0.91 (-1.60, -0.25)		0.51 (0.08, 0.97)
Bluehead chub <i>(Nocomis leptcephalus)</i>					1.26 (0.69, 1.88)		0.53 (0.12, 0.97)	
Bluegill <i>(Lepomis macrochirus)</i>							0.46 (0.08, 0.92)	0.51 (0.15, 0.88)
Bluespotted sunfish <i>(Enneacanthus gloriosus)</i>							0.84 (0.02, 1.76)	
Creek chubsucker <i>(Erimyzon oblongus)</i>		0.53 (0.03, 1.05)						0.59 (0.17, 1.12)
Chain pickerel (<i>Esox niger</i>)								2.03 (0.61, 2.95)
Coastal shiner <i>(Notropis petersoni)</i>	-0.81 (-1.60, -0.02)		0.69 (0.01, 1.43)					0.63 (0.13, 1.12)
Dusky shiner <i>(Notropis commingsae)</i>		0.87 (0.26, 1.50)	0.62 (0.17, 1.11)	-0.87 (-1.66, -0.15)		-0.62 (-1.16, -0.08)		0.58 (0.20, 0.98)
Dollar sunfish <i>(Lepomis marginatus)</i>	0.57 (0.15, 0.99)							0.46 (0.11, 0.84)
Eastern mudminnow <i>(Umbra pygmaea)</i>					-1.13 (-1.76, -0.56)		1.01 (0.12, 2.06)	
Flat bullhead <i>(Ameiurus platycephalus)</i>	-2.02 (-2.95, -0.31)			-1.54 (-2.85, -0.07)				
Flier <i>(Centrarchus macropterus)</i>	0.76 (0.24, 1.33)							
Golden shiner <i>(Notemigonus crysoleucas)</i>	1.23 (0.57, 1.93)		0.61 (0.09, 1.19)		-0.52 (-1.11, -0.01)			

Ironcolor shiner <i>(Notropis chalybaeus)</i>						-1.39 (-2.74, -0.14)	
Lake chubsucker <i>(Erimyzon sucetta)</i>	1.82 (0.96, 2.67)	-1.0 (-1.74, -0.28)					
Largemouth bass <i>(Micropterus salmoides)</i>						-0.53 (-1.01, -0.07)	0.75 (0.28, 1.32)
Mud sunfish <i>(Acantharchus pomotis)</i>							0.85 (0.11, 1.83)
Margined madtom <i>(Noturus insignis)</i>						-1.02 (-2.12, -0.09)	0.77 (0.30, 1.28)
Eastern mosquitofish <i>(Gambusia holbrooki)</i>			0.79 (0.13, 1.45)			-0.71 (-1.26, -0.16)	
Pirate perch <i>(Aphredoderus sayanus)</i>						-0.67 (-1.20, -0.15)	-0.56 (-1.02, -0.08)
Pumpkinseed <i>(Lepomis gibbosus)</i>						0.53 (0.13, 0.96)	-0.77 (-1.29, -0.28)
Redbreast sunfish <i>(Lepomis auritus)</i>		0.61 (0.13, 1.09)	1.17 (0.68, 1.72)			-0.56 (-0.95, -0.21)	0.96 (0.52, 1.40)
Redear sunfish <i>(Lepomis microlophus)</i>	1.42 (0.25, 2.59)		-1.57 (-2.74, -0.32)	1.75 (0.60, 2.84)			
Redfin pickerel <i>(Esox americanus)</i>			-0.65 (-1.32, -0.04)			-0.46 (-0.91, -0.01)	-0.48 (-0.97, -0.01)
Snail bullhead <i>(Ameiurus brunneaus)</i>							-0.43 (-0.81, -0.06)
Sawcheek darter <i>(Etheostoma serrifer)</i>	-1.26 (-2.5, -0.05)						
Lowland shiner <i>(Pteronotropis stonei)</i>						-1.95 (-2.86, -0.97)	
Spotted sunfish <i>(Lepomis punctatus)</i>			0.57 (0.12, 1.04)	-0.55 (-1.03, -0.12)	-0.69 (-1.2, -0.23)	-0.68 (-1.07, -0.30)	0.81 (0.38, 1.30)
Speckled madtom <i>(Noturus leptacanthus)</i>						0.54 (0.03, 1.06)	-0.76 (-1.82, -0.01)
							0.53 (0.08, 0.99)

Spotted sucker <i>(Minytrema melanops)</i>				1.39 (0.59, 2.44)
Savannah darter <i>(Etheostoma fricksium)</i>	-1.02 (-2.06, -0.01)		1.01 (0.18, 2.29)	0.60 (0.03, 1.22)
Swamp darter <i>(Etheostoma fusiforme)</i>	1.58 (0.50, 2.68)	1.18 (0.37, 2.18)		
Tadpole madtom <i>(Noturus gyrinus)</i>			-0.52 (-1.06, -0.01)	0.40 (0.02, 0.80)
Tessellated darter <i>(Etheostoma olmstedii)</i>		0.42 (0.004, 0.89)	-0.53 (-0.98, -0.11)	0.88 (0.47, 1.31)
Warmouth <i>(Lepomis gulosus)</i>	0.60 (0.09, 1.17)			1.12 (0.35, 2.02)
Yellow bullhead <i>(Ameiurus natalis)</i>	0.53 (0.06, 1.01)	-0.46 (-0.90, -0.03)		

Table 3. Abundance covariate effect size estimates for each species included in the analysis; posterior mean and (95% credible interval).

Species	Depth	Dissolved Oxygen	pH	Turbidity	Elevation	Forest Cover	Urban Cover	Watershed Area
American eel <i>(Anguilla rostrata)</i>			0.20 (0.08, 0.31)	-0.25 (-0.40, -0.11)	-0.55 (-0.71, -0.39)	-0.41 (-0.51, -0.31)		0.20 (0.13, 0.27)
Blackbanded darter <i>(Percina nigrofasciata)</i>	-0.79 (-1.10, -0.48)					0.41 (0.06, 0.74)		0.47 (0.29, 0.66)
Bluehead chub <i>(Nocomis leptoccephalus)</i>	-2.40 (-3.01, -1.85)		1.30 (0.74, 1.95)	-1.46 (-2.22, -0.78)	0.57 (0.42, 0.75)	-0.48 (-0.72, -0.25)		0.46 (0.28, 0.65)
Bluegill <i>(Lepomis macrochirus)</i>		-0.43 (-0.81, -0.19)	0.58 (0.41, 0.80)	0.46 (0.29, 0.67)	0.21 (0.11, 0.36)	0.37 (0.24, 0.49)	0.45 (0.41, 0.49)	0.33 (0.17, 0.44)
Bluespotted sunfish <i>(Enneacanthus gloriosus)</i>		0.28 (0.11, 0.45)		0.15 (0.06, 0.24)	-0.26 (-0.52, -0.01)	-0.41 (-0.53, -0.29)	-0.89 (-1.19, -0.62)	
Creek chubsucker <i>(Erimyzon oblongus)</i>		0.49 (0.30, 0.67)				-0.20 (-0.31, -0.10)	-0.29 (-0.47, -0.13)	
Chain pickerel <i>(Esox niger)</i>			-0.49 (-0.78, -0.19)				-0.63 (-1.10, -0.19)	
Coastal shiner <i>(Notropis petersoni)</i>	-0.41 (-0.78, -0.05)	-1.45 (-2.21, -0.67)						0.73 (0.60, 0.88)
Dusky shiner <i>(Notropis commingsae)</i>			0.52 (0.33, 0.72)	-0.42 (-0.58, -0.25)	0.11 (0.04, 0.18)	-0.22 (-0.31, -0.11)	-0.18 (-0.40, -0.03)	0.19 (0.09, 0.28)
Dollar sunfish <i>(Lepomis marginatus)</i>		-0.18 (-0.27, -0.09)			0.13 (0.05, 0.22)		-0.09 (-0.19, -0.001)	
Eastern mudminnow <i>(Umbra pygmaea)</i>	-0.40 (-0.67, -0.04)	0.84 (0.57, 1.08)	-1.11 (-1.32, -0.85)	0.26 (0.11, 0.38)		-0.18 (-0.36, -0.002)		
Flat bullhead <i>(Ameiurus platycephalus)</i>								
Flier <i>(Centrarchus macropterus)</i>	0.42 (0.29, 0.56)	-0.40 (-0.66, -0.15)			-0.32 (-0.65, -0.03)	0.26 (0.11, 0.40)	0.43 (0.23, 0.64)	-0.19 (-0.40, -0.01)

Golden shiner <i>(Notemigonus crysoleucas)</i>	0.23 (0.13, 0.32)		-0.66 (-0.88, -0.33)	0.12 (0.04, 0.20)		-0.09 (-0.19, -0.006)	-0.67 (-0.92, -0.42)	
Ironcolor shiner <i>(Notropis chalybaeus)</i>						-1.77 (-2.26, -0.84)		-3.79 (-4.86, -2.39)
Lake chubsucker <i>(Erimyzon sucetta)</i>	0.50 (0.23, 0.77)	0.69 (0.39, 1.00)		0.28 (0.01, 0.55)		-0.25 (-0.45, -0.06)	-0.83 (-1.37, -0.35)	-1.46 (-2.15, -0.78)
Largemouth bass <i>(Micropterus salmoides)</i>		-0.36 (-0.62, -0.08)	0.60 (0.34, 0.88)		-0.27 (-0.51, -0.06)		0.33 (0.22, 0.44)	0.17 (0.004, 0.33)
Mud sunfish <i>(Acantharchus pomotis)</i>	0.27 (0.05, 0.46)					-0.25 (-0.49, -0.03)		
Margined madtom <i>(Noturus insignis)</i>	-0.68 (-0.85, -0.50)	-0.39 (-0.60, -0.18)			0.44 (0.24, 0.65)	0.24 (0.03, 0.44)	0.30 (0.16, 0.45)	0.42 (0.29, 0.56)
Eastern mosquitofish <i>(Gambusia holbrooki)</i>	-0.58 (-0.62, -0.55)	-0.35 (-0.39, -0.31)	0.24 (0.20, 0.28)	0.10 (0.09, 0.12)	-1.44 (-1.49, -1.39)	-0.34 (-0.36, -0.31)	0.26 (0.25, 0.28)	
Pirate perch <i>(Aphredoderus sayanus)</i>	-0.26 (-0.33, -0.20)	0.14 (0.07, 0.21)		-0.43 (-0.52, -0.35)	-0.26 (-0.32, -0.20)			0.09 (0.05, 0.13)
Pumpkinseed <i>(Lepomis gibbosus)</i>	0.27 (0.09, 0.45)					-0.37 (-0.61, -0.14)	0.34 (0.17, 0.51)	
Redbreast sunfish <i>(Lepomis auritus)</i>			0.32 (0.24, 0.40)	0.12 (0.07, 0.16)	-0.22 (-0.29, -0.16)		0.10 (0.06, 0.14)	0.19 (0.14, 0.23)
Redear sunfish <i>(Lepomis microlophus)</i>		-1.22 (-1.82, -0.63)	2.58 (1.72, 3.47)	-0.94 (-1.58, -0.31)	0.55 (0.07, 1.04)	-1.68 (-2.45, -0.91)	-0.85 (-1.29, -0.44)	
Redfin pickerel <i>(Esox americanus)</i>		-0.34 (-0.42, -0.26)	0.08 (0.03, 0.14)	-0.17 (-0.23, -0.11)		-0.05 (-0.10, -0.003)		0.07 (0.01, 0.13)
Snail bullhead <i>(Ameiurus brunneus)</i>			1.31 (0.69, 1.98)	-1.64 (-3.21, -0.13)		-1.11 (-1.87, -0.37)		0.57 (0.006, 1.05)
Sawcheek darter <i>(Etheostoma serrifer)</i>	1.85 (1.17, 2.56)		1.44 (0.37, 2.40)	-3.21 (-4.53, -1.90)				-0.92 (-1.76, -0.03)
Lowland shiner <i>(Pteronotropsis stonei)</i>		0.63 (0.43, 0.87)				-0.22 (-0.37, -0.11)		0.13 (0.02, 0.30)

Spotted sunfish <i>(Lepomis punctatus)</i>		-0.30 (-0.40, -0.19)	0.34 (0.20, 0.52)			-0.11 (-0.22, -0.01)	-0.14 (-0.25, -0.05)
Speckled madtom <i>(Noturus leptacanthus)</i>	-0.38 (-0.63, -0.15)		-0.63 (-0.98, -0.34)	-0.75 (-1.55, -0.05)	0.78 (0.46, 0.12)	-0.51 (-0.90, -0.10)	0.43 (0.18, 0.67)
Spotted sucker <i>(Minytrema melanops)</i>		1.15 (0.09, 2.21)					
Savannah darter <i>(Etheostoma fricksium)</i>	0.81 (0.51, 1.11)			-1.12 (-1.54, -0.72)	-0.76 (-1.24, -0.30)	0.48 (0.04, 0.90)	
Swamp darter <i>(Etheostoma fusiforme)</i>		2.45 (1.74, 3.15)	-1.74 (-2.35, -1.16)	0.32 (0.12, 0.51)		-1.60 (-2.15, -1.09)	-0.71 (-1.55, -0.12)
Tadpole madtom <i>(Noturus gyrinus)</i>	-0.64 (-0.93, -0.36)					-0.29 (-0.53, -0.06)	
Tessellated darter <i>(Etheostoma olmstedii)</i>	-0.35 (-0.45, -0.25)		0.29 (0.19, 0.39)	-0.30 (-0.49, -0.10)	0.16 (0.06, 0.26)		0.33 (0.27, 0.39)
Warmouth <i>(Lepomis gulosus)</i>		-0.36 (-0.52, -0.19)				-0.18 (-0.33, -0.05)	
Yellow bullhead <i>(Ameiurus natalis)</i>	-0.65 (-0.77, -0.53)	-0.27 (-0.43, -0.12)		-0.41 (-0.58, -0.25)	-0.50 (-0.66, -0.34)		-0.14 (-0.28, -0.02)

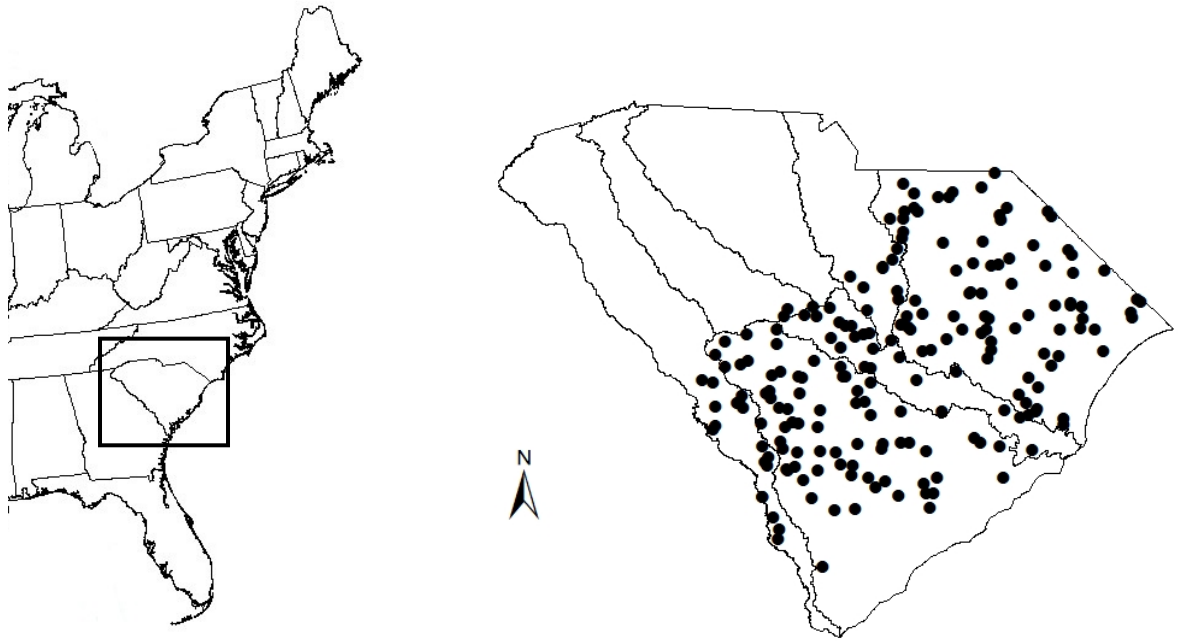
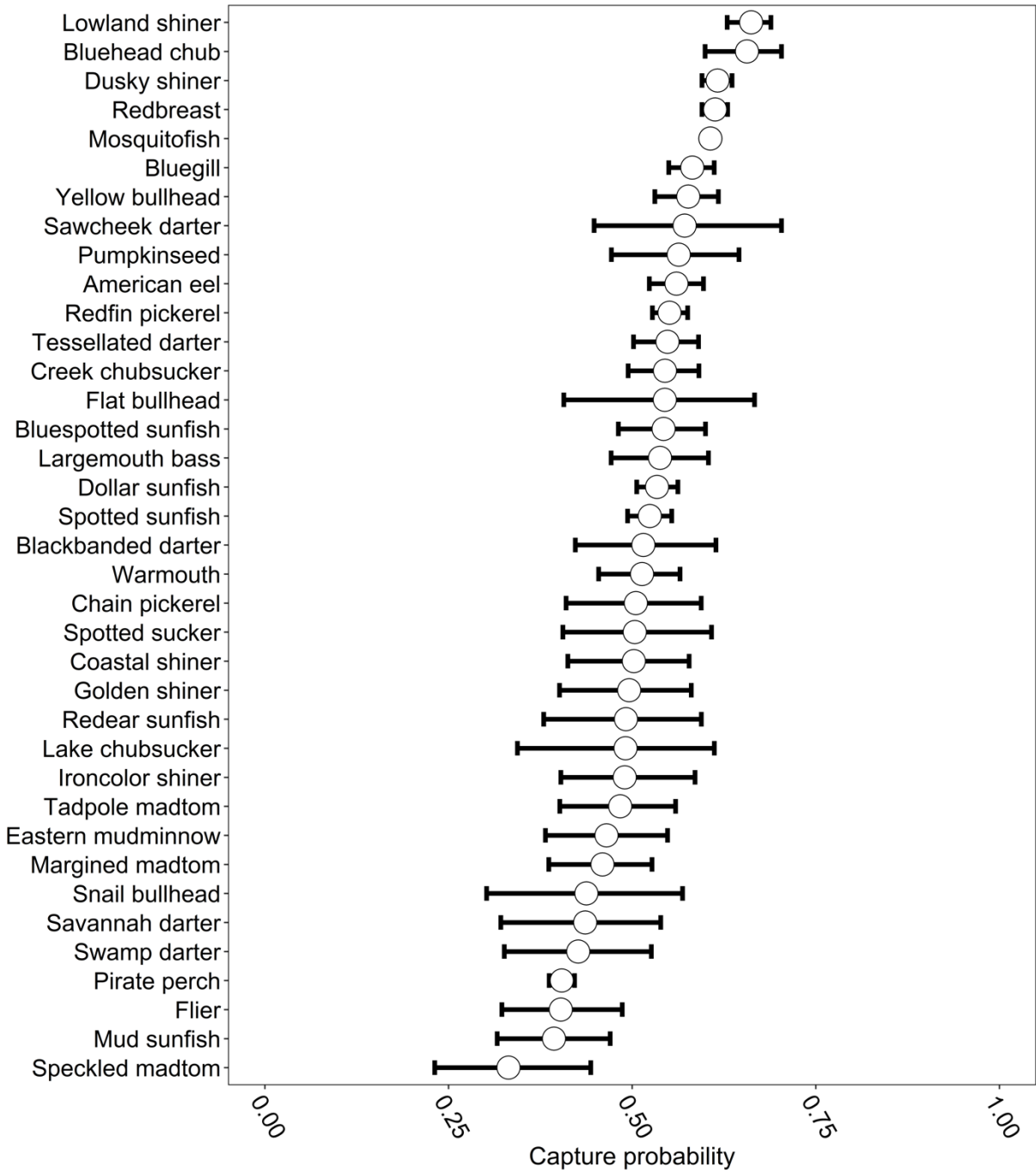
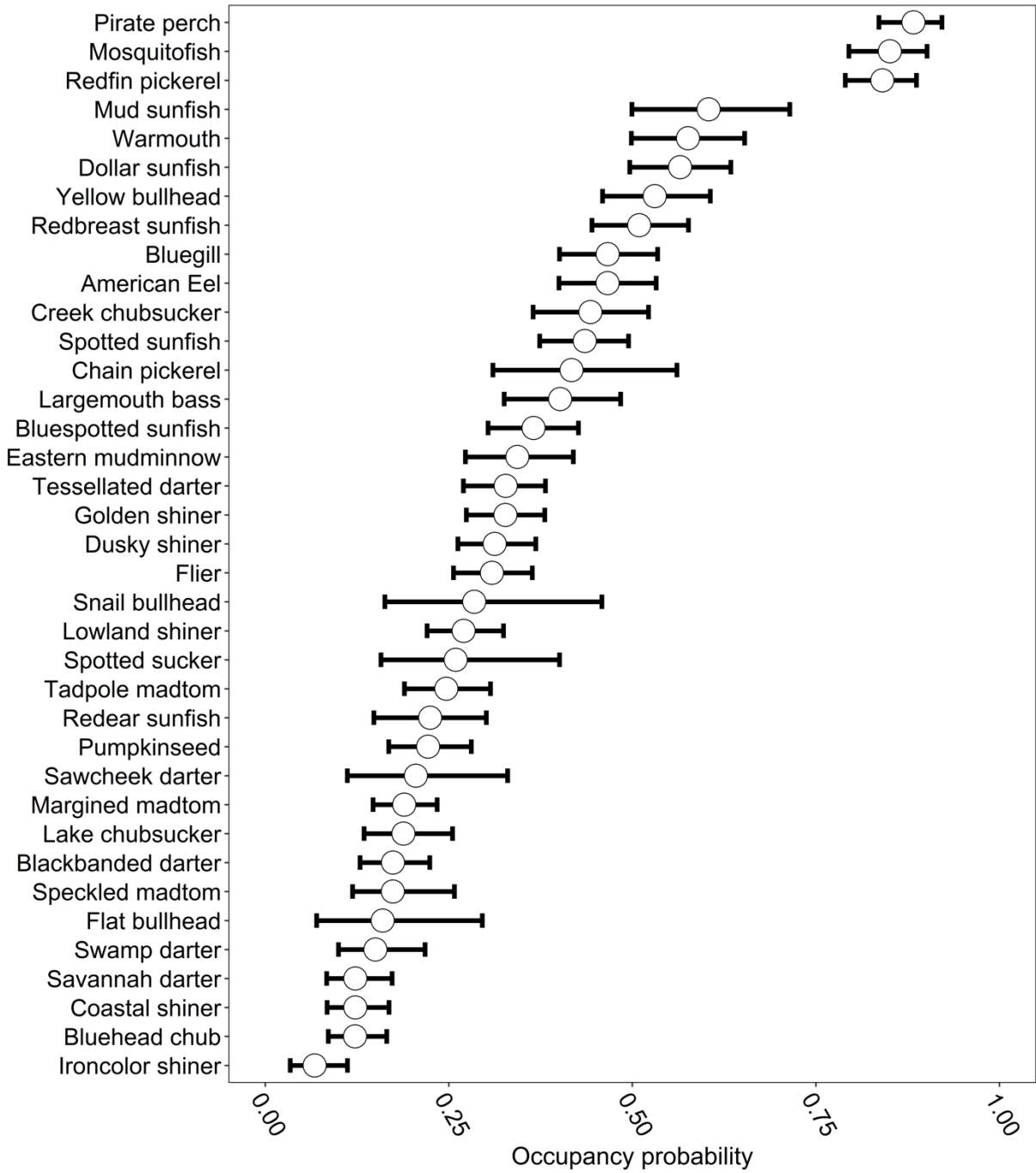


Figure 1. Map of eastern United States with distribution of the 203 South Carolina coastal plain sites included in the analysis.



(a.)



(b.)

Figure 2. Posterior mean and 95% credible intervals for capture (a.) and occupancy (b.) probabilities for all species.

Number of species with significant effect sizes

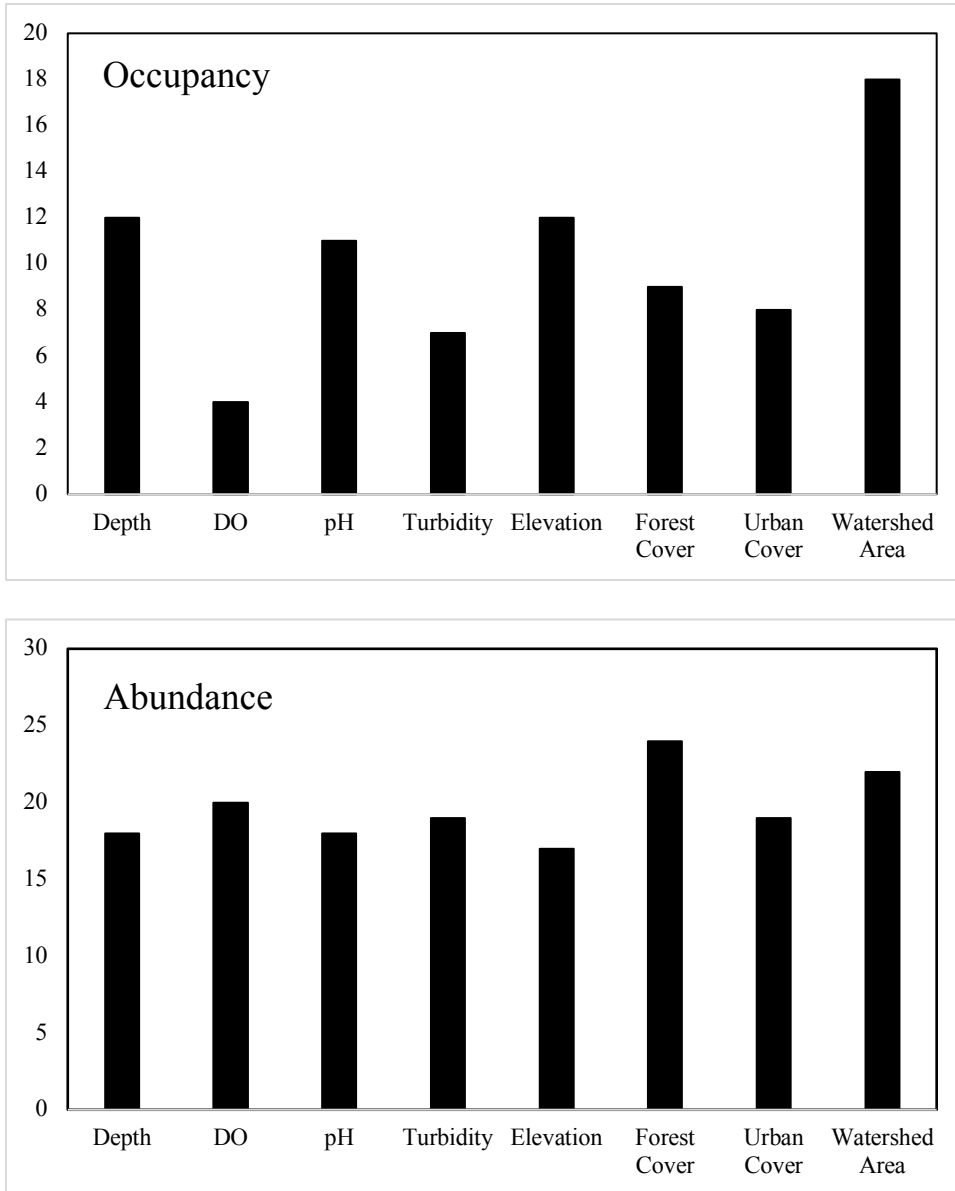


Figure 3. The number of species significant that had significant effect sizes for each covariate for occupancy (top panel) and abundance (bottom panel). Covariates were considered significant if the posterior mean and 95% credible interval did not overlap zero.

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CHAPTER 2: DRIVERS OF STREAM FISH DEMOGRAPHIC VARIATION AND SPATIAL ASYNCHRONY

Introduction

In a time of global change, identifying drivers of demographic variation remains a key aim for population ecologists (Muths et al.2017). Temporal fluctuations in populations and their environments are widespread in natural systems (Loreau and de Mazancourt 2008), and researchers have investigated the mechanisms involved in synchronizing population dynamics at different scales (Koenig 2001; Trenham 2003; Cayuela et al. 2016). Synchronous temporal variation in demographic parameters has been well documented among different populations of single species (Ranta et al. 1995; Robertson et al. 2015; Paradis et al. 2000).

Investigations of synchronous responses to temporal variation at the population level have generally focused on spatial synchrony, the degree to which geographically distinct populations fluctuate similarly in time (Grosbois et al. 2009). Spatial scale can influence the relative roles of regional factors like climate (e.g. Moran effect; Moran 1953) and dispersal, in shaping synchrony. Studies have identified that climate can drive synchrony at large spatial scales, and movement is more likely to act at intermediate or smaller scales (Ranta et al. 1995).

Theory predicts that two neighboring populations should exhibit synchronous dynamics, particularly if the species has high dispersal ability (Paradis et al. 1999; Kendall et al. 2000). Individuals of neighboring populations are more likely to experience the same climate drivers, an important characteristic that is associated with between-population synchrony. Recent studies have focused on the variation in demographic parameters using detailed information on individual life-histories (Lahoz-Monfort et al. 2011; Wu and Holan 2017; Swallow et al. 2016)

because analyses based on population counts cannot identify underlying mechanisms leading to synchrony (Tavecchia et al. 2008).

Much research has been done on spatial synchrony of multiple populations of individual species, but little attention has been paid to multi-species communities (Raimondo et al. 2004; but see Lahoz Monfort et al. 2011; Lahoz Monfort et. al 2013;). Species within a local community (i.e. interspecific synchrony) are exposed to similar biotic and abiotic environmental conditions (Begon, Harper, and Townsend 2006). Investigating synchrony among multiple species, in addition to spatial synchrony of different populations of the same species, can aid in uncovering the underlying causes of variation in demographic rates in a community, particularly since the underlying causes of synchrony at the community level are still poorly understood. Synchronization among different species within the same habitat can be influenced by shared stochastic effects such as weather and climate (Hansen et al. 2013); or shared predators (Raimondo et al. 2004; Vasseur and Fox 2007). While animals and plants are known to display synchronous population dynamics the relative degree of spatial and interspecific synchrony has been far less studied.

To investigate the relative degree of spatial and interspecific synchrony, I investigated two stream-fish communities by (1) examining variation of a demographic parameter (i.e., survival) to determine the degree of interspecific synchrony present within each stream community and spatial synchrony among populations of the same species, and (2) determine whether this variation can be explained by environmental variables. Given the close geographic proximity of my study sites I predicted that spatial synchrony would be greater than interspecific synchrony among species within the same sites.

Methods

Study sites

This study took place at Indian (34.741731°N, 82.849872°W), and Todd (34.749214°N, 82.813911°W) creeks in the Clemson Experimental Forest, SC, USA (Figure 1). Both are second-order streams, but Indian creek (mean wetted width = 2.6 m; range = 0.7 - 6.2 m) has a forested riparian zone whereas Todd (mean wetted width = 3.3 m; range = 1.4 - 7.0 m) has an open canopy located in a power-line corridor. Both streams are located within the same watershed and are approximately 3.35-km apart (Euclidean distance). Target species included four morphologically and ecologically diverse species, creek chub (*Semotilus atromaculatus*), striped jumprock (*Moxostoma rupicartes*), bluehead chub (*Nocomis leptocephalus*), and mottled sculpin (*Cottus bairdii*). Bluehead chub, creek chub, and striped jumprock were sympatric and found in both Todd and Indian creeks. These three species can be found in pool and run habitats of small to mid-sized streams, with bluehead chub and striped jumprock being more abundant in mid-sized streams and creek chub in smaller streams. Bluehead chub and creek chub are taxonomically and ecologically similar to one another in terms of diet, habitat, and thermal requirements (Rohde et al. 2009). Mottled sculpin was only present in Indian Creek and were found in riffle habitats.

Sampling methods

A bimonthly mark-recapture survey was conducted at two streams from November 2015 to March 2018. Streams were divided into 20-m sections with 26 sections in Todd Creek (520 m) and 37 sections in Indian (740 m). Indian Creek had a longer study area to increase sample size given its lower fish density. These 20-m sections were sampled by using pulsed-DC

backpack electrofishing with a Smith-Root LR-24 backpack unit (Smith-Root, Inc., Vancouver, Washington) and a Halltech HT-2000 backpack unit (Halltech Aquatic Research, Inc., Guelph, Ontario). A 2-pass depletion approach was used to increase recaptures. That is, each section was sampled twice, retaining fish captured in the first pass in a bucket when the section was sampled for the second time. On the first sampling occasion, all captured fish were identified to species and measured and weighed. Fish ≥ 50 -mm or greater in total length were then tagged with 8-mm passive integrated transponder (PIT) tags (Oregon RFID, Portland Oregon; or Biomark, Boise, Idaho). Detailed PIT tag incision protocols are described in Cary et al. (2016), and this previous study demonstrated that tagged fish had low mortality and tag loss from tagging procedures. On all subsequent occasions these 20-m sections were sampled in a similar fashion where all captured fish were scanned with a handheld PIT tag reader wand (Avid PowerTracker 7; Norco California), and previously tagged individuals (recaptures) were recorded, and non-tagged fish were implanted with a PIT tag before they were returned to the stream. Total length (mm) and weight (g) for all captured individuals were also recorded. Field sampling was completed as quickly as possible to conform to the assumption of instantaneous sampling on each occasion (Kéry and Schaub 2012). Sampling during each occasion was completed within 3 days (range = 1-10 days) in Indian Creek and within 4 days (range = 1-12 days) in Todd Creek. Intervals between sampling occasions lasted a mean of 60 days (range = 48 – 70; Table S2) in both Indian and Todd creeks. Temperature and water level loggers were deployed in each stream and measured hourly temperature and daily water level.

Statistical analysis

Data for statistical analysis was comprised of a capture history for each individual and occasion. Capture histories of all individuals (i), across sampling occasions (t) were created as a two-dimensional array, $y_{i,t}$, where 1s represent captures and 0s for non-captures for each

individual. Following Kéry and Schaub (2012), I fit multi-species CJS models representing an ecological process (Equations 1-2) and observation process (Equation 3).

$$z_{i,t+1}|z_{i,t} \sim \text{Bernoulli}(z_{i,t}\Phi_{i,t}), \quad \text{Equation 1}$$

$$\text{logit}[\Phi_{i,t}] = \mu_{g(i)} + \beta_{g(i)}x_t \quad \text{Equation 2}$$

$$y_{i,t}|z_{i,t} \sim \text{Bernoulli}(z_{i,t}p_t), \quad \text{Equation 3}$$

Where $\mu_{g(i)}$ represents the overall mean bimonthly survival rate for species g to which individual i belongs to, $\beta_{g(i)}$ represents the effect size of covariate x for each species $g(i)$, with a normal distribution with a mean of 0 and variance 1. Φ refers to the bimonthly survival rate on a given occasion t . Survival was modeled conditional on the latent state of each individual (i) on the immediately previous occasion (Equation 1). This ensured that a dead individual ($z_{i,t} = 0$) remained dead and a live individual ($z_{i,t} = 1$) would survive to the next occasion with a probability of Φ_t . Survival and detection were modeled to vary by occasion.

Five bi-monthly environmental covariates were fit in Equation 2 to determine which covariates were most important to variation in bi-monthly survival. These covariates included the maximum and mean stream temperature and water level for each occasion, as well as water level variation (coefficient of variation). Models were ranked in terms of their Deviance Information Criterion (DIC), a Bayesian analogue to AIC (Spiegelhalter et al. 2002). It was calculated as $\text{DIC} = D(\theta) + 2p_D$ where $D(\theta)$, the deviance when using the mean of the posterior distribution of the parameters is penalized by twice the effective number of parameters p_D . DIC was calculated in the jagsUI package and the lowest DIC value represented the most supported model of those that were considered.

Equation 2 was modified to include random effects (Eq 4; Appendix 2 Example JAGS Code) to characterize the amount of variation around the mean, where ε_{1t} was a time-specific random effect common to all species in the analysis and $\varepsilon_{2g(i),t}$ varied by time but separately for each species. Both random effects were sampled from a normal distribution with a mean of 0 and variances, σ_{common}^2 and $\sigma_{species}^2$ respectively.

$$\text{logit}[\Phi_{i,t}] = \mu_{g(i)} + \varepsilon_{1t} + \varepsilon_{2g(i),t} \quad \text{Eq 4}$$

Once covariates were determined by model selection, I ran a model with both the most supported covariate and temporal random effects in order to understand how much of the variance environmental covariates accounted for. Separate models were fit for the Indian and Todd Creek datasets.

I calculated an intra-class correlation coefficient (ICC), described in Lahoz-Monfort et al. (2011), to represent the synchrony of a given species with the rest of the species in the local community:

$$ICC = \frac{\sigma_{common}^2}{\sigma_{common}^2 + \sigma_{species}^2}$$

The ICC represented the proportion of between bi-monthly variance for the species of interest (either total or unexplained by covariates, if present) that was accounted for by the common random term (σ_{common}^2). When σ_{common}^2 is large relative compared to $\sigma_{species}^2$ the ICC value becomes larger and the species of interest shows more synchrony with the rest of the community. I calculated ICC values for models with random effects only, and models including both random effects and covariates. To further evaluate synchrony, I calculated Pearson's correlation coefficients of bi-monthly survival estimates for each pairwise species comparison within and between streams.

CJS models were fit with the jagsUI package (Kellner 2014) from program R (R Core Development Team 2008). Posterior distributions of model parameters were estimated by taking every 10th sample from 10,000 iterations after discarding 10,000 burn-in iterations for three Markov Monte Carlo chains. Model convergence was checked by visually examining plots of the Markov chains for good mixture and ensuring that the potential scale reduction factor value was less than 1.1 for all model parameters to assume model convergence (Gelman and Hill 2007).

Results

Over the duration of the study, I tagged 2,646 unique individuals in Indian Creek and 4,838 in Todd Creek (Table S3 and S4). Mottled sculpin had the greatest number of captured individuals in Indian Creek (39% of total tagged) whereas bluehead chub made up the majority of tagged individuals in Todd creek (81% of total tagged). More creek chub (765 vs. 226) were tagged in Indian Creek and more striped jumprock (673 vs. 283) were tagged in Todd creek.

Bi-monthly recapture probabilities ranged from 0.13 for bluehead chub to 0.59 for striped jumprock (Figure S2). Mean bi-monthly survival was similar across all species and ranged from 0.74 (creek chub; Todd creek) to 0.77 (striped jumprock; Todd creek). Survival differed greatly among sampling intervals (range = 0.04 – 0.99; creek chub and bluehead chub respectively), where low survival estimates occurred in late summer (July-September) (Figure 2). Survival was lower in Todd Creek where I observed a survival range of 0.04-0.47 (creek chub and striped jumprock) during summer months compared to Indian Creek.

Model selection results showed that different environmental covariates affected survival in each stream (Table 1). In Indian Creek, there was greater support for the maximum water level observed between bimonthly occasions. Survival increased with maximum water level for

Bluehead chub (effect size = 0.31), creek chub (effect size = 0.03), and striped jumrock (effect size = 0.11), and decreased for mottled sculpin (effect size = -0.25). There was more support for the maximum temperature observed between bimonthly occasions in Todd creek. Survival decreased with maximum temperature for all three species present in Todd Creek (effect size bluehead chub = -0.76; creek chub = -0.82; striped jumrock = -0.27). However, these effect sizes were not statistically significant since their 95% credible interval overlapped 0.

Intra-class correlation coefficients (ICC) ranged from 0.59 to 0.73 in Todd Creek and 0.51 – 0.71 in Indian, suggesting moderate to high synchrony across species within a stream (Table 2). Pearson's correlation coefficients for all pair-wise comparisons of species-specific survival probabilities were significant in both Todd and Indian creeks; however, species within Indian creek had lower correlation values relative to those within Todd Creek. Pearson's correlations for species pair-wise comparisons in Todd Creek resulted were all significant with a range of 0.77-0.97 correlation (Table 3). All six comparisons in Indian creek showed synchronous dynamics with significant correlation coefficients, however the coefficients were smaller relative to those in Todd creek (range = 0.60 to 0.86). When comparing species across streams, all three possible species pairs had non-significant Pearson's correlations (range = 0.16 to 0.55) and illustrate spatial asynchrony in bimonthly survival across the two streams.

To investigate whether there were local habitat differences that could potentially result in survival differences between the two creeks, I compared bi-monthly water temperature and water-level measurements for both sites. Average daily temperature across the study was similar for both sites, (Indian Creek, mean = 15.2 °C, range = 1.4 – 23.6; Todd Creek, mean = 15.8 °C, range = 0.7 – 25) (Figure 3) but I observed that differences in stream temperature were greatest during summer months in Todd Creek compared to Indian Creek by an average of 2.1 °C.

Stream water level also varied among streams; average water level was 0.17 m (range = 0.14 – 0.28 m) in Indian Creek and 0.26 (range = 0.20 – 0.54-m) in Todd Creek (Figure 4). Average difference in water level between the two streams was 0.08-m with greater differences observed during winter months. Todd Creek had a greater magnitude in peak flow after winter precipitation events relative to fall and summer.

Discussion

I observed that synchrony among species within a community was greater than spatial synchrony between populations of the same species across the two sites. Ecologically similar species were more similar in their responses (e.g. bluehead chub and creek chub in both streams). Other studies have linked interspecific synchrony to the biological characteristics of species where functionally similar (e.g. life history strategies or morphology) species have been observed to exhibit similar population dynamics (Tedesco and Hugueny 2006; Rocha et al. 2011). Notably, the degree of synchrony varied spatially between the two streams. The observed spatial asynchrony in survival may be attributed to habitat differences among the two streams. The study and modeling of multi-species synchrony can have numerous applications in ecology and conservation (Lahoz-Monfort et al. 2013). This study highlights how studying intra-annual variation in survival for multi-species communities can help identify key environmental drivers.

Despite close geographical proximity, the two study streams differed in habitat size and characteristics. These differences appeared to influence the observed dynamics in each stream where climate drivers such as precipitation and temperature interacted with local-scale conditions to generate spatial asynchrony. Recent advances in macrosystems ecology have

identified how multiscale systems, such as riverine networks, can drive the community patterns and processes (Heffernan et al. 2014; McCluney et al. 2014). River systems have a large degree of connectivity between the surrounding landscape and habitats within, where local (e.g. microhabitat) and regional (e.g. climate) drivers can interact to influence dynamics. The implication of this is that population and community responses to environmental change may also be structured at fine spatial scales.

While regional climate conditions can synchronize population dynamics, local environmental conditions can mediate the effects of regional drivers, such that local populations vary asynchronously and are more resilient to regional climate variation. Context dependency in the relationship between the abiotic environment and demographic variation has also been observed in other taxa such as amphibians (Cayuela et al. 2016). My results contrast with what is typically expected of spatial relationships of synchrony, where geographically close populations should be more likely to exhibit synchronous dynamics.

While spatial asynchrony has been reported at broad spatial scales (Tedesco et al 2006; Schindler et al. 2010), the present study is one of the few that demonstrates the presence of asynchrony in demography at finer spatial scales. Heterogenous responses of animals to climate can make conservation planning challenging (Muths et al 2017), given that it is generally expected that demographic responses are often considered to be controlled by a common driver. Although mismatches in the scaling of population synchrony and spatial environmental variation have been observed (Cayuela et al. 2016), the driving factors that are responsible for this variation still needs further research. Future research could include surveys across a number of populations to account for context dependency in demographic variation.

Recent work has also highlighted the importance of inter-population diversity to species persistence, where this diversity can lead to less variation in species' meta-population dynamics over time (Schindler et al. 2010). A likely consequence of global change is an increase in the occurrence of extreme climatic events (Easterling et al. 2000). Spatial asynchrony in survival among populations of the same species may contribute to the resilience against future change (Laliberté et al. 2010). Determining when low survival occurs within the annual cycle is important for an understanding of population dynamics and provide important knowledge for the conservation of species. There are advantages of conducting mark-recapture studies at fine temporal scales (e.g. bimonthly or seasonally). The present study revealed that survival was much lower during summer months compared to the rest of the year, particularly for Todd Creek. This could be due to higher temperatures during these months (Danehy et al. 2005) in combination with spawning timing. Annual sampling cannot reveal seasonal patterns in survival, and this bottleneck period would have otherwise been missed.

These results show that the abiotic environment influences demographic variation in lotic fishes and this study also emphasizes that the effect of the abiotic environment may be context dependent. More research is needed on the underlying mechanisms for the patterns observed in survival fluctuations for communities and the relative roles of the abiotic environment and biotic interactions (Kraft et al. 2015). Improved understanding of how the abiotic factors synchronize or desynchronize demographical parameters can be of great interest and this study draws attention to the need of paying attention to local habitat variation.

Tables and Figures

Table 1. Deviance information criterion for each environmental covariate included in the Cormack-Jolly Seber models for (a) Indian and (b) Todd creek.

(a) Indian Creek			(b) Todd Creek		
Model parameter	DIC	Δ DIC	Model parameter	DIC	Δ DIC
Maximum water level	15360	0	Maximum temperature	25484	0
Water level variation	15389	29	Mean temperature	26111	627
Mean water level	15407	47	Mean water level	27659	2175
Intercept	15575	215	Water level variation	28450	2966
Maximum temperature	15657	297	Maximum flow	28733	3249
Mean temperature	15853	493	Intercept	32216	6732

Table 2. Estimated residual and total variance of the common (ε_1) and species-specific (ε_2) random effect terms and inter-class correlation coefficients (ICC) For the survival (Φ) model with only random effects (Model $\Phi(\varepsilon_1 + \varepsilon_2)$), and the model with both the most supported covariate (*cov*; water-level in Indian and water temperature in Todd) and random effects (Model $\Phi(\text{cov} + \varepsilon_1 + \varepsilon_2)$).

	Interspecific variance component (σ_{common}^2)	Species-specific variance component ($\sigma_{species}^2$)	Intra-class correlation (ICC)
Indian Creek			
Model $\Phi(\varepsilon_1 + \varepsilon_2)$	3.10	1.22 (BHC)	0.71
		1.24 (CRC)	0.71
		2.92 (STJ)	0.51
		1.28 (MTS)	0.70
Model $\Phi(\text{cov} + \varepsilon_1 + \varepsilon_2)$	3.33	1.20 (BHC)	0.73
		1.29 (CRC)	0.72
		2.31 (STJ)	0.59
		1.55 (MTS)	0.68
Todd Creek			
Model $\Phi(\varepsilon_1 + \varepsilon_2)$	4.68	2.64 (BHC)	0.64
		3.63 (CRC)	0.56
		2.03 (STJ)	0.69
Model $\Phi(\text{cov} + \varepsilon_1 + \varepsilon_2)$	4.27	1.35 (BHC)	0.75
		3.45 (CRC)	0.55
		3.35 (STJ)	0.56

Table 3. Pearson’s correlations between bi-monthly survival estimates for bluehead chub (BHC), creek chub (CRC), striped jumprock (STJ), and mottled sculpin (MTS) for pairwise comparisons among species in (a) Indian Creek, (b) Todd Creek, and (c) between streams for species common to both sites.

Species pair	Correlation	<i>p</i> -value	Species pair	Correlation	<i>p</i> -value
(a) Indian creek					
BHC vs. CRC	0.76	< 0.005	STJ vs. CRC	0.83	< 0.005
BHC vs. STJ	0.61	0.06	STJ vs. MTS	0.60	0.02
BHC vs. MTS	0.86	0.03	MTS vs. CRC	0.78	0.07
(b) Todd Creek			(c) among sites		
BHC vs. CRC	0.97	< 0.005	BHC vs. BHC	0.55	0.20
BHC vs. STJ	0.83	< 0.005	CRC vs. CRC	0.32	0.32
STJ vs. CRC	0.77	< 0.005	STJ vs. STJ	0.16	0.66

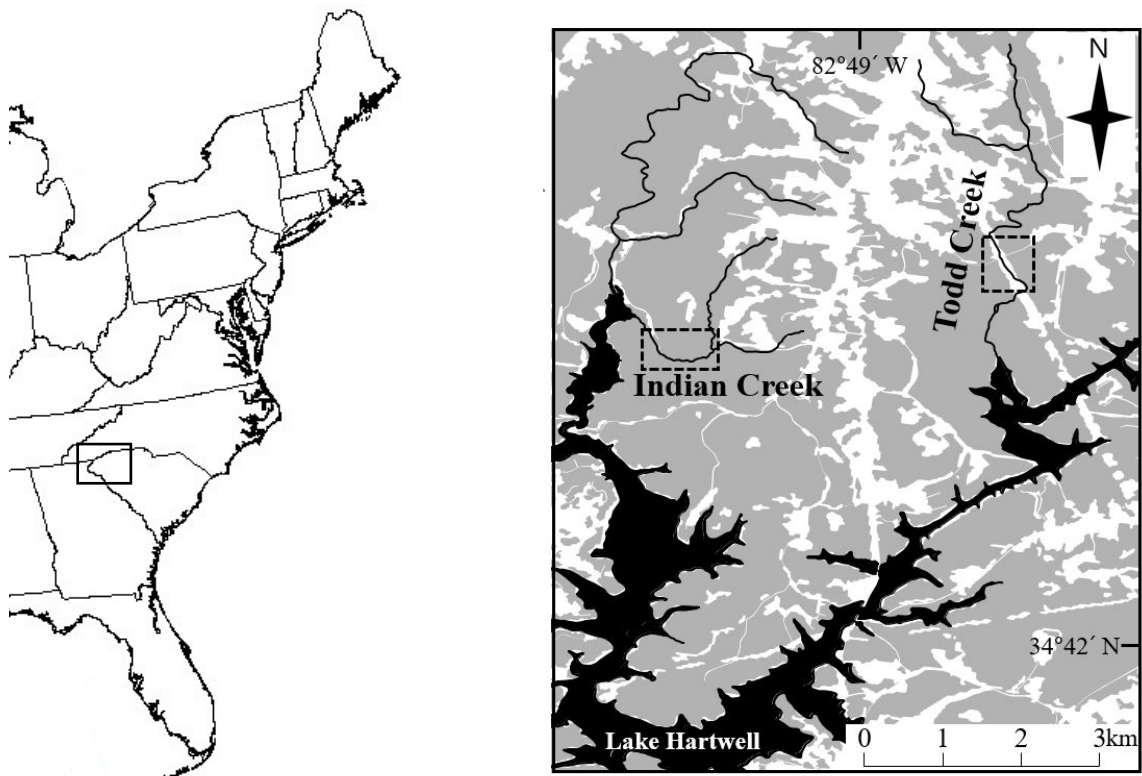
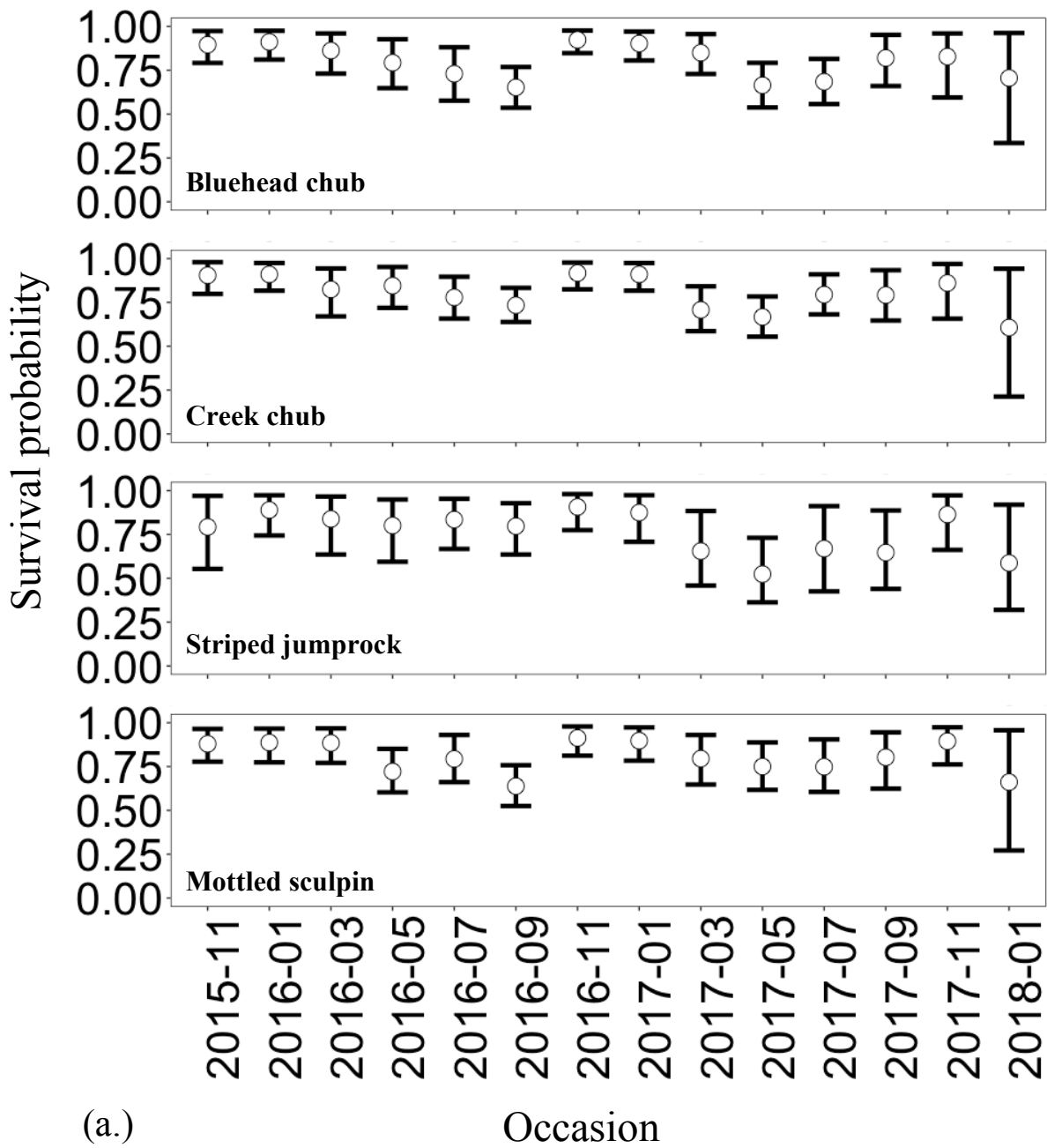


Figure 1. Study area map detailing the locations of Indian and Todd Creeks in Sixmile, South Carolina, USA. Shaded grey areas represent forested land.



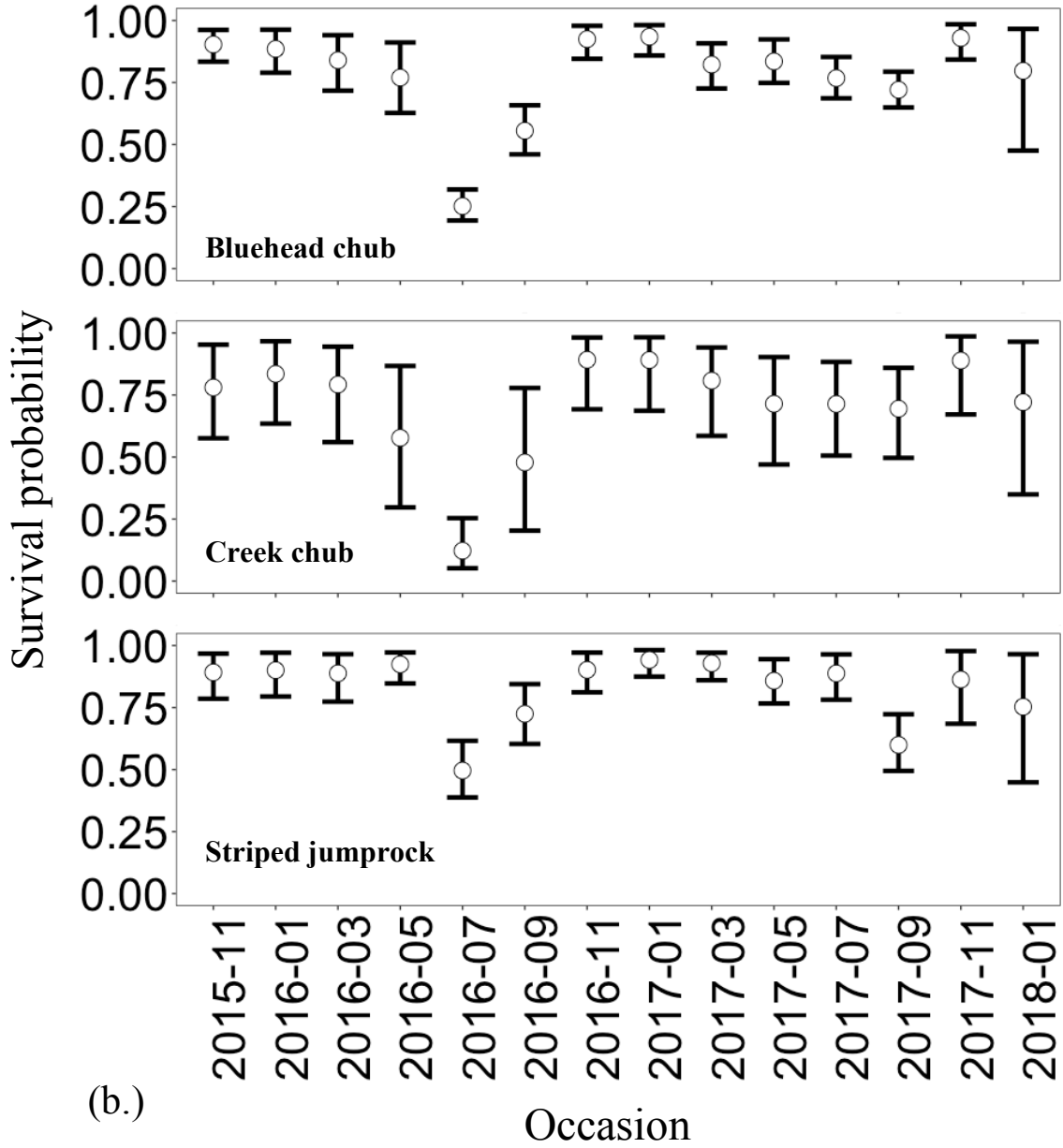


Figure 2. Estimated apparent bi-monthly survival probability for the species present in (a.) Indian and (b.) Todd creeks from model $\Phi(cov + \varepsilon_1 + \varepsilon_2)$. Where *cov* represents maximum water level in Indian Creek and maximum temperature in Todd Creek. “2015-11” represents the first bi-monthly occasion from November 2015 to January 2016. Point estimates are mean of the MCMC posterior distribution samples for survival of each species. Vertical bars show 95% credible intervals.

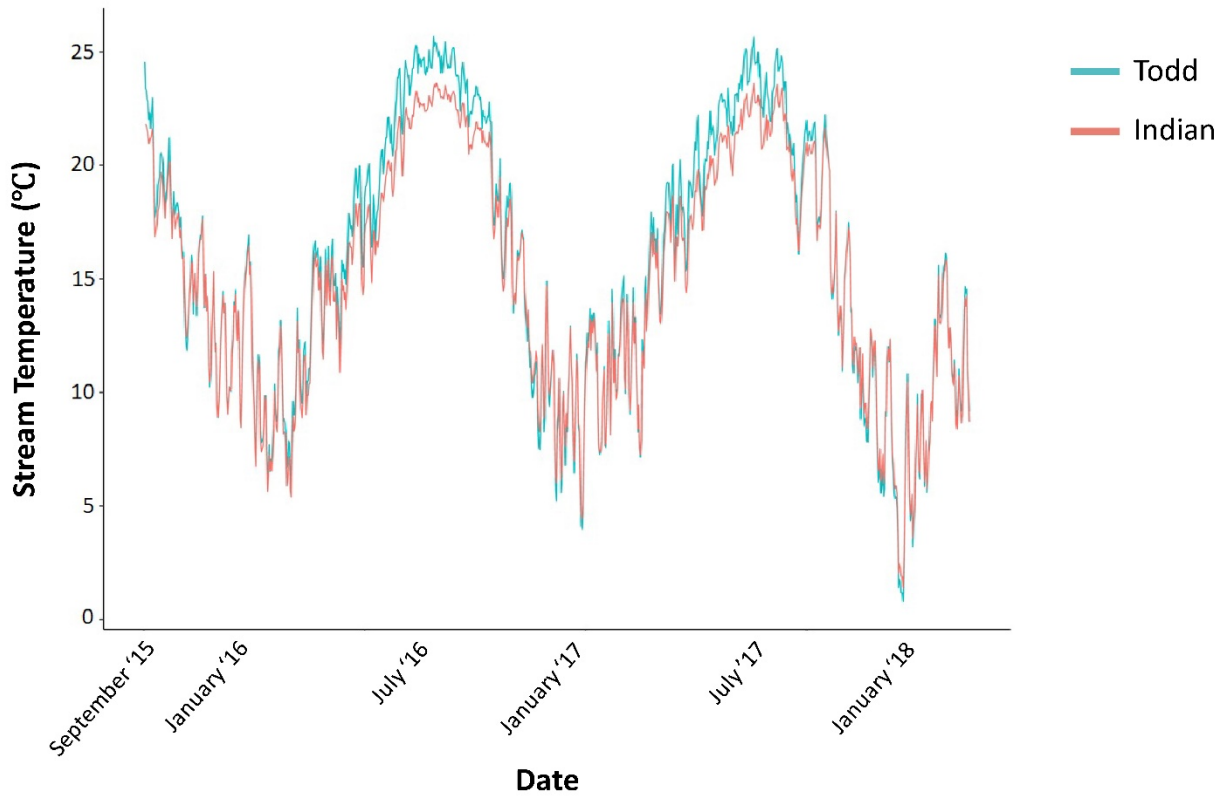


Figure 3. Mean daily temperature for Todd and Indian Creeks from September 2015 to March 2018.

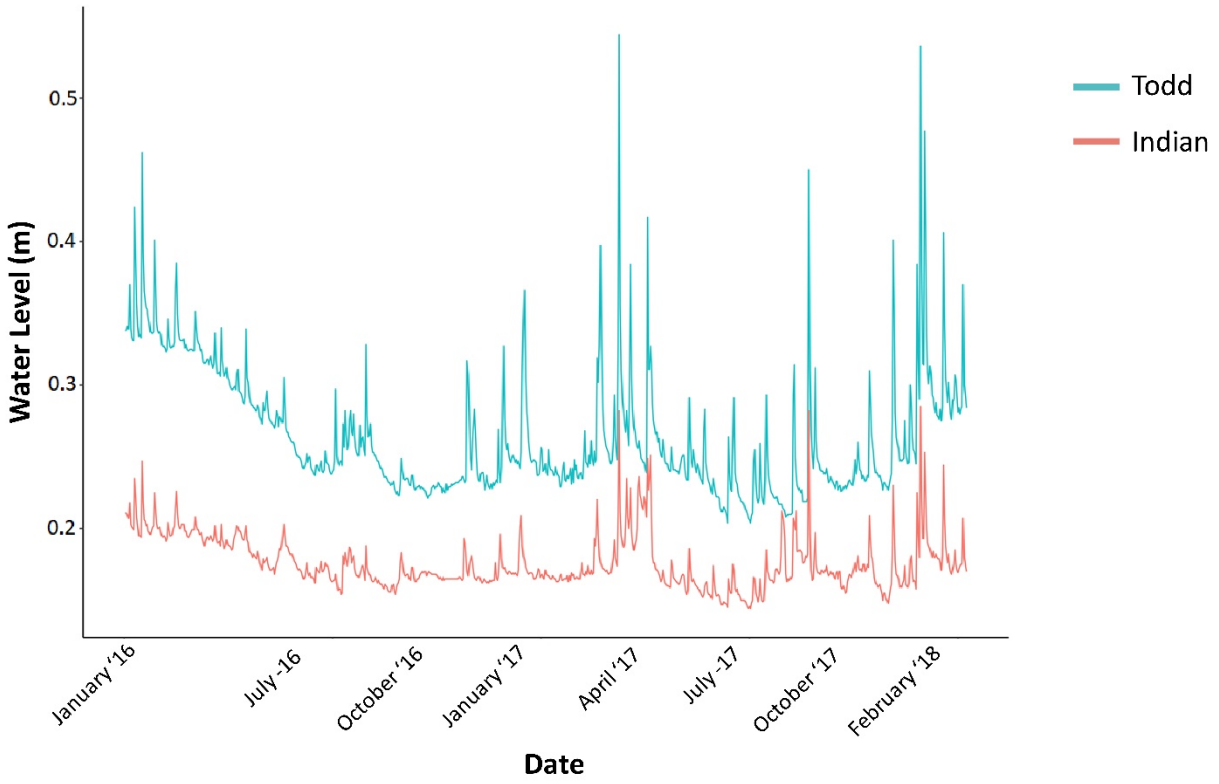


Figure 4. Daily water-level data for Todd and Indian creeks from January 2016 to March 2018.

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CHAPTER 3: INTRA- AND INTERSPECIFIC INTERACTIONS IN LOTIC FISH COMMUNITIES

Introduction

A major goal in community ecology is to understand the processes that shape patterns in the composition and diversity of species assemblages (Chesson 2000). In particular, community ecologists have long sought to understand how these patterns and processes maintain species-rich diversity and coexistence among species (HilleRisLambers et al. 2012). However, there are a large number of hypothesized processes that could underlie patterns of interest.

Community assembly processes have been described as species passing through multi-scale ecological filters (Poff 1997; Jackson et al. 2001). The theory begins with a regional pool of species upon which different filters (e.g. abiotic and biotic) act in sequence to determine local species membership (Violle et al. 2012). Some filters may act at broad spatial scales such as climate, while others operate at fine spatial scales such as microhabitat variation. Biotic interactions are also a potential filter influencing local community composition, and are thought to play a larger role at lower hierarchical levels of the filtering process since this is the scale at which species encounters occurs (Poff 1997). A disproportionate amount of attention has been paid to abiotic environmental filters rather than biotic factors in structuring communities (Kraft et al. 2015). While environmental filters are important, many studies fail to separate the influence of the abiotic environment from biotic interactions (Violle et al. 2012). For example, many community assembly studies represent environmental filtering and biotic interactions as sequential steps in the assembly process. However, both factors can influence one another to

drive community patterns, as the strength and direction of biotic interactions can be strongly influenced by the abiotic environment (Clark et al. 2010).

When population size increases and resources become limited, density dependence can influence different demographic rates such as movement, recruitment, and/or survival, all processes influencing population growth. These ecological interactions can occur within and among species in a communities and include interactions such as competition, predation, and mutualism, and determine community structure in conjunction with the abiotic environment (Polis and Strong 1996). These biotic interactions can also be body size dependent. Individuals undergo changes in body size and ontogeny throughout life with parallel changes in ecological performance. Body size is an important trait of an individual and can potentially influence the type and strength of ecological interactions, as well as influence life history processes such as foraging capacity, growth, and reproduction (De Roos et al. 2003). For instance, in size-structured predator-prey systems, capture success depends on the sizes of both predator and prey (Claessen et al. 2002; Taniguchi et al. 2002) where larger individuals are more likely to prey upon smaller individuals (Paradis et al. 1996). Larger and more experienced individuals may also have better competitive ability to outcompete smaller individuals for habitat space and foraging (Berec et al. 2006).

Recent advances in coexistence and competitive theory predict that the effects of intraspecific interactions should be greater than interspecific interactions for co-existence to occur (Chesson 2000; Clark et al. 2010). Competitive interactions should be expected to be primarily within species because over evolutionary time scales, competitive exclusion and niche diversification have led to resource partitioning among species (Forrester et al. 2006; Kraft et al. 2015). However, when different species have overlapping ecological niches, an increase in the

density of the individuals of one species can also intensify interspecific competition for these limited resources (Nakano et al. 1998; Baxter et al. 2004). There are few empirical investigations of the relative roles of intraspecific and interspecific competition in communities, and these studies are typically limited to comparisons for two species (Forrester et al. 2006; Hasegawa et al. 2014; Montorio et al. 2018).

The southeastern United States retains some of the highest freshwater fish diversity in North America and provides a suitable study system to evaluate biotic interactions given that few studies investigate pair-wise competition for multiple species. Researchers have identified the potential role of intra- and interspecific interactions in affecting behavior of stream fish (Petty et al. 2007; Hazelton and Grossman 2009; Grossman 2014). In a previous study (Pregler Chapter 2), I observed temporal variation in survival that differed among sites for two stream-fish communities from a mark-recapture study. While some of this variation was accounted for by environmental covariates, I was also interested in the role of biotic interactions in structuring these communities. My objectives were to investigate competition among species in two stream fish communities by estimating the effects of intra- and interspecific density on population growth rates. Because biotic interactions can also be size-dependent, I also investigated the effects of body size on competition in these two communities.

Methods

Study sites

The capture-mark-recapture study took place at Indian (34.741731°N, 82.849872°W), and Todd (34.749214°N, 82.813911°W) creeks in the Clemson Experimental Forest. Both are second order streams, and Indian Creek (mean wetted width = 2.6-m; range = 0.7 - 6.2-m) has a

well forested riparian zone whereas Todd Creek (mean wetted width = 3.33-m; range = 1.4 - 7.0-m) has an open canopy located in a power-line corridor. Both streams are located within the same watershed and are approximately 3.35-km apart (Euclidean distance). Target species included four species, creek chub (*Semotilus atromaculatus*), striped jumprock (*Moxostoma rupicartes*), bluehead chub (*Nocomis leptocephalus*), and mottled sculpin (*Cottus bairdii*). Bluehead chub, creek chub, and striped jumprock were sympatric and found in both Todd and Indian creeks. These three species can be found in pool and run habitats of small to mid-sized streams, with bluehead chub and striped jumprock being more abundant in mid-sized streams and creek chub in smaller streams. Bluehead chub and creek chub are taxonomically and ecologically similar to one another in terms of diet, habitat, and thermal requirements (Rohde et al. 2009). Mottled sculpin was only present in Indian Creek and were found in riffle habitats. I expected that negative intraspecific competition would be greater than interspecific competition, but perhaps with the exception of bluehead chub and creek chub which are the most ecologically similar.

Sampling methods.

Bimonthly mark-recapture was conducted at two streams from November 2015 to March 2018. Streams were divided into 20-m sections with 26 sections in Todd Creek (520 m) and 37 sections in Indian Creek (740 m). Indian Creek had a longer study area to increase sample size given its lower fish density. These 20-m sections were sampled by using pulsed-DC backpack electrofishing with a Smith-Root LR-24 backpack unit (Smith-Root, Inc., Vancouver, Washington), and a Halltech HT-2000 backpack unit (Halltech Aquatic Research, Inc., Guelph, Ontario). A two-pass depletion approach was used to increase recaptures where each section

was sampled twice by retaining fish captured in the first pass in a bucket when the section was sampled for the second time. On the first occasion, all captured fish were identified to species and measured and weighed. Fish 50-mm or greater in total length were then tagged with 8-mm passive integrated transponder (PIT) tags (Oregon RFID, Portland Oregon; or Biomark, Boise, Idaho). Detailed PIT tag incision protocols are described in Cary et al. 2016, and this previous study demonstrated that tagged fish had low mortality and tag loss from tagging procedures. On all subsequent occasions these 20-m sections were sampled again in a similar fashion where all captured fish were scanned with a PIT tag reader (Biomark) and previously tagged individuals (recaptures) were recorded. The remaining non-tagged fish were implanted with a PIT tag before they were returned to the stream.

Analysis

Abundance estimation

Mark-recapture data were analyzed using Jolly-Seber (JS) models following Kéry and Schaub (2012). Capture histories of all individuals (i), across sampling occasions (t) were created as a two-dimensional array, $y_{i,t}$, where 1s represent captures and 0s for non-captures for each individual. Given that the true abundance, N_t , is not known a priori, the JS model uses data augmentation to introduce a large number of potential unobserved individuals. The model can then infer how many more unique individuals should have been present in the population (i.e. abundance) by accounting for the degree of imperfect detection. The augmented dataset has dimensions M by t where M is greater than the number of observed individuals. I added sufficiently large numbers of rows of 0s until the posterior distribution of N was no longer truncated by the number of rows in the augmented dataset (Kéry and Schaub 2012). Data were

augmented by 300 rows of all 0 entries for all species except for bluehead chub in Todd Creek, which was augmented by 3000. Individuals in the mark-recapture study can be in one of three possible states: “not yet entered”, “alive”, and “dead”. The state transitions are controlled by two ecological processes, entry and survival. The entry probability, γ_t , is the probability that an individual in M first enters the population at occasion t . Separate Jolly-Seber (JS) model (Appendix 2 Example JAGS Code) were fit for each species in Indian and Todd Creeks. JS models represented an ecological process (Equations 1-3) where the state of individual i on the first occasion (f) (Equation 1) is:

$$z_{i,f} \sim \text{Bernoulli}(\gamma_f), \quad \text{Equation 1}$$

$$z_{i,t+1} | z_{i,t} = 1 \sim \text{Bernoulli}(\Phi_{i,t}) \quad \text{Equation 2}$$

Subsequent states are determined either by survival (Equation 2), for an individual already entered ($z_{i,t}=1$), or by entry for one that has not ($z_{i,t}=0$). Survival probability between occasion t and $t+1$ for individual i is denoted as $\Phi_{i,t}$, and comes from a normal prior distribution with mean of 0 and variance of 1. The observation process (Equation 3) is conditional on the state process and is:

$$y_{i,t} | z_{i,t} \sim \text{Bernoulli}(z_{i,t} p_{i,t}), \quad \text{Equation 3}$$

where if individual i is alive at occasion t , it may be recaptured with probability $p_{i,t}$. Several quantities of interest can be derived from the latent state variable z such as population size at time t which I estimated using $N_t = \sum_{i=1}^M z_{i,t}$. While JS models also estimate survival and capture probabilities, I only used the abundance estimates for the present study. Using the derived abundance estimates, I also calculated bi-monthly intrinsic rates of increase (λ_1) for each species by dividing N_{t+1} by N_t .

To evaluate size-dependent competition, I extended the Jolly-Seber model to a multi-state Jolly-Seber model (following Kéry and Schaub 2012) for each species. All species were divided into two size classes denoting small and large individuals. Body size cutoffs were determined by visualizing breaks in length-frequency histograms of captured individuals (Figures S3 and S4). The cutoff for mottled sculpin was 65-mm, 80-mm for bluehead chub and creek chub, and 100-mm for striped jumprock. The multi-state, mark-recapture data was represented by a two dimensional array for rows of individuals across occasions where data represented three possible states: where “0” denoted a noncapture, a “1” was a captured individual with small body size, or a “2” a large body size individual. The state-space model consisted of two model parts, the state equations were:

$$z_{i,f} = 1 \quad \text{Equation 4}$$

$$z_{i,t+1} | z_{i,t} \sim \text{Categorical}(\Omega_{z_{i,t},1\dots S,i,t}) \quad \text{Equation 5}$$

Equation 4 describes the state for each individual (i) at the first encounter (f). The multi-state model was conditional on first capture and given that there was no way to estimate γ_1 at the first occasion, this was overcome by adding a dummy occasion where all individuals in the augmented dataset were set in the state “not yet entered” at this first dummy occasion with a probability of 1 (Kéry and Schaub 2012). The state process (Equation 5) described how an individual transitioned from one state to another. Where Ω represented a state transition matrix to denote the probability that an individual transitions from its state at time t to a given state at time $t + 1$. Its state at time t is represented by a categorical variable, $z_{i,t}$, which is a matrix that contains the true state of individual i , at occasion t . States are numbered from 1 to S . The state transition matrix for Ω is described in Table 1, where ϕ_1 and ϕ_2 is the probability that an individual survives from survey t to survey $t + 1$ for size class 1 and 2 respectively, α_{12} is the

probability that an individual transitions from size 1 to size 2 between t and $t + 1$. It was not possible for the individuals in this study to shrink in body size from size 2 to size 1. The observation equation (Equation 6) linked the true state with the observed state:

$$y_{i,t} | z_{i,t} \sim \text{Categorical}(\Theta_{z_{i,t},1\dots S,i,t}) \quad \text{Equation 6}$$

where $y_{i,t}$ was the observed multi-state mark recapture data. The observation matrix, Θ , represented the probability that an individual i , is observed in a given state at time t . The probability of any observation is defined by the observation matrix for Θ in Table 2, where p_1 is the probability that an individual is observed at size 1, and p_2 is the probability that an individual is observed at size 2. Abundance estimates were derived similarly as in the Jolly-Seber model described above, where population size at time t was derived from the latent state variable z for each size category.

Bi-monthly abundance was estimated using Jolly-Seber (JS) models with the jagsUI package (Kellner 2014) from program R (R Core Development Team 2008). Posterior distributions of model parameters were estimated by taking every 10th sample from 10,000 iterations of three chains after discarding 1,000 burn-in iterations. Model convergence was checked by visually examining plots of the Markov chains for good mixture and by comparing the estimated between and within chain variances for each parameter, which is referred to as the potential scale reduction factor. I ensured that the potential scale reduction factor value was less than 1.1 for all model parameters to assume model convergence (Gelman and Hill 2007).

Estimating intraspecific and interspecific competition

I followed Adler et al. (2007) to estimate competition coefficients for the species in each stream community. The following model (Equation 7) describes the dynamics for two species:

$$N_{1,t+1} = \frac{\lambda_1 N_{1,t}}{1 + \alpha_{11} N_{1,t} + \alpha_{12} N_{2,t}} \quad \text{Equation 7}$$

Where $N_{1,t+1}$ is the abundance of individuals of species 1 at bimonthly occasion $t+1$. It equals the abundance on occasion t multiplied by the species-specific intrinsic rate of increase (λ_1) divided by total competition, represented by terms in the denominator. Since the maximum per capita growth rate is unknown for these species, I used the maximum observed λ_1 calculated from the JS model. Competition is the sum of intraspecific and interspecific effects, α_{11} and α_{12} respectively; α_{11} represents the effect of species 1 on itself and α_{12} represents the effect of species 2 on species 1. To solve for competition coefficients, I rearranged the terms to the following (Equation 8):

$$\lambda_1 \frac{N_{1,t}}{N_{1,t+1}} - 1 = \alpha_{11} N_{1,t} + \alpha_{12} N_{2,t} \quad \text{Equation 8}$$

Finally, using equation 5, I estimated the intraspecific and interspecific competition coefficients for each possible species pair in Indian and Todd creeks. This was performed using the model output from the Jolly-Seber model across all individuals for each possible species pair in Indian and Todd Creeks. Then using the multi-state Jolly-Seber results, I investigated if any size-dependent competition was present within these fish communities. Three body size grouping comparisons were performed for each species pair; competition between small body sizes, large body sizes, and the effect of large body size on small individuals.

Results

Over the duration of the study, I tagged 2,646 unique individuals in Indian Creek and 4,838 in Todd Creek. Mottled sculpin had the greatest number of individuals in Indian Creek (39% of total tagged) whereas bluehead chub made up the majority of tagged fish in Todd creek (81% of total tagged). More creek chub (765 vs 226) were tagged in Indian Creek and more striped jumprock (673 vs 283) were tagged in Todd creek. Following these patterns, abundance estimates from the Jolly-Seber model also differed between the two streams. In Indian Creek, mottled sculpin was the most abundant species (mean = 653; range = 208-653), followed by creek chub (mean = 292; range = 117-431), bluehead chub (mean = 208; range = 94-254), and striped jumprock (mean = 102; range = 56-230) (Figure 1). In Todd Creek, bluehead chub had the highest abundance (mean = 1725, range = 963-2375), followed by striped jumprock (mean = 290; range = 198-433), and creek chub (mean = 27; range = 89-190) with the lowest abundance. Creek chub was more abundant in Indian Creek relative to Todd Creek, and bluehead chub and striped jumprock were more abundant in Todd creek relative to Indian Creek.

Bi-monthly population growth rates were highest during September-November for bluehead chub, creek chub, and striped jumprock, whereas higher growth rates for mottled sculpin were observed between March-May and May-July (Figure 2). Decreases in population growth were observed in late summer (July-September). A previous study (Pregler Chapter 2) observed that survival for these species were lower during these intervals perhaps due to seasonal changes in abiotic stressors like temperature.

I observed a greater frequency of more negative intraspecific interactions (56% of total comparisons) than interspecific interactions (16% of total comparisons) (Table 3) in the non-

size-dependent results. Among species, there were few significant negative intraspecific interactions, and more significant positive interspecific interactions. The strongest negative interspecific interaction occurred between two ecologically similar species, bluehead chub and creek chub, but this relationship varied spatially. This was a one-way relationship where the population growth rate of creek chub was negatively impacted by higher bluehead chub densities in Indian Creek (interspecific competition coefficient = -0.006; $p < 0.005$) but not in Todd Creek (interspecific competition coefficient = 0.0005; $p = 0.03$).

Size-dependent competition estimates reflected similar patterns to competition results from across all individuals within species. I did not observe any size-dependent negative interspecific competition in these two stream communities (Table 4 and 5). While there was a negative interspecific interaction of bluehead chub on creek chub in Indian Creek, this relationship did not appear to be size-dependent. All significant interspecific competition coefficients were positive within each of the body size comparison groupings. While I observed a greater proportion of negative intraspecific interactions, only four of these values were significant (three in Indian Creek and one in Todd Creek).

Discussion

My study highlighted contrasting effects of intra- and interspecific density on species-specific population growth rates in these fish communities. While I observed more negative intraspecific interactions than interspecific, the majority of these were not statistically significant. There were more significant interspecific interactions than intraspecific, however these were positive interactions with the exception of a negative interaction between two species with high ecological overlap. These biotic interactions did not appear to be body size dependent.

This wasn't surprising given that there were few significant negative interactions when competition was investigated across all individuals. My results suggest that while biotic interactions can be important for stream communities, they may not be the dominating factor in regulating population dynamics in these systems.

Negative competitive interaction was inferred between bluehead chub and creek chub, the two most taxonomically and ecologically similar species but this interaction was not body size dependent. Interestingly, there were spatial differences in the competitive interactions between these two species where this negative interaction was observed in one stream but not the other. Spatial differences in these relationships may be attributed to habitat differences between the two streams. A previous study (Pregler Chapter 2) showed that habitat volume (water-level) is smaller in Indian Creek relative to Todd Creek. Given these species' overlapping habitat niche, this could potentially lead to competition for limited pool and run habitats in Indian Creek. Furthermore, the densities of the two species differed among the two creeks, creek chub is the second most abundant in Indian Creek whereas bluehead chub is the most abundant in Todd Creek. Spatial differences in competition has not been emphasized in the literature (Amarasekare 2003; Kneitel and Chase 2003); however, when habitat is limited, competitive interactions can increase and form dominance hierarchies between ecologically similar species (Nakano 1995a; Nakano 1995b). Creek chub tend to be more abundant in smaller streams (Harvey and Stewart 1991). These two species may be able to distribute themselves spatially among resources in Todd Creek because of the larger habitat volume (e.g. Ideal Free Distribution; Fretwell and Lucas 1970). A previous study showed that in the presence of asymmetrical competition, where one fish species was dominant over the other, the less dominant species was more likely to move in search of better access to resources (Berec et al.

2006). Perhaps where these species co-occurred provided enough habitat overlap in Indian Creek to interact and influence demography. More research would need to be conducted to investigate the spatial distribution of these two species relative to habitat volume.

Overall I observed a greater number of positive interactions among species. Although positive interactions between species have been documented, most ecological theory regarding the coexistence of multiple species focuses on antagonistic interactions such as competition and predation (Nelson et al. 2016). Positive interactions (e.g. facilitation) may provide an important mechanism for maintaining species-rich communities (Gross 2008). I observed in chapter 2 that abiotic stressors (such as maximum temperature and lower water-level) decreased survival probability and may keep fishes below their carry capacity so that one species isn't outcompeting another. If abiotic factors are driving populations dynamics more so than biotic factors, and species respond in synchrony to these drivers, perhaps this is why I observed more significant positive interspecific interactions. When conditions are favorable for population growth, all species tend to increase regardless of other species' densities (with the exception of bluehead chub and creek chub). Rivers are dynamic systems and lotic fish populations may not reach carrying capacity as quickly as fish do in lentic systems. Higher proportions of small-bodied, opportunistic (e.g. short generation time, high reproductive effort) species are endemic to the southeastern United States (Winemiller 2005). The greater proportions of opportunistic species in this region are linked to differences in hydrologic regimes (Mims and Olden 2012) where the abiotic environment can act as a disturbance to allow for such high diversity in these streams.

There is little documentation on competition among nongame fish in the literature, which suggests that this is an understudied system when it comes to biotic interactions. Nongame fishes are typically not thought of as interacting with each other enough to the degree that would

affect demography. Research on biotic interactions in nongame fishes has revealed that biotic interactions can be influenced by habitat factors such that the degree of an interaction may be context dependent (Inoue and Nakano 2001). The majority of studies focus on competition among salmonid species (Hasegawa et al. 2014; Montorio et al. 2018), or the negative impacts of nonnatives on native-nongame fish assemblages (Clarkson 2005; Hazelton and Grossman 2009; Weaver and Kwak 2013; Turek et al. 2016;).

While the majority of observed negative intraspecific interactions were not significant, there may still be important biological implications of intraspecific dynamics in these stream communities. There is growing empirical evidence that greater trait variation occurs within rather than among species (Clark et al. 2010; Messier et al. 2010; Violle et al. 2012). Individual variation is expected to break down competitive hierarchies and promote coexistence by decreasing the probability of competitive exclusion (Hart et al. 2016). Although research exists on the effects character displacement can have on the evolutionary processes that can lead to increased diversity via selection on individual variation (Brown and Wilson 1956), the implications of the ecological consequences of individual variation are rarely considered. In contrast, increased competitive relationships have been found when species did not evolve in sympatry (e.g. introduction of non-natives) (Nakano et al. 1997).

Although an increasing number of studies begin to document the importance of intraspecific dynamics to ecological and evolutionary processes (Clark et al. 2010; Bolnick et al. 2011; Violle et al. 2012), ecological theory still emphasizes interspecific variation. Community assembly is complex, and the relative influence of abiotic and biotic filters are difficult to separate (Kraft et al. 2015) given that both can interact together to drive local community dynamics. Advances have been made in using intra- and interspecific variation within a

community to help aid disentangling the role of both filters. This study adds to the growing knowledge that biotic interactions can be important for community assembly. Furthermore, given the importance of intraspecific competition in aiding species coexistence, additional research should be conducted into what density-dependent mechanisms (e.g. at the individual scale) are leading to the intraspecific dynamics. For instance, experiments that measure demographic responses while manipulating limiting resources of species can help understand how the strength and direction of within and among species interactions change.

Tables and Figures

Table 1. State transition matrix for the first two dimensions of Ω used for each species in the multi-state Jolly Seber model.

		True State at Time $t + 1$			
		Not yet entered	Size 1	Size 2	Dead
True State at Time t	Not yet entered	$1 - \gamma_1 - \gamma_2$	γ_1	γ_2	0
	Size 1	0	$\phi_1^*(1 - \alpha_{12})$	$\phi_1^*\alpha_{12}$	$1 - \phi_1$
	Size 2	0	$\phi_2^*(1 - \alpha_{21})$	$\phi_2^*\alpha_{21}$	$1 - \phi_2$
	Dead	0	0	0	1

Table 2. Observation transition matrix for the first two dimensions of Θ used for each species in the multi-state Jolly Seber model.

		Observation at Time t		
		Seen - Size 1	Seen - Size 2	Not seen
True state at Time t	Not yet entered	0	0	1
	Size 1	p_1	0	$1-p_1$
	Size 2	0	p_2	$1-p_2$
	Dead	0	0	1

Table 3. Competition Coefficients (p-value) comparing the effects of intraspecific (α_{11}) and interspecific (α_{12}) species density (N) on species-specific population growth rate (λ) for Indian and Todd Creeks for bluehead chub (BHC), creek chub (CRC), striped jumprock (STJ), and mottled sculpin (MTS). Significant p-values ($p < 0.05$) are bolded.

Comparison	Intraspecific (α_{11})	Interspecific (α_{12})
Indian		
BHC λ vs BHC N & CRC N	0.0008 (0.235)	-0.0002 (0.675)
BHC λ vs BHC N & STJ N	0.0004 (0.334)	0.0001 (0.922)
BHC λ vs BHC N & MTS N	-0.0004 (0.533)	0.0005 (0.150)
CRC λ vs CRC N & BHC N	-0.002 (0.02)	-0.006 (<0.005)
CRC λ vs CRC N & STJ N	0.0006 (0.649)	0.003 (0.356)
CRC λ vs CRC N & MTS N	-0.001 (0.188)	0.002 (<0.005)
STJ λ vs STJ N & BHC N	-0.005 (0.21)	0.008 (<0.005)
STJ λ vs STJ N & CRC N	-0.007 (0.175)	0.006 (<0.005)
STJ λ vs STJ N & MTS N	-0.0005 (0.888)	0.002 (0.01)
MTS λ vs MTS N & BHC N	-0.002 (0.057)	0.011 (<0.005)
MTS λ vs MTS N & CRC N	0.002 (0.194)	0.0007 (0.731)
MTS λ vs MTS N & STJ N	0.001 (0.154)	0.004 (0.361)
Todd		
BHC λ vs BHC N & CRC N	0.0002 (0.075)	-0.001 (0.523)
BHC λ vs BHC N & STJ N	0.00005 (0.481)	0.001 (0.005)
CRC λ vs CRC N & BHC N	-0.005 (0.1462)	0.0005 (0.03)
CRC λ vs CRC N & STJ N	-0.001 (0.222)	0.002 (0.001)
STJ λ vs STJ N & BHC N	0.0005 (0.372)	0.0001 (0.240)
STJ λ vs STJ N & CRC N	0.001 (0.03)	0.007 (0.509)

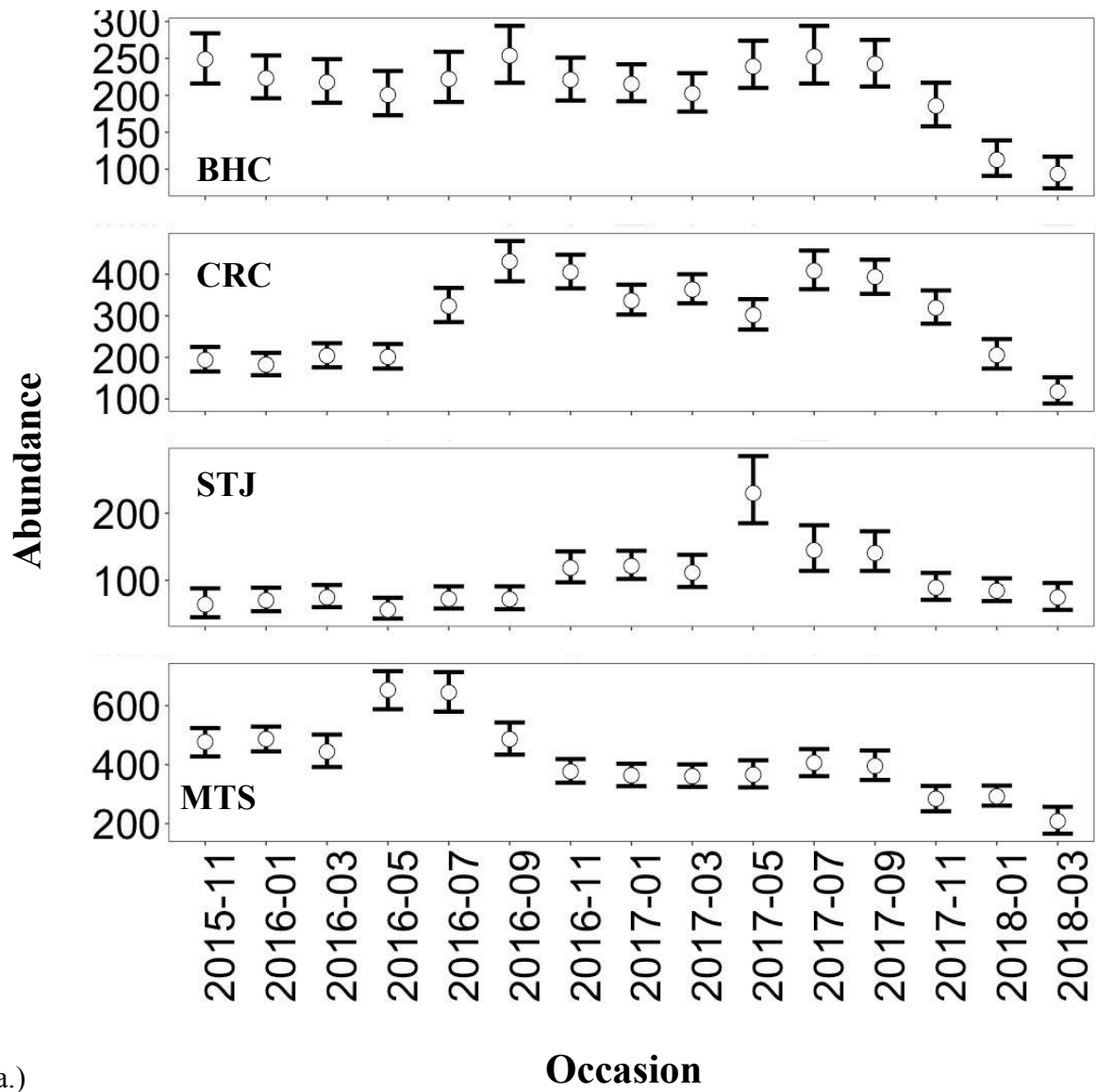
Table 4. Competition Coefficients (p-value) comparing the effects of intraspecific (α_{11}) and interspecific (α_{12}) species density (N) on species-specific population growth rate (λ) between small (denoted by a 1) and large body sizes (denoted by a 2) for species in Indian Creek (bluehead chub (BHC), creek chub (CRC), striped jumprock (STJ), and mottled sculpin (MTS)). Significant p-values ($p < 0.05$) are bolded.

Comparison	Intraspecific (α_{11})	Interspecific (α_{12})
Effect of small body size abundance on small body size population growth rate		
BHC1 λ vs BHC1 N & CRC1 N	0.00234 (0.221)	0.00026 (0.841)
BHC1 λ vs BHC1 N & STJ1 N	0.00419 (0.020)	-0.0022 (0.301)
BHC1 λ vs BHC1 N & MTS1 N	-0.00147 (0.672)	0.00241 (0.235)
CRC1 λ vs CRC1 N & BHC1 N	-0.01004 (0.072)	0.0291 (0.001)
CRC1 λ vs CRC1 N & STJ1 N	0.002617 (0.683)	0.01338 (0.268)
CRC1 λ vs CRC1 N & MTS1 N	-0.01064 (0.019)	0.01737 (0.0001)
STJ1 λ vs STJ1 N & BHC1 N	-0.00889 (0.229)	0.01855 (0.004)
STJ1 λ vs STJ1 N & CRC1 N	-0.00613 (0.357)	0.01192 (0.005)
STJ1 λ vs STJ1 N & MTS1 N	-0.00732 (0.319)	0.00989 (0.007)
MTS1 λ vs MTS1 N & BHC1 N	-0.00406 (0.241)	0.0141 (0.031)
MTS1 λ vs MTS1 N & CRC1 N	0.00344 (0.091)	0.00051 (0.829)
MTS1 λ vs MTS1 N & STJ1 N	0.00309 (0.107)	0.00189 (0.652)
Effect of large body size abundance on large body size population growth rate		
BHC2 λ vs BHC2 N & CRC2 N	0.00179 (0.475)	-0.00052 (0.721)
BHC2 λ vs BHC2 N & STJ2 N	-0.00236 (0.054)	0.01182 (0.010)
BHC2 λ vs BHC2 N & MTS2 N	0.000625 (0.625)	0.00016 (0.817)
CRC2 λ vs CRC2 N & BHC2 N	-0.00222 (0.352)	0.006029 (0.144)
CRC2 λ vs CRC2 N & STJ2 N	-0.004367 (0.0005)	0.03438 (0.00004)
CRC2 λ vs CRC2 N & MTS2 N	0.000228 (0.785)	0.001107 (0.172)
STJ2 λ vs STJ2 N & BHC2 N	-0.00339 (0.725)	0.00386 (0.173)
STJ2 λ vs STJ2 N & CRC2 N	0.01356 (0.314)	-0.00060 (0.784)
STJ2 λ vs STJ2 N & MTS2 N	-0.00247 (0.535)	0.002114 (0.004)
MTS2 λ vs MTS2 N & BHC2 N	-0.00048 (0.411)	0.001914 (0.088)
MTS2 λ vs MTS2 N & CRC2 N	0.00001 (0.981)	0.0006 (0.197)
MTS2 λ vs MTS2 N & STJ2 N	0.00018 (0.642)	0.00245 (0.349)
Effect of large body size abundance on small body size population growth rate		
BHC1 λ vs BHC1 N & CRC2 N	0.00511 (0.058)	-0.00168 (0.319)
BHC1 λ vs BHC1 N & STJ2 N	0.003246 (0.270)	-0.002305 (0.838)
BHC1 λ vs BHC1 N & MTS2 N	0.000906 (0.748)	0.001135 (0.518)
CRC1 λ vs BHC1 N & BHC2 N	-0.00530 (0.343)	0.02495 (0.011)
CRC1 λ vs CRC1 N & STJ2 N	-0.01418 (0.069)	0.13469 (0.004)

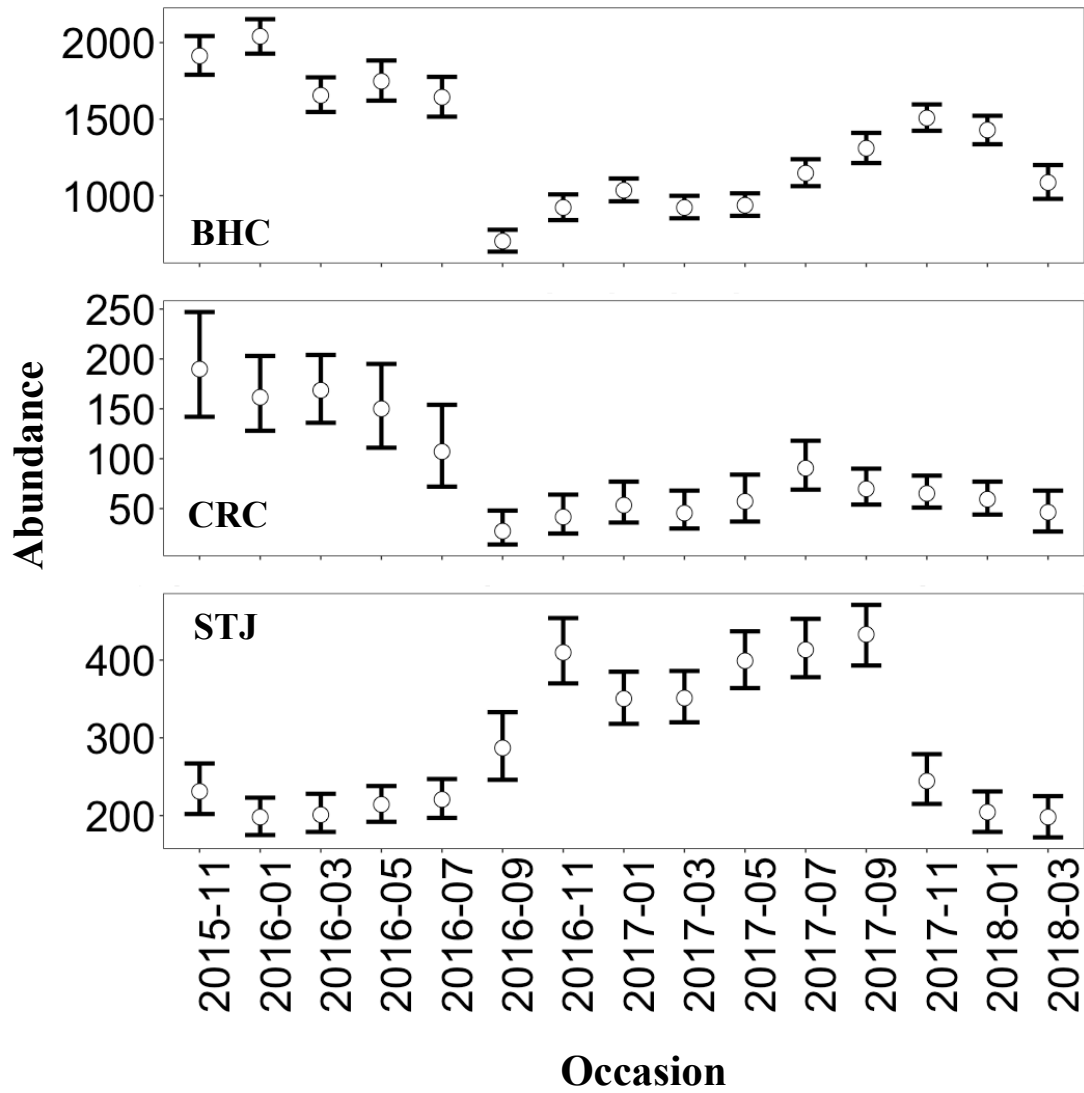
CRC1 λ vs CRC1 <i>N</i> & MTS2 <i>N</i>	-0.00335 (0.350)	0.01310 (0.0008)
STJ1 λ vs STJ1 <i>N</i> & BHC2 <i>N</i>	-0.01362 (0.170)	0.024061 (0.010)
STJ1 λ vs STJ1 <i>N</i> & CRC2 <i>N</i>	-0.01955 (0.077)	0.01723 (0.005)
STJ1 λ vs STJ1 <i>N</i> & MTS2 <i>N</i>	-0.00058 (0.935)	0.00747 (0.044)
MTS1 λ vs MTS1 <i>N</i> & BHC2 <i>N</i>	-0.000928 (0.810)	0.00946 (0.223)
MTS1 λ vs MTS1 <i>N</i> & CRC2 <i>N</i>	0.002032 (0.522)	0.00215 (0.559)
MTS1 λ vs MTS1 <i>N</i> & STJ2 <i>N</i>	0.00083 (0.805)	0.02119 (0.375)
BHC1 λ vs BHC1 <i>N</i> & BHC2 <i>N</i>	0.00454 (0.168)	-0.00213 (0.548)
CRC1 λ vs CRC1 <i>N</i> & CRC2 <i>N</i>	-0.00467 (0.521)	0.01372 (0.058)
STJ1 λ vs STJ1 <i>N</i> & STJ2 <i>N</i>	-0.027003 (0.012)	0.12501 (0.0006)
MTS1 λ vs MTS1 <i>N</i> & MTS2 <i>N</i>	-0.00254 (0.352)	0.00713 (0.028)

Table 5. Competition Coefficients (p-value) comparing the effects of intraspecific (α_{11}) and interspecific (α_{12}) species density (N) on species-specific population growth rate (λ) between small (denoted by a 1) and large body sizes (denoted by a 2) for species in Todd Creek (bluehead chub (BHC), creek chub (CRC), and striped jumprock (STJ)). Significant p-values ($p < 0.05$) are bolded.

Comparison	Intraspecific (α_{11})	Interspecific (α_{12})
Effect of small body size abundance on small body size population growth rate		
BHC1 λ vs BHC1 N & CRC1 N	0.000063 (0.854)	0.00261 (0.655)
BHC1 λ vs BHC1 N & STJ1 N	0.000020 (0.896)	0.00096 (0.095)
CRC1 λ vs CRC1 N & BHC1 N	-0.0126 (0.327)	0.0014 (0.075)
CRC1 λ vs CRC1 N & STJ1 N	0.0014 (0.759)	0.003 (0.007)
STJ1 λ vs STJ1 N & BHC1 N	0.0001 (0.975)	0.0050 (0.013)
STJ1 λ vs STJ1 N & CRC1 N	0.0055 (0.389)	0.0592 (0.066)
Effect of large body size abundance on large body size population growth rate		
BHC2 λ vs BHC2 N & CRC2 N	0.00075 (0.0483)	-0.0050 (0.2136)
BHC2 λ vs BHC2 N & STJ2 N	-0.00037 (0.202)	0.0016 (0.023)
CRC2 λ vs CRC2 N & BHC2 N	-0.03505 (0.064)	0.0049 (0.007)
CRC2 λ vs CRC2 N & STJ2 N	-0.01069 (0.393)	0.0066 (0.021)
STJ2 λ vs STJ2 N & BHC2 N	0.0006 (0.750)	0.0007 (0.392)
STJ2 λ vs STJ2 N & CRC2 N	0.0030 (0.040)	-0.0041 (0.532)
Effect of large body size abundance on small body size population growth rate		
BHC1 λ vs BHC1 N & CRC2 N	-0.0006 (0.222)	0.0152 (0.102)
BHC1 λ vs BHC1 N & STJ2 N	-0.00031 (0.276)	0.00213 (0.063)
CRC1 λ vs CRC1 N & BHC2 N	-0.0115 (0.249)	0.0022 (0.028)
CRC1 λ vs CRC1 N & STJ2 N	-0.00050 (0.948)	0.00289 (0.106)
STJ1 λ vs STJ1 N & BHC2 N	0.00060 (0.934)	0.0073 (0.041)
STJ1 λ vs STJ1 N & CRC2 N	0.00478 (0.448)	0.0681 (0.048)
BHC1 λ vs BHC1 N & BHC2 N	-0.0013 (0.039)	0.00247 (0.018)
CRC1 λ vs CRC1 N & CRC2 N	-0.0083 (0.599)	0.02039 (0.240)
STJ1 λ vs STJ1 N & STJ2 N	0.00317 (0.683)	0.01379 (0.110)

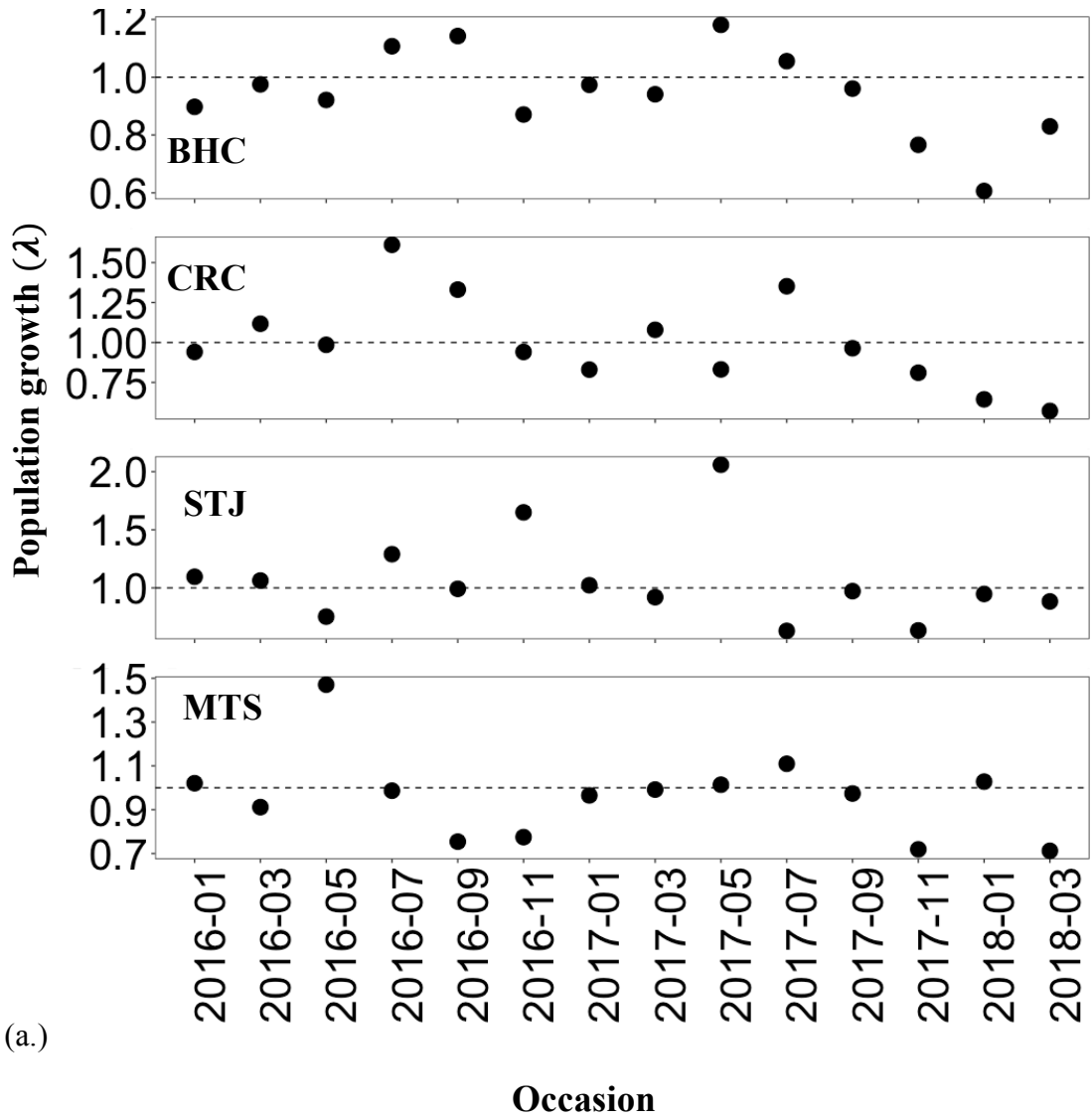


(a.)



(b.)

Figure 1. Abundance estimates over time for Indian (a.) and Todd (b.) creeks for bluehead chub (BHC), creek chub (CRC), striped jumprock (STJ), and mottled sculpin (MTS).



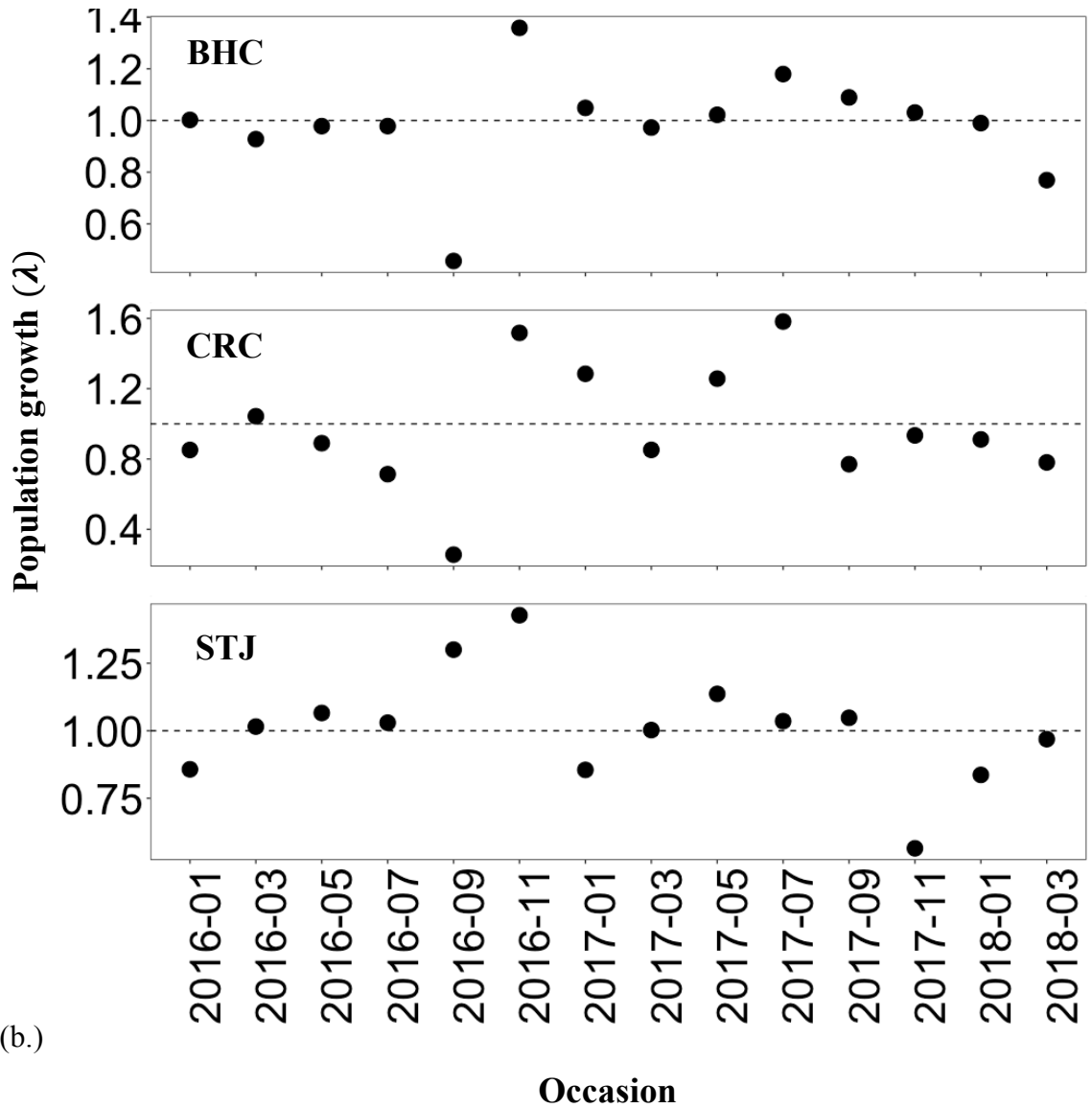


Figure 2. Population growth rate estimates (λ) over time for Indian (a.) and Todd (b.) Creeks for bluehead chub (BHC), creek chub (CRC), striped jumprock (STJ), and mottled sculpin (MTS). Dashed line at population growth rate of 1 (no change), values greater than 1 represent positive population growth, and values less than 1 represent population decrease.

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APPENDIX 1 - SUPPLEMENTARY TABLES AND FIGURES

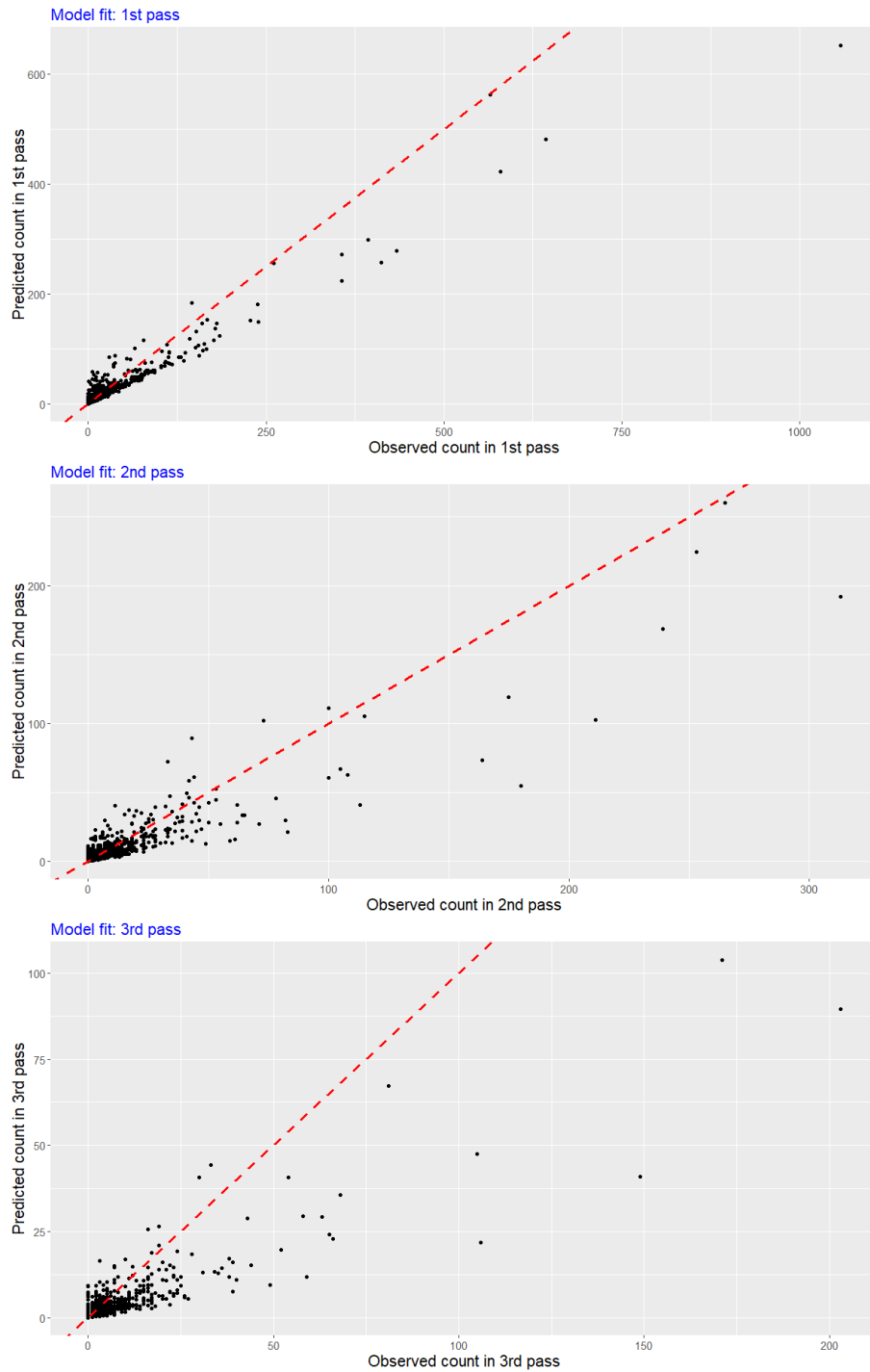
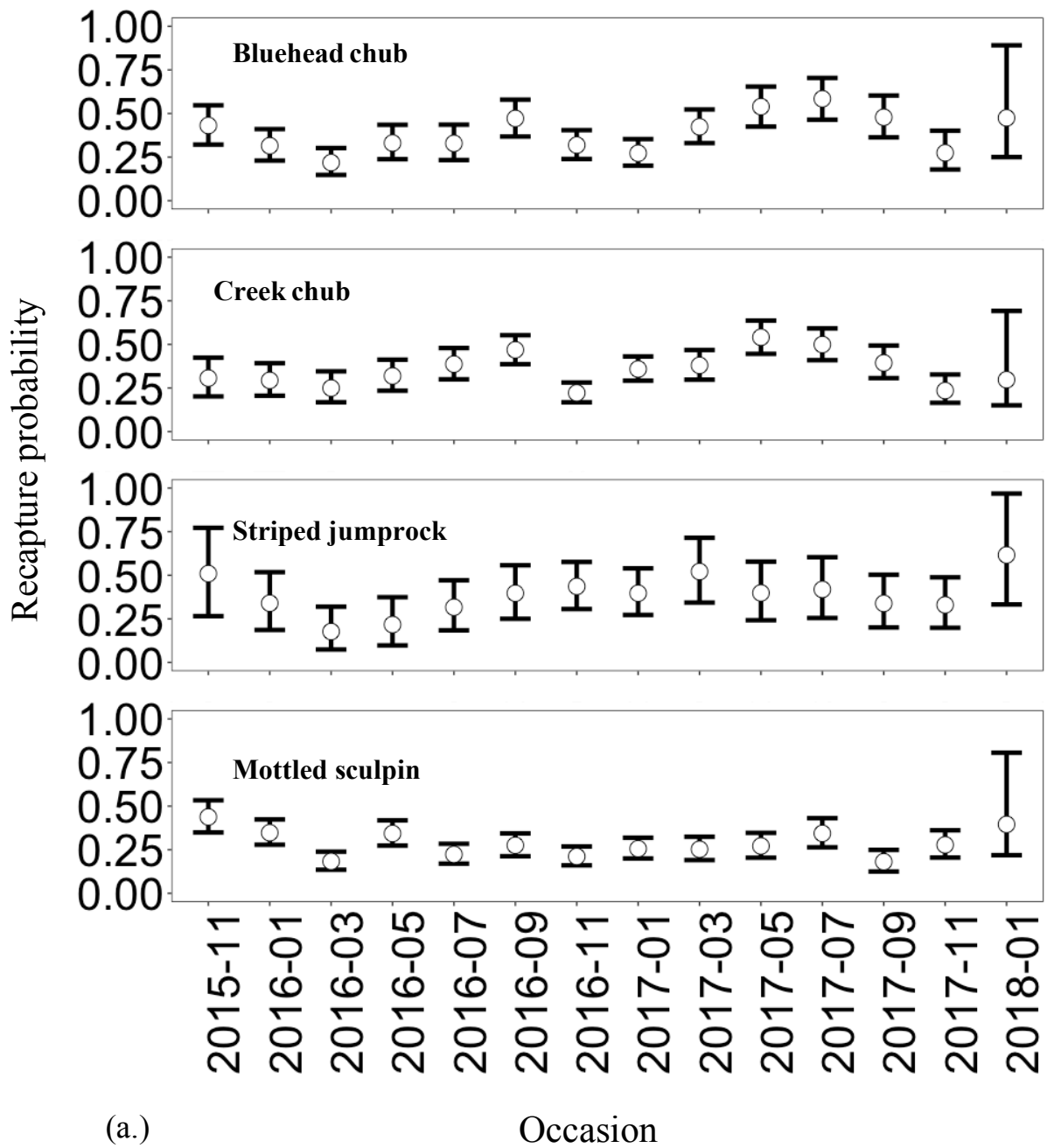
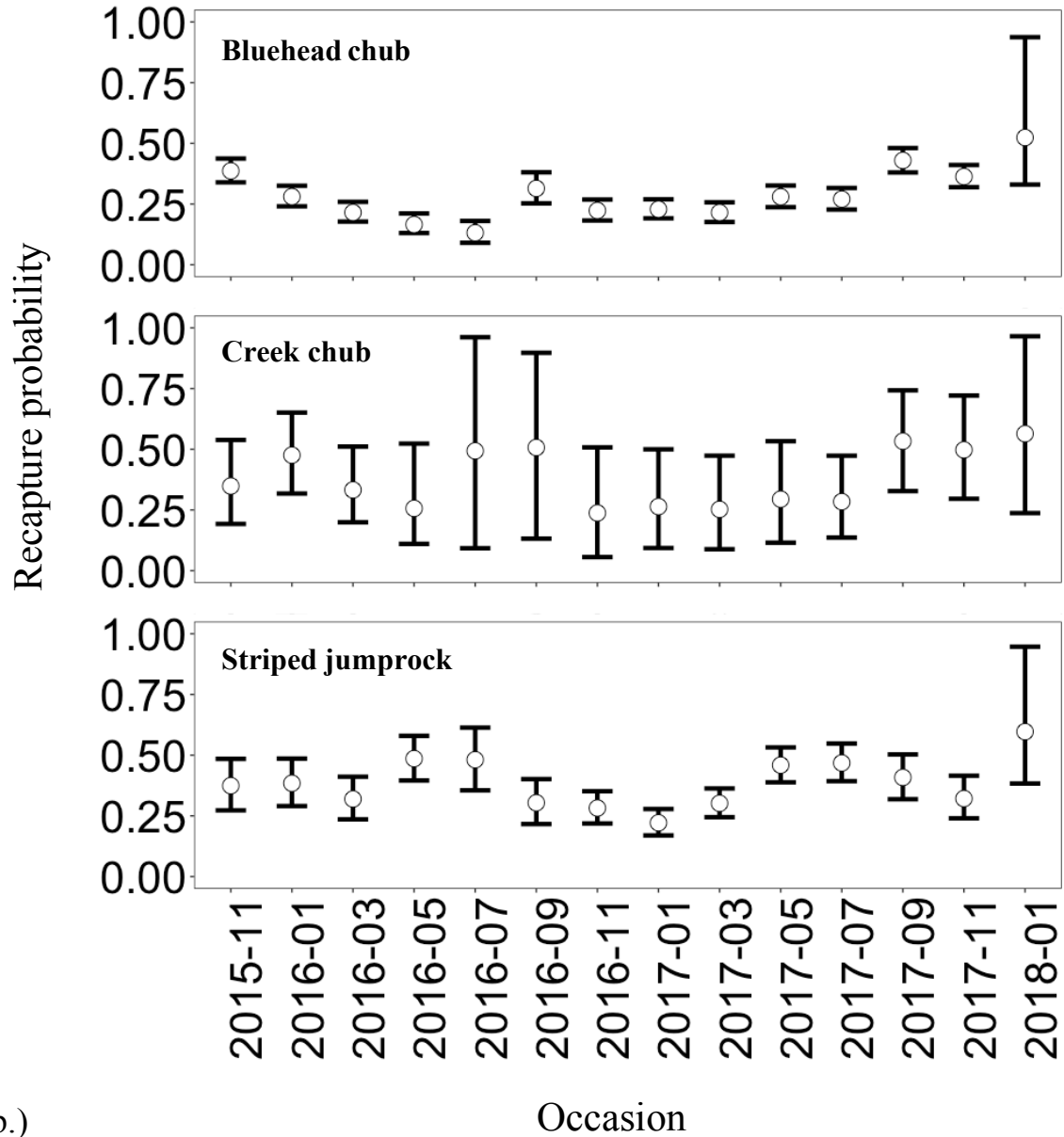


Figure S1. Model fit. Plot of predicted abundance versus observed abundance for each electrofishing pass for each species and site.





(b.) Occasion

Figure S2. Recapture probabilities for each species across the mark recapture study for Indian (a.) and Todd (b.) creeks. “2015-11” represents the first bi-monthly occasion from November 2015 to January 2016. Point estimates are mean of the MCMC posterior distribution samples for recapture probability of each species. Vertical bars show 95% credible intervals.

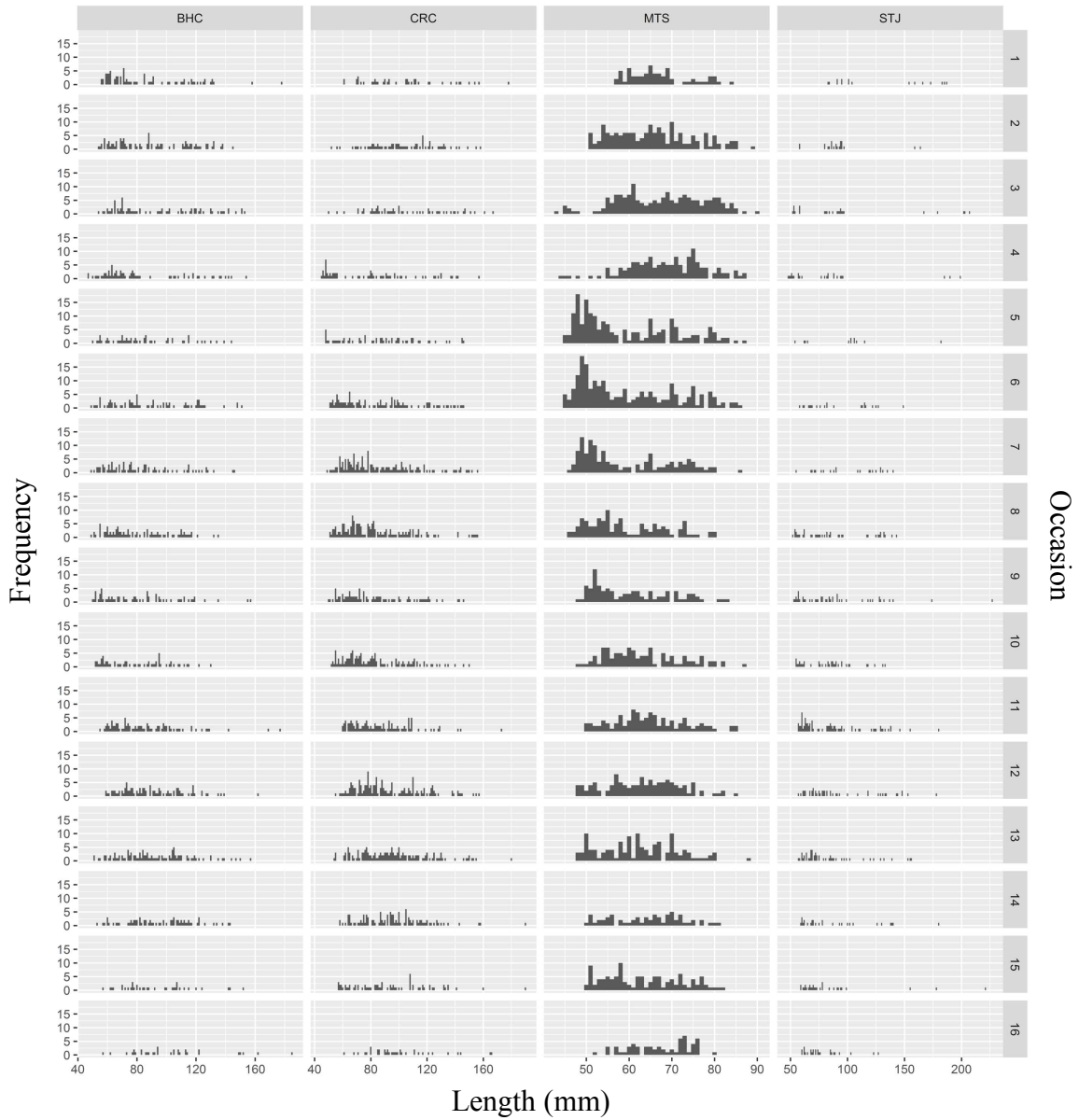


Figure S3. Length frequency histogram across occasions and species (BHC = bluehead chub, CRC = creek chub; MTS = mottled sculpin; STJ = striped jumprock) for Indian Creek.

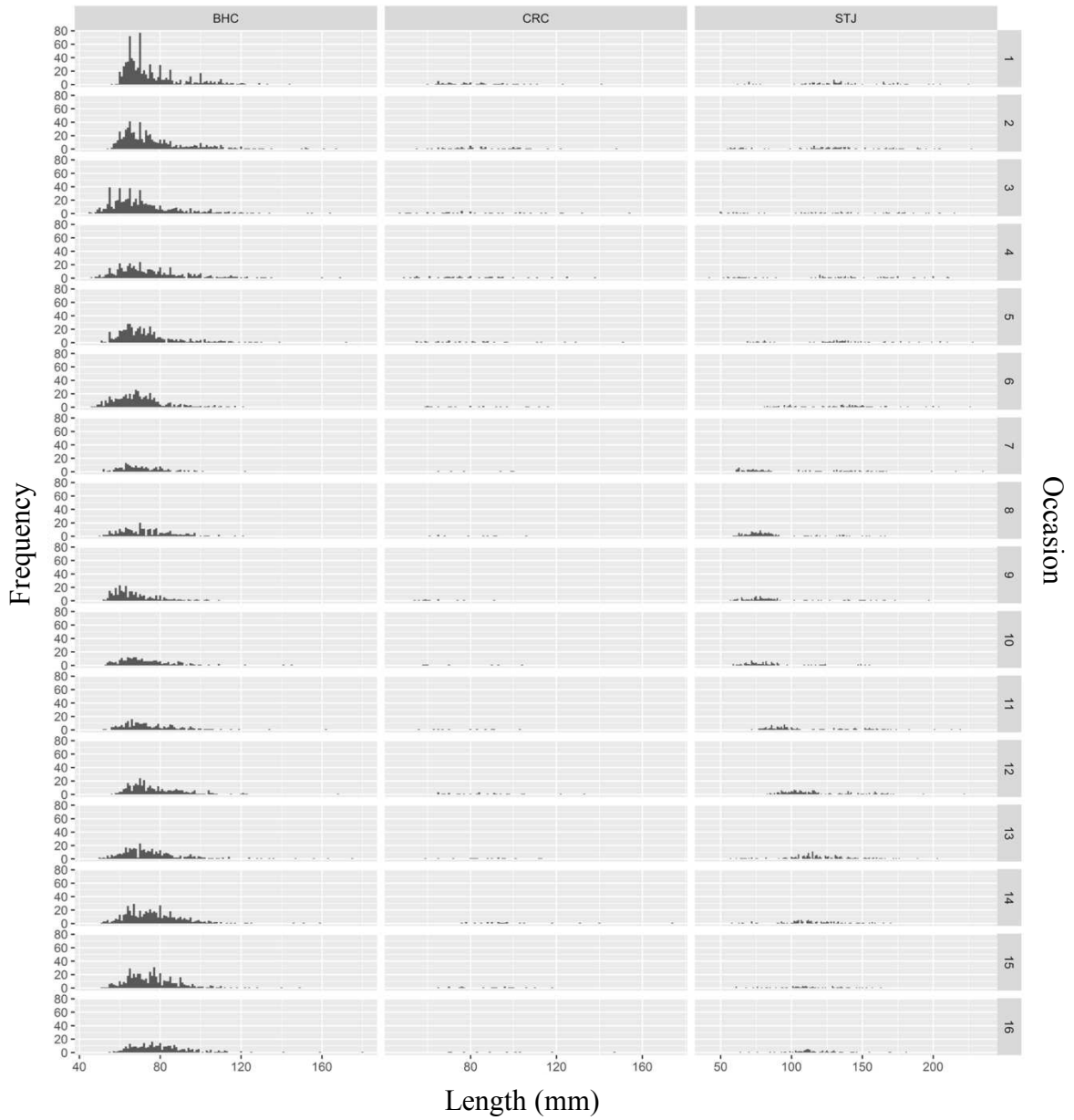


Figure S4. Length frequency histogram across occasions and species (BHC = bluehead chub, CRC = creek chub, STJ = striped jumrock) for Todd Creek.

Table S1. Summary of percent number of sites where each species was found, posterior mean and (95% credible intervals for capture, occupancy, and mean abundance across sites for each species.

Species	Family	% of sites	Est. capture probability	Est. occupancy probability	Mean abundance
American eel (<i>Anguilla rostrata</i>)	Anguillidae	44	0.56 (0.52-0.59)	0.46 (0.40-0.53)	5.18 (4.78-5.62)
Blackbanded darter (<i>Percina nigrofasciata</i>)	Percidae	15	0.51 (0.42-0.61)	0.17 (0.12-0.22)	1.89 (1.57-2.38)
Bluehead chub (<i>Nocomis leptcephalus</i>)	Cyprinidae	10	0.65 (0.59-0.70)	0.12 (0.08-0.16)	3.14 (2.84-3.48)
Bluegill (<i>Lepomis macrochirus</i>)	Centrarchidae	44	0.58 (0.54-0.61)	0.46 (0.40-0.53)	7.97 (7.48-8.49)
Bluespotted sunfish (<i>Enneacanthus gloriosus</i>)	Centrarchidae	35	0.54 (0.48-0.59)	0.36 (0.30-0.42)	2.98 (2.64-3.36)
Creek chubsucker (<i>Erimyzon oblongus</i>)	Catostomidae	39	0.54 (0.49-0.59)	0.44 (0.36-0.52)	3.42 (2.64-3.36)
Chain pickerel (<i>Esox niger</i>)	Esocidae	25	0.50 (0.41-0.59)	0.47 (0.31-0.56)	0.82 (0.62-1.08)
Coastal shiner (<i>Notropis petersoni</i>)	Cyprinidae	10	0.50 (0.41-0.57)	0.12 (0.08-0.16)	1.71 (1.39-2.21)
Dusky shiner (<i>Notropis commingsae</i>)	Cyprinidae	28	0.61 (0.59-0.63)	0.31 (0.26-0.36)	12.90 (12.22-13.63)
Dollar sunfish (<i>Lepomis marginatus</i>)	Centrarchidae	55	0.53 (0.50-0.56)	0.56 (0.49-0.63)	11.53 (9.30-15.65)
Eastern mudminnow (<i>Umbra pygmaea</i>)	Umbridae	29	0.46 (0.38-0.54)	0.34 (0.27-0.41)	2.81 (2.51-3.14)
Flat bullhead (<i>Ameiurus platycephalus</i>)	Ictaluridae	5	0.54 (0.40-0.66)	0.15 (0.07-0.29)	0.73 (0.09-4.80)
Flier (<i>Centrarchus macropterus</i>)	Centrarchidae	30	0.40 (0.32-0.48)	0.30 (0.25-0.36)	2.58 (2.25-2.96)
Golden shiner (<i>Notemigonus crysoleucas</i>)	Cyprinidae	32	0.49 (0.40-0.58)	0.32 (0.27-0.38)	4.09 (3.70-4.52)
Ironcolor shiner (<i>Notropis chalybaeus</i>)	Cyprinidae	5	0.49 (0.40-0.58)	0.06 (0.03-0.11)	2.05 (1.71-2.39)
Lake chubsucker (<i>Erimyzon sucetta</i>)	Catostomidae	15	0.49 (0.34-0.61)	0.18 (0.13-0.25)	1.15 (0.89-1.58)
Largemouth bass (<i>Micropterus salmoides</i>)	Centrarchidae	33	0.53 (0.47-0.60)	0.40 (0.32-0.48)	1.63 (1.37-2.01)
Mud sunfish (<i>Acantharchus pomotis</i>)	Centrarchidae	44	0.39 (0.31-0.47)	0.60 (0.49-0.71)	1.91 (1.45-3.48)

Margined madtom (<i>Noturus insignis</i>)	Ictaluridae	18	0.45 (0.38-0.52)	0.18 (0.14-0.23)	2.25 (1.91-2.67)
Eastern mosquitofish (<i>Gambusia holbrooki</i>)	Poeciliidae	79	0.60 (0.59-0.61)	0.85 (0.79-0.90)	62.20 (60.81-63.59)
Pirate perch (<i>Aphredoderus sayanus</i>)	Aphredoderidae	87	0.40 (0.38-0.42)	0.88 (0.83-0.92)	20.64 (20.02-21.25)
Pumpkinseed (<i>Lepomis gibbosus</i>)	Centrarchidae	20	0.56 (0.47-0.64)	0.22 (0.16-0.28)	1.44 (1.23-1.68)
Redbreast sunfish (<i>Lepomis auratus</i>)	Centrarchidae	50	0.61 (0.59-0.63)	0.50 (0.44-0.57)	12.09 (11.71-12.47)
Redear sunfish (<i>Lepomis microlophus</i>)	Centrarchidae	11	0.49 (0.37-0.59)	0.22 (0.16-0.28)	0.57 (0.42-0.80)
Redfin pickerel (<i>Esox americanus</i>)	Esocidae	83	0.55 (0.52-0.57)	0.84 (0.79-0.88)	13.50 (12.81-14.24)
Snail bullhead (<i>Ameiurus brunneus</i>)	Ictaluridae	10	0.43 (0.30-0.56)	0.28 (0.16-0.45)	0.63 (0.28-2.45)
Sawcheek darter (<i>Etheostoma serrifer</i>)	Percidae	10	0.57 (0.44-0.70)	0.20 (0.11-0.33)	0.41 (0.30-0.55)
Lowland shiner (<i>Pternotropis serrifer</i>)	Cyprinidae	24	0.66 (0.62-0.68)	0.27 (0.22-0.32)	12.3 (11.53-13.15)
Spotted sunfish (<i>Lepomis punctatus</i>)	Centrarchidae	42	0.52 (0.49-0.55)	0.43 (0.37-0.49)	7.34 (6.8-7.89)
Speckled madtom (<i>Noturus leptacanthus</i>)	Ictaluridae	13	0.33 (0.23-0.44)	0.17 (0.11-0.25)	2.42 (2.06-2.88)
Spotted sucker (<i>Minytrema melanops</i>)	Catostomidae	9	0.50 (0.40-0.60)	0.25 (0.15-0.40)	0.56 (0.38-0.86)
Savannah darter (<i>Etheostoma fricksium</i>)	Percidae	10	0.43 (0.32-0.53)	0.12 (0.08-0.17)	1.31 (1.06-1.63)
Swamp darter (<i>Etheostoma fusiforme</i>)	Percidae	12	0.42 (0.32-0.52)	0.15 (0.09-0.21)	0.78 (0.53-1.60)
Tadpole madtom (<i>Noturus gynrinus</i>)	Ictaluridae	22	0.48 (0.40-0.55)	0.24 (0.18-0.30)	1.25 (1.03-1.49)
Tessellated darter (<i>Etheostoma olmstedi</i>)	Percidae	32	0.54 (0.50-0.59)	0.32 (0.26-0.38)	6.19 (5.71-6.71)
Warmouth (<i>Lepomis gulosus</i>)	Centrarchidae	52	0.51 (0.45-0.56)	0.57 (0.49-0.65)	3.01 (2.57-4.14)
Yellow bullhead (<i>Ameiurus natalis</i>)	Ictaluridae	48	0.57 (0.53-0.61)	0.53 (0.45-0.60)	3.72 (3.37-4.08)

Table S2. Number of days between each bi-monthly sampling occasion across the mark-recapture study.

Occasion	Indian	Todd
1	64	65
2	57	65
3	68	63
4	56	48
5	66	69
6	58	56
7	58	60
8	58	60
9	69	66
10	54	51
11	66	70
12	56	57
13	70	69
14	48	52

Table S3. Number of tagged individuals for each species and stream and the percentage of tagged individuals caught only once (in parentheses) over the course of the mark-recapture study.

Species	Indian	Todd
Bluehead chub	535 (42%)	3908 (52%)
Creek chub	765 (46%)	226 (50%)
Striped jumprock	283 (50%)	673 (35%)
Mottled sculpin	1043 (52%)	NA

Table S4. Summary of marked (M) and recaptured (R) individuals for each species from occasion 1 (November 2015) to occasion 15 (March 2018) for Indian (a.) and Todd (b.) Creeks.
(a.)

Species		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
BHC	M	75	33	28	25	30	46	39	28	18	30	38	40	17	8	0
	R	20	44	43	31	47	37	49	42	40	60	60	64	56	29	33
CRC	M	61	34	35	35	71	97	74	39	44	30	77	60	36	26	0
	R	12	25	32	27	40	60	88	54	89	79	88	93	78	46	38
STJ	M	17	17	14	5	14	8	26	21	11	53	27	32	11	13	0
	R	5	8	11	7	8	14	17	26	28	19	23	20	18	18	26
MTS	M	128	101	47	136	111	65	47	40	34	48	63	53	27	53	0
	R	29	74	96	53	100	71	66	55	72	61	58	73	37	58	61

(b.)

Species		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
BHC	M	386	340	200	280	291	140	200	203	112	131	175	223	267	224	0
	R	236	320	293	223	182	41	83	97	133	123	167	164	259	289	329
CRC	M	33	27	22	13	9	3	8	10	4	7	20	7	8	4	0
	R	17	13	27	20	12	4	3	2	7	4	6	8	13	15	10
STJ	M	65	30	23	28	17	63	110	56	40	47	44	36	24	8	0
	R	32	36	50	44	69	39	31	56	54	79	117	129	73	54	77

APPENDIX 2 – EXAMPLE JAGS CODE

Chapter 1 Example JAGS Code

The following represents JAGS code (using package jagsUI in program R) for the hierarchical occupancy and abundance model used in Chapter 1.

```
#####  
## Coastal plain occupancy and abundance model ##  
#####  
# Author: Kasey C. Pregler  
  
model{  
  
  ## Ecological process  
  for(i in 1:nSites){  
    for(j in 1:nSpecies){  
      z[i,j] ~ dbern(omega[i,j])  
      logit(omega[i,j])<-mu.ome[j]+a[1,j]*DO[i] +  
        a[2,j]*elevation[i]+  
        a[3,j]*turbidity[i] + a[4,j]*pH[i] +  
        a[5,j]*forest[i] + a[6,j]*urban[i] + a[7,j]*wsarea[i] +  
        a[8,j]*depth[i]  
  
      N[i,j] ~ dpois(lam.eff[i,j])  
      lam.eff[i,j]<-z[i,j]*lambda[i,j]  
      log(lambda[i,j]) <- mu.lam[j] + b[1,j]*DO[i] +  
        b[2,j]*elevation[i] +  
        b[3,j]*turbidity[i] + b[4,j]*pH[i]+  
        b[5,j]*forest[i] + b[6,j]*urban[i] + b[7,j]*wsarea[i] +  
        b[8,j]*depth[i]  
  
    }  
  }  
  
  #### Detection  
  for(i in 1:nSites) {
```

```

for(j in 1:nSpecies){
  y[i,1,j] ~ dbin(p[i,j], N[i,j])
  y[i,2,j] ~ dbin(p[i,j]*(1-p[i,j]), N[i,j])
  y[i,3,j] ~ dbin(p[i,j]*(1-p[i,j])*(1-p[i,j]), N[i,j])
  #logit(p[i,j]) <- mu.p[j] +
  # c[6,j]*turbidity[i] + c[7,j]*velocity[i]
  logit(p[i,j]) <- mu.p[j]
}
}

```

Priors

```

for(j in 1:nSpecies){

  mu.ome[j]~dnorm(mu.a,tau.ome)
  mu.lam[j]~dnorm(mu.b,tau.lam)T(-2,2)
  mu.p[j]~dnorm(mu.c,tau.p)T(-3,3)

}

```

```

sd.ome ~dunif(0,3)
tau.ome <- 1/(sd.ome*sd.ome)
mu.a ~ dnorm(0,0.01)

```

```

sd.lam ~dunif(0,3)
tau.lam<- 1/(sd.lam*sd.lam)
mu.b ~ dnorm(0,0.01)

```

```

sd.p ~dunif(0,3)
tau.p <- 1/(sd.p*sd.p)
mu.c ~ dnorm(0,0.01)

```

```

for(h in 1:nCovs){
  for(j in 1:nSpecies){
    a[h,j]~dnorm(0,0.37)T(-3,3)
    b[h,j]~dunif(-2,2)
  }
}

```

```

}

```

```

## derived quantity
for(j in 1:nSpecies){
  omegaSpp[j] <- mean(omega[,j]) # mean occ prob for each species
across sites
  lamSpp[j] <- mean(lam.eff[,j]) # mean abundandace for each
species across sites
  pSpp[j] <- mean(p[,j]) # mean det prob for each species
across sites
}
}

```

Chapter 2 Example JAGS Code

The following represents JAGS code (using package jagsUI in program R; following methods described in Kéry and Schaub 2012 and Lahoz-Monfort et al. 2011) for an example Cormack Jolly Seber model with random effects to evaluate synchrony used in Chapter 2.

```

#####
## CJS Model Todd Creek - time varying phi and p ##
#####
# Author: Kasey C. Pregler

model {

# Priors and constraints
  # for (j in 1:nspecies){
  for (i in 1:nind){
    for (t in f[i):(n.occasions-1)){ # minus 1 (intervals)
      logit(phi[i,t]) <- mu.phi[species[i]] + epsilon[t] +
epsilon2[species[i],t]
      p[i,t] <- mean.p[species[i],t]
    } #t
  } #i

  for(t in 1:(n.occasions-1)){
    epsilon[t] ~ dnorm(0,tau)T(-1.5,1.5)

  }

sd ~ dunif(0,3)
sigma2 <- sd*sd
tau <- 1/sigma2

```

```

for(j in 1:3){
  sd.sp[j] ~dunif(0,3)
  sigma2.sp[j] <- sd.sp[j]*sd.sp[j]
  tau.sp[j] <- 1/sigma2.sp[j]
  for(t in 1:(n.occasions-1)){
    epsilon2[j,t] ~dnorm(0,tau.sp[j])T(-1.5,1.5)
  }
}

for (j in 1:3){
  mu.phi[j] ~ dnorm(0,0.001)T(-1.5,1.5) # prior for logit of mean
survival
  # for(h in 1:nCovs){
  for(t in 1:(n.occasions-1)){
    mean.p[j,t] ~ dunif(0, 1) # Prior for mean recapture

    phi.est[j,t] <- 1 / (1+exp(-mu.phi[j] - epsilon[t] -
epsilon2[j,t])) ### Bimonthly survival

  }
}
#}
# Likelihood
for (i in 1:nind){
  # Define latent state at first capture
  z[i,f[i]] <- 1
  for (t in (f[i]+1):h[i]){
    # State process
    z[i,t] ~ dbern(mu1[i,t])
    mu1[i,t] <- phi[i,t-1] * z[i,t-1]
    # Observation process
    y[i,t] ~ dbern(mu2[i,t])
    mu2[i,t] <- p[i,t-1] * z[i,t]
  } #t
} #i
}

```

Chapter 3 Example JAGS Code

The following represents JAGS code (using package jagsUI in program R; following methods described in Kéry and Schaub 2012) for an example Jolly-Seber model used in Chapter 3.

```
#####
## Jolly Seber Model ##
#####

model {
# Priors and constraints
for (i in 1:M){
  for (t in 1:(n.occasions-1)){
    logit(phi[i,t]) <- mean.lphi
  } #t
  for (t in 1:n.occasions){
    p[i,t] <- mean.p
  } #t
} #i
mean.p ~ dunif(0, 1) # Prior for mean capture
mean.phi ~ dunif(0, 1) # Prior for mean survival
mean.lphi <- log(mean.phi / (1-mean.phi))

for (t in 1:n.occasions){
  gamma[t] ~ dunif(0, 1)
} #t

# Likelihood
for (i in 1:M){
  # First occasion
  # State process
  z[i,1] ~ dbern(gamma[1])
  mu1[i] <- z[i,1] * p[i,1]
  # Observation process
  y[i,1] ~ dbern(mu1[i])

  # Subsequent occasions
  for (t in 2:n.occasions){
    # State process
    q[i,t-1] <- 1-z[i,t-1]
    mu2[i,t] <- phi[i,t-1] * z[i,t-1] + gamma[t] * prod(q[i,1:(t-
1)])
    z[i,t] ~ dbern(mu2[i,t])
  }
}
}
```

```

    # Observation process
    mu3[i,t] <- z[i,t] * p[i,t]
    y[i,t] ~ dbern(mu3[i,t])
  } #t
} #i

# Calculate derived population parameters
for (t in 1:n.occasions){
  qgamma[t] <- 1-gamma[t]
}
cprob[1] <- gamma[1]
for (t in 2:n.occasions){
  cprob[t] <- gamma[t] * prod(qgamma[1:(t-1)])
} #t
psi <- sum(cprob[]) # Inclusion probability
for (t in 1:n.occasions){
  b[t] <- cprob[t] / psi # Entry probability
} #t
for (i in 1:M){
  recruit[i,1] <- z[i,1]
  for (t in 2:n.occasions){
    recruit[i,t] <- (1-z[i,t-1]) * z[i,t]
  } #t
} #i
for (t in 1:n.occasions){
  N[t] <- sum(z[1:M,t]) # Actual population size
  B[t] <- sum(recruit[1:M,t]) # Number of entries
} #t
for (i in 1:M){
  Nind[i] <- sum(z[i,1:n.occasions])
  Nalive[i] <- 1-equals(Nind[i], 0)
} #i
Nsuper <- sum(Nalive[]) # Size of superpopulation
}

```