

THE ROLE OF HABITAT IN AQUATIC INTRA- AND INTERSPECIFIC INTERACTIONS

By

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To my parents

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LIST OF ABBREVIATIONS

AICc	Akaike's information criterion corrected for sample size
ANOVA	Analysis of variance
CDA	Canonical discriminant analysis
CI	Confidence or credible interval
CJS	Cormack-Jolly-Seber
CPUE	Catch per-unit effort
CWH	Coarse woody habitat
FR	Functional response
GPP	Generator powered pulsator
MLE	Maximum likelihood estimate
NLL	Negative log-likelihood
NUTS	No U-turn Sampler
TL	Total length

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THE ROLE OF HABITAT IN AQUATIC INTRA- AND INTERSPECIFIC INTERACTIONS

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Habitat restoration and augmentation are two common management strategies for aquatic systems. Advancing these approaches have often been mired in false dichotomies, such as the attraction-production debate. Seemingly simple questions such as how does habitat impact a given species or community remain unclear, greatly reducing the effectiveness of habitat augmentation. In this dissertation, I present strategies and guiding principles for the use of artificial habitat as the result of an experiment testing behavioral strategies of prey and predator across natural densities, a natural experiment in Florida lakes and a conceptualization of mechanisms of habitat effects across aquatic systems. Experimentally, I show strong local habitat filtering effects on fish community from habitat augmentation and discuss the implications limiting potential interspecies interactions. I also show evidence for diminishing returns for gamefish production as function of existing habitat diversity and coverage. Formulating my conceptualization, revealed that habitat structural components and location tend to have the strongest density-independent and density-dependent effects on population dynamics. Lastly, I discuss the lingering attraction-production debate as well as the prevailing 'if you build it, they will come' approach in the context of moving

the conversation forward to new hypotheses and approaches. I culminate this discussion by outlining pathways for effective habitat augmentation depending on management objective.

CHAPTER 1 SCALE-DEPENDENT MECHANISMS OF HABITAT MEDIATION ON FISHES

Introduction. Ecologists have sought to understand, “the origin and mechanisms of interactions of organisms with one another and with the nonliving world” Pianka (1974). Of principal interest to the field is describing the patterns and processes shaping a species’ occurrence and abundance (Krebs 1972). Intraspecific and interspecific organismal interactions strongly shape these collective properties (Salt 1979). Small changes in interaction rates cascade upwards, changing the locations where species can successfully colonize and the population growth rate. This has large attendant consequences for the population dynamics, community assemblages, and ecosystems that ecologists and natural resource managers are interested in. Therefore, it is important to understand how organismal interactions change across prey and predator densities as well as environmental conditions. The mechanisms regulating these interactions include density-independent and density-dependent processes (also termed scenopoetic vs. biometric variables (Hutchinson 1978), exogenous vs. endogenous factors (Turchin 1999), and conditions vs. resources (Begon et al. 2006)). The effects of these processes change across an individual’s age or size (Keast 1977, Schindler et al. 1997), a population’s density or abundance (Lindberg et al. 2006, White and Warner 2007), a community’s species assemblage or location (Hixon and Beets 1993, Estes and Duggins 1995, Chesson 2000), or any possible combination therein.

Theoretical and mathematical models have been the most ubiquitous methods used to represent our understanding of organisms’ interactions, endogenous and exogenous factors, and their collective and emergent properties ascending the ecological hierarchy (Allen and Starr 1982). Within this framework, considerable work

has been focused on determining whether density independent and density dependent effects dominate the changes observed in population abundance (Rosenzweig 1971, Shima and Osenberg 2003, Walters and Martell 2004). Density-independent processes limit resource availability to populations, either directly through abiotic constraints (e.g. temperature, light, turbulence, etc.) or indirectly by limiting primary production (Hutchinson 1941, Chesson and Huntly 1997, Hixon et al. 2002, White et al. 2010). Density-dependent processes regulate population growth through positive feedbacks on mortality (i.e. depensation) or through negative feedbacks (i.e. compensation).

Depensatory processes arise as an increase in the per capita mortality rate as population density decreases and result from passive (attack-abatement) and active responses in predator-prey interactions (May 1972, White et al. 2010). Passive responses include risk dilution and predator avoidance (e.g., lower detection risk or swamping) while active responses include shared vigilance (Lima 1995), quorum responses (Ward et al. 2008, 2011), or predator deterrence (Motta 1983).

Compensatory processes occur when the per capita mortality rate increases as population density increases and can be roughly partitioned into aggregative (Hassell and May 1974), functional (Holling 1959b, Murdoch 1973, Hunsicker et al. 2011), numerical (Holling 1959b, May and Oster 1976, Hörnfeldt 1994, Karell et al. 2009), and demographic responses (Murdoch 1971). Temporal compensation can arise from both short-term behaviors, namely functional responses (Holling 1959b), in combination with long-term population dynamics, namely numerical and demographic responses (Brook and Bradshaw 2006). Aggregative responses reflect spatial processes as predators

react to the relative density of prey in a patch and vice versa as prey react to the relative predation risk of a given patch (Stewart-Oaten and Murdoch 1990, White et al. 2010).

Habitat can be considered as a direct resource limiter and as density-independent effects (Verhulst 1838, Smith 1935), but its structuring role in predation, competition, and other interactions has led to numerous treatises on its density-dependent effects (Ricker 1954, Beverton and Holt 1957, Schoener 1971). Endogenous mediation either results through compensation, from limitations in refugia availability or foraging arenas (Walters and Juanes 1993, Ahrens et al. 2012), or through depensation, for example behavioral strategies (e.g., swarming or schooling, Allee 1927, 1931, Motta 1983) having minimum density requirements (often termed Allee effects, see May 1972 and Stephens et al. 1999). Consequently, considerable study has theorized how habitat and associated processes might regulate population growth (Holling 1959b, Charnov 1976, Hastings 1980, Abrams and Walters 1996) as well as searching for empirical support for these hypotheses (Solow and Steele 1990, Lindberg 1997, Shenk et al. 1998, Brook and Bradshaw 2006).

The representation of habitat in predator-prey theory (and other intra- and interspecific interactions) has focused on aggregative and functional responses, likely due to their short-term nature and the relative ease in quantifying them. An exception is density independent effects that are typically represented by simple single parameters denoting the aggregate resource cap on population growth, often termed the carrying capacity (Verhulst 1838, Berryman 1992). Compensation occurs continuously over population sizes with the biggest change in per capita mortality rates occurring as a population approaches (or exceeds) this resource limit (Rosenzweig and MacArthur

1963). Within fisheries, compensation is often implemented through a stock-recruit relationship in population models (Ricker 1954, Beverton and Holt 1957, Walters and Martell 2004). Classical mass-action predator-prey models have abstractly accounted for habitat-induced density dependence through simple attack rate parameters (Lotka 1925, Volterra 1931) or through more parameterized representations of predator consumption rates (termed functional responses, Solomon 1949), typically represented as changes in the predator search rate (Holling 1959b, Hassell and May 1974). Compensation has similarly been represented using functional responses (both in terms of changes to search and handling times) but also as a numerical response in population dynamics, most famously as Allee effects (McCarthy 1997, Courchamp et al. 1999, Stephens et al. 1999, Stephens and Sutherland 1999).

Mass-action models and functional responses received criticism from the lack of predator density-dependence (intraspecific competition) and gave rise to ratio-dependent predator-prey theory (Arditi and Ginzburg 1989, Arditi and Berryman 1991, Abrams and Ginzburg 2000). This theory states that predation rates vary as a function of the prey to predator ratio (thus inducing predator intraspecific competition) and resulting in a predator and prey equilibrium determined by prey production (versus solely predator densities in Lotka-Volterra derivatives)(Arditi and Ginzburg 1989). Ratio-dependence incorporates habitat processes in the assumption that spatial heterogeneity forces predators to interact through exploitative or interference competition by locally depleting prey or antagonistic behaviors (Arditi and Ginzburg 1989, Arditi and Saiah 1992). A key limitation of this theory is little mechanistic underpinning of these local

patch dynamics that would result in ratio-dependence and its inherent functional response form (Diehl et al. 1993, Abrams 1994).

Foraging arena theory is one approach that has sought to remedy the “fallacies” (Abrams 1994) of ratio-dependence by positing a mechanistic basis for predator density-dependence. It asserts that competition between predators arises from the behavioral, spatial, or temporal restriction of prey into arenas where prey are vulnerable and invulnerable to predation (Walters and Juanes 1993, Walters and Korman 1999, Ahrens et al. 2012). Exchange rates between vulnerable and invulnerable arenas dictate system dynamics instead of restrictive responses, which vary inter- and intraspecifically. Prey exchange thus “offers” predators opportunities to consume prey and where per-capita prey availability is inversely hyperbolic and prey mortality is hyperbolic across increasing predator densities (Ahrens et al. 2012). It is simple to envision various means that habitat may mediate prey exchange rates, such as acting as a refuge (or not) or altering advection/diffusion processes (Werner et al. 1983, Cury and Roy 1989, Werner and Anholt 1993, Heithaus et al. 2008).

Foraging arena theory predicts that arena structures should cascade across food webs as a result of changes in the exchange rates of any one species. This tenant is shared with many habitat-centric management strategies such as umbrella species (critical habitat is maintained from single-species conservation; Lambeck 1997, Simberloff 1998), reserves (spatial management intended to protect biodiversity and ecosystem functions as well as limiting localized harvest; Roberts et al. 2001, Hilborn et al. 2004), and restorations (repairing habitat degradation; Ewel 1987, Lake et al. 2007). Habitat augmentation is perhaps the most direct management example reliant on

organism-habitat relationships. Augmentation has pervaded aquatic resource management in the form of various habitat-centric strategies (e.g., artificial reefs, restorations, plantings, etc., Roberts et al. 2001, Tugend et al. 2002, Miranda et al. 2010, Bortone et al. 2011). The impact of augmentations has been highly variable ranging from positive (Brooks et al. 2004, Ahrenstorff et al. 2009), neutral (Bohnsack 1989, Sass et al. 2012), negative (Grossman et al. 1997), and unintended effects (Glasby et al. 2006, Sheehy and Vik 2010) on the species of interest. Without any generalized predictions arising from augmentation studies, further evaluation of habitat's role in mediating interactions in stochastic systems is necessary. Thus, further experimental and observational study with habitat as a central focus is warranted for progressing ecological theory and advancing natural resource management. In particular, study of density dependent processes may yield a better understanding of organism-habitat relationships and fruitful management strategies based on probable outcomes as well as tradeoffs.

This dissertation links three examinations of habitat-mediated mechanisms shaping population regulation with a conceptual framework. The framework was developed through a survey of the existing literature to identify commonalities in the assumed mechanism of habitat influence. An overview will build off the discussion above and construct a conceptual framework to integrate the theoretical and empirical outcomes in habitat-centric literature. Each empirical or experimental approach represents a different representation of mortality at spatial and temporal scales. At small spatial and short time scales, intense competition and predation risk result in foraging arena dynamics and rapid variation in organismal behavior (Walters and Korman 1999).

Within a population and over seasons or a year, cumulative mortality from competition and predation drives local population growth through recruitment of early life history stanzas (Walters and Korman 1999, Walters and Martell 2004) and species assemblages through habitat selection. This multi-scale approach is desirable as a central issue in ecology are changes in the attendant patterns of ecological processes across scales (Wiens 1989, Levin 1992, Hunsicker et al. 2011). Scaling from local dynamics to populations to communities to ecosystems inherently induces bias as nonlinear ecological processes are averaged over space or time (Hunsicker et al. 2011). Thus, the role habitat has in alternating predator functional responses are also scale-dependent. I seek to address two questions regarding habitat's role and its scale dependency: 1) at what spatial or temporal scales can the restructuring of predator functional responses by habitat be observed, 2) in what ways does habitat alter the expectations of population regulation and community assembly at each scale.

At the organismal level, an experiment will be conducted to test the underlying ratio-dependent assumptions of foraging arena theory in a simple bass-bluegill predator-prey system. Habitat, in this case, establishes a standardized invulnerable refuge for prey. Changes in prey and predator densities mediate the exchange rates of prey between arenas as well as may manifest behavioral externalities not predicted by ratio-dependent theory. These unpredicted behavioral responses have implications in the rates that stocks rebuild as modeled by ecosystem models, such as Ecopath with Ecosim. At the population level, a lake habitat augmentation experiment will be conducted to evaluate the strength of subsequent attractive and productive responses of game fish. Historically treated as binary outcomes of augmentation, fish attraction to

structure is highly conserved across taxa and an evolutionary stable strategy (Smith 1972). For attraction to persist, attracted individuals should have an improvement in fitness, observed as increases in production. These changes in production are invariably linked to foraging arena responses through density-dependent mortality and growth as well as resource variation. This study aims to ascertain if production can be observed above natural recruitment variation by taking advantage of a small, closed, more observable system than previously considered in comparison studies. The degree habitat influences population growth rates has implications for the performance of habitat-centric management strategies. At the community level, the habitat selection of the fish and turtle community for augmented habitat is assessed. The size and location of habitat are varied to evaluate changes in the species assemblage as a function of distance from existing habitat and size of structure.

CHAPTER 2 ALLEE EFFECTS FROM BEHAVIORAL VARIABILITY IN PREDATOR-PREY INTERACTIONS

Introduction

Ecologists have long sought generalizable predator-prey models that can flexibly describe a wide range of dynamics. These dynamics largely result from the predator's functional response, the per capita predation rate, with many formulations accounting for varying degrees of predator interference (Hassell and Varley 1969, Beddington 1975, DeAngelis et al. 1975, Arditi and Ginzburg 1989) but explicitly ignoring prey behavioral variation (Sih 1979, Okuyama 2008). However in the environment, prey and predators often adopt behaviors dependent on prey densities, predator densities (Werner and Hall 1988, Sih et al. 2003, Stier et al. 2013), and habitat complexity (Savino and Stein 1989a, 1989b). Prey antipredator behaviors and predator foraging modes may act synergistically or antagonistically with the potential for mortality rates to drastically depart from the expectations of a given functional response (Abrams 1993). With the ability of predation to regulate populations (Nicholson 1933), shape community organization (Holt 1977), and act as a major selective force (Abrams 2000), the effect of variable prey and predator behaviors on predation rates is of principal concern.

Many prey antipredator behaviors lead to reductions in predation risk as density increases (Abrams 1990). Passive responses such as risk dilution (*dilution effect*; Williams 1966; Hamilton 1971) and active responses such as shared vigilance (Lima and Dill 1990, Lima 1995), quorum responses (Ward et al. 2008, 2011), and predator deterrence (Motta 1983) often depend on 'safety in numbers' and reduce in effectiveness as prey density declines or are abandoned all together for other behaviors. As a result, inverse density dependence in the per capita prey mortality

arises at the scale of the aggregation (White and Warner 2007, Kramer and Drake 2010). Predator-prey interactions resulting in inverse density dependence are concerning as they can lead to population instability (Allee 1941, Rosenzweig 1971, Stephens and Sutherland 1999), i.e. to “Allee effects” (Courchamp et al. 1999, Stephens et al. 1999, Hutchings 2014). Allee effects resulting from behavior are often presented as a single behavior changing in efficacy as a function of prey density (Stephens et al. 1999) and most functional response formulations reflect this. Thus, commonly used predator-prey models are unlikely to account for prey and predators adopting a multitude of behaviors in response to biotic and abiotic cues.

All predator-prey models can arise from two rate equations, one for the prey population N and the other for the predator population P :

$$dN/dt = f(N) - g(N, P)P \quad (2-1)$$

$$dP/dt = \varepsilon g(N, P)P - \mu P \quad (2-2)$$

where $f(N)$ describes the production of prey, $g(N, P)P$ describes predation, $\varepsilon g(N, P)P$ describes the conversion of consumed prey into predator reproduction, and μP describes the mortality rate of predators. Prey production is typically assumed to follow logistic growth, but in short-term experiments with no prey reproduction it can be assumed to be zero. The prey population can also be assumed to decline through non-predatory means such as senescence, antagonistic behaviors, starvation, or non-lethal predation effects (Fraser and Gilliam 1992), such that Equation 2-1 is modified to include the non-predatory survival rate, S :

$$dN/dt = (0 - g(N, P)P)S \quad (2-3)$$

The per capita mortality rate $g(N, P)$ in simple two body systems, such as one prey and one predator, follows a functional response often one of the Holling functional response types (Holling 1959a, 1959b, 1966). The Holling functional responses types can be represented continuously using the generalized form developed by Real (1977):

$$g(N, P) = g(N) = \frac{aT_t N^n}{1+ahN^n} \quad (2-4)$$

where a is the predator search rate, T_t is the proportion of a predator's time spent foraging or for which prey are available, h is the time spent handling or digesting prey, and n is the number of encounters a predator must have with its prey before the predator is maximally efficient at feeding on that prey item (Real 1977). Typically, the predator's search rate, a , and the proportion of time foraging, T_t , are combined into a single parameter. The generalized form of the Holling functional response can take on the Type I form when $h = 0$ and $n = 1$ (i.e. no handling time or encounter effects), the Type II form when $h > 0$ and $n = 1$ (i.e. no encounter effects), and the Type III form when $h > 0$ and $n > 1$ (i.e. including handling time and encounter effects).

Predator-prey models that are prey-dependent, including only prey into the predator's functional response (i.e. $g(N, P) = g(N)$), are the classic Lotka-Volterra predator-prey models (Berryman 1992). Criticism of the Lotka-Volterra centers around the properties of the independence of equilibrium prey density from predator reproduction (Oksanen et al. 1981) and the production of limit cycles through increases in primary productivity (paradox of enrichment - Rosenzweig 1971). Fundamentally, the Lotka-Volterra models assume prey and predators move in a Brownian fashion akin to the behavior of reacting molecules. This assumption is incongruent with the wealth of

behaviors prey and predators adopt in their interactions. Additionally, foraging predators do not interfere with each other and limit their consumption rates.

Ratio-dependent predator-prey models were developed in order to include predator-dependence in the Lotka-Volterra models and correct its numerical instability (Arditi and Ginzburg 1989, Berryman 1992) by modifying the per capita mortality rate process to depend on the ratio of prey to predators $g(N/P)$. While the ratio-dependent models do relieve the numerical instability of the Lotka-Volterra models, the model formulation lacks behavioral mechanisms (Abrams 1994). Cosner et al. (1999) specifically derived the Type II ratio-dependent functional response as a predator group with constant frontal area foraging on homogeneously distributed prey, an assumption incongruent with restrictive prey behaviors.

An alternative to prey-dependent and ratio-dependent functional responses is foraging arena theory (Ahrens et al. 2012). Beginning as a series of experiments and models in the 1980s and '90s (Werner et al. 1983, Walters and Juanes 1993, Abrams and Walters 1996, Walters and Korman 1999), foraging arena has been widely used in fisheries and ecosystem models through Ecopath with Ecosim (Christensen and Walters 2004). In foraging arena theory, prey exchange from the total population (N) seeking to minimize predation risk by remaining invulnerable (Ware 1975), at rates v and v' , into and out of the foraging arena, or the vulnerable to predation state (V) where predators remove prey at rate aVP (Equation 2-5).

$$dV/dt = v(N - V) - v'V - aVP \quad (2-5)$$

Replacing N with V then modifies the per capita mortality rate in Equation 1-4. Predation rates increase asymptotically as a function of prey exchange rates (Ahrens et

al. 2012), with predation risk diluted among all vulnerable prey with the P/V chance of an individual vulnerable prey being the victim of predation (Lima and Bednekoff 1999). The utility of the foraging arena over the Lotka-Volterra or ratio-dependent models lies in the ability of the arena structure to represent variable prey behaviors and the models pathological flexibility to represent both Lotka-Volterra and ratio-dependence. The latter arises from changes in the exchange rate: strong 'ratio-dependence' from low exchange rates and Lotka-Volterra 'reaction vat' dynamics when exchange rates are high (Ahrens et al. 2012).

Here, we present a test of the ability of predator-prey models to describe mortality rates resulting from variable prey and predator behaviors. A factorial design of low, medium, and high densities of juvenile *Lepomis macrochirus* (Bluegill) predated by *Micropterus floridanus* (Florida Bass) was used to determine the density-dependence of predator-prey behaviors and the ability of predator-prey models to describe the resulting mortality rates. We discuss the applicability of each predator-prey model based on our results and the implications of variable prey and predator behavior on population regulation.

Materials and Methods

Experimental Setup

Experiments were conducted in three experimental 405 m² (one-tenth acre) ponds at the United States Geological Survey Wetland and Aquatic Research Center (Gainesville, FL, USA). Ponds were cleared of vegetation, divided into four treatment groups using block nets, and filled to ≈ 1 m deep in the center. This resulted in each treatment having two edges of shoreline and two edges of block net, all edges ≈ 9 m in length. Low, medium, and high predator and prey densities were chosen based on

empirical field surveys of 59 Florida lakes containing both Florida Bass and Bluegill (Hoyer and Canfield 1994). The low, medium, and high densities corresponded to oligotrophic, mesotrophic, and eutrophic lake nutrient statuses respectively. Prey densities were 20, 100, and 150 individuals while predator densities were one, three, and five individuals. Each pond housed three of the nine possible combinations of predator-prey densities plus a treatment consisting of a medium density of prey and no predators. Treatments were allocated non-randomly to maintain a total of 370 prey and 9 predators in each pond creating three sets of treatment combinations in that pond. This was done to maintain a similar ratio of prey to resources in each pond. Low and high prey densities were located catty-corner to one another and the low prey treatment was randomly allocated to one of the four treatments in each of the ponds for each experimental run. The treatment combinations were moved from pond to pond between each experimental run to reduce pond effects on a given treatment and done in a manner such that each treatment-pond combination was achieved. Three experimental runs were conducted to obtain replicates of the treatment groups. Refuge habitat was standardized to a 2 x 1 m 2.5 cm plastic hex mesh mat suspended from the water's surface along a depth gradient of approximately 15 to 60 cm. The mat was adorned with strips approximately 15 cm in length of plastic survey tape to simulate a natural grass bed.

Experimental Timeline

Experimental runs were conducted for seven days of predator-prey interactions starting April 20th, May 4th, and May 18th, 2016. Preliminary experimental trials indicated that seven days was a sufficient exposure time to ensure contrast in prey mortality rates but without complete removal of all prey in most of the treatments. Each pond was

emptied for two days before each run then filled and allowed to fallow for five days before adding prey. Preliminary experimental trials indicated this emptying-filling regime was sufficient to produce prey food resources, primarily benthofauna (midge larvae). Florida Bass were electrofished three days prior to the start of the experimental run using a 9.0 Generator Powered Pulsator electrofisher (Smith-Root, WA, USA) from Lake Santa Fe, FL (29.741165° N, 82.076767° W) with a median length of 350 mm. Florida Bass were fin clipped with unique within-treatment patterns, their total length measured, and released into their respective treatments for two nights prior to the beginning of the run. Juvenile Bluegill were obtained from Shongaloo Fish Hatchery (Hampton, FL, USA) the morning of the start of the experimental run with a median total length of 51 mm. Hatchery Bluegill were raised in open ponds subject to avian and testudine predators but no piscine piscivores. Approximately one-third of the medium and high prey densities and all of the low density were tagged with Visible Implant Elastomer Tags (Northwest Marine Technology, WA, USA) of a different color for each prey density and a unique color for the no predator treatment. Each prey stocking-group was observed for 15 minutes prior to stocking and any individuals that died during this period were replaced with untagged individuals, to minimize the effects of handling mortality. Prey modal length was measured from individuals that died during handling or were in excess of the required number to stock the treatments (the lengths of stocked individuals were not measured after preliminary experimental trials indicated mortality from measuring to be in excess of 50%). Bluegill were added to treatments directly along the shoreline and into the suspended mesh habitat structure at the start of the experimental run after ensuring the refuge was free of predators. Visual assessments of

the location of fish and their behavior were made through a standardized linear transect along the two shoreline edges of the pond twice over each experimental run. An approximate count and the location-behavior of fish were taken in the morning and in the afternoon to account for shading effects. Ponds were drained at the end of one week, and linear transects along the pond bottom were walked a minimum of three times with additional transects completed, up to six total, if a poor raw depletion signal was observed or if few prey were collected on any given transect. Prey modal length of each treatment and individual lengths and guts of Florida Bass were taken after collection from the drained ponds.

Mortality Rates

We modeled the prey mortality (in numbers of prey) as a latent random variable, $N_{loss,i}$, described by a Binomial distribution as $N_{loss,i} \sim Binomial(N_{stock,i}, \hat{M}_i)$, where $N_{stock,i}$ was the number of prey stocked in each treatment i and \hat{M}_i , assumed to be the product of daily mortality events. The prey mortality, $N_{loss,i}$, was estimated as $1 - N_{surv,i}$, where $N_{surv,i}$ was the maximum likelihood estimate of surviving prey using the Gould and Pollock depletion method (Gould and Pollock 1997) from the series of depletions after each pond was drained. The prey population N was assumed to change as a function of the predation rate, $g(N, P)P$, where $g(N, P)$ describes predator's functional response and P the predator population (prey production was assumed to be zero given the short experimental frame and non-reproductive status of the prey). The prey population was assumed to also decline through non-predatory means such as senescence, antagonistic behaviors, starvation, or non-lethal predation effects (Fraser and Gilliam 1992), modeled as the non-predatory survival rate, S using Equation 3.

We tested Lotka-Volterra, ratio-dependent, and foraging arena predator-prey relationships. A numerical scheme was implemented to predict the integrated accumulated predator consumption, $Q_{t,i}$, and change in prey abundance, $N_{t,i}$, over daily time steps $t = 0 \dots 7$ as:

$$Q_{t,i} = Q_{t-1,i} + g(N_{t,i}, P_i)P_i \quad (2-6)$$

$$N_{t+1,i} = S_i(N_{t,i} - g(N_{t,i}, P_i)P_i) \quad (2-7)$$

where $Q_{0,i} = 0$, $N_{0,i} = N_{stock,i}$, and prey abundance in each subsequent time step, $N_{t+1,i}$, was assumed to change discretely from predation, $g(N_{t,i}, P_i)P_i$, and then non-predation mortality components affecting the finite survival rate, S_i . Pond and experimental run effects for each treatment were incorporated as factors impacting the non-predation survival rate S_i :

$$\text{logit}(S_i) = S_0 + \beta_{pond,i} + \beta_{run,i} \quad (2-8)$$

where $\beta_{x,i}$ represent additive effects on the base survival rate, S_0 , in logit space. The total finite mortality rate, \widehat{M}_i , was calculated as:

$$\widehat{M}_i = 1 - N_{7,i}/N_{stock,i} \quad (2-9)$$

where $N_{7,i}$ was the estimated survivorship after a seven days of predator-prey interactions.

Type I and Type II Holling functional response were tested for each predator-prey relationship type by setting the number of encounters a predator must have with its prey before maximal efficient n to 1 and handling time h to 0 for Type I (Table 2-1). The parsimony of each functional response was compared using the corrected Akaike's information criterion (AICc) and model weights were determined after dropping models with ΔAICc values > 10 (Cavanaugh 1997, Burnham and Anderson 2002). Likelihood

profiles were made for the predator search rate as well as the predator handling time and vulnerable exchange rates if necessary from the top three models. Confidence intervals were estimated for the parameters using Wilk's theorem (Wilks 1938), assuming the test statistic from likelihood ratio tests between the maximum likelihood estimate (MLE) and potential parameter values are asymptotically chi-squared distributed and an $\alpha = 0.1$. Predictions of the expected mortality rate were calculated for each treatment level by pond and by experimental run from each functional response with model weights at the MLE of the parameters. Residuals between these predictions and the empirical data were calculated and visualized. The predicted predator functional response across prey densities from one to 150 individuals and for one, three, and five predators were also calculated for models with model weights at the MLE of the parameters. All models and information criterion calculations were made in program R (R Core Team 2015).

Behavioral Assessment

Observations on the location and behavior of prey and predators were aggregated by day (morning and afternoon transects combined) for each treatment and experimental run. Four post-hoc categories were used to score each treatment's prey locations / behaviors: in shoals along the deeper water edge of the provided weed mat refuge (in habitat), along the shoreline in shoals greater than 10 individuals (nearshore), in the shadows of the block nets (shadows), and immobile, solitary individuals, hidden from view (hiding). Bass locations / behaviors were also scored into four categories: stationary and high site fidelity (ambush), mobile and low site fidelity (shoaling), stationary and in the shadows of the block nets (shadows), as well as immobile and

hidden from view (hiding). The locations / behaviors of prey and predators were counted for each experimental run with a potential maximum score of three per treatment-behavior combination. Behavioral scores for each run and treatment were divided by the number of behaviors observed, such that if a single behavior was observed the treatment-behavior received a score of one and if two or three behaviors were observed the treatment-behavior received scores of one-half or one-third, respectively, in each treatment-behavior group. Behavior for control treatments were completely similarly but the total possible points was out of nine (three control treatments in each run for three experimental runs).

Canonical discriminant analysis (CDA) was applied to the classified prey and predator behaviors in order to determine the relative importance of prey abundance, predator abundance, or the prey-predator ratio in describing the exhibited behaviors. A multivariate analogue to the analysis of variance, CDA seeks to determine discriminant functions that maximize the distances between groups, the location / behavior categories, by using linear combinations of independent variables, the prey and predator abundances as well as the prey-predator ratio. Independent variables were standardized between zero and one to calculate standardized discriminant coefficients and determine the relative importance of each variable, similar to the effect size in regressions. Predictions were made from the resulting discriminant functions across prey abundances ranging from one to 150 individuals and for one, three, and five predator abundances to visualize the change in prey and predator behavior. The package *MASS* in program R was used to implement all CDAs.

Predator Stomach Contents

Gut contents of Florida Bass were examined at the end of each trial and the presence-absence of Bluegill (bones or whole) was assessed as well as whether the stomachs were empty or not. Logistic regressions were used to model the presence-absence of Bluegill and the presence-absence of empty stomachs. The set of logistic regressions used prey abundance, predator abundance, and the prey-predator ratio as covariates while the second set was used prey and predator behaviors. All covariates were standardized between zero and one. From the resulting logistic regressions using prey abundance, predator abundance, and the prey-predator ratio, predictions were made across prey abundances ranging from one to 150 individuals and for one, three, and five predator abundances to visualize the change in the presence of Bluegill and emptiness in Florida Bass stomachs. From the logistic regressions using prey and predator behaviors, predictions were made across probabilities of prey and predator behaviors ranging from zero to one.

Results

Maximum likelihood estimates of $N_{surv,i}$ showed high total finite prey mortality rates for all treatments, ranging from 25 to 100%. Control treatments without Florida Bass had mortality rates within the range of the treatments with Florida Bass indicating either high natural mortality rates or other predators consuming the bluegill, to which we concluded the latter. Numerous Cottonmouth Snakes (189 ha^{-1} , *Agkistrodon piscivorus*), Banded Water Snakes (74 ha^{-1} , *Nerodia fasciata*), and Bullfrogs (41 ha^{-1} , *Lithobates catesbeianus*) were observed in and adjacent to the ponds during pond preparation, and were capable of passing through the chain-link fence surrounding each pond.

Control treatments were not used for subsequent analysis as a result of this likely high external predation.

The top three parsimonious functional responses were all of the Holling Type II functional form and were, in order of parsimony: ratio-dependent, Lotka-Volterra, and foraging arena (Table 2-1). Respectively, the Holling type I functional form of these predator-prey models was 47, 16, and 8 AICc units higher than their Type II form. The negative log-likelihood for these Holling Type II models were nearly equal (Table 2-1). The predator search rate, a , was 0.148 (0.133, 0.164; 90% CI), 0.035 (0.022, 0.055), and 0.677 (0.190, 3.944) while the handling time, h , was 0.059 (0.043, 0.076), 0.688 (0.411, 1.141), and 0.059 (0.006, 0.124) corresponding to realized handling times of 1.4 (1.02, 1.82), 16.5 (11.3, 26.9), and 1.4 (0.144, 2.98) hours for the top three parsimonious models respectively. The foraging arena functional response had a low vulnerable exchange rate, v , of 0.184 (0.162, 0.738) that, using av , gave an effective predator search rate of the total prey population MLE of 0.124. The mean finite survival rate for the top three models was 0.994, 0.918, and 0.993 respectively with basal survival, pond, and run effects all specific to functional response structure. The coefficient of variation in the finite survival rate across ponds and runs of the top three models was lowest with a Lotka-Volterra functional response (1.28%) and higher with a ratio-dependent (1.43%) and the foraging arena functional response (1.58%).

Predictions of prey mortality rates from the top three models with pond and run effects (called full models hereafter) and the corresponding residuals (Figure 2-1A-C) showed that the full models had the greatest residual error in the predicted mortality rates for the low, then medium, then high prey treatments. The Lotka-Volterra and

foraging arena full models predicted 10% higher mortality rates than observed for the high prey treatments. The residual error showed that low prey treatments tended to be more variable than medium or high prey treatments and that the predator-prey formulations we considered were not able to accurately describe the variation.

The predicted per capita prey mortality rate, $Q_{t,i}/N_{t,i}$, from submodels without pond and run effects shared the characteristic of low prey treatments with the highest per capita mortality followed by the medium and then high prey treatments (Figure 2-1D-F). The shape of the per capita mortality fell into two general forms: wide and small disparities in the mortality rates as a function of prey abundance. The Lotka-Volterra submodel predictions showed the former and were nearly linear with little change in the slope as predator abundance increased (Figure 2-1D). The foraging arena and ratio-dependent submodel predictions showed the latter. Foraging arena per capita mortality rapidly approached the asymptote as a function of predator abundance with the same asymptote for each prey treatment (Figure 2-1E). Ratio-dependent per capita mortality approached the asymptote slower than foraging arena and had different asymptotes for each prey treatment (Figure 2-1F).

Predictions of the predator functional responses fell into two general forms: wide and negligible disparities in the per capita predator consumption as a function of the predator abundance (Figure 2-1G-I). Foraging arena and ratio-dependent functional responses exhibited wide disparities while Lotka-Volterra responses were negligible. The foraging arena and ratio-dependent functional responses were similar with minor differences in the asymptotes (Figure 2-1H&I). The highest per capita predator consumption occurred with only one predator (≈ 70 prey per predator) and a two- or

three-fold decrease when three or five predators were stocked. The Lotka-Volterra functional responses did not have different asymptotes of the per capita predator consumption (≈ 8 prey per predator) between different predator abundances but minor differences in the rate at which the asymptote was reached, fastest for one predator and slowest for five predators (Figure 2-1G).

Overall, ratio-dependent and foraging arena Type II predictions were similar across prey and predator densities with high finite daily survival rates and short handling times implying prey mortality coming largely from predation. The foraging arena Type II model had 4.6 and 19.3 times higher predator search rates than ratio-dependent and Lotka-Volterra formulations resulting in a rapid depletion of the vulnerable pool offset by low vulnerable exchange rates. Effectively, this predicted prey to be strongly spatially or behaviorally restricted with high predation risk upon entering the vulnerable pool in the foraging arena model. The Lotka-Volterra Type II model had lower finite daily survival rates ($\approx 8\%$ lower), lower predator search rate, and higher handling times implying prey mortality coming largely from low daily survival due to mortality agents other than Florida Bass. The likelihood of the data given the model and adjusted model weights was similar for each Type II predator-prey model yielding similar predictive performance.

Prey and Predator Behavior

Prey locations / behavior were predominantly split between hiding (33%), nearshore (38%), and in habitat (25%) with few observations (3%) in the shadows. The CDA had three discriminant functions but the majority of the variance in prey behavior was accounted for by the first one ($>96\%$). This discriminant function was predominantly driven by prey abundance (-3.96), then predator abundance (1.25), and lastly by the

prey to predator ratio (0.97) resulting in strong dependence of prey behavior on prey density. Predictions of prey behavior from the CDA (Figure 2-2A-D) showed the probability of being seen in refuge habitat to be highest in the high prey treatment across predator abundances and the probability being seen nearshore to be highest in the medium prey treatment, increasing as a function of predator abundance. Low-prey treatments across predator abundance had a high probability of exhibiting locations / behavior of the hiding type. Control treatments did not exhibit one consistent behavioral pattern with nearly equal probability of prey using the weed mat habitat, hiding, or occurring in nearshore shoals (Figure 2-2A-D). From the CDA predictions and our observations, Bluegill restricted their activity to refuge areas at low densities, shoaled in shallow water along the shoreline at medium densities, and utilized deeper water habitats along the edge of the weed mat at high densities. Increasing predator densities did not drastically change the predictions.

Predator locations / behavior were observed most frequently in the shoaling category (33%) and equally frequent (22%) in the ambush, shadows, and hiding categories. The CDA for predator behavior had three discriminant functions with the majority of the variance explained by the first one (91.4%). Prey to predator ratio drove this discriminant function (-3.21) followed by predator abundance (2.34) and prey abundance (1.83) resulting in strong ratio-dependence of predator behavior and weaker dependence on predator density. Predictions of predator behavior from the CDA (Figure 2-2E-H) showed the probability of observing the ambush category was high for the low predator treatment and increased as a function of prey abundance (Figure 2-2E). The probability of observing the shoaling or shadow category was high only during medium

and high predator treatments with the shoaling probability positively correlated with prey abundance and with the shadows probability negatively correlated with prey abundance (Figure 2-2F-G). For low and medium predator treatments there was a decreasing probability with prey abundance of observing the hiding category (Figure 2-2H). Predators did appear to interfere with one another because stationary ambush behavior with high site fidelity was never exhibited in medium or high predator treatments. Antagonistic behaviors among predators were observed as presumably males occasionally nipped females in the hopes of spawning. We did not observe any other spawning activity and the nipping behavior was observed infrequently (only in the second experimental run).

Predator Stomach Contents

Florida Bass stomachs were 59% empty and only 10% contained Bluegill. The first set of logistic regressions on Bluegill presence-absence and stomach emptiness using prey abundance, predator abundance, and the prey to predator ratio were poor fits to the data ($R^2 = 0.047$, $R^2 = 0.026$, respectively). Bluegill that were collected in Florida Bass Stomachs were most common in medium prey – high predator treatments and low prey – medium predator treatments (Table 2-2) but were not significantly different using a χ^2 test ($\chi^2 = 6.56$, $p = 0.16$). Empty Florida Bass stomachs were most common in high predator treatments (Table 2-2) but were not significantly different ($\chi^2 = 1.54$, $p = 0.82$). The second set of logistic regressions on Bluegill presence-absence and stomach emptiness using prey and predator behaviors had poor fits to the data ($R^2 = 0.106$, $R^2 = 0.042$, respectively). The strongest correlation between Bluegill

presence-absence and prey-predator behaviors had a Pearson's correlation coefficient of 0.09 and between stomach emptiness and prey-predator behaviors had an r of 0.13.

Discussion

The role of behavior in predator-prey systems is essential for an understanding of the mechanisms of density-dependent processes and the nature of population regulation (Nicholson 1933). Here, we showed evidence for Allee effects in Bluegill predated by Florida Bass through increasing per capita mortality with decreasing prey density as a result of prey antipredator behavior and predator foraging modes interacting. Our primary evidence for Allee effects stems from clear support across predatory-prey models for Type II functional responses, as mortality asymptotically increases as a function of prey density. The mechanism of this Allee effect was likely interactions between changes in prey antipredator behavior and predator interference, with the result of swapping from an ambush mode to a shoaling foraging mode. Density-dependent cooperative prey behaviors, principally antipredator behaviors (Allee 1931, Courchamp et al. 1999), and predator saturation in the Holling Type II functional response, called predator-driven Allee effects (Dennis 1989, Gascoigne and Lipcius 2004), have been long noted to result in Allee effects (for a review see Kramer et al. 2009). We cannot claim definitive support for either but found little evidence for predator saturation as Florida Bass stomachs (41% with any type of prey item) were less full than the estimated mean for North American piscivores ($\approx 68\%$) in Arrington et al. (2002).

Often, density-dependent processes are thought to stabilize populations through compensation, such as spatial restriction of prey from predators (Werner and Anholt 1993), with the result of increasing mortality as a population's size increases. However, passive and active responses of prey to predators, such as risk dilution (Williams 1966,

Hamilton 1971), shared vigilance (Lima 1995), quorum responses (Ward et al. 2008, 2011), or deterrence (Motta 1983), are often density-dependent and increase in effectiveness as a population's size increases. This 'safety in numbers' is likely responsible for the selection pressure behind many cooperative behaviors, one such is fish shoaling (Pitcher and Parrish 1993). For example, Sandin and Pacala (2005) found predation on aggregating Blue Chromis (*Chromis cyanea*) to decrease as a function of group size and Stier et al. (2013) found a similar pattern in shoaling Bluntnose Wrasse (*Thalassoma amblycephalum*). The degree to which inverse density dependence (Allee 1941, Neave 1953), leads to population instability depends on the strength of the Allee effect (Kramer et al. 2009) as well as co-occurring compensation (White 2011). Kramer and Drake (2010) showed evidence for instability with a predator-driven Allee effect in *Daphnia magnus* populations and a subsequent increase in the probability of extinction as prey density declined.

Unto to itself, our conclusion of compensatory mortality is not unusual as Kramer et al. (2009) showed an increasing prevalence of studies with evidence of predator-driven Allee effects. However, to our knowledge, few studies have explicitly manipulated both prey and predator densities to the end of showing the mortality rates from variable prey and predator behaviors. While the number of density combinations that we investigated was limited, we found prey per capita mortality increased as a function of predator density. These results are similar to the proportional scaling of per capita mortality rates when doubling the number of predators in Stier et al. (2013) and the increased extinction risk of an increased predator attack rate in Kramer and Drake (2010). Increasing per capita mortality as a function of predator density should lead to

population instability as prey densities become lower and predator densities become higher (Oaten and Murdoch 1975, Courchamp et al. 1999). However, Murdoch (1994) discusses the opposite phenomena in the California red scale (*Aonidiella aurantii*) parasitized by the Golden Chalcid wasp (*Aphytis melinus*) with remarkable population stability despite red scale densities <1% of those without their parasite-predator. This is not an isolated phenomena as other host-parasite systems and some predator-prey systems exhibit such behavior (Hassell et al. 1991, Murdoch 1994).

We must admit one serious caveat about the whole study. The observed mortality rates over the seven-day trials were obviously much higher than would lead to sustainable Florida Bass – Bluegill dynamics on longer time scales. It is quite possible that much of the high mortality was due to using hatchery Bluegill naive to piscine predators and did not, at least initially, behave as wild fish would have. Additionally, we very likely restricted some of the behavior of the natural Florida Bass – Bluegill system that would otherwise stabilized the behavioral-driven Allee effect we observed. Redistribution of prey and predators across the landscape would likely occur in response to the local decline of prey density as prey seek to reduce predation risk through aggregation (Sutherland 1983) and predators seek to reduce mutual interference (Kacelnik et al. 1992). White et al. (2010) and White (2011) proposed that the “patch” defined by predators may exceed the size of the prey aggregation resulting in little effect on predator foraging behavior and stabilization of the effects of inverse density dependent mortality. This phenomena may explain the inverse density dependence we observed as the predators’ “patch” could have exceeded the size of our experimental system and prey were subjugated to concentrated predation pressure that

would have otherwise been distributed over other local aggregations. We feel that this effect may have been somewhat minimized as Bluegill were often observed forming more than one shoal, creating multiple local aggregations, and Florida Bass were observed repeatedly occupying the same spatial locations in each treatment, though it is worth noting these could be symptoms of concentrated predation pressure rather than a lack of.

Perhaps more importantly than finding Allee effects, variation in prey and predator behaviors resulted in departures from expectations in the mortality rate, especially at low prey densities. Prey behaviors and spatial arrangements changed as a function of their own density, reflecting a switch to active responses rather than passive (risk-dilution) ones as prey density increased. For example, extreme spatial restriction of prey from predators (to the point that observers had difficulty finding Bluegill in clear water with fluorescently marked fish) was observed only in low prey treatments while shoaling and movement to deeper water along the edge of the provided habitat occurred in medium and high prey treatments, respectively. Predator behavior changed as a function of the prey-predator ratio possibly reflecting predator interference. Ambush behavior, always exhibited in the low predator treatments, appears to be preferential to other behaviors for consuming Bluegill as observed in the Florida Bass stomach contents analysis. There are obvious benefits to this strategy, Bluegill use auditory and visual cues for proximate detection of predators that a stationary predator foraging strategy would impair (Spotte 2007 pp. 19–32) as well as allowing the characteristic Florida Bass camouflage to further impede visual detection by prey.

As we used prey and predator densities similar to naturally occurring ones, we may not have been able to observe the extreme effects of density-dependent prey and ratio-dependent predator behaviors would have on the per capita mortality rate. However, Tupper and Juanes (2017) recently showed strong effects of predation risk on prey mortality as mediated by habitat complexity on natural reefs in young-of-year Cunner (*Tautoglabrus adspereus*). At higher prey densities than our high prey treatment, we may have observed the “dilution + detection” effect described in White (2011) when an aggregation’s size become so large as to increase their detection by predators resulting in survival not monotonically decreasing as in risk dilution but the formation of a hump shape as detection effects surpass dilution effects as prey density increases.

Variation in prey and predator behavior also indicates a violation of the homogeneity assumption in the Lotka-Volterra predator-prey models. While the Lotka-Volterra Type II model fit nearly as well as the other top models, strong spatial restriction of prey suggests that the predator interference models, foraging arena and ratio-dependent, were more likely to be representative of the predator-prey interactions in our experiment. However, the ratio-dependent predator-prey model may not be appropriate as the derivation from mass-action principles by Cosner et al. (1999) assumed an explicit spatial arrangement of predator foraging groups (constant frontal area) and homogeneously distributed prey which, from our behavioral observations, did not occur in our experiment. Additionally between similar prey:predator ratios, we observed different prey behaviors (nearshore vs. in habitat and hiding vs. nearshore) as well as predator behaviors (ambush/hiding vs. shoaling and shoaling/in shadows vs.

shoaling). This leaves the foraging arena predator-prey model as potentially the most appropriate for describing the behavioral dynamics we observed.

Despite the pathology of the foraging arena agreeing with the behaviors we observed, it was not the most parsimonious model of the mortality rates. Both the ratio-dependent and Lotka-Volterra were more parsimonious with the ratio-dependent model only marginally more so than the Lotka-Volterra. In the Lotka-Volterra models, prey died by non-predatory means and the mortality patterns we observed were accounted for by low survival rates as well as larger pond and run effects. Conversely, the ratio-dependent models had higher predation rates as well as smaller pond and run effects. This contradiction between poor accounting of behavioral pathology but better description of the mortality rates can occur purely as a result of the modeling framework. Had we been able to account for natural mortality and model purely the predation rates, it is likely the most parsimonious model would have changed.

Despite not being the most parsimonious model, foraging arena is still useful as it described the mortality rates nearly as well as the Lotka-Volterra and ratio-dependent models. In our experiment, prey foraging activity was heavily restricted into arenas occupying tiny spatial areas at low prey densities (as to be barely observable), then shallow nearshore arenas at the size of the shoal for medium prey densities, and at high prey densities occupying a larger arena along the deeper water edge with exchange into and out of the weed mat refuge. These behaviors and spatial restrictions are not describable by predator-prey models assuming homogeneity, the Lotka-Volterra and derivatives set (Abrams and Walters 1996), nor by ratio-dependent models that lack mechanisms translating fine-scale behaviors to the attendant population dynamics

(Abrams 1994). As Ahrens et al. (2012) described, the foraging arena exchange rate v and the predator attack rate a can dictate whether the predator-prey dynamics are 'bottom-up' or 'top-down' controlled. Low exchange rates and high predator search rates limit predation by the prey exchange rate into the vulnerable arena vN creating the 'donor-controlled' state while under high exchange rates predation approaches the mass action rate aNP , the 'reaction vat' (Ahrens et al. 2012). Without totally retreading ground that has been covered in the foundational foraging arena papers (see Walters and Juanes 1993, Abrams and Walters 1996, Walters and Korman 1999, Ahrens et al. 2012), arena structures are a useful logical abstraction for envisioning the breadth of predator-prey interactions. In this study, the arenas changed between refuges and fish shoals but most predator-prey systems are easy to envision in an arena context (others that have been put forth previously are: frontal boundaries, diel vertical migrations, advection of 'prey' to sessile predators, drift of benthic stream insects, antagonistic behaviors, and more in Ahrens et al. 2012). We contend, as Walters et al. (2016) recently has, that foraging arena theory can flexibly represent fine-scale predator-prey behaviors that result in density-dependent processes and population regulation. With respect to the 200+ years of predator-prey theory since Malthus (1798), perhaps, focusing on theoretical representations of fine-scale predator-prey interactions will advance theoretical ecology and its applications further than perpetuation of the prey-dependent / ratio-dependent debate.

Table 2-1. Predator-prey models considered in this study with generalized per capita predation, Q/P , the Holling functional response type, the functional response (FR) formulation, the change in the corrected Akaike's Information Criterion from the most parsimonious model $\Delta AICc$, the model weights, and the negative log-likelihood (NLL). *Due to $\Delta AICc$ values > 10 , these functional responses were dropped in the calculation of model weights

Name	Q/P	Holling Type	FR Formulation	$\Delta AICc$	Model wt. (%)	NLL
Lotka-Volterra*	$g(N)$	I	aN	16.13	—	162.33
Lokta-Volterra	$g(N)$	II	$\frac{aN}{1 + ahN}$	0.06	47.76	152.00
Ratio-dependent*	$g(N, P)$	I	$a\left(\frac{N}{P}\right)$	46.84	—	177.68
Ratio-dependent	$g(N, P)$	II	$\frac{a\left(\frac{N}{P}\right)}{1 + ah\left(\frac{N}{P}\right)}$	0.00	49.33	151.97
Foraging Arena Theory*	$g(V, P)$	I	aV	14.33	—	159.13
Foraging Arena Theory	$g(V, P)$	II	$\frac{aV}{1 + ahV}$	5.66	2.91	152.61

Table 2-2. Frequency of Florida Bass stomachs containing Bluegill and completely empty (no prey items) by prey and predator densities.

Prey Density	Predator Densities		
	Low	Medium	High
Bluegill Presence			
Low	0.012	0.025	0.000
Medium	0.000	0.000	0.037
High	0.000	0.012	0.012
Empty Presence			
Low	0.025	0.049	0.136
Medium	0.037	0.062	0.086
High	0.025	0.074	0.099

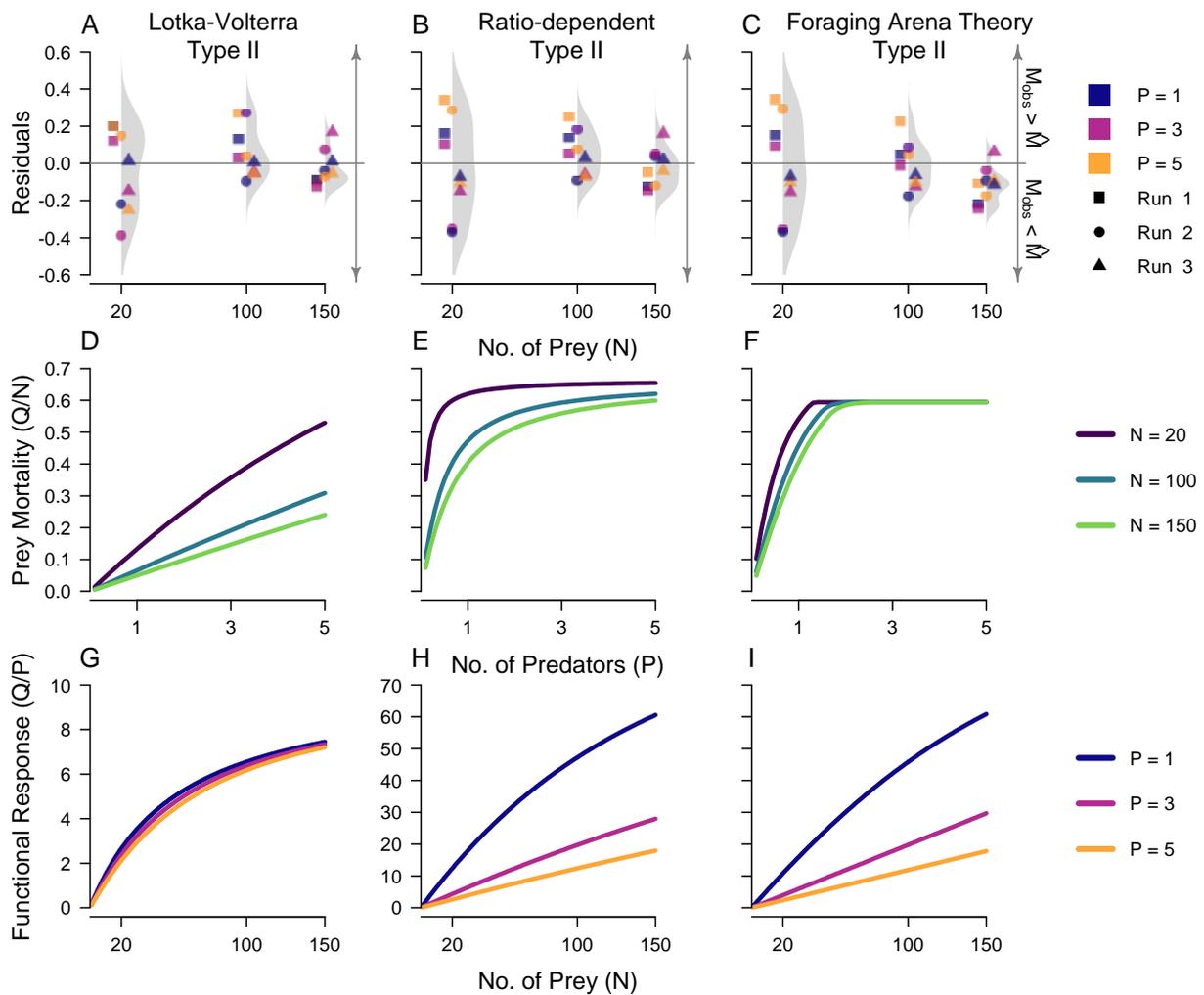


Figure 2-1. Predictions from the Lotka-Volterra, foraging arena, and ratio-dependent Type II predator-prey models. Model residuals of the prey mortality rate (observed mortality, M_{obs} , minus predicted mortality \hat{M}) are shown with warmer colors indicating higher predator densities and each experimental run, 1-3, indicated by triangles, circles, and squares, respectively (A-C). The density distribution of model residuals is indicated by gray polygons. Smooth predictions of the per capita prey mortality rate across a range of predator densities are shown with warmer colors indicating higher prey densities (D-F). Smooth predictions of the per capita predator consumption rate across a range of prey densities are shown with warmer colors indicating higher predator densities (G-I).

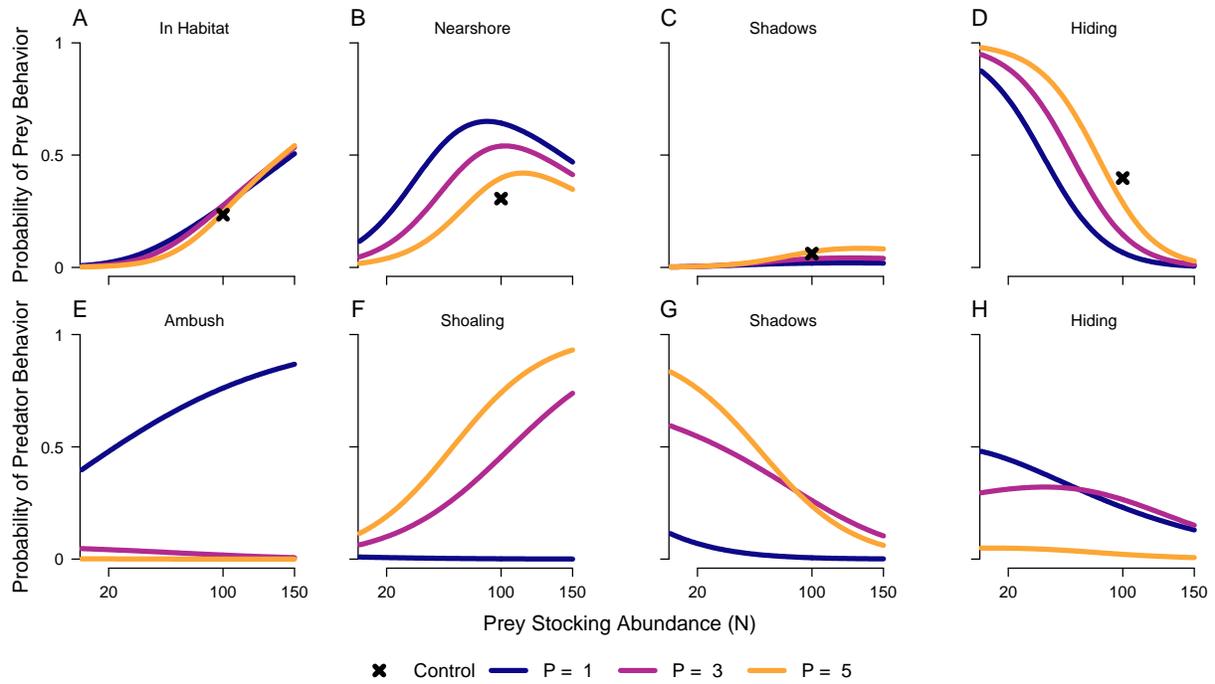


Figure 2-2. Predictions of probability of prey (A-D) and predator behaviors (E-H) across a range of prey densities and three different predator densities as well as the control treatments. Warmer colors indicated higher predator densities while the black x indicates the control treatment.

CHAPTER 3 ASSESSMENT OF THE PRODUCTION POTENTIAL OF ENHANCED AQUATIC SYSTEMS

Introduction

Habitat restoration and augmentation are two of the most common management strategies for aquatic systems in the United States (Ewel 1987, Tugend et al. 2002, Lake et al. 2007, Bortone et al. 2011). Management objectives vary from creating fish attractors (Prince and Maughan 1978, Smith et al. 1979, Johnson and Lynch 1992), nursery habitat (Coen et al. 2007, Lewis and Gilmore 2007), adult refuge (Bohnsack et al. 1994, Miranda et al. 2010), spawning habitat (Kondolf et al. 1996, Koenig et al. 2000), or meeting societal expectations to augment habitat (Tugend et al. 2002). Improvements to meet these objectives vary widely, but rely on modifying the existing levels of habitat through the addition of some structure, artificial (e.g. concrete, tires, derelict ships) or natural (e.g. woody debris, vegetation, stones). Such habitat improvements concentrate fish for anglers and may improve catch rates, however the degree to which population-level production can be improved is unknown (Lindberg 1997, Pickering and Whitmarsh 1997, Bortone et al. 2011). This lingering unknown production potential hinders the effective use of habitat-based management strategies and has led to considerable scientific debate, largely focused on whether fish attract to new structure out of behavioral preference or new habitat confers production (Prince and Maughan 1978, Bohnsack and Sutherland 1985, Lindberg 1997).

The limited evidence of population-level production seen in artificial reef studies extends into freshwater studies. Attraction in freshwater is a near ubiquitous feature of studies aimed at gamefish (Willis and Jones 1986, Barwick et al. 2004, Newbrey et al. 2005, Miranda et al. 2010) but few studies have focused on non-gamefish species,

typically the foraging base for gamefish, outside of stream systems (though see Wills et al. 2004, Sass et al. 2006, Roth et al. 2007). Sass et al. (2006) showed that removal of woody debris changed the diet composition and negatively affected growth rates of Largemouth Bass *Micropterus salmoides*. Gaeta et al. (2011) showed that Largemouth Bass depressed their growth rates in lakes with high levels of shoreline development (e.g. lower densities of woody debris), compared to undeveloped lakes. However additions of habitat in the same lake systems have not had the opposite effect, Sass et al. (2012) found no response in fish growth or recruitment to the addition of coarse woody debris in a second whole-lake experiment with minimal fishing pressure.

Habitat augmentations influence population-level production by creating new habitat where an individual's fitness (Fisher 1930) might improve through occupation or use. The means through which individuals can locate augmented habitat is habitat selection, the process of an individual choosing one habitat over another based on its characteristics that affect vital rates (Greene and Stamps 2001). During habitat selection, organisms redistribute themselves across habitats in order to maximize their fitness. Under an ideal free distribution, individuals experience equal fitness, or realized habitat quality, by modulating competition through varying their density in response to differences in intrinsic habitat quality, or density-independent suitability (Fretwell and Lucas 1969, Bernstein et al. 1991). Under an ideal despotic distribution, a proportional relationship between fitness and intrinsic habitat quality arises from unequal competitors; strong competitors occupying the highest quality habitat while weaker competitors occupy lower quality habitat (Fretwell 1972, Parker and Sutherland 1986, Johnson 2007).

Assuming a system is in equilibrium with respect to individual fitness prior to adding habitat, the potential result of an augmentation is to sequentially redistribute individuals from occupied habitats, change individual fitness as a result of redistribution, and engender a change in population-level production as a result of increasing individual fitness. Redistribution to augmented habitats requires discovery of new habitat from non-oriented (responses to current conditions), oriented (reliance on perceptual cues), and memory mechanisms (use of historical information; sensu Mueller and Fagan 2008). Changes in individual fitness occur through increases in survival or increases in the production of offspring. Increases in fitness result from alleviating competition and predation related to the intrinsic habitat quality of new habitat (Van Horne 1983). In the case of very low intrinsic quality, competition for resources in existing habitat may still be alleviated as individuals with a low likelihood of surviving or reproducing choose to occupy new habitat (Van Horne 1983, Greene and Stamps 2001). New habitat with higher intrinsic habitat quality might also provide higher resource acquisition rates, reduce predation rates, offer more critical habitat, or facilitate positive social interactions (Van Horne 1983).

Any of these processes that improve fitness can result in population-level production. However in aquatic systems, redistribution to new habitat is largely dominated by adult gamefish colonizing new structures rapidly (Moring and Nicholson 1994, Wills et al. 2004), as predicted by their dispersal ability. This likely a result of predation limiting the dispersal of smaller-bodied individuals and fishes to habitats with potentially higher fitness (Werner and Hall 1988). Changes in adult fitness may occur as increases in growth rates, survivorship, or fecundity but these do not necessarily

translate to changes in recruitment (Smokorowski and Pratt 2007). In many aquatic systems, the recruitment bottleneck occurs during the juvenile life phase (Pauly 1980, Walters and Juanes 1993, Walters and Korman 1999) and without contemporaneous improvements in juvenile survivorship by augmented habitat it is unlikely population-level productivity, measured as the number of recruits, will change. Increases in freshwater adult gamefish production without explicit targeting of the juvenile life stage have occurred in relatively bare systems, such as reservoirs (Wills et al. 2004, Miranda et al. 2010). However, many habitat augmentations occur in systems with existing habitat that have typically show no increases in production (Sass et al. 2012, Marsden et al. 2016) and predominantly under the objective of providing fish attractors for anglers (Tugend et al. 2002). This disparity between habitat-poor and habitat-rich augmentation outcomes necessitates comparisons on the changes in gamefish fitness and population-level productivity from habitat augmentations to lakes of different existing habitat quantity.

The purpose of this study is to assess the efficacy of habitat enhancement on influencing the growth, survival, and recruitment of adult Florida Bass *Micropterus floridanus* populations in two Florida lakes with differing levels of existing habitat, rich and poor. We hypothesized that augmentation of brush piles into the habitat-poor lake would increase growth rates and adult survival while the habitat-rich lake would experience little to no increase in growth and survival. As increases in adult growth and survival should increase adult fitness, we hypothesized that Florida Bass adult population estimates would increase post-augmentation in the habitat-poor lake and remain relatively the same in the habitat-rich lake, the latter consistent with previous

lacustrine habitat augmentations (Sass et al. 2012). While we expected to see changes in the fitness and recruitment of Florida Bass post-augmentation we did not expect these changes to exceed the background variability in population size compared to two non-augmented lakes adjacent to the augmented lakes. Shaw and Allen (2016) showed recruitment of Florida Bass in the augmented and comparison lakes to be highly variable as well as Shaw and Allen (2014) showed spawning effort to be sporadic over time.

Materials And Methods

System Characteristics

We experimentally manipulated two of four small lakes with a wealth of prior information on gamefish recruitment, abundance, and lake characteristics (Table 3-1). Private access lakes located on the BJ Bar Ranch southeast of Hawthorne, FL were used for the experiment (Figure 3-1). The four lakes fell into two size groups, small: Big Fish Lake (3.2 ha) and Keys Lake (3.6 ha), and large: Devil's Hole Lake (11.6 ha) and Speckled Perch Lake (12.4 ha). We chose to augment habitat in one small (Big Fish Lake) and one large lake (Speckled Perch Lake) and as a result one small (Keys Lake) and one large lake (Devil's Hole Lake) were used as non-augmented comparisons. Speckled Perch Lake and Devil's Hole were considered habitat-rich with wider littoral zones (9.2 and 10.6 m, respectively; consisting of emergent and floating-level vegetation) while Big Fish Lake and Keys Lake were considered habitat-poor with narrower littoral zones (4.1 and 5.8 m, respectively). Speckled Perch Lake also had the highest submersed aquatic vegetation (percent volume infested, 7.4%) while Big Fish Lake had the lowest (1.7%).

The fish communities in each lake differed in various ways (e.g. the number of Cyprinid species, the presence/absence of Florida Gar *Lepisosteus platyrhincus* or Brown Bullhead *Ameiurus nebulosus*, and the number of *Lepomis* species) but were similar in that the dominant *Lepomis* species was Bluegill *Lepomis macrochirus* and the dominant aquatic predator was Florida Bass. Evidence of other apex predators, such as Alligator *Alligator mississippiensis* or River Otter *Lontra canadensis*, was limited to only five occasions over three years. The bottom contours of each system differed quite considerably (Figure 3-1A) with Speckled Perch Lake having a relatively uniform maximum depth at 2.4-2.6 m while the rest of the lakes showed more variability in lake depth and deeper maximum depths (ranging from 5.5 to 7.6 m).

Augmentation

Sand Live Oaks *Quercus geminata* were logged from the BJ Bar Ranch ranging in heights from four to seven meters and divided into two categories of brush piles consisting of a single tree (termed small) or three trees (termed large). The augmentation effect was a 15-20% increase in habitat by surface area in Big Fish Lake and 12-16% by surface area in Speckled Perch Lake resulting in 16 and 64 brush piles in each lake, respectively (Figure 3-1B-C). Brush piles were transported by boat to randomly selected locations from two strata, nearshore and offshore environments that were less than and greater than 65 m from shore, respectively, in Speckled Perch Lake and 20 m in Big Fish Lake. In Big Fish Lake, brush piles in the nearshore category were typically in depths of 2–3 m and in the offshore category in depths of 3–4 m. In Speckled Perch Lake, brush piles in the nearshore category were in depths 1.5–2 m and in the offshore category were in depths 2–2.5 m. Small and large brush piles were divided evenly between these two categories. Four brush pile strata resulted in Big Fish

Lake: 1) small brush pile – nearshore (small, close), 2) small brush pile – offshore (small, far), 3) large brush pile – nearshore (large, close), and 4) large brush pile – offshore (large, far). Six brush pile strata resulted in Speckled Perch Lake: 1) small brush pile – nearshore, 2) small brush pile – offshore, 3) small brush pile – *Nuphar* (small, *Nuphar*), 4) large brush pile – nearshore, 5) large brush pile – offshore, and 6) large brush pile- *Nuphar* (large, *Nuphar*). The *Nuphar* strata resulted from the placement of offshore brush piles in patches of Spatterdock *Nuphar advena* in the center of the lake.

Capture Survey Design

Electrofishing and angler surveys were conducted on each lake from 2009 to 2015 under a variety of objectives (Figure 3-2). Electrofishing surveys were conducted from 2009 to 2012 during the day using a generator powered Smith-Root Type VI-A electrofisher (Smith-Root, Vancouver, WA) using one stainless dropper rig and one to two netters on a 4.88 m modified aluminum V-hulled vessel, coded as MS-DE (Hangsleben et al. 2013). Output settings ranged between 170 to 500V and modulated the DC pulse frequency to maintain 4 – 5 amps and the sampling objective was to capture gamefish (Florida Bass, Black Crappie, Bluegill) as well as Lake Chubsuckers (*Erymizon succetta*). From 2014 to 2015, daytime, coded as ZS-DE, and nighttime, coded as ZS-NE, electrofishing surveys were conducted using the same electrofishing rig as used for 2009 – 2012 but the objective was to capture all fish species and tag Florida Bass and Bluegill over 250 mm and 175 mm, respectively. In 2015, a nighttime electrofishing survey routine, coded as GS-NE, was conducted in only Devil's Hole Lake using a Smith-Root 7.5 generator-powered pulsator (GPP) with two stainless steel eight dropper rigs and two netters on a 5.5 m aluminum vessel. Output settings ranged

between 335 and 500 V and modulated the DC pulse frequency to maintain 4 – 5 amps with a sampling objective of targeting (> 250 mm) Florida Bass for marking and recapturing.

Angling surveys were conducted year-round from 2009 – 2012 using an open gear set for marking and recapturing Florida Bass, coded as MS-AN. In 2013, angling surveys were conducted in late spring and late fall in Devil’s Hole Lake with a fixed gear set, swapping gears every hour (Gary Yamamoto Senkos and Bill Lewis Rat-L-Traps in spring with the addition of a Zoom Super Fluke and Bomber Square A crankbait in the fall), aimed at marking and recapturing Florida Bass, coded as NS-AN. Angling conducted between summer and fall of 2014 in all lakes used an open gear set aimed at marking and recapturing Florida Bass and adult Bluegill, coded as ZS-AN. In late fall 2014 and into late spring 2015, angling surveys were conducted using a fixed gear set (Z-man ElaZtech Diezel Minnows, Floating WormZ, Pop FrogZ, and StreakZ) aimed at marking and recapturing Florida Bass, coded as GS-AN. All captured Florida Bass were measured for total length (TL). Recapture histories for Florida Bass across gears were determined and multiple marks were consolidated into one identifying record for each lake. The gear at capture and date at capture were kept as metadata for mark-recapture analysis.

Growth Analysis

Growth increments, the difference in the total length at capture between capture events, were used to estimate von Bertalanffy growth parameters and predict total length at age using an improved Fabens method developed in Wang (1998):

$$L_{t+1} - L_t = [l_{\infty} + \beta(L_t - \bar{L}_t) - L_t](1 - \exp(-K(T_{t+1} - T_t))) + \gamma D_t \quad (3-1)$$

where L_{t+1} is the length at the next capture, L_t is the length at capture, \bar{L}_t is the sample mean length at capture, T_{t+1} is the date at next capture, T_t is the time at capture, l_∞ is the mean maximum length of the recapture population (different than the standard von Bertalanffy L_∞ , [$L_\infty \approx l_\infty + \beta(L_t - \bar{L}_t)$]), β controls the degree of individual variation in the growth increment, K is the Brody growth coefficient, γ is the post-augmentation increment effect, and D_t is the proportion of the time increment that occurred during the post-augmentation (ranging from 0 to 1). An increment level effect, γ , was chosen to encapsulate changes in l_∞ or K during the post-augmentation rather than making an explicit assumption as to whether one or the other was impacted. If $\beta = 0$, then there is no individual variation in the growth increment while $\beta > 0$ entails greater individual variation. The residuals between the observed growth increment and the predicted increment was assumed to be normally distributed:

$$L_{t+1} - L_t \sim N(\widehat{L_{t+1}} - L_t, \sigma) \quad (3-2)$$

where σ is the residual error. Priors were weakly informative for l_∞ , β , and γ while informative for K and σ to generate the probability mass in likely parameter values (Table 2). Convergence was assessed using the Gelman-Rubin statistic (<1.001; Gelman and Rubin 1992) and visually. The significance of the post-augmentation increment effect, γ , was assessed at an $\alpha = 0.2$ and determined significant if the 80% credible intervals did not overlap zero.

Due to measurement error, length increments were pre-processed to drop records of length at capture that resulted in negative growth increments. As there was no way to ascertain whether the initial length at capture or the subsequent length at capture was in error (e.g. the first length measured fish longer than reality or the second

measured fish shorter than reality), the pre-processing compiled two growth increments sets using a forward projection (dropping future records lower than the initial capture) and a backward projection (dropping past records higher than the last capture). Overall, the projection pre-processing removed combinations of observations that resulted in negative growth. Estimation of von Bertalffy growth parameters for each lake was conducted in JAGS (Plummer 2003) using runjags (Denwood 2013) in R (R Core Team 2015).

Mark – Recapture Analysis

A modified Cormack-Jolly-Seber (CJS) was used to analyze the recapture history dataset to determine yearly survival rates for Florida Bass, yearly population sizes, and gear-specific detection probabilities (Cormack 1964, Jolly 1965, Seber 1965). The CJS conditions on first capture, ignoring the possible latent state variable of entered or not as estimated by the Jolly-Seber class of models (Jolly 1965, Seber 1965). We chose the CJS model over Jolly-Seber models due to this restriction as our recapture histories resulted from irregular sampling over seven years leading to issues with estimating the entrance probability of fish. A state-space formulation of the Cormack-Jolly-Seber (Royle 2008, Kéry and Schaub 2011) was used where the latent state variable of individual survival is estimated (Equations 3-3 and 3-4). The state-space formulation is useful as it allows for modeling heterogeneity at the scale of individuals and sampling events. Given the sampling heterogeneity we encountered from combining multiple survey routines, the state-space formulation was the most practical.

$$z_i f_i = 1 \tag{3-3}$$

$$z_{i,t+1} | z_t \sim \text{Bernouli}(z_{i,t} \phi_{i,t}^{\Delta t}) \tag{3-4}$$

where $z_{i,t}$ is the latent state variable for individual i at time t , f_i is the first capture event of individual i , and $\phi_{i,t}$ is the survival rate for individual i at time t . Thus, survival from t to $t+1$ (Δt) is Bernoulli distributed with probability of surviving equal to the latent survival state times the survival probability. Annual survival rates were raised to the Δt to scale the survival probability from sampling t to $t+1$ as a factor of the time interval Δt .

Observations of the latent state are also Bernoulli distributed (Equation 3-5):

$$y_{i,t}|z_{i,t} \sim \text{Bernoulli}(z_{i,t}p_{i,t}) \quad (3-5)$$

where $y_{i,t}$ is the recapture history and $p_{i,t}$ is the detection probability. Both the survival ($\phi_{i,t}$) and the detection ($p_{i,t}$) were assumed to vary with sampling events (t):

$$\phi_{i,t} = \mu_{\phi,t_{yr}} \quad (3-6)$$

$$p_{i,t} = \mu_{p,t_{gear}} + \varepsilon_t \quad (3-7)$$

where $\mu_{\phi,t_{yr}}$ is the mean survival probability for sampling event t based on the year of the event, $\mu_{p,t_{gear}}$ is the mean detection probability for sampling event t based on the gear used during the event, and ε_t is the random effect of a given sampling event.

These random effects were assumed to come from a normal hyperdistribution (Equation 8):

$$\varepsilon_t \sim N(0, \sigma) \quad (3-8)$$

$$\sigma \sim U(0,5) \quad (3-9)$$

where σ is the standard deviation of the hyperdistribution and has an informative uniform prior between 0 and 5 (Equation 3-9). Random effects for sampling events were used to account for any variation that may have accounted from one sampling event to the next such as changes in effort, environmental conditions, or changes in lure sets during angling surveys. We implemented the state-space CJS model in STAN (STAN

Development Team 2017a) using the no U-turn sampler (NUTS) with a burn-in of 1,000 and gross sampling of 10,000 with a thinning rate of every 10th for a total of 1,000 samples. The STAN model was computed using RStan (STAN Development Team 2016) in R (R Core Team 2016). Posteriors were assessed for convergence using the Gelman-Rubin diagnostic (<1.001; Gelman and Rubin 1992) as well as visually assessed.

Population estimates for each sampling event k were calculated as:

$$\hat{N}_t = \frac{\omega_t}{p_t} \quad (3-10)$$

$$\omega_t = \sum_{i=1}^I X_{i,t} \quad (3-11)$$

where \hat{N}_t is population estimate at sampling event t and ω_t is the summation of capture histories, $X_{i,t}$, for sampling event t . Yearly population estimates were derived similarly to the sampling event estimates (Equation 3-12 –3-14):

$$\hat{N}_{s,year} = \frac{\omega_{s,year}}{p_{s,year}} \quad (3-12)$$

$$\omega_{s,year} \sim \text{Poisson}(\lambda_{year}) \quad (3-13)$$

$$\text{logit}(p_{s,year}) \sim N(\mu_{p_{year}}, \sigma_{p_{year}}) \quad (3-14)$$

where $\hat{N}_{s,year}$ is one sample of the population estimate in a given year, $\omega_{s,year}$ is one sample from a Poisson distribution with mean λ_{year} describing the distribution of the number of recaptures in a given year, and $p_{s,year}$ is one sample from a Normal distribution with mean $\mu_{p_{year}}$ and standard deviation $\sigma_{p_{year}}$ describing the distribution of logit transformed detection probabilities in a given year. The $\mu_{p_{year}}$ and $\sigma_{p_{year}}$ are mean and standard deviation of the values of p_t at t through T sampling events in a given year; where p_t is calculate using Equation 7. A thousand samples were generated for

$\omega_{s,year}$ and $p_{s,year}$ to generate 1,000 samples of \hat{N}_{year} . The median, the 10th, and the 90th quantiles were calculated from the estimates of \hat{N}_{year} . The significance of the augmentation on survival and population estimates was assessed by taking the difference between estimates for 2014 and 2015 (last pre-augmentation and only post-augmentation years, respectively) and estimating the 80% credible intervals of the difference. Significance at an $\alpha = 0.2$ was assessed as the 80% credible intervals not overlapping zero.

Results

von Bertalanffy Growth

Florida Bass were estimated to have very different von Bertalanffy growth curves among lakes but consistent growth curves within a lake pre- and post-augmentation (Figure 3-3A). Prior to augmentation, the larger lakes, Speckled Perch Lake and Devil's Hole Lake, had similar growth curves with low Brody growth coefficients (K ; Figure 3-3B), mean maximum length of the recapture population around 459–472 mm (l_{∞} ; Figure 3-3C), but high values for the growth variation parameter in Speckled Perch Lake and low values in Devil's Hole Lake (β ; Figure 3-3D). Keys Lake had higher estimates of the Brody growth coefficient and slightly lower l_{∞} than the larger lakes with a similar low growth variation to the Devil's Hole Lake. Big Fish Lake had a considerably different growth curve, appearing almost deterministic in nature, with a high Brody growth coefficient median estimate of 0.78, low l_{∞} around 343 mm, and low growth variation. Post augmentation, mean growth increased slightly in the large augmented lake, Speckled Perch Lake ($\bar{\gamma} = 1.5$) and in the large comparison lake, Devil's Hole Lake ($\bar{\gamma} = 1.0$). In the smaller augmented lake, Big Fish Lake, mean growth increased slightly more than the larger lakes ($\bar{\gamma} = 3.2$) but was not identifiable in Keys Lake. None of the

post-augmentation increment effects, γ , were significant with all 80% credible intervals overlapping zero (Figure 3-3E).

Cormack-Jolly-Seber Performance

The Cormack-Jolly-Seber model converged on survival and detection probabilities for all lakes across years and gears with the exception of Big Fish Lake and Keys Lake. In these lakes, the estimation of the mean detection probability for ZS-NE nighttime electrofishing was unidentifiable from intrinsic and extrinsic nonidentifiability. Intrinsic nonidentifiability resulted from the inability of the CJS model structure to resolve the detection probability of the last sampling event. Extrinsic nonidentifiability resulted from a low number of sampling events in these lakes by ZS-NE gear and few fish recaptured on these events. Subsequent analyses disregarded these sampling events when estimating survival and detection probability.

Detection Probabilities

Average detection probabilities across lakes were lowest in Devil's Hole Lake (0.013), then Keys Lake (0.034), then Speckled Perch Lake (0.040), and highest in Big Fish Lake (0.046). Across gears, angling had lower average detection probabilities (NC-AN, 0.02; ZS-AN, 0.021; GS-AN, 0.024; and MH-AN, 0.030) than daytime electrofishing (ZS-DE; 0.037 and MH-DE, 0.042). Nighttime electrofishing had the lowest (GS-NE, 0.004) and highest (ZS-NE, 0.087) average detection probability with gear saturation likely the cause of the lowest detection probability. In the large augmented lake, Speckled Perch Lake, ZS-AN had the lowest mean detection probability while ZS-NE had the highest (Figure 3-4). Mean detection probabilities in small augmented lake, Big Fish Lake, were lowest for MH-AN and highest for ZS-DE. In large comparison lake, Devil's Hole Lake, ZS-AN had the lowest while NC-AN had the highest mean detection

probabilities. Mean detection probabilities were lowest for ZS-DE and highest for MH-DE in small comparison lake, Keys Lake.

Inclusion of sampling event random effects, called effective detection probability hereafter, dampened the differences between the mean detection probabilities between gears to some extent (Table 3-3). In Speckled Perch Lake, ZS-AN had the lowest and ZS-NE had the highest mean effective detection probability across sampling events. Mean effective detection probabilities in Big Fish Lake were lowest for MH-AN and highest for ZS-DE. In Devil's Hole Lake, GS-NE had the lowest mean effective detection probability while GS-AN had the highest with NC-AN and MH-DE having similar probabilities. The gear with the lowest mean effective detection probability in Keys Lake was ZS-AN and the highest was MH-DE.

Survival Probabilities

"Apparent survival" for each lake varied considerably (Figure 3-5). For all lakes except Devil's Hole Lake, the median survival probability was highest in 2009. In the augmented lakes, Speckled Perch Lake and Big Fish Lake, very low survival in 2010 and 2014 were followed by moderately higher survival in 2011 and 2015 (Figure 3-5A and 3-5B). In the larger comparison lake, Devil's Hole Lake, median survival probabilities followed a sawtooth pattern; increasing from 2009 to 2010, decreasing in 2011, then increasing from 2011 to 2013, then severely decreasing in 2014 and increasing moderately in 2015 (Figure 3-3C). In the small comparison lake, Keys Lake, median survival probabilities remained relatively the same from 2009 to 2011, decreased in 2012, and then again decreased in 2015 (Figure 3-5D).

The 80% confidence intervals for apparent survival were on average the widest in Big Fish Lake and Keys Lake likely from lower sample sizes. On average, the last

year with sampling (2015 and the post-augmentation block for all lakes except Keys Lake which was in 2014) had the highest uncertainty in survival probabilities followed by the first sampling event. This is largely an artifact of the CJS model structure, which has greater uncertainty in parameter estimates for the initial and final sampling events. Higher degrees of uncertainty in last year of sampling is also due in part to some reductions in sampling effort relative to early years of sampling.

Post-augmentation survival increased significantly in Speckled Perch Lake (80% CI: 0.036 – 0.518 in Speckled Perch Lake) and in Big Fish Lake (80% CI: 0.090 – 0.531), the two augmented lakes. The smaller augmented lake, Big Fish Lake had a slightly greater median difference between pre- and post-augmentation survival rates (0.383) than the larger augmented lake, Speckled Perch Lake (0.307). The larger comparison lake, Devil's Hole Lake, survival rates from pre- to post-augmentation were insignificantly different with a small median difference (0.085). Survival rates were not identifiable for the post-augmentation period in the smaller comparison lake, Keys Lake.

Abundance Estimates

Across lakes, Keys Lake had the lowest median adult abundance (Florida Bass > 250 mm) at 80 individuals, then Big Fish Lake (81), then Speckled Perch Lake (276), and lastly Devil's Hole Lake (770). In the larger augmented lake, Speckled Perch Lake, median adult abundance estimates decline from 2009 to 2011 four-fold, increased seven-fold in 2014, then declined slightly in 2015 during the post-augmentation period (Figure 3-6A). Big Fish Lake median adult abundance declined from 2009 to 2015 in the post-augmentation period by 85% (Figure 3-6B). In Devil's Hole Lake, median adult abundance exhibited a saw-tooth pattern, increasing and decreasing year to year, while trending upward for a 163% increase from 2009 to 2015 during the post-augmentation

period (Figure 3-6C). Mean adult abundance declined four-fold in Keys Lake from 2009 to 2011, doubled in 2012, and doubled again in 2014 (Figure 3-6D).

Post-augmentation adult population estimates decreased significantly in Speckled Perch Lake (80% CI: -275 – -25 in Speckled Perch Lake) and decreased insignificantly in Big Fish Lake (80% CI: -54 – 3), the two augmented lakes. The larger augmented lake, Speckled Perch Lake, had a greater median difference between pre- and post-augmentation survival rates (-123 adults) than the smaller augmented lake, Big Fish Lake (-27 adults). Relative to the median population estimate prior to the post-augmentation period, Speckled Perch Lake declined by 50% and Big Fish Lake declined by 28%. The larger comparison lake, Devil's Hole Lake, population estimates post-augmentation were significantly greater with a largest median difference of the three lakes with estimates (+405 adults). Population estimates were not identifiable for the post-augmentation period in the smaller comparison lake, Keys Lake.

Discussion

Habitat augmentations in freshwater systems seem to possess feedback between the amount of existing habitat and the conferred increases in vital rates and production of gamefish. Systems replete with existing habitat or even possessing a modicum of existing habitat have been observed to experience little changes in growth (Sass et al. 2012) or recruitment following augmentations (Allen et al. 2003, Sass et al. 2012, Marsden et al. 2016) while systems with sparse habitat experience large increases in growth and recruitment (Willis and Jones 1986, Wills et al. 2004, Miranda et al. 2010). Here, we experimentally manipulated two small, Florida lakes with different levels of existing habitat, rich and poor, and assessed the changes in Florida Bass growth, survival, and adult abundance before and after a habitat augmentation.

Contrary to our hypothesis that existing habitat quantity would lead to different responses in growth, survival, and adult abundance, we observed the same median response for both augmented lakes. Growth only had a minor increase while survival increased significantly post-augmentation in both augmented lakes. Adult population estimates decreased significantly in the habitat-rich augmented lake, Speckled Perch Lake, and decreased insignificantly in the habitat-poor augmented lake, Big Fish Lake. We had hypothesized that the population estimate would increase from changes in growth and survival (we only observed positive changes in survival) instead we observed declines in the adult abundance. Compared to the augmented lakes, the large comparison lake had no significant changes in growth or survival but a significant increase in the adult abundance indicating the dynamics in the augmented lakes were likely from an augmentation effect.

To our knowledge, few habitat augmentation studies have estimated adult survival as a function of the augmentation typically focusing on growth, diet, behavior, or density (Allen et al. 2003, Gaeta et al. 2011, 2014, Sass et al. 2012). We observed significant increases in median “apparent survival” while simultaneously observing declines in the adult population estimates following the habitat augmentations. Median “apparent survival” estimates were low in 2010 in our augmented lakes, Speckled Perch Lake and Big Fish Lake, and low in 2014 across all lakes. These observations could arise from either environmental perturbation or changes in vulnerability to the gear. Delayed effects in “apparent survival” from the prolonged drought in 2010 – 2011 and the resultant low lake levels in 2012 (Figure 3-7) could be linked to declines in the foraging base for gamefish. Reductions in zooplankton (e.g. cladocerans) from little

rainfall and low lake height (as described by Havens et al. 2016) could lead to declines in forage fish and produced the subsequent low gamefish survival in 2014, the last pre-augmentation year. Low “apparent survival” in our augmented lakes could have resulted from this drought in 2010 as well, as Speckled Perch Lake and Big Fish Lake are less connected to aquifers and more reliant on surficial water input through precipitation than Devil’s Hole Lake and Keys Lake.

Despite these environmental possible mechanisms, it is unlikely that adult median survival rates changed as much as we estimated. Allen et al. (2002), in their survey of Florida Bass mortality in Florida Lakes, found a mean annual survival of 0.51 and, including fishing mortality, 70% of annual survival rates were between 40 and 60%, considerably less variation that predicted in our study lakes. Allen et al. (2008), confirmed this pattern in their survey of Largemouth Bass mortality, finding mean annual survival rates (including all mortality sources) in peninsular Florida of 0.5, a nationwide mean of 0.42, and an estimated natural mortality of 0.49. We suspect that the most plausible explanation for our low pre-augmentation survival and decline in adult abundance arises from changes in catchability after our augmentation.

Generally, the number of recaptured Florida Bass declined as a function of the number of sampling events by gear indicating, at minimum, declining catchability for each gear (Figure 3-8). This is not wholly unexpected as Hanglshoben et al. (2013) found catchability in these lakes to vary considerably during daytime electrofishing. In 2014, the last pre-augmentation year, angling became a predominant survey method in the augmented lakes and had the potential to sample a different vulnerable pool of the gamefish population. High initial capture rates from accessing this new vulnerable pool

coupled with low recapture rates had the potential to bias population estimates high. There is evidence for this phenomenon in the other large lake, Devil's Hole Lake, and in our other small lake, Keys Lake, as angling became a dominant survey method in 2013 and 2014, respectively, and co-occurred with a sizeable increase in their population size.

Declining catchability does not explain the overall decline of the population estimate in Big Fish Lake however. One possibility is drought during 2010 and 2011 had long lasting effects on the foraging base for Florida Bass. Another possibility is that the increase use of Big Fish Lake by a small herd of Water Buffalo *Bubalus bubalis* starting in 2013 (Figure 3-9) adversely impacted the gamefish population in some way (e.g. bioturbation, eutrophication from excrement, or littoral habitat disturbance). Anecdotally, adult Florida Bass did not seem to exhibit negative behavioral responses to Water Buffalo presence and were often angled in close proximity, potentially taking advantage of the animal-based structure in a mostly featureless lake.

While declining catchability is the most likely driver of observed survival and abundance dynamics we observed, the various growth trajectories across lakes could be contributing. Density-dependent adult somatic growth is often linked to changes in the food supply (Beverton and Holt 1957). Somatic growth curves like those predicted in Big Fish Lake where fish grow quickly to the mean maximum length predict strong density-dependent growth in adults. It is very unlikely our habitat augmentation increased the production of forage fish and perhaps even stunted primary production through reducing nutrient resuspension in the lake by reducing fetch (visibility increased from < 1m from 2009 – 2014 to > 4 m in 2015). This could have contributed to the

overall decline in Big Fish Lake especially post-augmentation. In contrast, growth trajectories like those in Devil's Hole Lake and Speckled Perch Lake where fish grow slowly and rarely reach their mean maximum length could indicate density-dependence in early life stanzas. Gaeta et al. (2014) simulated Largemouth Bass growth across a range of coarse woody habitat densities based on empirical data and found slow growth at low coarse woody habitat (CWH) densities as a result of the decline of their prey base. Interestingly, the lakes in our study with the highest abundance of pre-augmentation vegetation and CWH, Speckled Perch Lake and Devil's Hole Lake, also had the slowest growth; the opposite of Gaeta et al. (2011, 2014). The structurally simple lakes, Big Fish Lake and to a lesser degree Keys Lake, may allow Florida Bass to achieve high predation rates and high initial growth rates. Conversely, structurally complex systems such as Speckled Perch Lake and Devil's Hole Lake may limit the foraging opportunities of young Florida Bass and limit their growth (Savino and Stein 1989b).

Irrespective of the mechanisms driving survival, and adult abundance dynamics, our estimates were very uncertain. Few other augmented systems have matched the degree of recapture sampling, the augmentation amount by surface area, the plethora of pre-augmentation information, or the closed system we had in this study (though see Sass et al. 2006, 2012, Gaeta et al. 2011). Even with this approach, we are not able to say habitat augmentations confer population-level production. There are obvious issues in our study common to all augmentation studies, such as a lack of replication and temporal autocorrelation confounding augmentation effects with other regimes. There is a clear tradeoff in the use of closed versus open systems in assessing augmentation

effects. Open systems suffer from immigration-emigration processes masking discrete effects from redistributing fishes but can augment in many locations to generate replicates. Conversely, closed systems, such as our small study lakes, remove the confounding immigration-emigration processes but lack the replication to address the question.

We experienced another factor that has not been frequently mentioned in augmentation studies: changing catchability. We infer this changing catchability to stem from gear saturation as declining capture rates over time were observed in multiple gears (Figure 3-8). Thus, our system and other small lakes might suffer Heisenberg's uncertainty principle where the attempts to measure the system with greater precision alter the trajectory of the system. In our lakes, saturating sampling effort may have resulted in changes in the vulnerability to the gear over time and biased recapture rates, detection probabilities, and the population estimates derived from them. We could have supplemented our sampling protocol with additional metrics such as condition (weights were recorded intermittently across gears so we were not able to include it in our analyses), measured growth using otoliths, conducted sampling aimed at young-of-year fish or other metrics of early life stages. However, these would not have resulted in more precise population estimates and may not have provided better inferences on the dynamics. For example, little discernible relationship can be made between the "apparent survival" estimates and brood success and relative age-1 density (Figure 3-10) collected by Shaw and Allen (2016). However, the variability in brood success and age-1 recruitment estimates do suggest that the highly variable "apparent survival" estimates we observed is are more likely resulting from changes in catchability rather

than environmental processes, as they are less variable than our estimates but should be greater.

Given the uncertainty in estimating vital rates and population-size, the study system tradeoffs, and the potential to alter the dynamics through sampling, it may be more tractable to focus on the mechanisms through which habitat augmentations affect gamefish in future studies (Smokorowski and Pratt 2007). Fundamentally, the issue of measuring population-level production mechanisms resides in measuring vital rates over time with precision. When the habitat augmentation effects are localized this may be possible, such as structures aimed at providing nursery habitat (Pickering and Whitmarsh 1997). However, the majority of artificial habitat augmentations are not narrowly aimed at a single life stanza or, if they are, are aimed at adults (Grossman et al. 1997, Tugend et al. 2002, Miranda et al. 2010). In this case, effects are dispersed and often occur in changes in the spatial use (Werner et al. 1977, Lowe et al. 2003, Topping et al. 2005, Schroeffer and Szedlmayer 2006, Ahrenstorff et al. 2009, Topping and Szedlmayer 2011, Marsden et al. 2016), the diet (Crowder and Cooper 1982, Ahrenstorff et al. 2009), and growth (Gaeta et al. 2011, Sass et al. 2012).

Translating these effects to changes in vital rates is lacking, though often assumed, and the impacts of these dispersed effects on population-level production remain unknown. Principally, these effects can occur but fail to alleviate recruitment bottlenecks (Pauly 1980) and result in no change to fish production as a result of the density-dependent survival (Walters and Korman 1999, Shaw and Allen 2016). Even habitat augmentations aimed at pre-recruits could result in no changes in production if adults become cannibalistic at high pre-recruit densities, likely a factor in our lakes

(Shaw and Allen 2016) and observed in other Florida / Largemouth Bass populations (Post et al. 1998). Thus, the relationship between amount of existing habitat, augmentation amount, and population-level production question may remain unanswered. Despite this, management goals structured around increasing angler catch per unit effort or augmenting systems with zero habitat (Miranda et al. 2010) are very likely to be successful. Habitat restoration strategies aimed at increasing ecosystem function and broad food web effects (Ruiz-Jaen and Aide 2005, Lake et al. 2007) are more likely to meet the production-oriented management goals in systems with existing habitat albeit over longer time-scales (Walker et al. 2007).

Table 3-1. Lake characteristics as described by Hangsleben et al. 2013 and the number of fish species identified in (Hoyer and Canfield 1994), where the value for Speckled Perch is inferred from the semi-permanent connection to Devil's Hole.

Lake	Area (ha)	Mean Depth (m)	Average Secchi Disk Depth (m)	Littoral zone width (m)	Percent volume infested	Number of fish species
Devil's Hole Lake	11.8	4.64	4.48	10.6	4.8	22
Speckled Perch Lake	12.6	1.86	1.57	9.2	7.4	22?
Big Fish Lake	3.0	3.25	3.02	4.1	1.7	6
Keys Lake	3.6	2.92	2.90	5.8	5.2	10

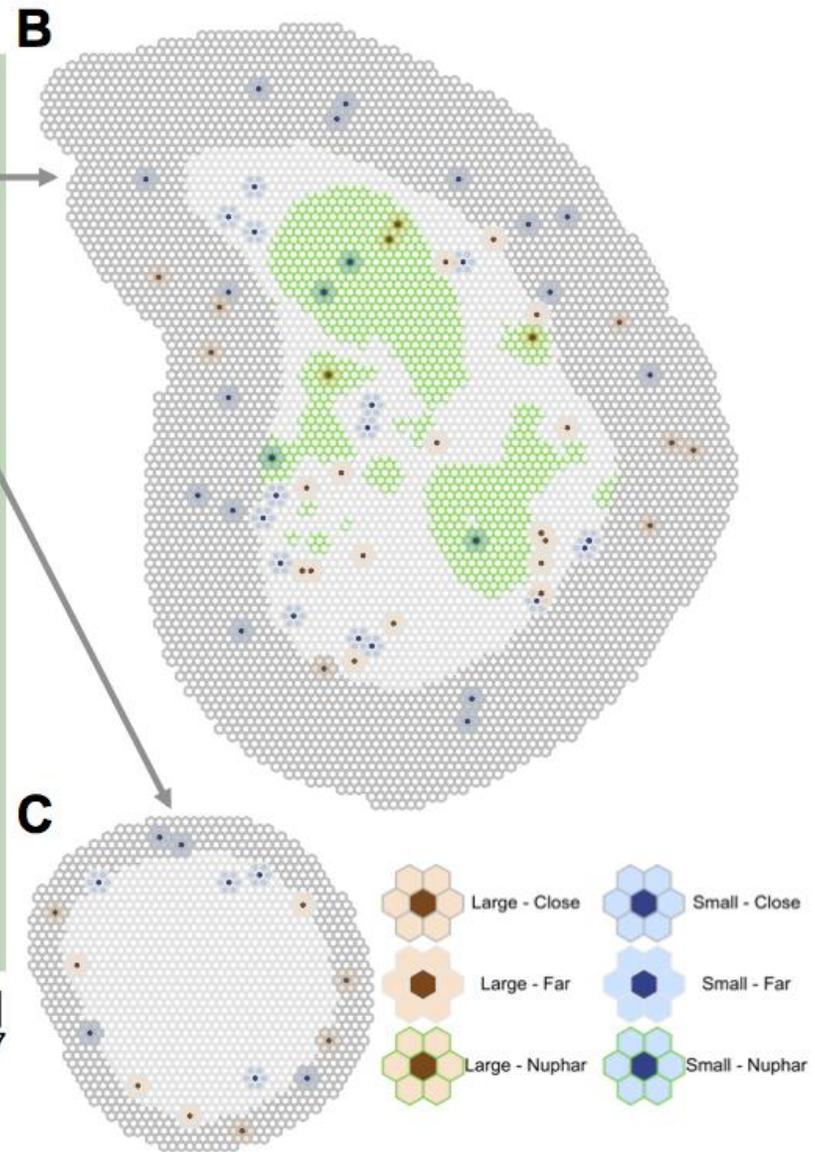
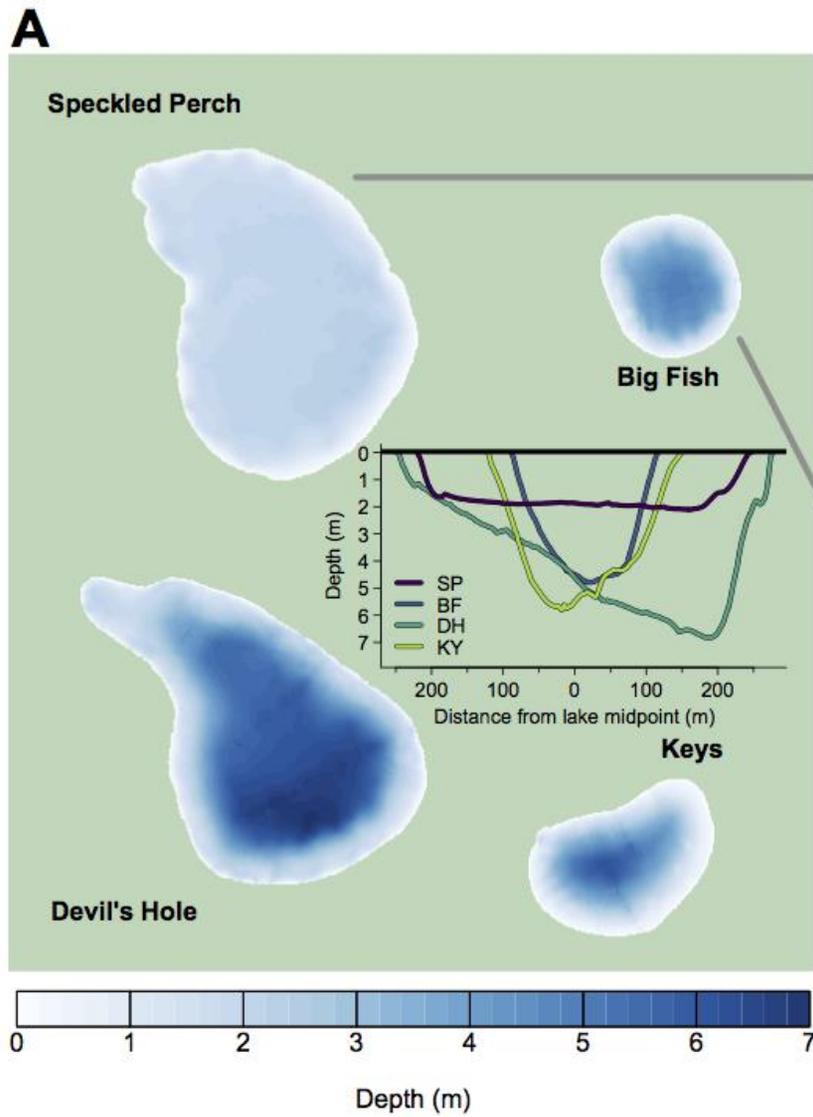
Table 3-2. Priors for von Bertalanffy growth parameters used in the Wang (1998) improved Fabens estimation. The prior distribution of $N(\mu, \sigma)T(0)$ corresponds to a half-normal prior distribution to prevent zero values (STAN Development Team 2017b).

Parameter	Prior
l_{∞}	$N(0,100)T(0)$
β	$N(0, \sqrt{1000})T(0)$
K	$N(0,1)T(0)$
γ	$N(0, \sqrt{1000})$
τ	$Gamma(1,0.05)$
σ	$\frac{1}{\sqrt{\tau}}$

Table 3-3. Mean effective detection probabilities for each gear in each lake.
 Probabilities were calculated as the mean gear detection probability plus the sampling event random effect.

Gear	Speckled Perch Lake	Big Fish Lake	Devil's Hole Lake	Keys Lake
MH-DE	0.0570	0.0464	0.0196	0.0488
MH-AN	0.0444	0.0197	0.0156	0.0307
NC-AN	—	—	0.0207	—
ZS-DE	0.0271	0.0667	0.0084	0.0247
ZS-AN	0.0062	0.0403	0.0087	0.0251
GS-AN	0.0115	0.0323	0.0219	—
GS-NE	—	—	0.0045	—
ZS-NE	0.0773	—	—	—

Figure 3-1. Bathymetric profiles for the four surveyed lakes (A). Inset is a cross-section of each lake's bathymetry at the widest point. Brush piles were added to Speckled Perch (B) and Big Fish (C) into six and four potential groups, respectively. Large brush piles (three trees) are indicated in brown while small brush piles (one tree) are indicated in blue with darker tones indicating the brush piles location and lighter tones indicating the six adjacent cells. Brush piles are indicated by dark grey in the nearshore zone, light grey in the offshore zone, and green in Spatterdock (*Nuphar lutea*; applies to Speckled Perch only).



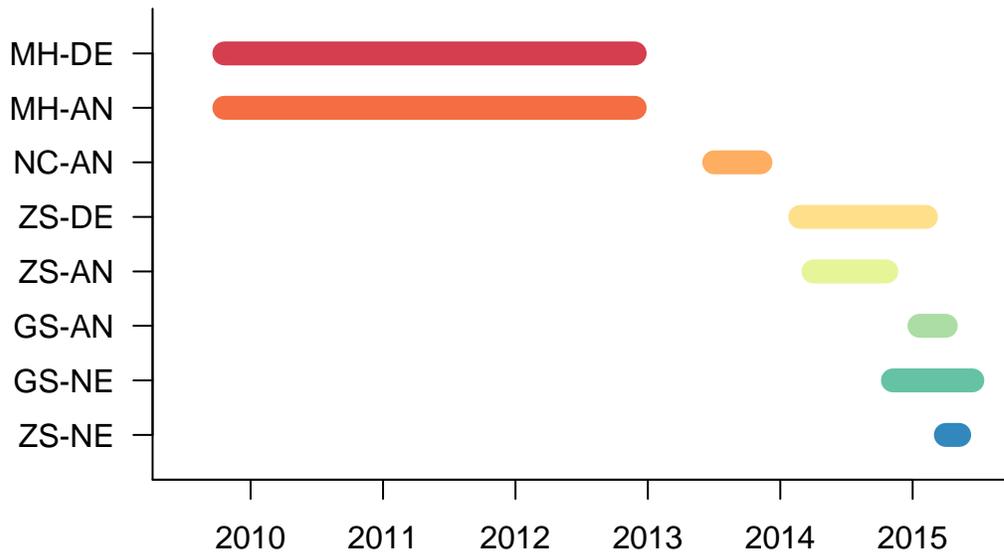


Figure 3-2. Duration and type of gear deployed in the four lakes from 2009 - 2015. Project leads Matt Hangsleben (MH), Nicholas Cole (NC), Zach Siders (ZS), and Grant Scholten (GS) are shown with the gear deployed: daytime electrofishing (DE), nighttime electrofishing (NE), and angling (AN).

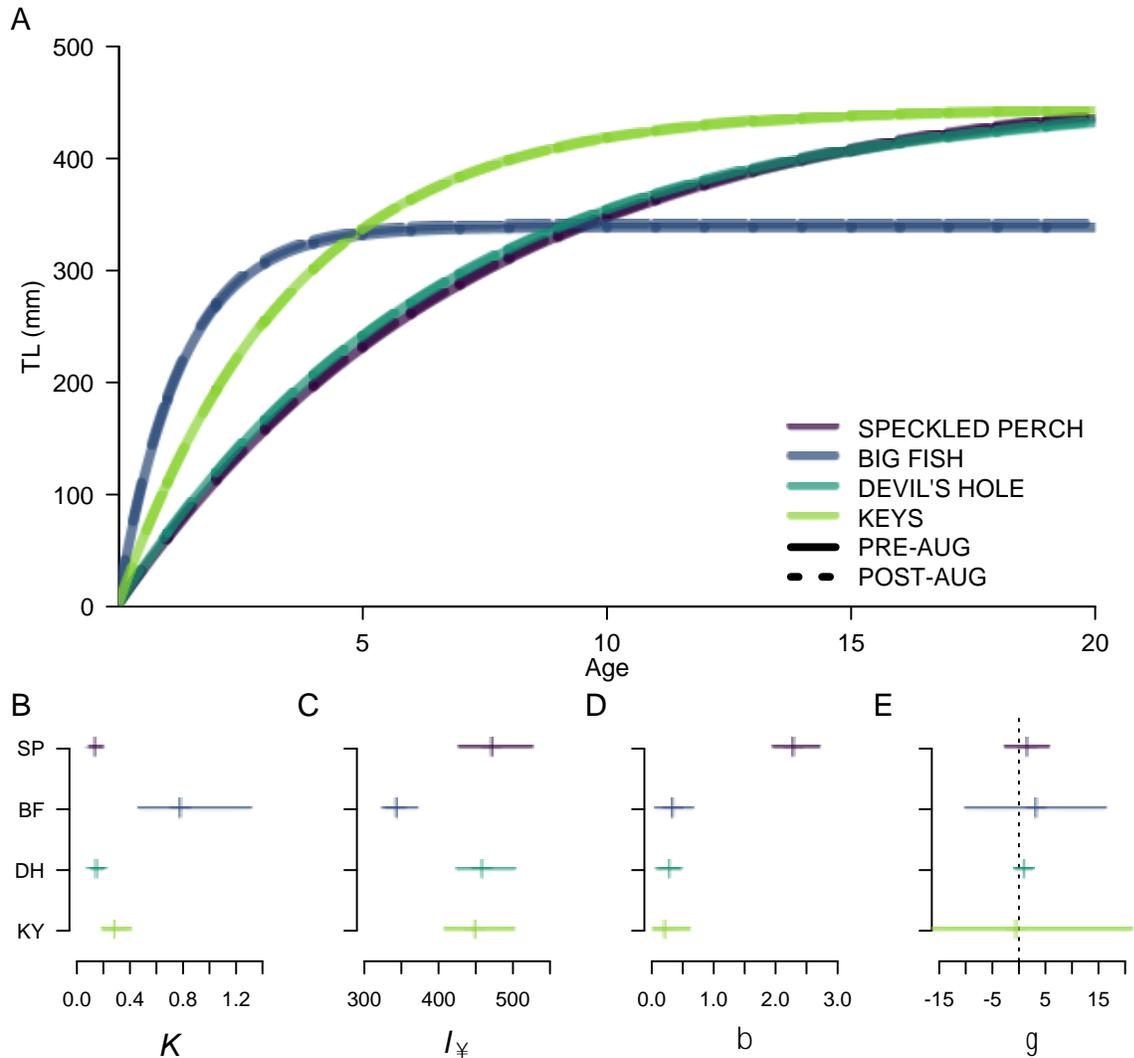


Figure 3-3. Mean von Bertalanffy growth (in millimeters of total length, TL) at age (in years) for Florida Bass in each lake based on length at recapture using Wang's (1998) method for the Faben estimation of the von Bertalanffy growth parameters (A). Parameter estimates and their 80% credible intervals for K (B), l_{∞} (C), β (D), and γ (E) of the Faben estimation with the dashed line indicating zero for the post-augmentation increment effect (E).

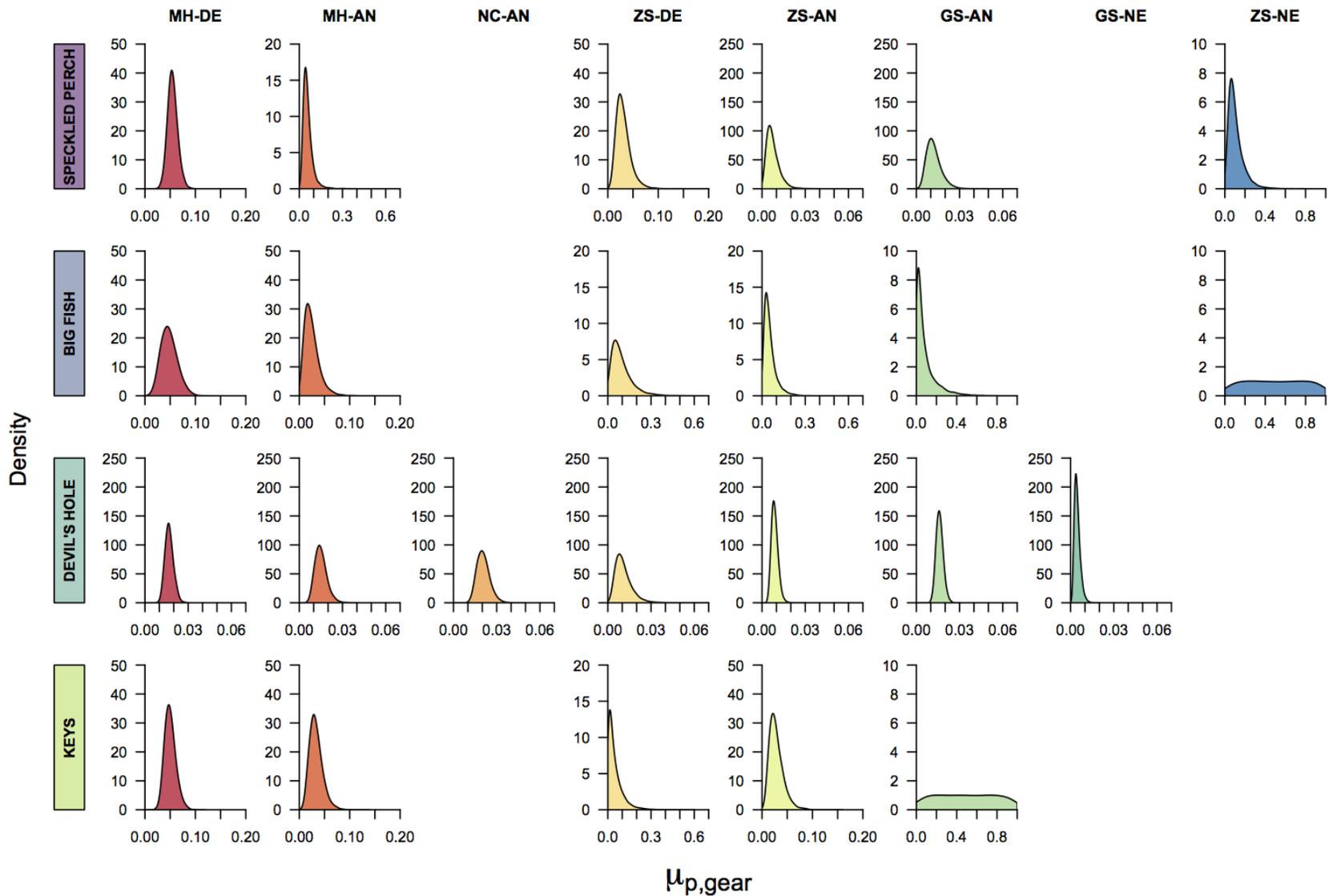


Figure 3-4. Probability density of the detection probability, p_{gear} , for each gear fished and each lake as estimated by a Cormack-Jolly-Seber mark-recapture model.

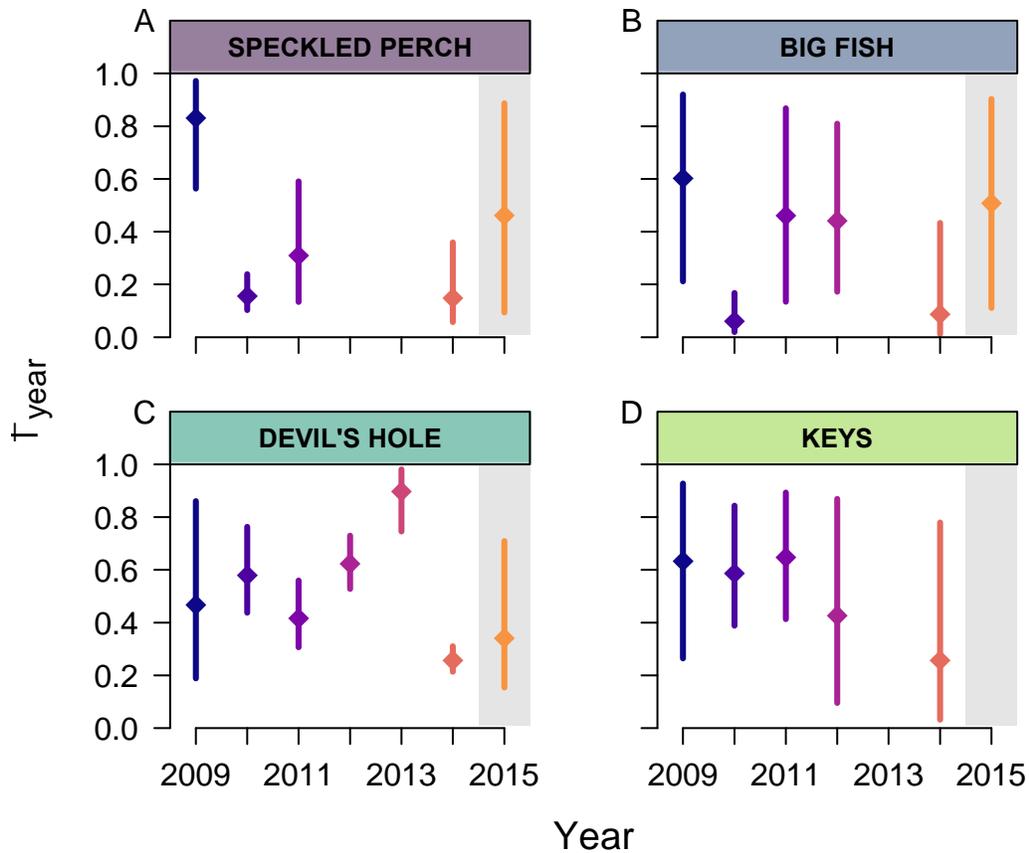


Figure 3-5. Yearly survival rates, ϕ_{year} , from 2009 to 2015 for each lake as estimated by a Cormack-Jolly-Seber mark-recapture model. Lines indicate the 80% credible interval and diamonds indicate the median point estimate. Warmer colors indicate years closer to present. The grey block indicates the post-augmentation period occurring after brush pile additions to Speckled Perch Lake and Big Fish Lake.

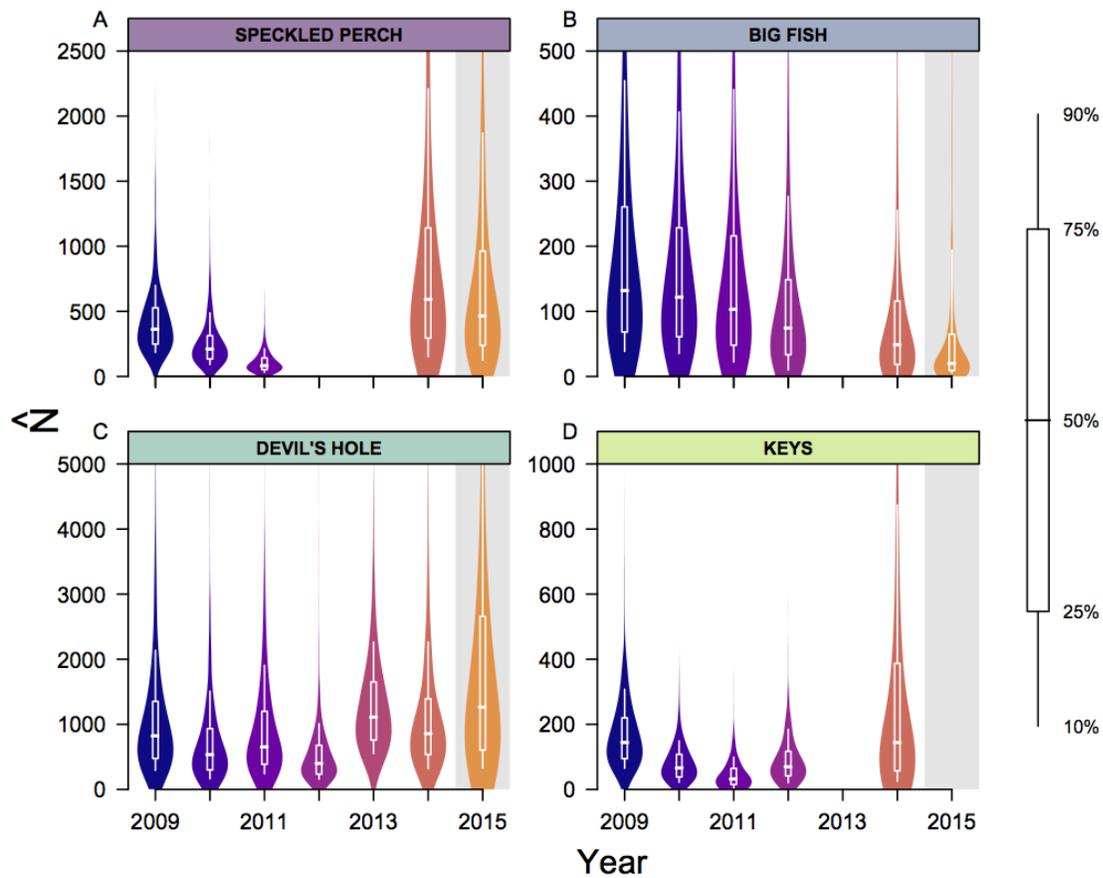


Figure 3-6. Yearly population estimates, \hat{N} , from 2009 to 2015 for each lake as derived from a Cormack-Jolly-Seber population model. Lines indicate the 80% credible interval, boxes indicate the 50% credible intervals, and the dash indicates the median. Warmer colors indicate years closer to present. The grey block indicates the post-augmentation period occurring after brush pile additions to Speckled Perch Lake and Big Fish Lake.

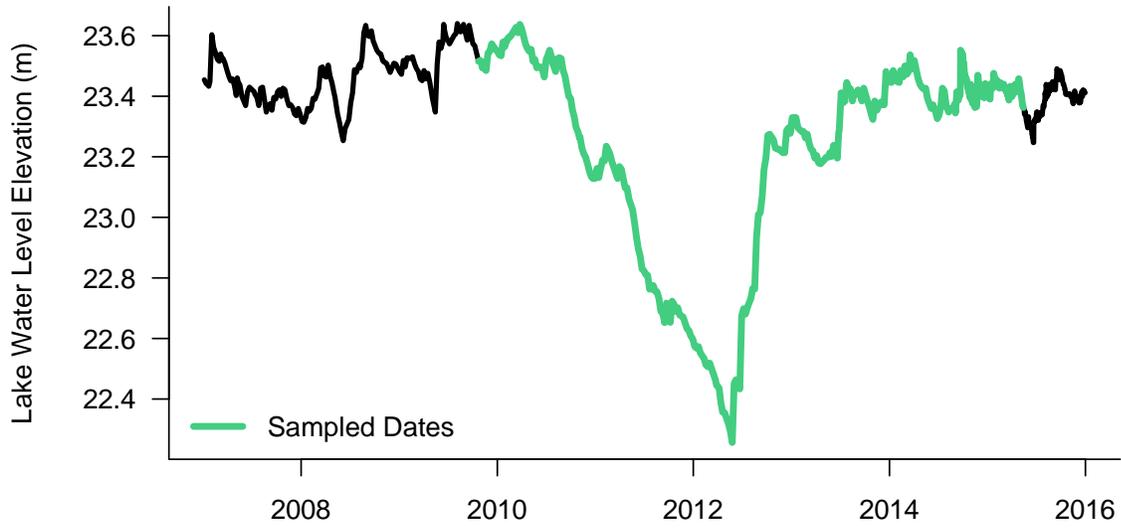


Figure 3-7. Lake water level elevation (m) at Star Lake (5.92 km, 3.68 mi away from surveyed lakes).

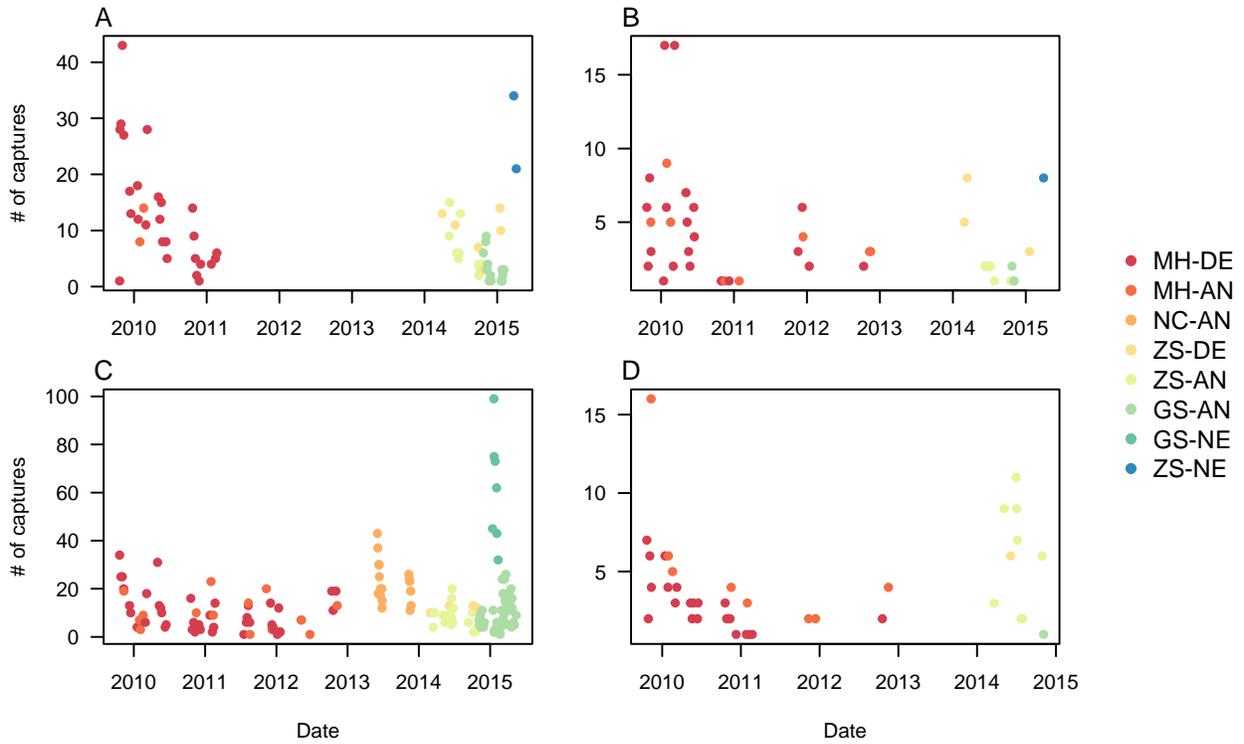


Figure 3-8. Number of recaptures of Florida Bass for each gear type by capture date.



Figure 3-9. Evidence for the attractiveness of brush piles in our augmented lakes.
Photo courtesy of author.

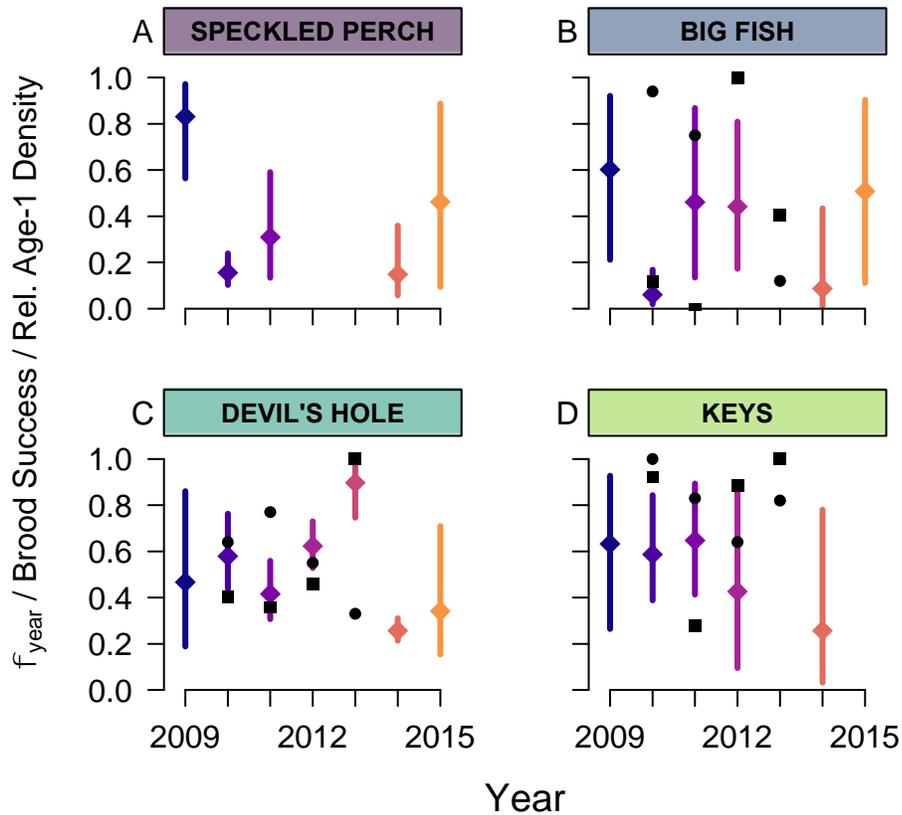


Figure 3-10. “Apparent survival” estimates from this study with estimates of brood success (circles) and relative age-1 density (squares) from Shaw and Allen (2016). Relative age-1 density was calculated by taking the age-1 density and dividing by the max for that lake. No estimates of brood success or age-1 density were made for Speckled Perch Lake.

CHAPTER 4
ABIOTIC AND BIOTIC FILTERING DRIVES DEPAUPERATE SPECIES
ASSEMBLAGES ON AUGMENTED HABITAT

Introduction

Habitat selection processes determine the species that attract to augmented habitat (Pulliam and Danielson 1991, Greene and Stamps 2001). Augmentation based management explicitly and implicitly relies on the habitat selection process to meet management objectives. Explicit selection by target species or complexes is needed for most augmentation management objectives, such as increasing catch per unit effort (CPUE), adding nursery habitat, providing adult sanctuary, or increasing spawning habitat (Tugend et al. 2002). These strategies also implicitly rely on the habitat selection of non-target species in a myriad of ways, such as predators of target species not selecting new habitat or prey of target species benefiting from the augmentation to increase the target species' food availability. Historically, habitat augmentations have utilized available structures, such as coarse woody debris, concrete, tires, and stakes, to attract a single species or a small species complex (Polovina 1991, Johnson and Lynch 1992, Pickering et al. 1999, Bortone et al. 2011). These structures can have greater, equal, or less intrinsic habitat quality found in natural structure, such as vegetation, reefs, and rock formations, with disparate effects of the resulting species assemblage that colonize new habitat from each species' habitat selection.

Habitat selection processes are often partitioned into abiotic constraints on colonization and persistence (Darwin 1859) and biotic interactions as the source of depauperate community assemblages (Diamond 1975, Keddy 1992). Abiotic constraints can arise from structural components or from dispersal limitation (e.g. the augmented habitat is farther away than the dispersal distance of a given species). Many of the

structural components, such as complexity, location, orientation, height, and shape, of augmented habitat have been investigated in previous attraction-production studies (Phillips 1990, Brickhill et al. 2005, Bortone et al. 2011). However, the individual effect of a single structural component is difficult to parse from interacting biotic processes. The abundance and diversity of interstitial space for refuge availability is a critical component of intrinsic habitat quality and many augmented structures approximate the refuge availability of natural habitat (Johnson et al. 1988, Lynch and Johnson 1989, Caddy and Stamatopoulos 1990, Walters et al. 1991, Caddy 2007). Dispersal limitation, on the other hand, is often of little consequence as the augmentation scale is smaller than the dispersal scale of fishes. In addition to the other abiotic constraints, physiological and behavioral constraints may limit the colonization of a particular species such as species that utilizes camouflage that requires a particular background (Armbruster and Page 1996, Magoulick 2004, Cox et al. 2009).

While abiotic constraints have a role in reducing the species assemblage, biotic interactions, predominantly competition and predation, likely determine the species assemblage more. Competitive processes can engender strong density-dependent growth and mortality increasing the likelihood that a given species will redistribute to new habitat to improve their fitness (i.e. the ideal free distribution; Fretwell and Lucas 1969). Post-colonization, competitive processes can constrain resource availability and result in high species turnover, termed by community ecologists as bottom-up sequential dependency (Holt 1997, 2009, Gravel et al. 2011). This is a common feature of most augmentations with depauperate species assemblages changing over time

post-augmentation but remaining different than those on natural habitat (Walsh 1985, Bohnsack et al. 1994, Caley and John 1996, Brosse et al. 2007).

Similar to competition, predation can operate on fishes in the natural and augmented habitat to influence species assemblages but also acts on dispersing fishes (Hixon and Menge 1991, Carr and Hixon 1995). On existing habitat, high predation rates reduce the likelihood of survival and generate a high likelihood of seeking a new habitat (Křivan 1996, 1997). Dispersing individuals are likely to move through refuge-less habitat greatly increasing their predation risk (Anderson 1984, Savino and Stein 1989a, Sih and Wooster 1994). It is this dispersal predation that likely limits many small-bodied fishes from successfully dispersing to new habitat, not dispersal distance, as they are well within the gape size of many aquatic predators (Lewis and Helms 1964). Predation also can operate differentially between existing habitat and new habitat as the abundance of a given predator can change or the predator guild can change in composition (Hixon and Beets 1993, Bohnsack et al. 1994).

Competition and predation can act synergistically to influence the species assemblage (Hixon and Menge 1991). Depauperate species assemblages may reduce refuge space competition and allow colonizing species to better avoid predators (Hixon and Beets 1993, Caley and John 1996). Conversely, a depauperate species assemblage might increase the predation risk relative to a richer species assemblage through passive and active responses. Passive responses such as risk dilution, or safety in numbers, can decline if only a few members of a predation guild are attracted to new structure, especially if non-attracted members of the guild are more vulnerable to predation. Additionally, differential attraction to structure across a predation guild can

limit active responses such as cooperative interspecific anti-predator behaviors and increase the per capita predation rate. These behaviors include predator deterrence (Motta 1983, Turner and Mittelbach 1990), shared vigilance (Lima 1995, Ward et al. 2011), and quorum responses (Turner and Pitcher 1986, Ward et al. 2008).

Cumulatively, competition and predation can determine the species assemblage in a myriad of ways and it is likely impossible to parse the effects of a single process from co-occurring processes.

Despite augmented habitat often having similar interstitial space diversity (Caddy 2007 p. 81), depauperate species assemblages often occur (Walsh 1985, Bohnsack et al. 1994, Brosse et al. 2007). The purpose of this study was to assess how the location and size of augmented habitat interact to subset the species assemblage in two augmented lakes compared to two adjacent non-augmented lakes in north central Florida. A stratified design of new structure, near and far from existing habitat as well as large and small in size, allowed for differential patterns of attraction. Species unattracted to any new structure, even those exceptionally close to existing habitat, could indicate abiotic constraints while species that colonize intermittently may be responding to other environmental characteristics or could be limited by dispersal predation. With the strong likelihood of depauperate species assemblages, we also sought to compare the prey and predator species of the augmentation's target species, Florida Bass *Micropterus floridanus*, to those in existing habitat. Changes in the predation or predator guild are likely to have strong effects on the fitness benefits associated with colonizing new habitat and the efficacy of habitat augmentation management.

Materials and Methods

System Characteristics

We experimentally manipulated four small private-access lakes located on the BJ Bar Ranch east of Hawthorne, FL (Figure 4-1). The four lakes fell into two size groups, smaller systems: Big Fish Lake (3.2 ha) and Keys Lake (3.6 ha), and larger systems: Devil's Hole Lake (11.6 ha) and Speckled Perch Lake (12.4 ha). We chose to augment habitat in one small (Big Fish Lake) and one large lake (Speckled Perch Lake) and as a result one small (Keys Lake) and one large lake (Devil's Hole Lake) were used as comparisons.

Previous sampling at these lakes had quantified fish community characteristics, and the communities differed in some ways. For example, lakes varied in the number of cyprinid species, the presence/absence of Florida Gar *Lepisosteus platyrhincus* or Brown Bullhead *Ameiurus nebulosus*, and the number of *Lepomis* species. However, overall they were fairly similar in that the dominant *Lepomis* species was Bluegill *Lepomis macrochirus* and the dominant aquatic predator was Florida Bass *Micropterus floridanus*. Evidence of other apex predators, such as American Alligator *Alligator mississippiensis* or River Otters *Lontra canadensis*, was limited to only five occasions over three years. The bottom contours of each system differed quite considerably (Figure 4-1A) with Speckled Perch Lake having a relatively uniform maximum depth at 2.4-2.6 m while the rest of the lakes showed more variability in lake depth and deeper maximum depths (ranging from 5.5 to 7.6 m).

Augmentation

Sand Live Oaks *Quercus geminata* were logged from the BJ Bar Ranch ranging in heights from 4 to 7 m and divided into two categories of brush piles consisting of a

single tree (termed small) or three trees (termed large). The augmentation effect was a 15-20% increase in habitat by area in Big Fish Lake and 12-16% by area in Speckled Perch Lake resulting in 16 and 64 brush piles in each lake, respectively (Figure 4-1B–C). Brush piles were transported by boat to randomly selected locations from two strata, nearshore and offshore environments that were less than and greater than 65 m from shore, respectively, in Speckled Perch Lake and 20 m in Big Fish Lake. In Big Fish Lake, brush piles in the near shore category were typically in depths of 2–3 m and in the off shore category in depths of 3–4 m. In Speckled Perch Lake, brush piles in the near shore category were in depths 1.5–2 m and in the off shore category were in depths 2–3 m. Small and large brush piles were divided evenly between these two categories. Four brush pile strata resulted in Big Fish Lake: 1) small brush pile – near shore (small, close), 2) small brush pile – off shore (small, far), 3) large brush pile – near shore (large, close), and 4) large brush pile – off shore (large, far). Six brush pile strata resulted in Speckled Perch Lake: 1) small brush pile – near shore, 2) small brush pile – off shore, 3) small brush pile – Nuphar (small, Nuphar), 4) large brush pile – near shore, 5) large brush pile – off shore, and 6) large brush pile- Nuphar (large, Nuphar). The Nuphar strata resulted from the placement of off shore brush piles in patches of Spatterdock Nuphar lutea in the center of the lake.

Survey Design and Processing

Each lake was surveyed using cameras (GoPro Hero 3+/4 Black Edition, 1080p, Wide format; Mateo, CA, USA) to assess the abundance and distribution of all observable fish and turtle species. Lakes were initially broken into four strata (Figure 4-6) using characteristics of distance to shore, depth, and an emergent vegetation index—as assessed from Google Maps satellite imagery in R (R Core Team 2015) using the

RgoogleMaps package (Loecher and Ropkins 2015) and the raster package (Hijmans 2015). Pre-augmentation surveys were conducted in December 2014 with four sites per lake strata for Big Fish Lake and Keys Lake, 8 for Devil's Hole Lake, and 10 for Speckled Perch Lake. Surveys were conducted every 3–4 months following the augmentation, occurring in December 2014 after the surveys were completed, for a total of five post-augmentation blocks, roughly in March 2015, June 2015, September 2015, January 2016, and May 2016. All lakes were surveyed within a 4–6 week period during each survey block. The survey frequency in the September 2015 and January 2016 blocks was reduced due to low visibility. Post-augmentation, a minimum of 10 and 22 brush piles were surveyed in Big Fish Lake and Speckled Perch Lake, respectively.

Each camera survey consisted of at least a five minute burn-in period to allow fish / turtle behaviors to resume after the disturbance of placing the camera and a 15 minute survey. Cameras were oriented randomly in 45° declinations from 0–360° as well as vertically placed in the middle of the water column for sites less than 1 m in depth and at approximately 1 m for sites greater than 1m in depth. Visibility was measured using a handcrafted visibility instrument consisting of 2.44 m (8 feet) long PVC rod delineated at 15.24 cm (6 inches) increments with a plastic fishing lure in the shape and color of a 10 cm Florida Bass at the end. Cameras were mounted on 3 m fiberglass rods (Stick It Anchor Pins; Palm Beach, FL, USA) for anchoring into the substrate when surveying. Surveys in shallow areas (< 3 m deep) were conducted from a boat (Alumacraft 1542 Jon; Arkadelphia, AR, USA) using electric trolling motors (Minn Kota Endura Max; Racine, WI, USA) to minimize disturbance. Surveys in deeper areas (> 3 m deep) were conducted using divers on an Air Line Hookah Dive System (The Air

Line R360XL by J. Sink; Ocala, FL, USA). Longer burn-in periods were used for diver-placed surveys and were determined *post-hoc* by video processors by assessing when substrate flocculent resettled. Surveys were decomposed into five-second clips every 30 seconds for a minimum of 20 clips. All fishes / turtles on each clip were enumerated and recorded. Two observers enumerated clips with numerous individuals or multiple species and the maximum was taken of both observations. Florida Bass were enumerated by life stage into categories of fryball, age-0, juveniles, and adults. Visual characteristics were used to determine each Florida Bass life stage: fryballs were less than ≈ 20 mm in length, brown in color with a characteristic broad black stripe; age-0's were less than ≈ 50 mm, pale in color with a characteristic black stripe; juveniles were less than ≈ 150 mm in length, pale in color without significant barring and a fusiform body shape; and adults greater than ≈ 150 mm in length typically had significant barring and more rotund than juveniles. Some adults did not possess barring instead displaying a golden-olive color but were always much larger than juveniles. Bluegill were also enumerated by life stage into categories of fryball, fry, juveniles, and adults. Bluegill "fryballs" were considered as very small fry to which the enumeration of individual fry was impossible while "fry" were larger fry and enumerable. Juveniles were considered as Bluegill no greater than 100 mm typically less than 70 mm without significant body pigmentation and no characteristic white fin tips. Golden Shiner *Notemigonus crysoleucas* were also enumerated by life stage into categories of juveniles and adults upon expert consultation (Travis Tuten, pers. comm.).

Environmental Variables

We used a variety of environmental variables in subsequent analyses. Lake depth was measured using sonar and then imputed for the whole lake using a digital elevation model onto a raster grid with cells 2.5 x 2.5 m. This depth layer was used to determine aspect (slope direction) and distance to shore. Observations were made during the processing of each camera survey of the bottom type (muck or sand) and vegetation types: aquatic bladderworts (*Utricularia floridana* and *Utricularia foliosa*), Banana Lily (*Nymphoides aquatica*), grasses (Maidencane - *Panicum hemitomon* and Torpedo Grass - *Panicum repens*), Lemon Bacopa (*Bacopa caroliniana*), rushes (*Eleocharis baldwinii* and *Eleocharis interstincta*), and Spatterdock (*Nuphar lutea*); and algae types: Filmentatous, Musk-grass (*Chara spp.*), and Periphyton. These point observations were then kriged using the gstat package and a inverse distance weighting power of 3 (Gräler et al. 2016) to create layers for each lake. Vegetation and algae layers were only imputed for lakes with observations of those types.

Occupancy Modeling

We used a three-level occupancy model (described by Aing et al. 2011, Mordecai et al. 2011) to model the multiscale occupancy (Nichols et al. 2008) of fishes and turtles observed in our lakes. Each lake was modeled identically but independently. The multiscale occupancy model was formulated as a state-space model (Royle and Kéry 2007) with a state process model for the occupancy (site-level) and use (survey-level) latent state variables as well as an observation model for repeated detections during camera surveys. The state process model consisted of an equation for the site-level occupancy (Equation 4-1) and the survey-level occupancy (Equation 4-2):

$$z_{ik} \sim \text{Bernoulli}(\psi_k) \tag{4-1}$$

where z_{ik} is the latent state for the site-level occupancy at site i and ψ_k is the permanent occupancy probability for species k (Efford and Dawson 2012, Pavlacky et al. 2012).

$$a_{ijk}|z_{ik} \sim \text{Bernoulli}(z_{ik}, \theta_{ik}) \quad (4-2)$$

where a_{ijk} is the latent state for the survey-level occupancy and θ_{ik} is the temporary occupancy probability for survey j (Kéry and Royle 2015). Temporary occupancy is conditional on a species permanently occupying a site ($z_{ik} = 1$). In this formulation, species permanently occupying site z_{ik} can vary from survey to survey in their site occupancy. The observation model is denoted as:

$$y_{ijk}|a_{ijk} \sim \text{Binomial}(J_{ijk}, a_{ijk} * p_{ijk}) \quad (4-3)$$

where y_{ijk} is the detection of a species during a survey at a site and conditional on the temporary occupancy ($a_{ijk} = 1$), p_{ijk} is the detection probability over J_{ijk} clips during a camera survey. The prior distributions for ψ_k , θ_{ik} , and p_{ijk} for each species were assumed to come from normal hyperdistributions with flat priors (Table 4-1).

Detection between individual clips was assumed to be independent after preliminary camera survey trials indicated 30 seconds between clips eliminated the same individuals lingering in front of the camera (the average time on the video frame was approximately 5 seconds). Enumerated individuals were collapsed to binary states indicating detection / nondetection (0,1) for all clips. Occupancy models were implemented in JAGS (Plummer 2003) using the runjags package (Denwood 2013). All traces of parameters and posterior probabilities were visually assessed using the Gelman-Rubin diagnostic (Gelman and Rubin 1992) for convergence (Figure 4-7).

Lakewide Predictions

We evaluated how environmental site characteristics influenced site occupancy across all four lakes. Estimates of the survey-level temporary occupancy latent state variable, a_{ijk} , from the multiscale occupancy models were matched with environmental site characteristics for each lake and the survey block for each camera survey. Markov Chain Monte Carlo estimates of the temporary occupancy latent state were averaged over 1,000 samples to obtain a mean estimated latent state (between 0 and 1) for each site–survey combination. Weak correlations between multiple environmental characteristics and the probability of a species occurring at a site as well as processing of the camera surveys indicated that many covariates were interacting to shape a species' occupancy. Rather than attempt to model this procedure using a model-selection framework, we employed an artificial neural network approach to blend environmental characteristics into new variables using the neuralnet package. Artificial neural networks are linear models that use weights (roughly regression coefficients) to mix covariates into a hidden layer(s). Hidden layers then have weighted contributions to predicting the response variable. We used one hidden layer to predict the species by site by lake median estimates using three times the number of environmental covariates for the number of hidden nodes. Artificial neural networks had 63, 33, 63, 39 hidden nodes in Speckled Perch Lake, Big Fish Lake, Devil's Hole Lake, and Keys Lake, respectively. This sacrifices ease of tracing covariate influence for predictive performance, which we maximized by modulating the conversion threshold of the artificial neural networks until we achieved R^2 values over 0.85. The resulting networks

were used to make predictions of the probability of species occurrence for each survey of every possible site in each lake

To predict at every possible site in each lake, we divided each lake into a hexagonal grid with cells of equal area (31 m²) and extracted the mean of the environmental characteristics for each cell from their layers using a bilinear sampling method in the raster package. We parsed predictions into brush pile strata (see Materials and Methods - Augmentation) and the “natural” areas subsuming all areas that were not brush piles. Brush piles areas were assigned by determining the cell a brush pile occurred in. Probabilities of species presence in each brush pile stratum were averaged by survey to obtain pre- and post-augmentation estimates. The sampling to multiscale occupancy model to neural network model to lakewide predictions is graphically summarized in Figure 4-8.

Species-level Brush Pile Effects

Species-specific predictions of the temporary occupancy at all possible sites from the artificial neural networks were *logit* transformed to make them approximate a normal distribution. The effect of brush pile stratum and pre- and post-augmentation survey periods on site predictions was modeled as a linear regression. The significance of group effect sizes was assessed using two-tailed t-tests as well as the overall significance of brush pile strata and pre- / post-augmentation was assessed using an analysis of variance (ANOVA). Significance was assessed at an $\alpha = 0.05$. A separate linear regression was used to compare all brush pile stratum effect sizes to the non-brush areas for each post-augmentation survey and averaged across brush pile strata for comparison in Speckled Perch Lake and Big Fish Lake.

Brush Pile Effects on Diversity

Lake diversity was assessed from the species-specific lakewide predictions from the artificial neural networks using a weighted richness index (WR_i) for each survey:

$$WR_i = \frac{\sum n_k * p_{ik}}{n_k} \quad (4-13)$$

where n_k is the number of species at site i and p_{ik} is the vector of predicted probabilities for site i for species k to n_k . The effect of brush pile strata on weighted richness was assessed against the expected weighted richness for non-brush pile areas in Speckled Perch Lake and Big Fish Lake. Due to the differing total species richness between lakes, the weighted richness index was normalized to vary between zero and one (maximum - minimum standardization) for inter-lake comparisons. Jackknife sampling was used to test the effect of each species on the weighted richness pre- and post-augmentation for each brush pile strata. Standardized scores (Z-scores) were used to compare effects and significance was assessed at an $\alpha = 0.05$. The effect of brush piles on weighted richness was assessed relative to all non-brush areas and littoral non-brush areas using standardized scores.

Results

Surveys

A total of 642 surveys were conducted over the six survey blocks with 245 in Speckled Perch Lake (155/90, non-brush/brush), 156 in Big Fish Lake (88/68, non-brush/brush), 149 in Devil's Hole Lake, and 92 in Keys Lake. Over 12,947 clips, 18 species of 9,620 fish / turtles were observed, 9,575 were fish, and 45 were turtles (Table 4-2). Our camera surveys did not observe the expected total species richness. For example, concurrent electrofishing surveys (Siders, unpublished data) detected

some species in each lake that were not observed on cameras in that lake. Similar studies have noted this to not be an unlikely result (Bacheler and Shertzer 2015, Bacheler et al. 2017). Striped Musk Turtles were captured electrofishing in Speckled Perch Lake, but were not detected on cameras. Grass pickerel (*Esox americanus vermiculatus*) and Bluespotted Sunfish (*Enneacanthus gloriosus*) were electrofished in Devil's Hole Lake ($n=1$ each over 100+ surveys) and Tadpole Madtom (*Noturus gyrinus*) were electrofished in Speckled Perch Lake ($n=1$ over 60+ surveys) but none were detected on camera. Other species that may have been present in the lakes can be discerned from rotenone studies conducted by Hoyer and Canfield (1994) during 1987-1991, such as Bowfin (*Amia calva*), Dollar Sunfish (*Lepomis marginatus*), Everglades Pygmy Sunfish (*Elassoma evergladei*), Least Killfish (*Heterandria formosa*), Taillight Shiner (*Notropis maculatus*), and Yellow Bullhead (*Ameiurus natalis*). Many of these species are either small or cryptic or with such low abundances that detection is extremely difficult. There is also the possibility these unobserved species have been extirpated since the Rotenone surveys were conducted in the late 1980s.

Observed Species Richness

Observed species richness generally correlated with lake size with the larger lakes, Speckled Perch Lake and Devil's Hole Lake Lake, having 14 and 16 species, respectively (Figure 4-2). Species not shared between those lakes were Brown Bullhead and Florida Gar in Speckled Perch Lake with Warmouth, Golden Topminnow, Seminole Killifish, and Striped Musk turtles in Devil's Hole Lake. All of these species except Golden Topminnow have been observed in both large lakes using other survey techniques (Siders, unpublished data). Keys Lake and Big Fish Lake had 8 and 5 species respectively. Lake Chubsucker, Warmouth, Lined Topminnow, and Florida

Softshell turtle were found in Keys Lake but not in Big Fish Lake whereas Seminole Killifish were found in Big Fish Lake but not in Keys Lake. All stages of Florida Bass, Bluegill, and Golden Shiner were observed in Speckled Perch Lake and all stages of Florida Bass and Bluegill were observed in Big Fish Lake. Florida Bass fry and Golden Shiner adults were not seen in Devil's Hole Lake while Florida Bass fryballs were not seen in Keys Lake.

Permanent Occupancy

Most species had similar permanent occupancy probability, akin to the prevalence of the species across all sites in a given lake, as measured by the cameras across lakes and occupancy probabilities lower than 0.25. A notable exception to consistently lower permanent occupancy probabilities was Bluegill fry with consistently high probabilities in all lakes ($\bar{\psi} > 0.5$). Eastern Mosquitofish also had had on average high occupancy probabilities in all lakes ($\bar{\psi} > 0.25$). Some species had disparate permanent occupancy probabilities such as Lake Chubsuckers ($\overline{\psi_{SP,DH}} < 0.25$; $\overline{\psi_{KY}} > 0.8$) and Black Crappie ($\overline{\psi_{SP}} < 0.1$; $\overline{\psi_{DH}} > 0.75$). The high predictions in these cases stem from exceptionally low detections in particular lakes: $\frac{1}{1855}$ clips for Lake Chubsuckers in Keys Lake and $\frac{1}{3059}$ clips for Black Crappie in Devil's Hole Lake. These detections should be perhaps discarded as even two more detection events can prevent exceptionally high permanent occupancy probabilities (e.g. juvenile Golden Shiners in Devil's Hole Lake had three detections and a $\bar{\psi} < 0.25$).

In Speckled Perch Lake, most species had low site-level occupancy probabilities as measured by the cameras except for Bluegill fry, Florida Gar, and Mosquitofish had probabilities greater than 0.25 (Figure 4-2A). Site-level occupancy in Keys Lake was

similar to Speckled Perch Lake in that most species had low permanent occupancy probabilities except Lake Chubsuckers, Bluegill fry, Mosquitofish had probabilities greater than 0.5 (Figure 4-2D). Seven species / stages in Devil's Hole Lake had permanent occupancy probabilities close to 0.25, Brook Silversides, Florida Bass fryballs, age-0 Florida Bass, Bluegill juveniles, Warmouth, Black Crappie, and Lined Topminnow, while. Bluegill fry, Black Crappie, and Mosquitofish had occupancy probabilities greater than 0.5 (Figure 4-2C). In Big Fish Lake, Florida Bass fryballs, Bluegill fryballs, Bluegill fry, Bluegill adults, and Mosquitofish had occupancy probabilities greater than 0.25 (Figure 4-2B).

Detection Probability

Devil's Hole Lake had the lowest median detection probability across species (0.09), followed by Keys Lake (0.112), Speckled Perch Lake (0.113), and Big Fish Lake (0.23). Detection probabilities were weakly negatively correlated with permanent occupancy probabilities in Speckled Perch Lake ($R = -0.23$), weakly positively correlated in Big Fish Lake ($R = 0.05$), weakly positively correlated in Devil's Hole Lake ($R = 0.21$), and modestly positively correlated in Keys Lake ($R = 0.38$). In Speckled Perch Lake, Florida Bass juveniles, Bluegill adults, Warmouth, Lined Topminnow, and Florida Softshells had detection probabilities greater than 0.25 (Figure 4-2A). Bluegill fry, juveniles, and adults as well as Seminole Killifish had detection probabilities greater than 0.25 in Big Fish Lake (Figure 4-2B). In Devil's Hole Lake, Brook Silversides, Bluegill juveniles, Warmouth, Redear Sunfish, and Mosquitofish had detection probabilities greater than 0.25. Lake Chubsucker, Bluegill juveniles, and Warmouth had detection probabilities greater than 0.25 in Keys Lake. Many of these species / stages make intuitive sense to have relative high detection probabilities, such as the large

schools of Bluegill fry and juveniles or the large conspicuous size of Florida Softshell. Generally, species that were on average detected in the majority of clips in a survey or were detected in one clip on a survey had high detection probabilities.

Species-level Brush Pile Effects

Predicted temporary occupancy of fishes and turtles were different between pre- and post-augmentation surveys as well as across brush pile strata with occupancy generally increasing in the augmented lakes and variable in the non-augmented lakes. Comparisons between the species-specific predictions of temporary occupancy at all possible sites in each lake revealed significant pre- and post-augmentation effects. In all lakes, pre- and post-augmentation effects in the linear regression were significant overall indicating changes in each species' temporary occupancy between the two survey groups (Speckled Perch Lake, $F > 7.23$, $p < 0.001$; Big Fish Lake, $F > 594$, $p < 0.0001$; Devil's Hole Lake, $F > 133$, $p < 0.0001$; Keys Lake, $F > 133$, $p < 0.0001$). In the augmented lakes, the brush pile strata were significant overall on each species' temporary occupancy at all possible brush piles in each lake. All brush pile strata effects were significant overall ($F > 3.43$, $p < 0.0022$) for Speckled Perch Lake and all brush pile stratum effects were significant overall ($F > 5.18$, $p < 0.001$) except for Bluegill fry ($F = 1.03$, $p = 0.39$) and adult Bluegill ($F = 2.24$, $p = 0.06$) in Big Fish Lake.

Overall, the survey group (pre- or post-augmentation) had significant effect sizes for predicting most species' temporary occupancy in each lake indicating that temporary occupancy is variable over time regardless of augmentation effects. Assessment of the effect size significance for pre- and post-augmentation effects indicated that all species had significant effect sizes between pre- and post-augmentation surveys except adult Golden Shiners in Speckled Perch Lake as well as Lined Topminnow and Swamp

Darters in Devil's Hole Lake (Figure 4-3). In Speckled Perch Lake, all species had significant increases in the effect size between survey groups except age-0 and adult Florida Bass, adult Bluegill, Black Crappie, and Florida Softshells that had significant decreases. In Big Fish Lake, all species had significant increases in occupancy post-augmentation except Florida Bass fryballs, age-0's, and adults, Bluegill fryballs, and Seminole Killifish that had significant decreases in the effect size between survey groups. Brook Silversides, Lake Chubsucker, adult Florida Bass, juvenile Bluegill, adult Bluegill, juvenile Golden Shiners, and Golden Topminnows had significant increases between survey groups while Florida Bass fryballs and age-0's, Bluegill fryballs, Warmouth, Redear Sunfish, Black Crappie, Peninsula Cooter, Striped Musk Turtle, and Florida Softshell had significant decreases in Devil's Hole Lake. In Keys Lake, Brook Silverside, Lake Chubsucker, age-0 Florida Bass, Bluegill fryballs and fry, Warmouth, and Mosquitofish had significant increases while juvenile and adult Florida Bass, juvenile and adult Bluegill, Lined Topminnow, and Florida Softshell had significant decreases.

Many species had different responses to brush piles strata some attracting or not attracting to all types, others a limited subset, and, in a few species, attraction to some brush pile strata and not attracting to others. In Speckled Perch Lake, juvenile Florida Bass and Florida Softshell were the only species to have significant increases in effect size on all brush piles relative to the pre-augmentation survey (Figure 4-3). Bluegill fry, juvenile Bluegill, adult Bluegill, Redear Sunfish, Lined Topminnow, Swamp Darter, Mosquitofish, and Peninsula Cooter had significant decreases in effect size. Brook Silversides decreased on close-small, far-large and -small, and Nuphar-small. Brown

Bullhead decreased on close-small and Nuphar-large, and Florida Gar decreased on all brush piles except Nuphar-small. Lake Chubsucker increased on far-large and -small as well as Nuphar-large, Florida Bass fryballs increased on close-large and -small, age-0 Florida Bass increased close-large and -small, far-large, and Nuphar-large. Bluegill fryballs increased on far-large and Nuphar-small and Black Crappie increased on close-large, far-large and -small, and Nuphar-large. Adult Florida Bass increased on far-large but decreased on close-small brush piles. Juvenile Golden Shiner increased on close-small but decreased on close-large as well as far-large and -small brush piles while adults exhibited the same pattern.

Compared to Speckled Perch Lake, fewer species had significant effect sizes of brush pile strata in Big Fish Lake. Adult Florida Bass significantly increased in effect size on all brush piles while Brook Silversides, juvenile Florida Bass, and Mosquitofish significantly decreased on all brush piles strata. Florida Bass age-0's decreased on close-large and -small as well as far-large. Bluegill fryballs decreased on far-large and -small, juvenile Bluegill decreased on close-large and far-large, adult Bluegill decreased on far-large, and Seminole Killifish decreased on close-large and far-large. Florida Bass fryballs decreased on close-small and far-large but increased on close-large. On average, Speckled Perch Lake had smaller positive and negative effect sizes ($\mu_{(+)} = 4.69, \mu_{(-)} = -6.87$) than Big Fish Lake ($\mu_{(+)} = 9.69, \mu_{(-)} = -22.47$).

In the augmented lakes, the two primary gamefish species, Florida Bass and Bluegill, had disparate responses to brush pile strata relative to pre-augmentation (Figure 4-3). Florida Bass had on average significantly positive effect sizes while Bluegill had on average significantly negative responses. In Speckled Perch Lake,

Florida Bass fryballs, age-0, and juveniles were significantly positive on all close brush pile strata, while all life stages but fryballs had significantly positive effects on far-large brush piles. All Bluegill life stages except fryballs had significantly negative effects on all brush pile strata while Bluegill fryballs had mixed responses. In Big Fish Lake, Florida Bass fryballs had significantly positive effects on close-large while adults had significantly positive effects on all brush pile strata. Age-0's had significantly negative effects on close-large and -small as well as far-large while adults had significantly negative effects on all brush pile strata. Bluegill had significantly negative effects on some brush piles and insignificant on the rest.

Over all the post-augmentation surveys, the proportion of species / life stages with consistently positive or negative differences in effect sizes in brush pile strata versus non-brush areas was 84% in Speckled Perch Lake and 54% in Big Fish Lake (Figure 4-4). In Speckled Perch Lake, Lake Chubsuckers, Florida Bass age-0's and adults, Bluegill fryballs, Black Crappie, and Florida Softshells had consistently higher effect sizes relative to non-brush areas. Brook Silversides, all Bluegill life stages, Redear Sunfish, adult Golden Shiners, Lined Topminnows, Brown Bullhead, Florida Gar, Swamp Darters, Mosquitofish, and Peninsula Cooters had consistently lower effect sizes. In Big Fish Lake, adult Florida Bass, Bluegill fry, and adult Bluegill had consistently higher effect sizes while Brook Silversides, juvenile Bluegill, and Seminole Killifish had consistently lower effect sizes relative to non-brush areas. A spawning bout of Florida Bass was seen with an increase in effect size for Florida Bass fryballs and adult Florida Bass in the first post-augmentation survey (corresponding to March 2015) in Big Fish Lake.

Patterns from comparing pre- and post-augmentation (Figure 4-3) were mostly consistent when comparing within a survey brush pile strata to non-brush pile areas (Figure 4-4). In Speckled Perch Lake and over post-augmentation surveys 1-4, many species had large effect sizes. This is in contrast to Big Fish Lake, which has considerably smaller effect sizes for many species / life stages in all surveys. Only in the last post-augmentation survey did Speckled Perch Lake have considerably lower effect sizes on brush piles and, of these, most were negative. The spawning bout of Florida Bass present in pre- and post-augmentation comparisons (Figure 4-3) was still present in Big Fish Lake with larger, positive effect sizes for fryballs and adults.

Across brush pile strata, close and far brush piles had the 11 species / life stage significantly positive effects with eight in Nuphar strata in Speckled Perch Lake. In Big Fish Lake, close brush piles had three significantly positive effects and far had two. Speckled Perch Lake far brush piles had 24 significantly negative effects, close brush piles had 22, and Nuphar had 21. In Big Fish Lake, far brush piles had 13 significantly negative species / life stage effects and close brush piles had 11. On average in both lakes, large brush piles had larger effect sizes (positive or negative) than small brush piles. Close brush piles had on average smaller effect sizes than far brush piles but were larger than Nuphar for negative effects but smaller for positive effects.

Brush Pile Effects on Diversity

At the lake-wide level, Keys Lake had the highest spatial variability in species richness across the lake followed by the two large lakes, Speckled Perch Lake and Devil's Hole Lake (Figure 4-5). Big Fish Lake had initially fairly low weighted richness during the pre-augmentation survey and increased by the last survey. In Speckled Perch Lake, pockets of high weighted richness occurred along the northeastern shore in

an area with high vegetation diversity (comprised of aquatic bladderworts, Banana Lily, grasses, rushes, and Spatterdock), in the middle of the lake in Spatterdock patches, and smaller areas along the edge of the littoral zone in the pre-augmentation surveys (Figure 4-5A). In the first post-augmentation survey, the weighted richness of these pockets increased (Figure 4-5B) and continued to increase as well as spread by the last post-augmentation survey (Figure 4-5C).

Similar temporal dynamics occurred in Big Fish Lake and Devil's Hole Lake with pockets of high weighted richness along the littoral zone in the pre-augmentation survey (Figure 4-5D & G) with those pockets increasing in weighted richness by the last post-augmentation (Figure 4-5E–F & H–I). In Keys Lake, pockets of high weighted richness along the littoral zone (Figure 4-5J) became a swath of high weighted richness along the littoral zone by the last post-augmentation survey (Figure 4-5K–L). Pockets of high weighted richness in Devil's Hole Lake and Keys Lake corresponded to areas of high vegetation diversity. In Devil's Hole Lake, a particular rich area along the eastern shore had Maidencane, Lemon Bacopa, Spatterdock, and Periphyton along with sand / limestone cobble substrate (80 / 20%, respectively). Anecdotally, this area is known for high angling and electrofishing catch per unit effort (CPUE) and a groundwater connection keeping ambient water temperatures lower than the surrounding lake. In Keys Lake, pockets of high richness along the western and southern shores had aquatic bladderworts and rushes while a particularly rich area along the northern shore had aquatic bladderworts, rushes, and Spatterdock. While comprised of two and three vegetation types, these areas are high in vegetated diversity compared to the solely aquatic Bladderwort or denuded rest of Keys Lake.

Brush piles in Speckled Perch Lake had a significant negative effect on species richness relative to the pre-augmentation surveys. Jackknife sampling revealed the critical species / life stages that drove the richness on brush piles. Adult Bluegill, Redear Sunfish, and Swamp Darters significantly drove species richness on close-large brush piles as well as on far-large brush piles. On far-brush piles, Brook Silversides, adult Florida Bass, Florida Gar, and Peninsula Cooters also significantly contributed to species richness. Brook Silversides, age-0 Florida Bass, adult Florida Bass, Bluegill fry, adult Bluegill, Florida Gar, Redear Sunfish, adult Golden Shiners, Swamp Darters, and Peninsula Cooters significantly drove species richness on far-small as well as Nuphar-large and -small brush piles. Relative to the post-augmentation surveys, Bluegill fryballs significantly drove species richness on Nuphar-large brush piles. Overall, mean weighted richness in Speckled Perch Lake increased from 5.37 to 8.53 with an increasing standard deviation of 1.75 to 1.86 between pre- and post-augmentation surveys. This resulted in brush piles being most significantly different from pre-augmentation surveys than post-augmentation surveys.

Brush piles in Big Fish Lake had no significant effects on weighted richness relative to pre- or post-augmentation surveys indicating species richness did not change between brush piles and surrounding habitat. Mean lake-wide weighted richness was 2.21 and increased to 2.79 with an increasing standard deviation of 0.84 to 0.95 between pre- and post-augmentation surveys. Keys Lake showed similar temporal dynamics in weighted richness ($\mu_{PRE} = 6.69, \mu_{POST} = 7.43$) indicating that lake-wide weighted richness across lakes was likely positively correlated with the number of surveys consistent with standard discovery curves in biodiversity sampling.

Discussion

Habitat augmentation induces habitat selection processes restructuring species assemblages through abiotic constraints and biotic interactions. As a result, augmented habitat is likely to result in different local species assemblages from existing ones (Walsh 1985, Bohnsack et al. 1994, Moring and Nicholson 1994). Here, we showed evidence for depauperate and different communities resulting from disparate effects of brush piles across species, over life history stages, between lakes, and over time. Larger-bodied species, on average, attracted to brush piles with the effect of decreasing species richness as a function of distance from littoral habitat. The disparate effects we observed indicate abiotic constraints limit some species from colonizing any augmented habitat, dispersal predation likely limits smaller-bodied species from colonizing habitat far away from existing refuges, and a suite of biotic interactions determines co-colonizing species. The result of each species' habitat selection alludes to a more complex relationship between augmentation effectiveness and system characteristics than implied by the "if you build it, they will come" approach implicit in many single-species habitat augmentations.

Unintended and inconsistent effects, such as we observed, could almost be considered the norm of habitat augmentation strategies using coarse woody habitat. Additions of this habitat have yielded limited results (Moring and Nicholson 1994, Lewin et al. 2004, Sass et al. 2012) though removals can impact diet, growth, and condition of target species (Sass et al. 2006, Ahrenstorff et al. 2009, Gaeta et al. 2011). Artificial reefs, the analogous structure in marine environments, have also yielded limited predictable outcomes with considerable scientific introspection aimed at resolving the issue (Lindberg 1997, Pickering and Whitmarsh 1997, Carr and Hixon 1997, Pickering

et al. 1999, Osenberg et al. 2002). Despite this, habitat augmentations with simple structures often assume new structure is universally attracting target species. This assumption likely derives from the high biomass attributed to early artificial reefs (reviewed by Bohnsack and Sutherland 1985) as well as a plethora of evidence for fish attraction to structure.

In our lakes, the target gamefish species, adult Florida Bass and Bluegill, had variable responses to new structure, with Florida Bass being attracted and Bluegill both attracted and deterred compared to pre-augmentation surveys. Compared to post-augmentation surveys, Florida Bass had moderate positive effect sizes and Bluegill had strong increasing negative effect sizes in Speckled Perch Lake, the larger augmented lake, as well as moderate positive effect sizes for both species in Big Fish Lake, the smaller augmented lake. We attribute Speckled Perch Lake's failure to universally attract gamefish to differences in the lake characteristics. Speckled Perch Lake has a more diverse complement of 25+ plant species, wider littoral zones (9.2 m), and more submersed aquatic vegetation (7.4 %) than Big Fish Lake which has only 11 plant species, narrower littoral zones (4.1 m), and less submersed aquatic vegetation (1.7 %) (Hangsleben et al. 2013). As a result, Speckled Perch Lake had considerably high interstitial space diversity and abundance prior to augmentation relative to Big Fish Lake. Thus, habitat augmentation effectiveness at attracting fish is probably related to the amount of existing natural structure (and the attendant diversity and abundance of interstitial spaces) as in the case with Big Fish Lake. Brush pile augmentations dramatically increase the availability and diversity of interstitial spaces in the case of low amounts of existing natural structure (Schindler et al. 2000, Miranda et al. 2010, Gaeta

et al. 2011) but only minimally so in the case of high amounts of existing natural structure (Newbrey et al. 2005).

During the timescale of most augmented habitat studies' *in situ* observations (lasting a few years to a decade), coarse woody habitat (Johnson and Lynch 1992, Schindler et al. 2000, Sass et al. 2012), concrete debris (Bortone et al. 1994, 2011, Marsden et al. 2016), tire piles (Bohnsack et al. 1994), or other simple habitat (Moring and Nicholson 1994, Sheehy and Vik 2010) possess little structural resemblance to natural habitat (Pickering and Whitmarsh 1997, Brickhill et al. 2005). These structures lack natural habitat's interstitial space diversity afforded by accreting organisms that accumulate on augmented habitat often beyond the timescale of observations (Carr and Hixon 1997). In many freshwater systems, accreting organisms are lacking and augmented habitat remains perpetually hypodiverse relative to vegetation. Further, the distribution of interstitial spaces on simple habitat is truncated to larger spaces leading to a dearth of available refuge for species or life stages with small body sizes (Shulman 1984, Hixon and Beets 1989, Brickhill et al. 2005). This refuge availability imparts a strong environmental filter on the species likely to persist after colonization of the site, selecting only for species that can utilize the available interstitial space or structure characteristics (Caley and John 1996, Brickhill et al. 2005, Newbrey et al. 2005).

In our lakes, brush piles were strongly selected for by large-bodied species with small bodied and cryptic species typically failing to occupy brush piles. These large-bodied species were Lake Chubsucker, adult Florida Bass, Black Crappie, and Florida Softshell in Speckled Perch Lake and adult Florida Bass as well as adult Bluegill in Big Fish Lake. Reductions in the species assemblage of this kind likely reflects the large

interstitial spaces on brush piles versus vegetation (Heck and Thoman 1981, Savino and Stein 1989b, Newbrey et al. 2005). The few occupying small-bodied fishes were early Florida Bass life stages (i.e. fryballs, age-0's, and juveniles) in Speckled Perch Lake and Florida Bass fryballs and Bluegill fry in Big Fish Lake. As the most abundant species in our lakes, Florida Bass and Bluegill are the also the most likely to be undergoing strong density-dependent mortality and growth through intra- and interspecific competition and predation (Werner et al. 1983, Werner and Anholt 1993). The colonization of pre-adult life stages for both of these species is likely in response to density-dependent mortality (Werner and Gilliam 1984, Hixon and Jones 2005). Even with potentially larger interstice sizes on brush piles, new structure provides greater refuge availability and access to new resources that were otherwise limited by advection of prey into existing refuges (Walters and Juanes 1993, Ahrens et al. 2012). Further, colonization of brush piles by the early life stages may reduce the high predation risk associated with the littoral zone (Lewis and Helms 1964, Werner and Hall 1988, Savino and Stein 1989b).

There was limited inference to be made based on the number of species / life stages attracted to a given brush pile stratum. In both lakes, large brush piles had larger effect sizes than small ones either reflecting the disparity in interstitial space abundance or a greater variety of interstice sizes between the two sizes of brush piles. In Speckled Perch Lake, brush pile distance from shore had little impact on the number of species / life stages filtered likely reflecting the large patch of Spatterdock in the lake disrupting a clear distance to shore (and the littoral zone) gradient. In Big Fish Lake, close brush piles had one more species / life stage with a significant effect size indicating only a

small difference between brush pile distance groups. This likely reflects the steep bathymetric gradient present in Big Fish Lake (Figure 4-1A) limiting the distance between close and far brush piles. Close brush piles in both lakes were more likely to have small-bodied species / life stages occupy them while far brush piles were more likely to have large bodied species / life stages. This difference could arise from the high predation risk associated with moving from littoral zone refuges for small-bodied organisms or limitations due to swimming ability, more likely the former (Ware 1975, Shulman 1984, Walters and Juanes 1993). Overall, differences in species-specific attraction or deterrence resulted in impoverished and different brush pile species assemblages in Speckled Perch Lake as well as diminished but similar brush pile species assemblages in Big Fish Lake.

The depauperate and different communities we observed may have numerous consequences to the local as well as lake population and community dynamics. The most obvious of these is changes in the predation risk of brush pile occupying species / life stages. Brush piles in Speckled Perch Lake had significantly higher occupancy of Florida Softshell than the typical nursery habitat in the littoral vegetation. Occupancy of brush piles by young Florida Bass life stages might reduce the predation risk of littoral zone predators only to induce a different predation risk from Florida Softshell. Access to higher prey concentrations may occur as brush piles were located in open water or Spatterdock away from the high competitor abundance in the littoral zone.

Reduced species richness on brush piles may have had subtler effects. Augmented habitat may provide greater refuge availability and alleviate density-dependent mortality associated with nursery habitat but this loss of prey items could

potentially increased predation on other species located in the littoral zone. For instance, spawning Florida Bass adults and fryballs moving from spawning beds in littoral zones to deeper water habitat on brush piles in Big Fish Lake could reduce the vulnerability of adults to avian predators (Heck and Thoman 1981, Biro et al. 2003) such as Osprey *Pandion haliaetus*, herons *Ardea* spp., and egrets *Egretta* spp. as well as the vulnerability of fryballs to piscine predators located along the littoral zone. In turn, this reduction in prey availability to avian piscivores could increase predation on species that remain in the littoral zone. Another subtle potential effect from brush pile occupancy is indirect effects on the target species prey base. Reductions in vulnerability for early life stages by movement to brush piles has the potential to increase the strength of density-dependent growth on predatory species of those life stages with downstream effects on their fecundity. A similar phenomena occurs when high refuge availability through vegetation limits the growth of predators (Crowder and Cooper 1982). An interspecies interaction where this could have arisen was the use of brush piles by spawning bass that likely decreased the vulnerability of Florida Bass eggs and fry, which could have reduced the available prey, Florida Bass eggs and fry, to adult Bluegill predators, and result in less production of Bluegill early life stages, one of the main prey populations for adult Florida Bass, and could result in reductions in growth, condition, and fecundity.

We made many assumptions in our surveying and modeling process. During our survey, we assumed that camera deployments were minimally disruptive and normal fish behavior and movement would occur shortly after deployment. For the most part, we feel this assumption was not violated. Some instances during diver-based camera deployments disturbed sediment and vegetation had the potential to attract or disperse

fishes and turtles from the survey volume but those instances of this nature were limited to less than 10 out of 642 surveys. Other potential violations may have resulted from attracting fishes to the camera as occurred semi-frequently with juvenile and adult Bluegill and intermittently with Florida Softshell and Brown Bullhead (Figure 4-9). We concluded this effect to be minimal as despite the occasional inquisitive fish most fishes moved rapidly through the survey volume. Perhaps the most worrisome survey violation is false positives, both from double counting and species misidentification. Double counting was not a factor for us as we assumed from the occupancy framework that each survey was a series of Bernoulli trials and that individuals could leave or enter between each clip. We observed minimal instances of fish remaining in the survey volume between clips and these instances were limited to adult Florida Bass on spawning beds in Big Fish Lake during the first post-augmentation survey. Misidentification was a more prevalent issue in our *post-hoc* survey analysis with 10-20% of species misidentified by technicians. We attributed this error to low visibility and technician naivety with system characteristics. The lead author watched every clip with fish presences and corrected any undercounting or misidentifications to minimize this error.

Our multiscale occupancy modeling structure also made assumptions about the nature of the occupancy process and observations. The latent state z_{ik} of the permanent occupancy assumed that over the course of the six surveys that a species either occupied or unoccupied a given site. We knowingly violated this assumption, as the purpose of study was to manipulate occupancy through brush pile augmentations. Fortunately, we did not intend to use the permanent occupancy latent state to make any

inference other than the overall prevalence of given species in the lakes across surveys. Instead, we used the latent state a_{ijk} of the temporary occupancy to vary site-level (permanent) occupancy survey to survey and infer the gradual change in occupancy at sites as a result of brush pile augmentations and time. Another option we could have implemented was a dynamic occupancy model (Royle and Kéry 2007) but we did not have the requisite number of pre-augmentation surveys to truly assess changes in occupancy with this formulation. Another assumption our model framework made is the sharing of information between species for the permanent occupancy probability, the temporary occupancy probability, and the detection probability through hyperdistributions and random effects. We feel this is a reasonable assumption in our lakes given a diversity of body sizes and species. Had we included a single turtle species or an outlier body size this assumption would have been less appropriate.

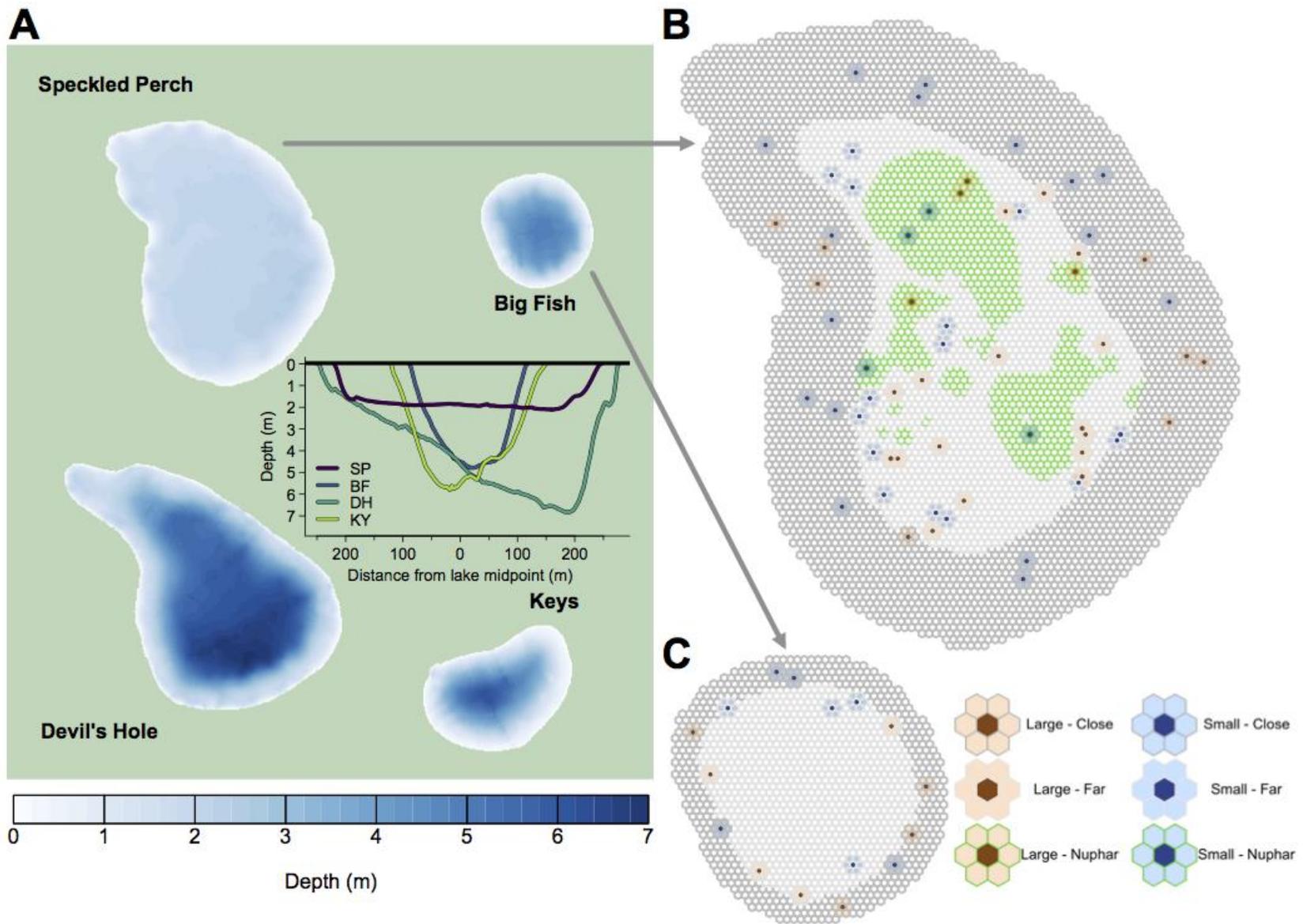
Conclusion. Habitat augmentations are a ubiquitous fisheries management strategy worldwide with the ability to be excellent tests of the mechanisms underlying ecological processes. Despite the prevalence of augmented habitat producing changing and different species assemblages (Walsh 1985, Bohnsack et al. 1994, Caley and John 1996, Brosse et al. 2007), the assumption of many habitat augmentations is for target species to be attracted and to increase in productivity (Turner et al. 1969, Polovina 1991, Pickering et al. 1999). We tested this universal attraction of target species, adult Florida Bass and Bluegill, and found Florida Bass to attract to new habitat in both lakes but only Bluegill fryballs to attract in our larger lake. Additionally, the majority of the fish community did not attract to brush piles, 3 out of 15 species in our large lake and 2 out of 5 species in our small lake.

These depauperate communities could benefit target species through alleviating density-dependent mortality and growth, as they were intended. However, changes in the local species assemblage may result in unintended consequences for target species and drive the variability observed in habitat augmentation studies (Lindberg 1997, Pickering and Whitmarsh 1997). Future research should focus developing candidate species for effective augmentation and determining the effects of the highly likely depauperate species assemblages on augmentation efficacy. It is unrealistic to assume providing additional refuges increases the system's carrying capacity without considering how the food web responds. Habitat augmentations provide an excellent experimental setup to test the mechanisms and stability of community assemblage processes. We inferred the depauperate assemblages arose from co-occurring abiotic filtering and lumped biotic interactions. However, it would be useful to determine which biotic interactions, such as density-dependent mortality and growth as well as food availability, competition, and predation, are doing the species filtering. With the advent of 3D printing, it may be possible to determine such components using large-scale, manipulable, standardized, and complex habitat.

Table 4-1. Prior and hyperprior distributions for parameters of the multiscale occupancy model.

Component	Eq. #
<i>Priors</i>	
$\psi_k \sim N(\mu_\psi, \sigma_\psi)$	4-4
$\theta_{ik} \sim N(\mu_\theta, \sigma_\theta)$	4-5
$p_{ijk} \sim N(\mu_p, \sigma_p)$	4-6
<i>Hyperpriors</i>	
$\mu_\psi \sim \text{logit}(U(0,1))$	4-7
$\sigma_\psi \sim U(0,5)$	4-8
$\mu_\theta \sim \text{logit}(U(0,1))$	4-9
$\sigma_\theta \sim U(0,5)$	4-10
$\mu_p \sim \text{logit}(U(0,1))$	4-11
$\sigma_p \sim U(0,5)$	4-12

Figure 4-1. Bathymetric profiles for the four surveyed lakes (A). Inset is a cross-section of each lake's bathymetry at the widest point. Brush piles were added to Speckled Perch (B) and Big Fish (C) into six and four potential groups, respectively. Large brush piles (three trees) are indicated in brown while small brush piles (one tree) are indicated in blue with darker tones indicating the brush piles location and lighter tones indicating the six adjacent cells. Brush piles are indicated by dark grey in the nearshore zone, light grey in the offshore zone, and green in Spatterdock (*Nuphar lutea*; applies to Speckled Perch only).



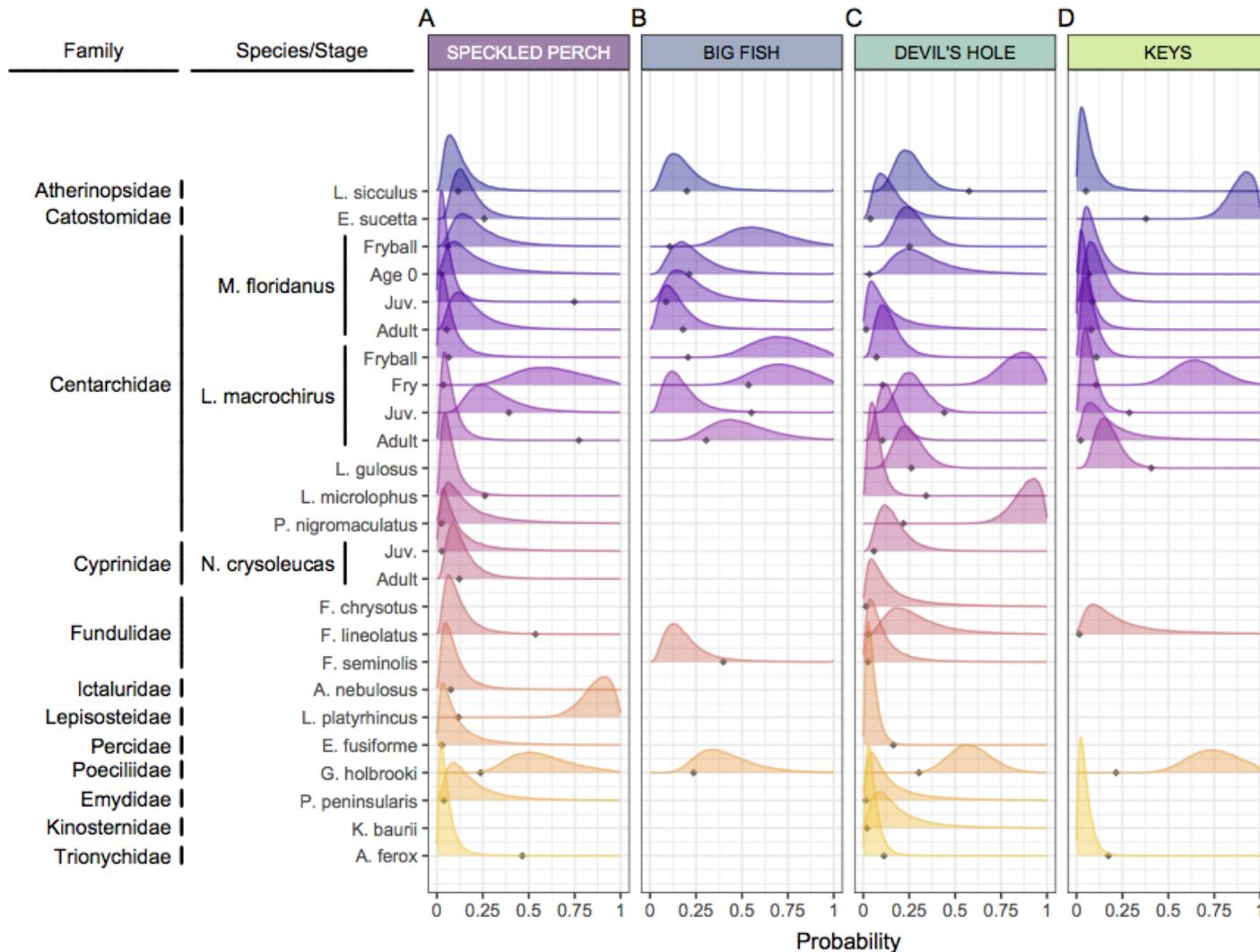
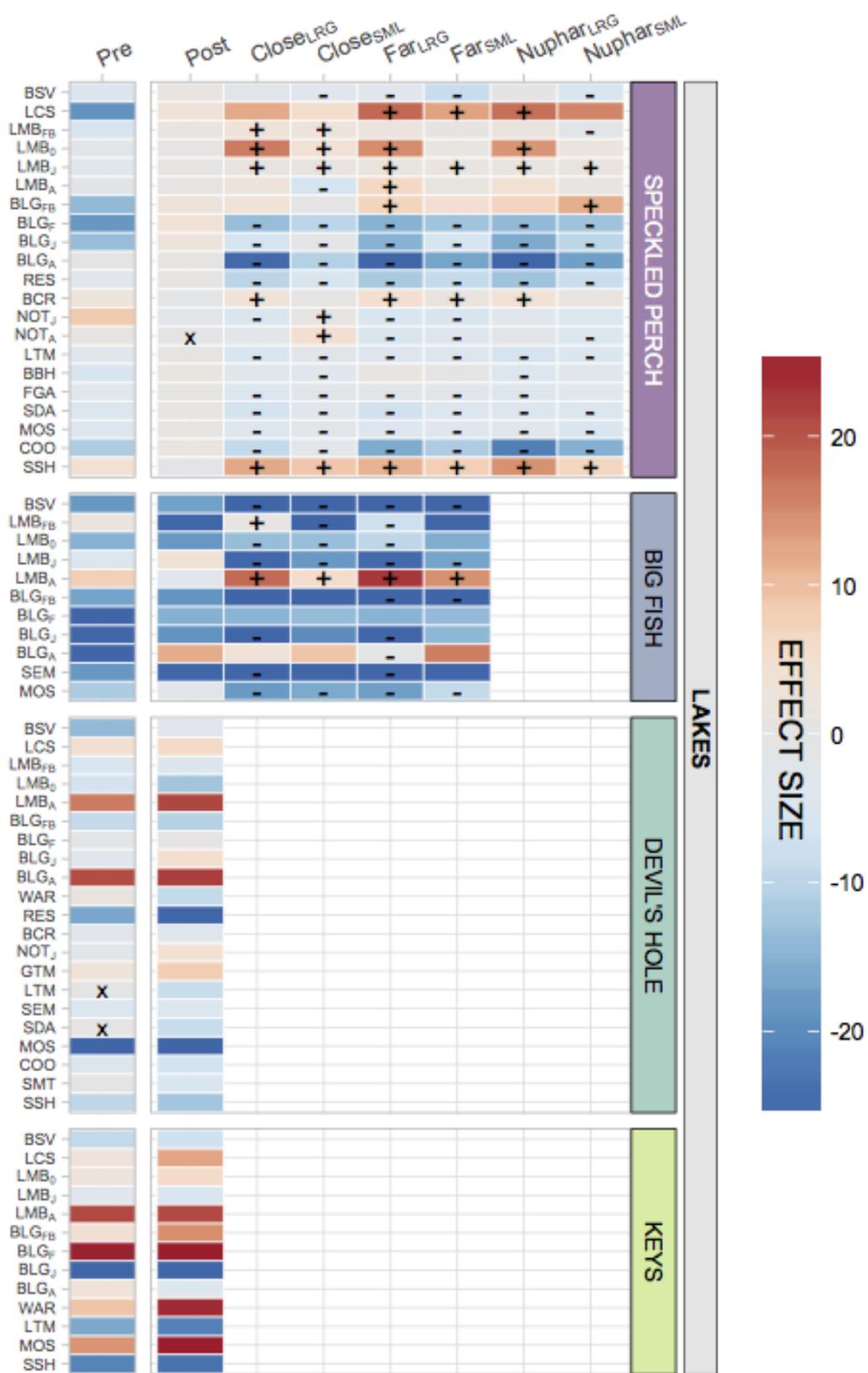


Figure 4-2. Site-level probabilities of occupancy of each fish / turtle species by lake estimated from the multiscale occupancy model. Density distributions indicate the occupancy probability and gray diamonds indicate the median detection probability for each species.

Figure 4-3. Effect sizes for each species in each lake for all non-brush pile areas pre- (Pre) and post-augmentation (Post) as well as six brush piles: close, far, and Nuphar for large (LRG) and small (SML) sizes. Warmer colors indicate higher probabilities. Significant brush effects were denoted with “+” for positive and “-“ for negative effects with insignificant pre- or post-augmentation effects denoted with “x”. Florida Bass stages are denoted as LMB_{FB} for fryball, LMB₀ for age-0’s, LMB_J for juveniles, and LMB_A for adults. Bluegill stages are denoted as BLG_{FB} for fryball, BLG_F for fry, BLG_J for juveniles, and BLG_A for adults. Golden Shiner stages are denoted as NOT_J and NOT_A for juveniles and adults, respectively. Other species codes are: Brook Silversides (BSV), Lake Chubsucker (LCS), Redear Sunfish (RES), Black Crappie (BCR), Golden Topminnow (GTM), Lined Topminnow (LTM), Seminole Killifish (SEM), Brown Bullhead (BBH), Florida Gar (FGA), Swamp Darter (SDA), Eastern Mosquitofish (MOS), Peninsula Cooter (COO), Striped Musk Turtle (SMT), and Florida Softshell Turtle (SSH).



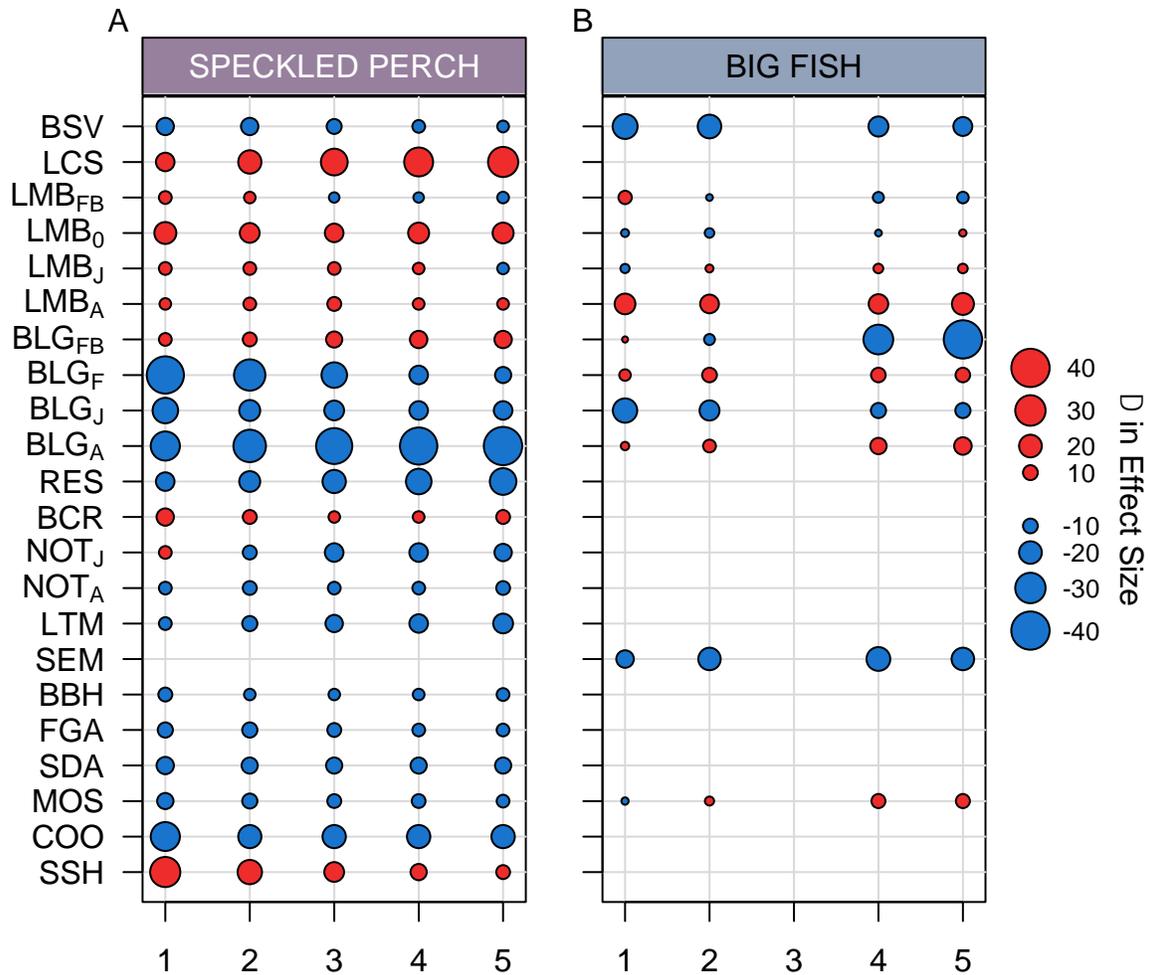


Figure 4-4. Difference in effect size of brush pile strata from non-brush areas for each post-augmentation survey for each species in Speckled Perch (A) and Big Fish (B). Positive differences in relative effect (colored red) indicate a species had a higher probability of brush pile versus the non-brush areas and vice versa for negative differences (colored blue). Symbol size indicates the magnitude of the effect. Species abbreviations are equivalent to Figure 4-3.

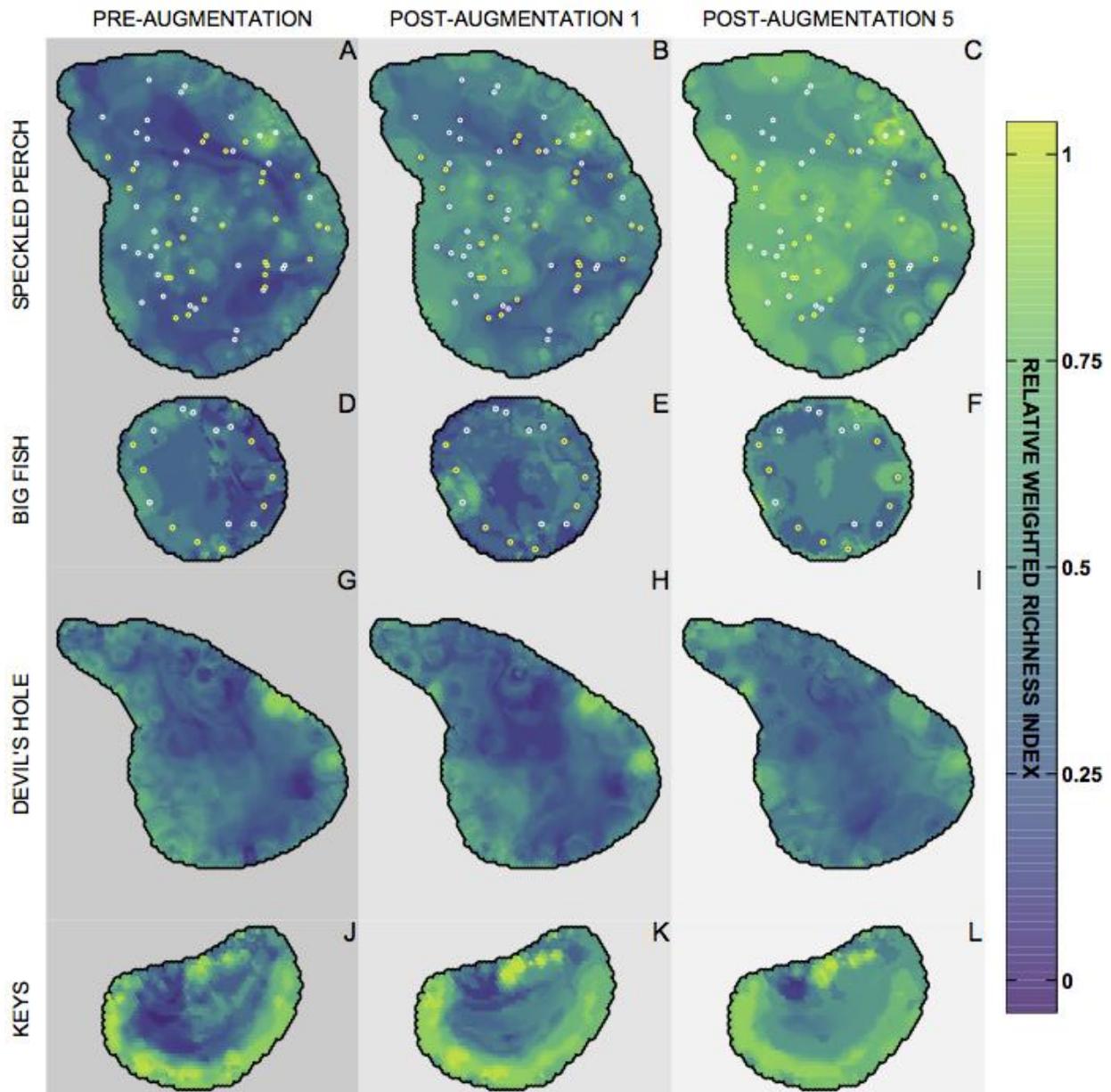


Figure 4-5. Relative weighted richness (standardized between 0 and 1) for each lake for pre-augmentation, first post-augmentation, and fifth (last) post-augmentation surveys (left to right). Warmer colors indicate higher relative weighted richness (higher diversity). Yellow and white borders indicated large and small brush piles, respectively, in Speckled Perch and Big Fish.

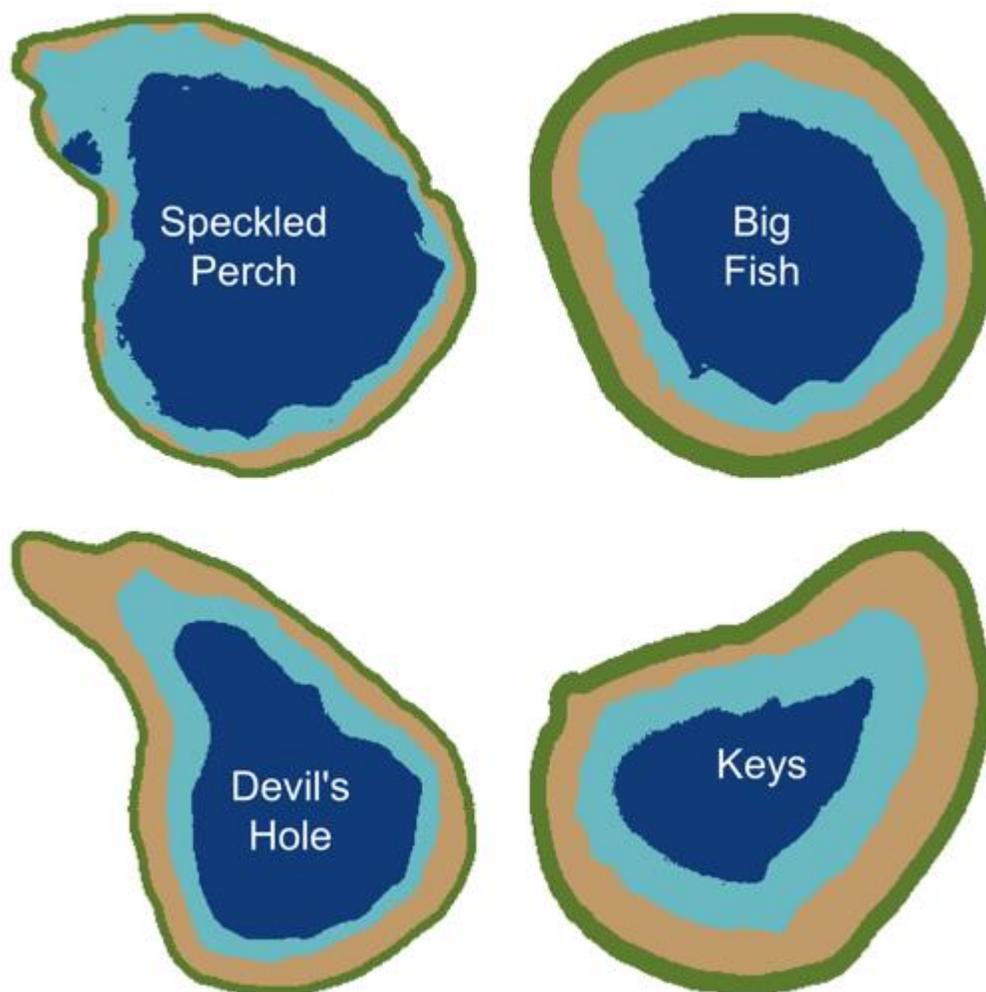


Figure 4-6. The four strata each lake was divided into for purposes of the camera survey of natural habitats based on depth, distance to shore, and an emergent vegetation index calculated by Google Earth satellite imagery.

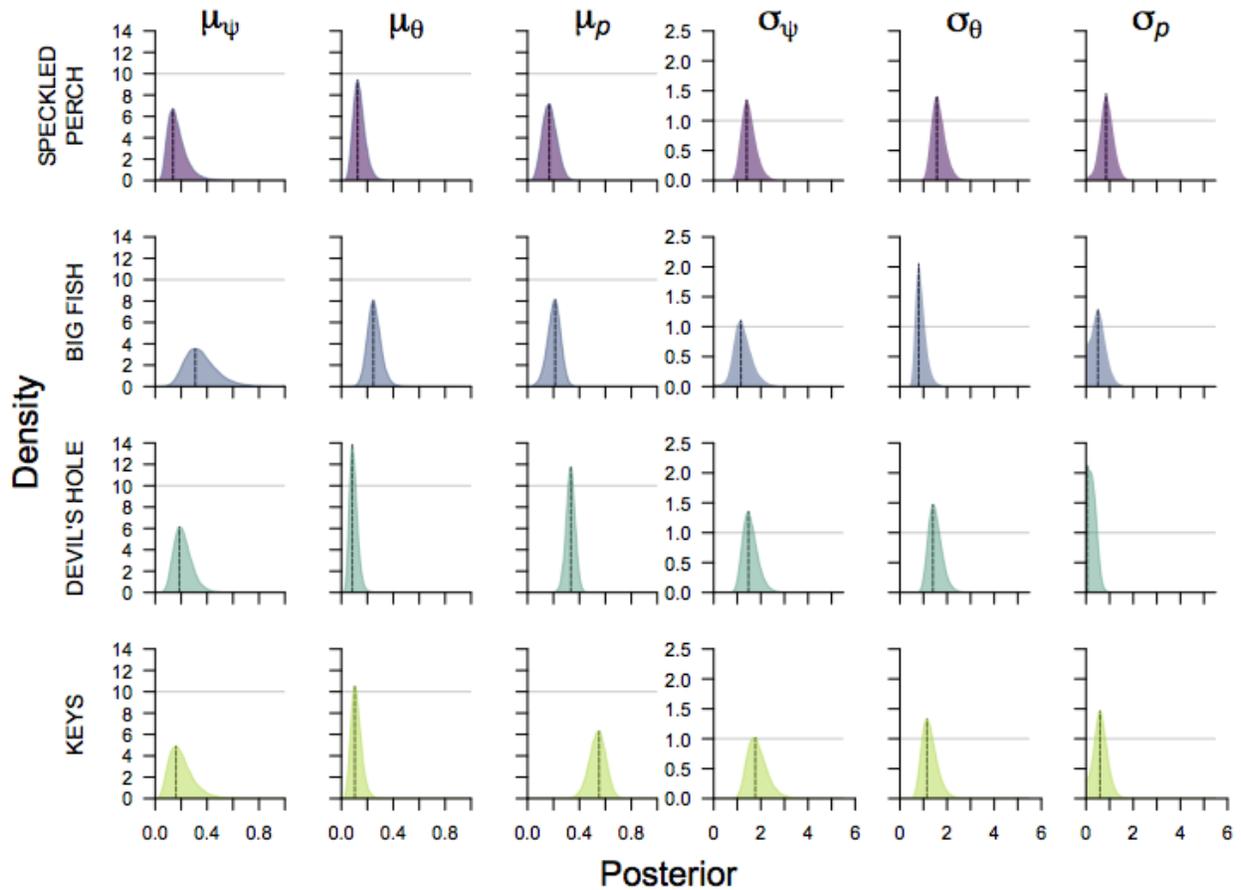


Figure 4-7. Marginal posterior distributions for hyperparameters (μ_x, σ_x) of Normal hyperdistributions for ψ_k , θ_{jk} , and p_k (the permanent occupancy probability for species k , the temporary occupancy probability for species k on survey j , and the detection probability for species k , respectively). Hypermeans ($\mu_\psi, \mu_\theta, \mu_\rho$) were back-converted from the logit scale for ease of interpretation. Dashed lines indicate the maximum of the marginal posterior distributions. Gray solid line indicates the flat prior distribution for the hyperparameters.

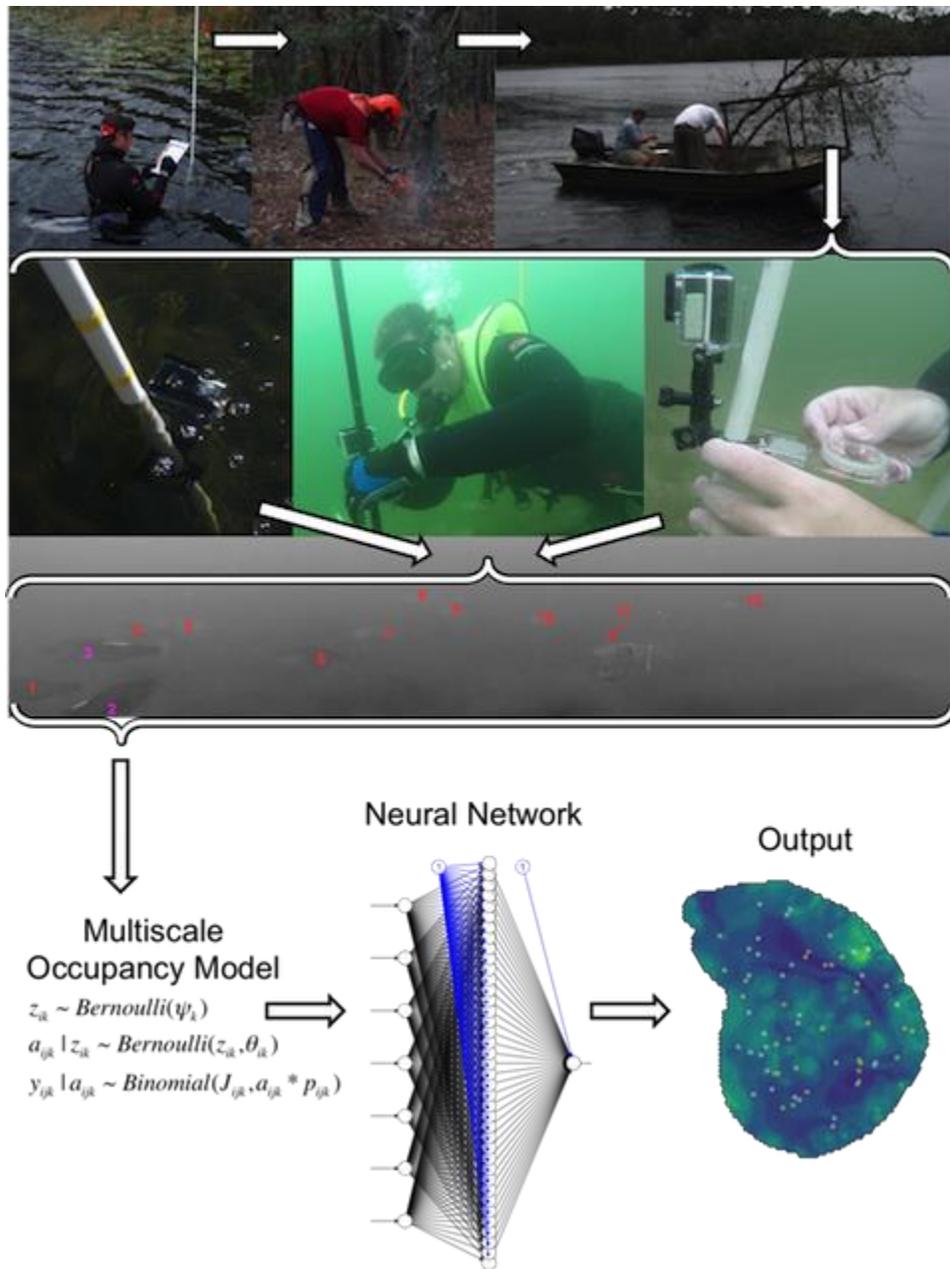


Figure 4-8. General framework for the study. Pre-augmentation surveys (top, left) were followed by logging of brush piles (top, center) then habitat augmentation (top, right). Post-augmentation surveys (center, three panel) followed habitat augmentation from March 2015 to May 2016 and were conducted by boat (center, left) and divers (center) measuring environmental and survey characteristics (center, right). Clips from surveys were enumerated (center, full width). Counts were converted to presence / absence and used in a multiscale occupancy model (bottom, left), then the Markov Chain Monte Carlo predictions of the survey-level latent state were used to train a neural network with environmental covariates (bottom, center). The neural network was then used to produce lakewide predictions. Photos courtesy of author.

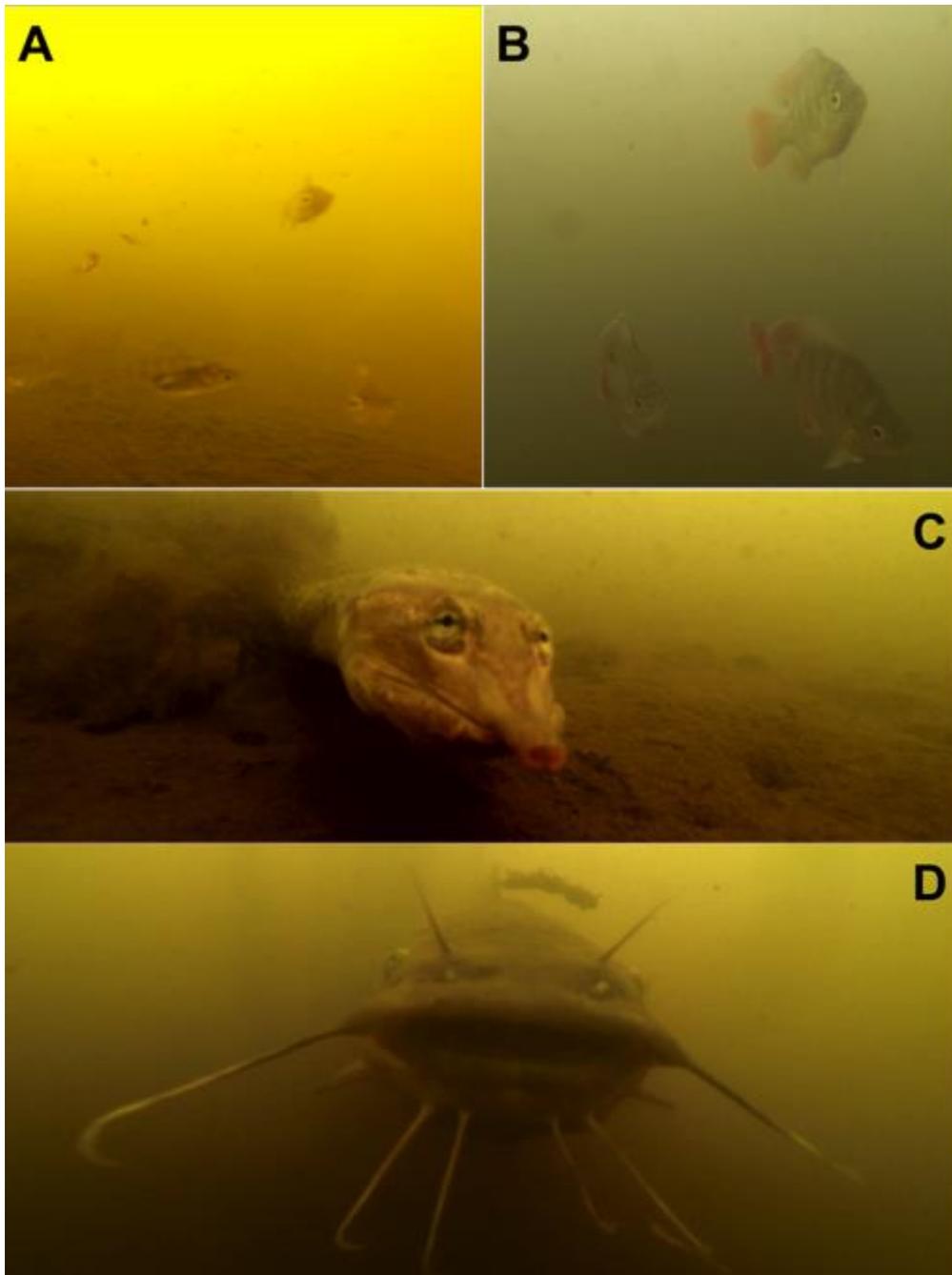


Figure 4-9. Examples of species / life stages that were attracted to the camera: (A) juvenile Bluegill, (B) adult Bluegill, (C) Florida Softshells, (D) Brown Bullhead. Photo courtesy of author.

CHAPTER 5 CONCEPTUAL MODEL FOR HABITAT EFFECTS

Introduction

Habitat augmentations have resulted in variable attendant dynamics and a corresponding litany of potential processes attempting to explain them. Principally, these processes have to account for several key patterns: 1) the ubiquitous attraction of fish to structure; 2) the dynamic community assemblages on augmented habitat (Walsh 1985, Hixon and Beets 1989, Bohnsack et al. 1994, Caley and John 1996); and 3) the exceptionally high biomass found on artificial structure. The latter pattern has resulted in a false dichotomy between early artificial reef proponents uncritically accepting that artificial reefs lead to increased fish production (Turner et al. 1969, Talbot et al. 1978, Smith et al. 1979) and fisheries scientists contending habitat could not be limiting exploited fish stocks that were presumably near carrying capacity with the same amount of hard bottom prior to heavy exploitation (Bohnsack and Sutherland 1985, Bohnsack 1989, Polovina 1991). Bohnsack (1989) contended that the association with habitat by fishes is the result of behavioral preference. However, for behavioral preference to arise so ubiquitously across fishes, natural selection must act upon fitness benefits garnered from attraction (Morris 1992, Greene and Stamps 2001, Mayor et al. 2009). This extension of Bohnsack's (1989) tautology to evolutionary time-scales simply entails attraction precipitating production and revealing the attraction-production debate to result from a false dichotomy.

Despite this, the key patterns of habitat augmentations remain largely unexplained as well as why is there so little evidence for production from habitat augmentations. To explain these phenomena, we propose a new conceptual framework

for the effects of habitat augmentations on aquatic systems. The framework consists of six components: 1) an existing system to be augmented; 2) the habitat augmentation; 3) attraction to new structure; 4) density-independent effects resulting from the augmentation; 5) fitness benefits; and 6) selection. In the following text, these components will be discussed and the results of Chapters 2 – 4 integrated into the framework. Our objective is to integrate the considerable scientific inference made throughout the attraction-production debate into a single framework that can be applied across aquatic systems. The motivation behind this objective is to allow researchers and managers to make decisions about the use and implementation of habitat augmentations with a clear understanding of the likely processes that will be impacted and possible outcomes that may result. Further, the processes that govern habitat augmentation effects are similar between aquatic systems and coalescing research across systems may result in new inferences and hypothesis.

Conceptual Framework

Existing System

Prior to habitat augmentations, environmental resources (bottom-up control) and predator abundances (top-down control) determine how fishes allocate themselves in space, time, and through behavior. There are numerous ways to envision these processes including Lotka-Volterra and ratio-dependent predator-prey models (Lotka 1925, Volterra 1931, Arditi and Ginzburg 1989) but we choose to focus on foraging arena theory. Foraging arena theory envisions spatial, temporal, and behavioral patterns as the result of organisms seeking to maximize consumption and minimize predation (Ware 1975, Werner and Hall 1988) by exchanging between vulnerable and

invulnerable states (Walters and Juanes 1993, Ahrens et al. 2012). These foraging arena dynamics are the result of intraspecific competition and their density-dependent feedback on exchange rates from refugia and each foraging bout incurring a risk of predation. When the foraging arenas are viewed in aggregate across the system, prey should be distributed according to an ideal free distribution (Fretwell and Lucas 1969) to maximize fitness (e.g. minimizing competition and predation while maximizing per capita consumption rates). Summarizing the existing system: foraging arena dynamics determines the spatial, temporal, and behavioral restrictions fishes undertake to maximize survival and when aggregated over space and time the foraging arena dynamics produce the ideal free distribution of fishes maximizing their fitness. It is these dynamics, and by association the processes of competition and predation, that habitat augmentations can modify.

In our augmented lakes, Chapters 3 and 4, the foraging arena and ideal free distribution dictated the pre-augmentation conditions. Across lakes, the production of Florida Bass prior to augmentation was highly variable by evidence of wide confidence intervals in our population estimates and high interannual variation in adult “apparent survival.” These likely resulted from intense competition for food resources (anecdotally, many individuals were of very poor condition) resulting in density-dependent growth, survival, and, subsequent, high variability in recruitment or the production of new Florida Bass. Further evidence is derived from skip spawning (Shaw and Allen 2014) and the likely cannibalistic origin of a Ricker stock-recruit relationship in the lakes (Ricker 1975, Shaw and Allen 2016). Similar to many other systems (Pauly 1980, Walters and Juanes 1993), the survival bottleneck within our lakes was likely in the juvenile life stanza as

nest survival was considerably less variable than adult “apparent survival” (Slagle et al. 2017). Fish communities within the lakes were typically localized and codependent on interacting environmental characteristics. Species richness was asymptotically stratified as a function of distance from shore, with higher species richness near the shoreline and lower species richness farther away. Habitat complexity and dispersal predation likely drove this relationship with the result of small areas of high abundance / occurrence and many areas of low or no abundance / occurrence.

Habitat Augmentation

The process of augmenting habitat is concurrently the simplest component in our framework and of the greatest consequence. Choices in habitat structure and location precipitate vastly different dynamics within aquatic systems and the limited ability of scientists to explicitly replicate most structures is partly to blame for the lingering attraction-production debate (Bohnsack et al. 1994, Carr and Hixon 1997, Wills et al. 2004). We argue that rather than continue to distinguish natural versus artificial habitat it more useful to quantify the structural components and location characteristics that distinguish them (Bohnsack 1989). Natural habitat already exists along a continuum (a classic example is the reef to sandy bottom gradient) and somewhere between the most complex, fractious habitats and the simplest falls artificial ones. Structural components might be represented in a multi-dimensional space with structural complexity, shape, orientation, depth, reef size, material composition, current flow, adjacency to other structures, and so on as its axes. Placing the entire suite of natural habitat into this space would reveal they span the continuum of habitat quality. The addition of artificial habitat to this space might yield some skewness relative natural habitat on a few axes, such as composition and complexity, but for many of the axes the similarity to natural

reefs would be apparent. One potential metric that may incorporate the availability of interstitial space for various sizes of fish is the fractal coefficient proposed by Caddy (2007).

Another component of the augmentation process is the objective. These objectives range from creating fish attractors (Prince and Maughan 1978, Smith et al. 1979, Johnson and Lynch 1992), nursery habitat (Caddy 2007, Coen et al. 2007, Lewis and Gilmore 2007), adult refuge (Bohnsack et al. 1994, Miranda et al. 2010), spawning habitat (Kondolf et al. 1996, Koenig et al. 2000), or meeting societal expectations to augment habitat (Tugend et al. 2002). Broadly, these can be classified into restoration objectives or increasing catch per unit effort (CPUE) objectives. Restoration objectives have predominantly occurred in streams (Kauffman et al. 1997, Lake et al. 2007) and nearshore environments (Coen et al. 2007, Lewis and Gilmore 2007) while increasing CPUE objectives have typically occurred in reservoirs (Tugend et al. 2002, Miranda et al. 2010), lakes (Moring and Nicholson 1994, Roth et al. 2007, Sass et al. 2012), and the marine environment (Bohnsack and Sutherland 1985, Polovina 1991, Bortone et al. 2011). While the management objective may seem a trivial choice it has consequences in the choice of structure to use and the potential metrics necessary to judge fulfillment.

Under a restoration objective, the augmented structure is often of equal or greater complexity than that of natural habitat, such as out planting vegetation or adding any habitat to featureless systems (Redfield 2000, Barwick et al. 2004, Lepori et al. 2005, Santos et al. 2008). Concurrently, a restoration objective is often more ecosystem focused and improves the carrying capacity of the system rather than a single species (Ehrenfeld and Toth 1997). In contrast, a increasing CPUE objective is often aimed at a

single-species and utilizes habitat that is available and placed where convenient. It is much easier to haphazardly deploy concrete, fallen trees, and debris than grow or build complex, connected structure, but has the potential effect of providing a narrower range of interstice sizes, thus offering refugia to a narrow size class (Caley and John 1996, Caddy 2007, Campbell et al. 2011). The result is a filtering on the species assemblage and size classes that can utilize augmented habitat. Despite augmenting the same habitat in each lake, we expected in our lakes to induce the effects akin to a restoration objective in our small lake with little structure and akin to an increasing CPUE objective in our larger lake with considerable existing structure.

Attraction

Direct effects of habitat stem from attraction to augmented habitat and these effects can be split into dispersal and persistence phases. Dispersal to novel habitats can be viewed analogously to an island biogeographic process where the size of the habitat and distance from source populations is limiting (MacArthur and Wilson 1967); however, in almost all cases the landscape scale is smaller than the physiological dispersal limitations of most fish species. The size of the artificial habitat does seem to influence dispersal dynamics in the marine environment but varies species to species (Campbell et al. 2011, Brown et al. 2016). This leaves predation of dispersers to new habitat as perhaps the dominant limitation to dispersal (McNair 1986, Persson and Greenberg 1990a). Predation is likely minimized in enhancements aimed at adult gamefish due to gape limitations, but could be a major limiter of the dispersal of juvenile and small-bodied fishes (Schmitt and Holbrook 1984, Christensen 1996, Persson et al. 1996).

For attraction, or occupancy of the site by the species, to be detected, either dispersal to structure has to equal or exceed the dispersal predation rate or dispersed individuals have to persist on the new structure. Typically, three habitat characteristics determine this: (1) suitability, (2) competitors, and (3) resource availability. Suitability is largely determined by the type of structure that is used in the enhancement, with numerous freshwater (Lynch and Johnson 1989, MacRae and Jackson 2001, Wills et al. 2004) and marine (Brock and Norris 1989, Sherman et al. 2002, Gregalis et al. 2009) studies aimed at elucidating optimum designs. A principal component of suitability is the distribution of interstitial spaces determining the refuge composition and abundance at a given structure (Russ 1980, Johnson et al. 1988, Lynch and Johnson 1989, Eklöv 1997). Intra- and interspecific interference competition for these refuges can drive differences in the species assemblage at structures or result in changing assemblages seasonally or evolving post-enhancement (Persson and Greenberg 1990b, Ruxton 1995, Toscano et al. 2010). Persistence beyond short-time scales is constrained by the resource availability to the prey, termed by community ecologists as bottom-up sequential dependency (Holt 1997, 2009, Gravel et al. 2011).

In our augmented lakes, brush piles strongly filtered for typically large-bodied species with small bodied and cryptic species failing to occupy brush piles. These large-bodied species were Lake Chubsuckers, adult Florida Bass, Black Crappie, and Florida Softshells in the larger lake with more habitat, Speckled Perch Lake, and adult Florida Bass as well as adult Bluegill in the smaller lake with less habitat, Big Fish Lake. Filtering of this kind likely reflects differences in the characteristics between brush piles and vegetation (Heck and Thoman 1981, Savino and Stein 1989b, Newbrey et al. 2005,

Caddy 2007 p. 81) as well as dispersal predation (McNair 1986, Sih and Wooster 1994, Stamps et al. 2005). Some early life stages of Florida Bass and Bluegill occupied brush piles indicating these species survived dispersal predation and, with intense density-dependent growth and mortality as the most abundant species, had a strong impetus to colonize new habitat (Werner and Gilliam 1984, Hixon and Jones 2005).

As expected with the small landscape scale of our lakes (4 – 12 ha), there were little differences across brush piles closer or farther from shore as well as larger or smaller piles (i.e. a lack of island biogeography dynamics). In both lakes, large brush piles had attracted species more strongly than small ones likely reflecting the disparity in interstitial space abundance between the two sizes. In the larger lake, distance from shore had a moderate impact on the number of species / life stages filtered by brush piles. In smaller lake, close brush piles only had one more species / life stage than far brush piles. Close brush piles in both lakes were more likely to have small-bodied species / life stages occupy them while far brush piles were more likely to have large bodied species / life stages. This difference likely arose from the high predation risk associated with moving from littoral zone refuges for small-bodied organisms (Ware 1975, Shulman 1984, Walters and Juanes 1993). Differences in species-specific attraction resulted in depauperate and different brush pile species assemblages in the larger lake as well as depauperate but similar brush pile species assemblages in the smaller lake.

Density-Independent Effects

Habitat enhancement effects can be differentiated into density-independent and density-dependent processes. New habitat can directly increase resources through the colonization of periphyton and epifauna (van Dam et al. 2002) or provide allochthonous

nutrient inputs (Muotka and Laasonen 2002) or alter environmental physical interactions, such as flow regimes in lotic systems or advection in lentic systems (Kauffman et al. 1997, Bunn and Arthington 2002). These resource improvements can be most simply envisioned as an increase in the system's carrying capacity under logistic population growth (Verhulst 1838).

In our augmented lakes, we saw some anecdotal density-independent effects of the habitat augmentation. In the smaller lake and mostly featureless lake, the addition of habitat correlated with improved water clarity during the winter that was typically low due to wind-driven resuspension. Periphyton colonized the brush piles over the course of six months and after a year had grown to 0.1 – 0.33 m clumps on most branches of the pile. In the larger lake, water pH was typically around 3.8 – 4 and tannin-stained which likely reduced the periphyton production. Allochthonous input from the brush piles and leaf litter did not seem to affect the production of gamefish or alter the benthos considerably. Low pH in both augmented lakes likely slowed the breakdown of leaf litter, as distinguishable leaves were still present after 1.5 years post-augmentation.

Fitness Benefits

Attraction to new habitat has the potential for direct fitness benefits but these are density-dependent in nature. Higher growth rates of attracted individuals may result from access to new resources or previously inaccessible resources. Increased growth rates could also result from dietary shifts as a result of attraction to habitat. Sass et al. (2006) showed that removal of woody debris changed the diet composition and negatively affected growth rates of Largemouth Bass *Micropterus salmoides*. Gaeta et al. (2011) showed that Largemouth Bass depressed growth rates in lakes with high levels of shoreline development (e.g. lower densities of woody debris), compared to

undeveloped lakes. However, Sass et al. (2012) found no response in fish growth or recruitment to addition of coarse woody debris in a second whole-lake experiment.

Improved growth rates can occur at different life stages depending on the location of the habitat, the food availability, and the refuge availability. Improving juvenile growth allows escape from the gape size of predators, reductions in exploitative competition by growing a larger gape size, and can alter reproductive strategies taken later in life (territorial vs. sneaker males; Gross and Charnov 1980). Alternatively, improving adult growth or condition can alter reproductive success (nest guarding or brood care) or reproductive output (the number or quality of the eggs). Changes in juvenile growth rates are likely to be easier to detect from a higher signal to noise ratio than adult growth rates due to the strong predation and competition pressures in the recruitment bottleneck (Pauly 1980, Walters and Juanes 1993).

Habitat augmentations also have the potential to reduce predation risk, especially in featureless systems. MacRae and Jackson (2001) found that small-bodied fish species were restricted, both in presence and abundance, to complex habitat that offered refuge from smallmouth bass *Micropterus dolomieu* predation and when afforded predator release occupied all parts of the littoral zone, including simple habitat. A proportional decrease in mortality from predation—and an increase in survival—should accompany reductions in predation risk and be most effective in juveniles undergoing the highest degree of predation across life history stanzas (Pauly 1980, Walters and Juanes 1993). Predator type may also change as a result of attraction to artificial structures. This is likely to be expected in many habitat enhancement projects as fish assemblages often differ between types of structures and between artificial and

natural structures. Bohnsack et al. (1994) found that planktivores and benthic feeding fishes were more present on artificial reefs than comparison natural reefs while herbivorous fishes and meiofauna predators were more present on natural reefs.

While the relationship between refuge availability and fitness benefits might seem proportional, our foraging arena pond experiment indicated habitat use to density dependent. The prey in our experiment, Bluegill, utilized cover at intense spatial restriction at low densities, shoaled at intermediate densities, and used habitat at high densities. The weed mat we provided for refuge from our experimental predator, Florida Bass, did not seem to provide refuge from predators until very high densities of prey. This has strong consequences for systems seeking to augment habitat especially those that have been exploited (Greene and Stamps 2001). Habitat-based management strategies to improve the fitness of fish within the system may remain ineffective if fish behavior is density-dependent as we observed in our ponds. These effects are likely compounded when the added structure does not allow for the full range of antipredator behaviors (for example, camouflage designed for heavy vegetation but new structure is not).

In addition to observing density dependent prey behavior, we also observed ratio-dependence in our predator behavior. At low predator densities, sessile ambush behaviors (camouflaged and waiting) prevailed while at intermediate to high predator densities predators swapped from mobile ambush behaviors (hiding in the shadows) to active searching (shoaling) as a function of prey density. This ratio-dependent predator foraging modes has consequences for the effectiveness of new refuge on reducing predation rates. Some predators are able to swap foraging modes at will and take

advantage of different behaviors depending on the prey density. Thus, across prey densities predators are able to likely maintain high foraging rates and reduce strong effects of habitat on the predation rate. Further, augmented habitat has the potential to restructure interactions between predators and prey. Carey and Wahl (2010) found that Largemouth Bass *Micropterus salmoides* and Muskellunge *Esox masquinongy* when both present were able to impart higher predation rates than separately and cruising Largemouth Bass predominantly benefited from the relationship. In our augmented lakes, habitat augmentations may have benefited the ambush predators more such as Florida Gar *Lepisosteus platyrhincus* or Florida Bass that were able to adopt an ambush foraging mode as we observed in our pond experiments. Thus, augmented habitats may reduce predation risk, increase it, or result in completely different predation strategies. From our community analyses in the larger lake, we showed that the predator assemblages changed between the littoral zone and the brush piles. Brush piles had more Florida Softshell *Apalone ferox* and Black Crappie *Pomoxis nigromaculatus* than the littoral zone increasing the abundance of these predators while reducing the abundance of predatory Florida Bass. In our smaller lake, brush piles provided refuge for brooding adult Florida Bass from Ospreys *Pandion haliaetus* and refuge for early life stages of Florida Bass and Bluegill from wading birds such as Snowy Egrets *Egretta thula*, Tricolor Herons *Egretta tricolor*, Little Blue Herons *Egretta caerulea*, and Great Egrets *Ardea alba* (Newbill and Siders, unpublished data).

Selection

Fitness improvements have the potential for two effects, production and selection. Production seems a likely outcome if increases in growth and survival accompany attraction to new structure. As outlined above, fitness improvements

depend highly on the life history stanza targeted by habitat enhancement, the change in prey availability or predation risk from the new structure, and low dispersal costs. Enhancement targeted at juveniles within the recruitment bottleneck, a period of typically the highest mortality rates across life history stanzas (Pauly 1980, Persson and Greenberg 1990a), have the greatest chance for observable changes in production. Changes in adult fish survival or growth are likely to result in changes in fecundity—increases in the numbers or quality of offspring—but these pre-recruit effects may not translate into production from density-dependence in the stock-recruit relationship (Beverton and Holt 1957, Walters and Korman 1999). Intense competition and predation of pre-recruits without any accompanying abatement of these effects by new structure would be predicted to result in no change in production. Selection for attraction to structure as a behavioral trait could still occur. Offspring of attracted individuals might have lower dispersal costs, be spawned earlier than conspecifics, have higher growth rates, better yolk sac nutrition, or reduced predation rates. This might result in offspring from attracted individuals displacing those of non-attracted individuals over time resulting in a high prevalence of the alleles responsible for attraction. Increased frequency of attracted individuals in populations can also occur through their improved survival or their offspring and result in attraction to be an evolutionary stable strategy (Smith 1972, Smith and Price 1973).

Utility

With our conceptual framework outlined, it is important to state what the envisioned utility of the framework is. Foremost, there is multitude of studies across systems focused on augmenting habitat to systems but poor transference of information between systems. This framework was designed to be used in all systems (even

terrestrial, though our examples are focused on the aquatic for the above discussion) and provide a mode to translate research across systems as well as relate their patterns and processes. Secondly, it is necessary to synthesize the abundance of scientific studies and management trials into a single framework. While there is room for improvement and refinement in our framework, there is not, to our knowledge, one that integrates from behavioral to evolutionary scales and incorporates the abiotic and biotic components of the systems. Key processes such as density-dependence, predator-prey relationships, community assembly, and selective pressures encompass the central patterns of ubiquitous attraction, dynamic assemblages, and high biomass of augmented habitat studies.

Lastly, just as Bohnsack (1989) did after 10+ years of augmented habitat research as well as Lindberg (1997), Pickering and Whitmarsh (1997), and Grossman et al. (1997) did after 20+ years, it is critical to revisit and revise the existing theory, empirical work, and experiments that form the basis of knowledge of habitat studies. It is reasonable to say habitat-based management has outstripped new inference from habitat-based studies but not without variable effectiveness (Tugend et al. 2002, Bortone et al. 2011). From our experiment, empirical, and conceptual work we have determined a few principal management recommendations. Over short time scales, habitat augmentations aimed at increasing CPUE are successful. The near-ubiquitous attraction of predatory gamefish to structure works in the managers' (and fishers') favor to increase biomass on augmented habitat and increase CPUE. In our own augmentation, colonization of new habitat was rapid and survey CPUE was far greater on augmented habitat than natural for gamefish. Simple, available structures work well

in these management plans as the generally large interstitial spaces of such structure provide refuge for the larger-bodied species associated with a desire to increase CPUE.

Over long time scales, the effects of this increase CPUE are likely to decline as the system equilibrates to a new ideal free distribution or as fishers deplete the attracted fish. Perception may remain unchanged as hyperstable catchability dampens the signal of decline of the fish stock system-wide. Restoration approaches are likely to yield higher returns in this case. Increasing the carrying capacity through restorative ecosystem wide effects such as improving forage fish abundance or augmenting habitat for small-bodied fishes is likely result in greater gamefish production or condition, thus, slowly increasing CPUE over time. Restorative approaches are also often successful at improving system-wide productivity especially in degraded system. Typically, the only systems with marginal system-wide effects are those that either had an abundance of existing habitat or where the limiting habitat was not restored.

Fundamentally, the question that must be addressed by scientists and managers is the same question that has plagued the attraction-production debate since the 1970s: is habitat limiting? For highly degraded systems, featureless systems, or new systems (such as reservoirs), the potential impact of augmenting habitat is grandiose. Additions of habitat yield gains in primary productivity, fish growth, and gamefish CPUE. For systems replete with existing habitat, the potential impact of augmenting habitat is likely negligible. With diminishing returns for augmenting habitat as a function of existing habitat, it is necessary for augmenters to decide if habitat is truly limiting the system, and if so, how to approach the choice of structure, location, and target species / life stages to best achieve the augmentation objective.

LIST OF REFERENCES

- Abrams, P. A. 1990. The effects of adaptive behavior on the type-2 functional response. *Ecology* 71:877–885.
- Abrams, P. A. 1993. Why predation rate should not be proportional to predator density. *Ecology* 74:726–733.
- Abrams, P. A. 1994. The fallacies of "ratio-dependent" predation. *Ecology*:1842–1850.
- Abrams, P. A. 2000. The evolution of predator-prey interactions: theory and evidence. *Annual Review of Ecology and Systematics* 31:79–105.
- Abrams, P. A., and L. R. Ginzburg. 2000. The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology & Evolution* 15:337–341.
- Abrams, P. A., and C. J. Walters. 1996. Invulnerable prey and the paradox of enrichment. *Ecology*:1125–1133.
- Ahrens, R. N., C. J. Walters, and V. Christensen. 2012. Foraging arena theory. *Fish and Fisheries* 13:41–59.
- Ahrenstorff, T. D., G. G. Sass, and M. R. Helmus. 2009. The influence of littoral zone coarse woody habitat on home range size, spatial distribution, and feeding ecology of largemouth bass (*Micropterus salmoides*). *Hydrobiologia* 623:223–233.
- Aing, C., S. Halls, K. Oken, R. Dobrow, and J. Fieberg. 2011. A Bayesian hierarchical occupancy model for track surveys conducted in a series of linear, spatially correlated, sites. *Journal of Applied Ecology* 48:1508–1517.
- Allee, W. C. 1927. Animal aggregations. *The Quarterly Review of Biology* 2:367–398.
- Allee, W. C. 1931. Co-operation among animals. *American Journal of Sociology*:386–398.
- Allee, W. C. 1941. Integration of problems concerning protozoan populations with those of general biology. *American Naturalist*:473–487.
- Allen, M. S., W. Scheaffer, W. F. Porak, and S. Crawford. 2002. Growth and mortality of largemouth bass in Florida waters: implications for use of length limits. Pages 559–566 *American Fisheries Society Symposium*. American Fisheries Society.
- Allen, M. S., K. I. Tugend, and M. J. Mann. 2003. Largemouth Bass Abundance and Angler Catch Rates following a Habitat Enhancement Project at Lake Kissimmee, Florida. *North American Journal of Fisheries Management* 23:845–855.

- Allen, M. S., C. J. Walters, and R. Myers. 2008. Temporal trends in largemouth bass mortality, with fishery implications. *North American Journal of Fisheries Management* 28:418–427.
- Allen, T. F. H., and T. B. Starr. 1982. *Hierarchy: perspectives for ecological complexity*. University of Chicago Press, Chicago.
- Anderson, O. 1984. Optimal foraging by largemouth bass in structured environments. *Ecology* 65:851–861.
- Arditi, R., and A. A. Berryman. 1991. The biological control paradox. *Trends in ecology & evolution* 6:32.
- Arditi, R., and L. R. Ginzburg. 1989. Coupling in predator-prey dynamics: ratio-dependence. *Journal of Theoretical Biology* 139:311–326.
- Arditi, R., and H. Saiah. 1992. Empirical evidence of the role of heterogeneity in ratio-dependent consumption. *Ecology*:1544–1551.
- Armbruster, J. W., and L. M. Page. 1996. Convergence of a cryptic saddle pattern in benthic freshwater fishes. *Environmental Biology of Fishes* 45:249–257.
- Arrington, D. A., K. O. Winemiller, W. F. Loftus, and S. Akin. 2002. How often do fishes “run on empty”? *Ecology* 83:2145–2151.
- Bacheler, N. M., N. R. Geraldi, M. L. Burton, R. C. Muñoz, and G. T. Kellison. 2017. Comparing relative abundance, lengths, and habitat of temperate reef fishes using simultaneous underwater visual census, video, and trap sampling. *Marine Ecology Progress Series* 574:141–155.
- Bacheler, N. M., and K. W. Shertzer. 2015. Estimating relative abundance and species richness from video surveys of reef fishes. *Fishery Bulletin* 113:15–27.
- Barwick, R. D., T. J. Kwak, R. L. Noble, and D. H. Barwick. 2004. Fish populations associated with habitat-modified piers and natural woody debris in piedmont carolina reservoirs. *North American Journal of Fisheries Management* 24:1120–1133.
- Beddington, J. R. 1975. Mutual interference between parasites or predators and its effect on searching efficiency. *The Journal of Animal Ecology*:331–340.
- Begon, M., C. R. Townsend, and J. L. Harper. 2006. *Ecology: from individuals to ecosystems*. Blackwell.

- Bernstein, C., J. R. Krebs, and A. Kacelnik. 1991. Distribution of birds amongst habitats: theory and relevance to conservation. Pages 317–345 in C. M. Perrins, J. D. Lebreton, and G. J. M. Hirons, editors. *Bird population studies: relevance to conservation and management*. Oxford University Press, Oxford, U.K.
- Berryman, A. A. 1992. The origins and evolution of predator-prey theory. *Ecology*:1530–1535.
- Beverton, R. J. H., and S. J. Holt. 1957. *On the dynamics of exploited fish populations*. Reprint of First Edition. The Blackburn Press, Caldwell, New Jersey.
- Biro, P. A., J. R. Post, and E. A. Parkinson. 2003. Population consequences of a predator-induced habitat shift by trout in whole-lake experiments. *Ecology* 84:691–700.
- Bohnsack, J. A. 1989. Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? *Bulletin of Marine Science* 44:631–645.
- Bohnsack, J. A., D. E. Harper, D. B. McClellan, and M. Hulsbeck. 1994. Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off southeastern florida, u.s.a. *Bulletin of Marine Science* 55:796–823.
- Bohnsack, J. A., and D. L. Sutherland. 1985. Artificial reef research: a review with recommendations for future priorities. *Bulletin of Marine Science* 37:11–39.
- Bortone, S. A., F. P. Brandini, G. Fabi, and S. Otake. 2011. *Artificial reefs in fisheries management*. CRC Press.
- Bortone, S. A., J. V. Tassell, A. Brito, J. M. Falcon, J. Mena, and C. M. Bundrick. 1994. Enhancement of the nearshore fish assemblage in the Canary Islands with artificial habitats. *Bulletin of Marine Science* 55:602–608.
- Brickhill, M. J., S. Y. Lee, and R. M. Connolly. 2005. Fishes associated with artificial reefs: attributing changes to attraction or production using novel approaches. *Journal of Fish Biology* 67:53–71.
- Brock, R. E., and J. E. Norris. 1989. An analysis of the efficacy of four artificial reef designs in tropical waters. *Bulletin of Marine Science* 44:934–941.
- Brook, B. W., and C. J. Bradshaw. 2006. Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology* 87:1445–1451.
- Brooks, A. P., P. C. Gehrke, J. D. Jansen, and T. B. Abbe. 2004. Experimental reintroduction of woody debris on the Williams River, NSW: geomorphic and ecological responses. *River Research and Applications* 20:513–536.

- Brosse, S., G. D. Grossman, and S. Lek. 2007. Fish assemblage patterns in the littoral zone of a European reservoir. *Freshwater Biology* 52:448–458.
- Brown, C. J., A. R. Harborne, C. B. Paris, and P. J. Mumby. 2016. Uniting paradigms of connectivity in marine ecology. *Ecology* 97:2447–2457.
- Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30:492–507.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd edition. Springer, New York.
- Caddy, J. F. 2007. *Marine habitat and cover: their importance for productive coastal fishery resources*. UNESCO Publishing, Paris.
- Caddy, J. F., and C. Stamatopoulos. 1990. Mapping growth and mortality rates of crevice-dwelling organisms onto a perforated surface: the relevance of 'cover' to the carrying capacity of natural and artificial habitats. *Estuarine, Coastal and Shelf Science* 31:87–106.
- Caley, M. J., and J. S. John. 1996. Refuge availability structures assemblages of tropical reef fishes. *Journal of Animal Ecology* 65:414–428.
- Campbell, M. D., K. Rose, K. Boswell, and J. Cowan. 2011. Individual-based modeling of an artificial reef fish community: Effects of habitat quantity and degree of refuge. *Ecological Modelling* 222:3895–3909.
- Carey, M. P., and D. H. Wahl. 2010. Interactions of multiple predators with different foraging modes in an aquatic food web. *Oecologia* 162:443–452.
- Carr, M. H., and M. A. Hixon. 1995. Predation effects on early post-settlement survivorship of coral-reef fishes. *Marine ecology progress series*. Oldendorf 124:31–42.
- Carr, M. H., and M. A. Hixon. 1997. Artificial reefs: the importance of comparisons with natural reefs. *Fisheries* 22:28–33.
- Cavanaugh, J. E. 1997. Unifying the derivations for the Akaike and corrected Akaike information criteria. *Statistics & Probability Letters* 33:201–208.
- Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical population biology* 9:129–136.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual review of Ecology and Systematics*:343–366.

- Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist* 150:519–553.
- Christensen, B. 1996. Predator foraging capabilities and prey antipredator behaviours: pre-versus postcapture constraints on size-dependent predator-prey interactions. *Oikos*:368–380.
- Christensen, V., and C. J. Walters. 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* 172:109–139.
- Coen, L. D., R. D. Brumbaugh, D. Bushek, R. Grizzle, M. W. Luckenbach, M. H. Posey, S. P. Powers, and Sg. Tolley. 2007. Ecosystem services related to oyster restoration. *Marine Ecology Progress Series* 341:303–307.
- Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51:429–438.
- Cosner, C., D. L. DeAngelis, J. S. Ault, and D. B. Olson. 1999. Effects of spatial grouping on the functional response of predators. *Theoretical population biology* 56:65–75.
- Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. *Trends in ecology & evolution* 14:405–410.
- Cox, S., S. Chandler, C. Barron, and K. Work. 2009. Benthic fish exhibit more plastic crypsis than non-benthic species in a freshwater spring. *Journal of ethology* 27:497–505.
- Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802–1813.
- Cury, P., and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Canadian Journal of Fisheries and Aquatic Sciences* 46:670–680.
- van Dam, A. A., M. C. Beveridge, M. E. Azim, and M. C. Verdegem. 2002. The potential of fish production based on periphyton. *Reviews in Fish Biology and Fisheries* 12:1–31.
- Darwin, C. 1859. *On the origin of species by means of natural selection, or, The preservation of favored races in the struggle for life.* J. Murray, London.
- DeAngelis, D. L., R. A. Goldstein, and R. V. O’neill. 1975. A model for trophic interaction. *Ecology* 56:881–892.

- Dennis, B. 1989. Allee effects: population growth, critical density, and the chance of extinction. *Natural Resource Modeling* 3:481–538.
- Denwood, M. J. 2013. runjags: An R Package Providing Interface Utilities, Distributed Computing Methods and Additional Distributions For MCMC Models in JAGS. *Journal of Statistical Software*.
- Diamond, J. M. 1975. Assembly of species communities. Pages 342–444 in M. L. Cody and J. M. Diamond, editors. *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, MA.
- Diehl, S., P. A. Lundberg, H. Gardfjell, L. Oksanen, and L. Persson. 1993. Daphnia-phytoplankton interactions in lakes: is there a need for ratio-dependent consumer-resource models? *American Naturalist*:1052–1061.
- Efford, M. G., and D. K. Dawson. 2012. Occupancy in continuous habitat. *Ecosphere* 3:1–15.
- Ehrenfeld, J. G., and L. A. Toth. 1997. Restoration ecology and the ecosystem perspective. *Restoration Ecology* 5:307–317.
- Eklöv, P. 1997. Effects of habitat complexity and prey abundance on the spatial and temporal distributions of perch (*Perca fluviatilis*) and pike (*Esox lucius*). *Canadian Journal of Fisheries and Aquatic Sciences* 54:1520–1531.
- Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs* 65:75–100.
- Ewel, J. J. 1987. Restoration is the ultimate test of ecological theory. Pages 31–33 *Restoration ecology: a synthetic approach to ecological research*.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon Press, Oxford, U.K.
- Fraser, D. F., and J. F. Gilliam. 1992. Nonlethal impacts of predator invasion: facultative suppression of growth and reproduction. *Ecology* 73:959–970.
- Fretwell, S. D. 1972. *Populations in a seasonal environment*. Princeton University Press.
- Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16–36.

- Gaeta, J. W., M. J. Guarascio, G. G. Sass, and S. R. Carpenter. 2011. Lakeshore residential development and growth of largemouth bass (*Micropterus salmoides*): a cross-lakes comparison. *Ecology of Freshwater Fish* 20:92–101.
- Gaeta, J. W., G. G. Sass, and S. R. Carpenter. 2014. Drought-driven lake level decline: effects on coarse woody habitat and fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 71:315–325.
- Gascoigne, J. C., and R. N. Lipcius. 2004. Allee effects driven by predation. *Journal of Applied Ecology* 41:801–810.
- Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical science*:457–472.
- Glasby, T. M., S. D. Connell, M. G. Holloway, and C. L. Hewitt. 2006. Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions? *Marine Biology* 151:887–895.
- Gould, W. R., and K. H. Pollock. 1997. Catch-effort maximum likelihood estimation of important population parameters. *Canadian Journal of Fisheries and Aquatic Sciences* 54:890–897.
- Gräler, B., E. Pebesma, and G. Heuvelink. 2016. Spatio-temporal interpolation using gstat. *The R Journal* 8:204–218.
- Gravel, D., F. Massol, E. Canard, D. Mouillot, and N. Mouquet. 2011. Trophic theory of island biogeography. *Ecology letters* 14:1010–1016.
- Greene, C. M., and J. A. Stamps. 2001. Habitat selection at low population densities. *Ecology* 82:2091–2100.
- Gregalis, K. C., M. W. Johnson, and S. P. Powers. 2009. Restored oyster reef location and design affect responses of resident and transient fish, crab, and shellfish species in Mobile Bay, Alabama. *Transactions of the American Fisheries Society* 138:314–327.
- Gross, M. R., and E. L. Charnov. 1980. Alternative male life histories in bluegill sunfish. *Proceedings of the National Academy of Sciences* 77:6937–6940.
- Grossman, G. D., G. P. Jones, and W. J. Seaman Jr. 1997. Do artificial reefs increase regional fish production? A review of existing data. *Fisheries* 22:17–23.
- Hamilton, W. D. 1971. Geometry for the selfish herd. *Journal of theoretical Biology* 31:295–311.

- Hangsleben, M. A., M. S. Allen, and D. C. Gwinn. 2013. Evaluation of electrofishing catch per unit effort for indexing fish abundance in Florida lakes. *Transactions of the American Fisheries Society* 142:247–256.
- Hassell, M. P., and R. M. May. 1974. Aggregation of predators and insect parasites and its effect on stability. *The Journal of Animal Ecology*:567–594.
- Hassell, M. P., R. M. May, S. W. Pacala, and P. L. Chesson. 1991. The persistence of host-parasitoid associations in patchy environments. i. a general criterion. *The American Naturalist* 138:568–583.
- Hassell, M. P., and G. C. Varley. 1969. New inductive population model for insect parasites and its bearing on biological control. *Nature* 223:1133–1137.
- Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. *Theoretical population biology* 18:363–373.
- Havens, K. E., R. S. Fulton, J. R. Beaver, E. E. Samples, and J. Colee. 2016. Effects of climate variability on cladoceran zooplankton and cyanobacteria in a shallow subtropical lake. *Journal of Plankton Research* 38:418–430.
- Heck, K. L., and T. A. Thoman. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. *Journal of Experimental Marine Biology and Ecology* 53:125–134.
- Heithaus, M. R., A. Frid, A. J. Wirsing, and B. Worm. 2008. Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution* 23:202–210.
- Hijmans, R. J. 2015. *Raster: geographic data analysis and modeling*.
- Hilborn, R., K. Stokes, J.-J. Maguire, T. Smith, L. W. Botsford, M. Mangel, J. Orensanz, A. Parma, J. Rice, J. Bell, and others. 2004. When can marine reserves improve fisheries management? *Ocean & Coastal Management* 47:197–205.
- Hixon, M. A., and J. P. Beets. 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bulletin of Marine Science* 44:666–680.
- Hixon, M. A., and J. P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* 63:77–101.
- Hixon, M. A., and G. P. Jones. 2005. Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology* 86:2847–2859.

- Hixon, M. A., and B. A. Menge. 1991. Species diversity: prey refuges modify the interactive effects of predation and competition. *Theoretical Population Biology* 39:178–200.
- Hixon, M. A., S. W. Pacala, and S. A. Sandin. 2002. Population regulation: historical context and contemporary challenges of open vs. closed systems. *Ecology* 83:1490–1508.
- Holling, C. S. 1959a. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Canadian Entomologist* 91:293–320.
- Holling, C. S. 1959b. Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist* 91:385–398.
- Holling, C. S. 1966. The functional response of invertebrate predators to prey density. *Memoirs of the Entomological Society of Canada* 98:5–86.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical population biology* 12:197–229.
- Holt, R. D. 1997. From metapopulation dynamics to community structure: some consequences of spatial heterogeneity. Pages 149–164 in I. Hanski and M. E. Gilpin, editors. *Metapopulation Biology: Ecology, Genetics and Evolution*. Academic Press, San Diego.
- Holt, R. D. 2009. Toward a trophic island biogeography: reflections on the interface of island biogeography and food web ecology. Pages 143–185 in J. B. Losos and R. E. Ricklefs, editors. *The theory of island biogeography revisited*. Princeton University Press, Princeton.
- Hörnfeldt, B. 1994. Delayed density dependence as a determinant of vole cycles. *Ecology*:791–806.
- Hoyer, M. V., and D. E. J. Canfield. 1994. *Handbook of common freshwater fish in florida lakes*. University of Florida, Institute of Food and Agricultural Sciences, Gainesville, FL.
- Hunsicker, M. E., L. Ciannelli, K. M. Bailey, J. A. Buckel, J. Wilson White, J. S. Link, T. E. Essington, S. Gaichas, T. W. Anderson, R. D. Brodeur, and others. 2011. Functional responses and scaling in predator–prey interactions of marine fishes: contemporary issues and emerging concepts. *Ecology Letters* 14:1288–1299.
- Hutchings, J. A. 2014. Renaissance of a caveat: Allee effects in marine fish. *ICES Journal of Marine Science* 71:2152–2157.

- Hutchinson, G. E. 1941. Ecological aspects of succession in natural populations. *American Naturalist*:406–418.
- Hutchinson, G. E. 1978. *An introduction to population ecology*. Yale University Press, New Haven and London.
- Johnson, D. L., R. A. Beaumier, and W. E. Lynch Jr. 1988. Selection of habitat structure interstice size by bluegills and largemouth bass in ponds. *Transactions of the American Fisheries Society* 117:171–179.
- Johnson, D. L., and W. E. Lynch Jr. 1992. Panfish use of and angler success at evergreen tree, brush, and stake-bed structures. *North American Journal of Fisheries Management* 12:222–229.
- Johnson, M. D. 2007. Measuring habitat quality: a review. *The Condor* 109:489–504.
- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52:225–247.
- Kacelnik, A., J. R. Krebs, and C. Bernstein. 1992. The ideal free distribution and predator-prey populations. *Trends in Ecology & Evolution* 7:50–55.
- Karell, P., K. Ahola, T. Karstinen, A. Zolei, and J. E. Brommer. 2009. Population dynamics in a cyclic environment: consequences of cyclic food abundance on tawny owl reproduction and survival. *Journal of Animal Ecology* 78:1050–1062.
- Kauffman, J. B., R. L. Beschta, N. Otting, and D. Lytjen. 1997. An ecological perspective of riparian and stream restoration in the western United States. *Fisheries* 22:12–24.
- Keast, A. 1977. Mechanisms expanding niche width and minimizing intraspecific competition in two centrarchid fishes. Pages 333–395 in M. Stere and B. Wallace, editors. *Evolutionary biology*. Plenum, New York.
- Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* 3:157–164.
- Kéry, M., and J. A. Royle. 2015. *Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in r and bugs: volume 1: prelude and static models*. Academic Press.
- Kéry, M., and M. Schaub. 2011. *Bayesian population analysis using WinBUGS: a hierarchical perspective*. Academic Press.

- Koenig, C. C., F. C. Coleman, C. B. Grimes, G. R. Fitzhugh, K. M. Scanlon, C. T. Gledhill, and M. Grace. 2000. Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelf-edge reefs of Florida. *Bulletin of Marine Science* 66:593–616.
- Kondolf, G. M., J. C. Vick, and T. M. Ramirez. 1996. Salmon spawning habitat rehabilitation on the Merced River, California: an evaluation of project planning and performance. *Transactions of the American Fisheries Society* 125:899–912.
- Kramer, A. M., B. Dennis, A. M. Liebhold, and J. M. Drake. 2009. The evidence for Allee effects. *Population Ecology* 51:341.
- Kramer, A. M., and J. M. Drake. 2010. Experimental demonstration of population extinction due to a predator-driven Allee effect. *Journal of Animal Ecology* 79:633–639.
- Krebs, C. J. 1972. *Ecology*. Harper and Row, New York.
- Křivan, V. 1996. Optimal foraging and predator–prey dynamics. *Theoretical Population Biology* 49:265–290.
- Křivan, V. 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator-prey dynamics. *The American Naturalist* 149:164–178.
- Lake, P. S., N. Bond, and P. Reich. 2007. Linking ecological theory with stream restoration. *Freshwater Biology* 52:597–615.
- Lambeck, R. J. 1997. Focal species: a multi-species umbrella for nature conservation. *Conservation biology*:849–856.
- Lepori, F., D. Palm, E. Brännäs, and B. Malmqvist. 2005. Does restoration of structural heterogeneity in streams enhance fish and macroinvertebrate diversity? *Ecological Applications* 15:2060–2071.
- Levin, S. 1992. The Problem of Pattern and Scale in Ecology. *Ecology* 73:1943–1967.
- Lewin, W.-C., N. Okun, and T. Mehner. 2004. Determinants of the distribution of juvenile fish in the littoral area of a shallow lake. *Freshwater Biology* 49:410–424.
- Lewis, R. R., and R. G. Gilmore. 2007. Important considerations to achieve successful mangrove forest restoration with optimum fish habitat. *Bulletin of Marine Science* 80:823–837.
- Lewis, W. M., and D. R. Helms. 1964. Vulnerability of forage organisms to largemouth bass. *Transactions of the American Fisheries Society* 93:315–318.

- Lima, S. L. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour* 49:11–20.
- Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *The American Naturalist* 153:649–659.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Lindberg, W. J. 1997. Can science resolve the attraction-production issue? *Fisheries* 22:10–13.
- Lindberg, W. J., T. K. Frazer, K. M. Portier, F. Vose, J. Loftin, D. J. Murie, D. M. Mason, B. Nagy, and M. K. Hart. 2006. Density-dependent habitat selection and performance by a large mobile reef fish. *Ecological Applications* 16:731–746.
- Loecher, M., and K. Ropkins. 2015. Rgooglemaps and loa: unleashing r graphics power on map tiles. *Journal of Statistical Software* 63:1–18.
- Lotka, A. J. 1925. *Elements of physical biology*. Williams & Wilkins, Baltimore, Maryland, USA.
- Lowe, C. G., D. T. Topping, D. P. Cartamil, and Y. P. Papastamatiou. 2003. Movement patterns, home range, and habitat utilization of adult kelp bass *Paralabrax clathratus* in a temperate no-take marine reserve. *Marine Ecology Progress Series* 256:205–216.
- Lynch, W. E., Jr., and D. L. Johnson. 1989. Influences of interstice size, shade, and predators on the use of artificial structures by bluegills. *North American Journal of Fisheries Management* 9:219–225.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press.
- MacRae, P. S., and D. A. Jackson. 2001. The influence of smallmouth bass (*Micropterus dolomieu*) predation and habitat complexity on the structure of littoral zone fish assemblages. *Canadian Journal of Fisheries and Aquatic Sciences* 58:342–351.
- Magoulick, D. D. 2004. Effects of predation risk on habitat selection by water column fish, benthic fish and crayfish in stream pools. *Hydrobiologia* 527:209–221.
- Malthus, T. R. 1798. *An essay on the principle of population*. Reprinted from 1798 edition, Johnson, London, as *Malthus-Population: the first essay*. Ann Arbor Paperbacks, University of Michigan, Ann Arbor, Michigan, USA.

- Marsden, J. E., T. R. Binder, J. Johnson, J. He, N. Dingledine, J. Adams, N. S. Johnson, T. J. Buchinger, and C. C. Krueger. 2016. Five-year evaluation of habitat remediation in Thunder Bay, Lake Huron: Comparison of constructed reef characteristics that attract spawning lake trout. *Fisheries Research* 183:275–286.
- May, R. M. 1972. Limit cycles in predator-prey communities. *Science* 177:900–902.
- May, R. M., and G. F. Oster. 1976. Bifurcations and dynamic complexity in simple ecological models. *American Naturalist*:573–599.
- Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales.
- McCarthy, M. A. 1997. The Allee effect, finding mates and theoretical models. *Ecological Modelling* 103:99–102.
- McNair, J. N. 1986. The effects of refuges on predator-prey interactions: a reconsideration. *Theoretical population biology* 29:38–63.
- Miranda, L. E., M. Spickard, T. Dunn, K. M. Webb, J. N. Aycock, and K. Hunt. 2010. Fish habitat degradation in u.s. reservoirs. *Fisheries* 35:175–184.
- Mordecai, R. S., B. J. Mattsson, C. J. Tzilkowski, and R. J. Cooper. 2011. Addressing challenges when studying mobile or episodic species: hierarchical Bayes estimation of occupancy and use. *Journal of Applied Ecology* 48:56–66.
- Moring, J. R., and P. H. Nicholson. 1994. Evaluation of three types of artificial habitats for fishes in a freshwater pond in maine, usa. *Bulletin of Marine Science* 55:1149–1159.
- Morris, D. W. 1992. Scales and costs of habitat selection in heterogeneous landscapes. *Evolutionary Ecology* 6:412–432.
- Motta, P. J. 1983. Response by potential prey to coral reef fish predators. *Animal Behaviour* 31:1257–1259.
- Mueller, T., and W. F. Fagan. 2008. Search and navigation in dynamic environments – from individual behaviors to population distributions. *Oikos* 117:654–664.
- Muotka, T., and P. Laasonen. 2002. Ecosystem recovery in restored headwater streams: the role of enhanced leaf retention. *Journal of Applied Ecology* 39:145–156.
- Murdoch, W. W. 1971. The developmental response of predators to changes in prey density. *Ecology*:132–137.

- Murdoch, W. W. 1973. The functional response of predators. *J. appl. Ecol* 10:335–342.
- Murdoch, W. W. 1994. Population regulation in theory and practice. *Ecology* 75:271–287.
- Neave, F. 1953. Principles affecting the size of pink and chum salmon populations in British Columbia. *Journal of the Fisheries Board of Canada* 9:450–491.
- Newbrey, M. G., M. A. Bozek, M. J. Jennings, and J. E. Cook. 2005. Branching complexity and morphological characteristics of coarse woody structure as lacustrine fish habitat. *Canadian Journal of Fisheries and Aquatic Sciences* 62:2110–2123.
- Nichols, J. D., L. L. Bailey, N. W. Talancy, E. H. Campbell Grant, A. T. Gilbert, E. M. Annand, T. P. Husband, J. E. Hines, and others. 2008. Multi-scale occupancy estimation and modelling using multiple detection methods. *Journal of Applied Ecology* 45:1321–1329.
- Nicholson, A. J. 1933. The Balance of Animal Populations. *Journal of Animal Ecology* 2:131–178.
- Oaten, A., and W. W. Murdoch. 1975. Functional response and stability in predator-prey systems. *American Naturalist*:289–298.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist*:240–261.
- Okuyama, T. 2008. Individual behavioral variation in predator–prey models. *Ecological Research* 23:665–671.
- Osenberg, C. W., C. M. S. Mary, J. A. Wilson, and W. J. Lindberg. 2002. A quantitative framework to evaluate the attraction–production controversy. *ICES Journal of Marine Science: Journal du Conseil* 59:S214–S221.
- Parker, G. A., and W. J. Sutherland. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Animal Behaviour* 34:1222–1242.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil* 39:175–192.
- Pavlacky, D. C., J. A. Blakesley, G. C. White, D. J. Hanni, and P. M. Lukacs. 2012. Hierarchical multi-scale occupancy estimation for monitoring wildlife populations. *The Journal of Wildlife Management* 76:154–162.

- Persson, L., J. Andersson, E. Wahlström, and P. Eklöv. 1996. Size-specific interactions in lake systems: predator gape limitation and prey growth rate and mortality. *Ecology*:900–911.
- Persson, L., and L. A. Greenberg. 1990a. Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*)-roach (*Rutilus rutilus*) interaction. *Ecology*:44–56.
- Persson, L., and L. A. Greenberg. 1990b. Interspecific and intraspecific size class competition affecting resource use and growth of perch, *Perca fluviatilis*. *Oikos*:97–106.
- Phillips, S. H. 1990. A guide to the construction of freshwater artificial reefs. Sport Fishing Institute, Washington, D.C.
- Pianka, E. R. 1974. Evolutionary ecology. Harper-Row.
- Pickering, H., and D. Whitmarsh. 1997. Artificial reefs and fisheries exploitation: a review of the 'attraction versus production' debate, the influence of design and its significance for policy. *Fisheries research* 31:39–59.
- Pickering, H., D. Whitmarsh, and A. Jensen. 1999. Artificial reefs as a tool to aid rehabilitation of coastal ecosystems: investigating the potential. *Marine Pollution Bulletin* 37:505–514.
- Pitcher, T. J., and J. K. Parrish. 1993. Functions of shoaling behaviour in teleosts. Pages 363–439 in T. J. Pitcher, editor. *Behaviour of teleost fishes*. 2nd edition. Chapman & Hall.
- Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.
- Polovina, J. J. 1991. Fisheries applications and biological impacts of artificial habitats. Pages 153–176 in W. Seaman and L. M. Sprague, editors. *Artificial habitats for marine and freshwater fisheries*. Academic Press, San Diego, CA.
- Post, D. M., J. F. Kitchell, and J. R. Hodgson. 1998. Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2588–2600.
- Prince, E. D., and O. E. Maughan. 1978. Freshwater artificial reefs: biology and economics. *Fisheries* 3:5–9.

- Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *The American Naturalist* 137:S50–S66.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Real, L. A. 1977. The kinetics of functional response. *The American Naturalist* 111:289–300.
- Redfield, G. W. 2000. Ecological research for aquatic science and environmental restoration in south Florida. *Ecological Applications* 10:990–1005.
- Ricker, W. E. 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada* 11:559–623.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Department of the Environment, Fisheries and Marine Service, Ottawa, CAN.
- Roberts, C. M., J. A. Bohnsack, F. Gell, J. P. Hawkins, and R. Goodridge. 2001. Effects of marine reserves on adjacent fisheries. *Science* 294:1920–1923.
- Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385–387.
- Rosenzweig, M. L., and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. *The American Naturalist* 97:209–223.
- Roth, B. M., I. C. Kaplan, G. G. Sass, P. T. Johnson, A. E. Marburg, A. C. Yannarell, T. D. Havlicek, T. V. Willis, M. G. Turner, and S. R. Carpenter. 2007. Linking terrestrial and aquatic ecosystems: the role of woody habitat in lake food webs. *Ecological Modelling* 203:439–452.
- Royle, J. A. 2008. Modeling individual effects in the Cormack–Jolly–Seber model: a state–space formulation. *Biometrics* 64:364–370.
- Royle, J. A., and M. Kéry. 2007. A Bayesian state-space formulation of dynamic occupancy models. *Ecology* 88:1813–1823.
- Ruiz-Jaen, M. C., and T. M. Aide. 2005. Restoration success: how is it being measured? *Restoration Ecology* 13:569–577.

- Russ, G. R. 1980. Effects of predation by fishes, competition, and structural complexity of the substratum on the establishment of a marine epifaunal community. *Journal of Experimental Marine Biology and Ecology* 42:55–69.
- Ruxton, G. D. 1995. Short term refuge use and stability of predator-prey models. *Theoretical Population Biology* 47:1–17.
- Salt, G. W. 1979. A comment on the use of the term emergent properties. *American Naturalist*:145–148.
- Sandin, S. A., and S. W. Pacala. 2005. Fish Aggregation Results in Inversely Density-Dependent Predation on Continuous Coral Reefs. *Ecology* 86:1520–1530.
- Santos, L. N., F. G. Araújo, and D. S. Brotto. 2008. Artificial structures as tools for fish habitat rehabilitation in a neotropical reservoir. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18:896–908.
- Sass, G. G., S. R. Carpenter, J. W. Gaeta, J. F. Kitchell, and T. D. Ahrenstorff. 2012. Whole-lake addition of coarse woody habitat: response of fish populations. *Aquatic sciences* 74:255–266.
- Sass, G. G., J. F. Kitchell, S. R. Carpenter, T. R. Hrabik, A. E. Marburg, and M. G. Turner. 2006. Fish community and food web responses to a whole-lake removal of coarse woody habitat. *Fisheries* 31:321–330.
- Savino, J. F., and R. A. Stein. 1989a. Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. *Environmental Biology of Fishes* 24:287–293.
- Savino, J. F., and R. A. Stein. 1989b. Behavioural interactions between fish predators and their prey: effects of plant density. *Animal behaviour* 37:311–321.
- Schindler, D. E., S. I. Geib, and M. R. Williams. 2000. Patterns of fish growth along a residential development gradient in north temperate lakes. *Ecosystems* 3:229–237.
- Schindler, D. E., J. R. Hodgson, and J. F. Kitchell. 1997. Density-dependent changes in individual foraging specialization of largemouth bass. *Oecologia* 110:592–600.
- Schmitt, R. J., and S. J. Holbrook. 1984. Gape-limitation, foraging tactics and prey size selectivity of two microcarnivorous species of fish. *Oecologia* 63:6–12.
- Schoener, T. W. 1971. Theory of feeding strategies. *Annual review of ecology and systematics*:369–404.

- Schroepfer, R. L., and S. T. Szedlmayer. 2006. Estimates of residence and site fidelity for red snapper *Lutjanus campechanus* on artificial reefs in the northeastern Gulf of Mexico. *Bulletin of Marine Science* 78:93–101.
- Seber, G. A. 1965. A note on the multiple-recapture census. *Biometrika* 52:249–259.
- Shaw, S. L., and M. S. Allen. 2014. Localized spatial and temporal variation in reproductive effort of Florida Bass. *Transactions of the American Fisheries Society* 143:85–96.
- Shaw, S. L., and M. S. Allen. 2016. Quantifying recruitment compensation in florida largemouth bass, with implications for fisheries. *Transactions of the American Fisheries Society* 145:462–475.
- Sheehy, D. J., and S. F. Vik. 2010. The role of constructed reefs in non-indigenous species introductions and range expansions. *Ecological Engineering* 36:1–11.
- Shenk, T. M., G. C. White, and K. P. Burnham. 1998. Sampling-variance effects on detecting density dependence from temporal trends in natural populations. *Ecological monographs* 68:445–463.
- Sherman, R. L., D. S. Gilliam, and R. E. Spieler. 2002. Artificial reef design: void space, complexity, and attractants. *ICES Journal of Marine Science: Journal du Conseil* 59:S196–S200.
- Shima, J. S., and C. W. Osenberg. 2003. Cryptic density dependence: effects of covariation between density and site quality in reef fish. *Ecology* 84:46–52.
- Shulman, M. J. 1984. Resource limitation and recruitment patterns in a coral reef fish assemblage. *Journal of experimental marine biology and ecology* 74:85–109.
- Sih, A. 1979. Stability and prey behavioural responses to predator density. *Journal of Animal Ecology* 48:79–89.
- Sih, A., L. B. Kats, and E. F. Maurer. 2003. Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. *Animal Behaviour* 65:29–44.
- Sih, A., and D. E. Wooster. 1994. Prey behavior, prey dispersal, and predator impacts on stream prey. *Ecology* 75:1200–1207.
- Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological conservation* 83:247–257.
- Slagle, Z., M. S. Allen, and S. L. Shaw. 2017. Factors influencing nest survival in florida bass. *Transactions of the American Fisheries Society* 146:696–702.

- Smith, G. B., D. A. Hensley, and H. H. Matthews. 1979. Comparative efficacy of artificial and natural gulf of mexico reefs as fish attractants. Florida Department of Natural Resources, St. Petersburg, FL.
- Smith, H. S. 1935. The role of biotic factors in the determination of population densities. *Journal of Economic Entomology* 28:873–898.
- Smith, J. M. 1972. Game theory and the evolution of fighting. Page On evolution. Edinburgh University Press.
- Smith, J. M., and G. R. Price. 1973. The Logic of Animal Conflict. *Nature* 246:15.
- Smokorowski, K. E., and T. C. Pratt. 2007. Effect of a change in physical structure and cover on fish and fish habitat in freshwater ecosystems – a review and meta-analysis. *Environmental Reviews* 15:15–41.
- Solomon, M. E. 1949. The natural control of animal populations. *The Journal of Animal Ecology*:1–35.
- Solow, A. R., and J. H. Steele. 1990. On sample size, statistical power, and the detection of density dependence. *The Journal of Animal Ecology*:1073–1076.
- Spotte, S. 2007. Bluegills: biology and behavior. American Fisheries Society.
- Stamps, J. A., V. V. Krishnan, and M. L. Reid. 2005. Search costs and habitat selection by dispersers. *Ecology* 86:510–518.
- STAN Development Team. 2016. RStan: the R interface to Stan.
- STAN Development Team. 2017a. STAN.
- STAN Development Team. 2017b. Stan modeling language: user's guide and reference manual.
- Stephens, P. A., and W. J. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology & Evolution* 14:401–405.
- Stephens, P. A., W. J. Sutherland, and R. P. Freckleton. 1999. What is the Allee effect? *Oikos*:185–190.
- Stewart-Oaten, A., and W. W. Murdoch. 1990. Temporal consequences of spatial density dependence. *The Journal of Animal Ecology*:1027–1045.

- Stier, A. C., S. W. Geange, and B. M. Bolker. 2013. Predator density and competition modify the benefits of group formation in a shoaling reef fish. *Oikos* 122:171–178.
- Sutherland, W. J. 1983. Aggregation and the “ideal free” distribution. *The Journal of Animal Ecology*:821–828.
- Talbot, F. H., B. C. Russell, and G. R. Anderson. 1978. Coral Reef Fish Communities: Unstable, High-Diversity Systems? *Ecological Monographs* 48:425–440.
- Topping, D. T., C. G. Lowe, and J. E. Caselle. 2005. Home range and habitat utilization of adult California sheephead, *Semicossyphus pulcher* (Labridae), in a temperate no-take marine reserve. *Marine Biology* 147:301–311.
- Topping, D. T., and S. T. Szedlmayer. 2011. Home range and movement patterns of red snapper (*Lutjanus campechanus*) on artificial reefs. *Fisheries Research* 112:77–84.
- Toscano, B. J., F. J. Fodrie, S. L. Madsen, and S. P. Powers. 2010. Multiple prey effects: Agonistic behaviors between prey species enhances consumption by their shared predator. *Journal of Experimental Marine Biology and Ecology* 385:59–65.
- Tugend, K. I., M. S. Allen, and M. Webb. 2002. Use of artificial habitat structures in US lakes and reservoirs: a survey from the Southern Division AFS Reservoir Committee. *Fisheries* 27:22–27.
- Tupper, M., and F. Juanes. 2017. Testing foraging arena theory: The effects of conspecific density and habitat type on time and energy budgets of juvenile cunner. *Journal of Experimental Marine Biology and Ecology* 487:86–93.
- Turchin, P. 1999. Population regulation: a synthetic view. *Oikos*:153–159.
- Turner, A. M., and G. G. Mittelbach. 1990. Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. *Ecology* 71:2241–2254.
- Turner, C. H., E. E. Ebert, and R. R. Given. 1969. Man-made reef ecology. *Fish Bulletin*, State of California, Department of Fish and Game.
- Turner, G. F., and T. J. Pitcher. 1986. Attack abatement: a model for group protection by combined avoidance and dilution. *American Naturalist*:228–240.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *The Journal of Wildlife Management* 47:893–901.

- Verhulst, P.-F. 1838. Notice sur la loi que la population suit dans son accroissement. *Correspondance Mathématique et Physique* Publiée par A. Quetelet 10:113–121.
- Volterra, V. 1931. Variations and fluctuations of the number of individuals in animal species living together. Page *Animal ecology*. Translated from 1928 edition by R.N. Chapman. Arno, New York, New York, USA.
- Walker, L. R., J. Walker, and R. J. Hobbs. 2007. *Linking restoration and ecological succession*. Springer.
- Walsh, W. J. 1985. Reef fish community dynamics on small artificial reefs: the influence of isolation, habitat structure, and biogeography. *Bulletin of Marine Science* 36:357–376.
- Walters, C., V. Christensen, B. Fulton, A. D. M. Smith, and R. Hilborn. 2016. Predictions from simple predator-prey theory about impacts of harvesting forage fishes. *Ecological Modelling* 337:272–280.
- Walters, C. J., and F. Juanes. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2058–2070.
- Walters, C. J., and S. J. D. Martell. 2004. *Fisheries ecology and management*. Princeton University Press.
- Walters, C., and J. Korman. 1999. Linking recruitment to trophic factors: revisiting the Beverton–Holt recruitment model from a life history and multispecies perspective. *Reviews in Fish Biology and Fisheries* 9:187–202.
- Walters, D. A., W. E. Lynch Jr., and D. L. Johnson. 1991. How depth and interstice size of artificial structures influence fish attraction. *North American Journal of Fisheries Management* 11:319–329.
- Wang, Y.-G. 1998. An improved Fabens method for estimation of growth parameters in the von Bertalanffy model with individual asymptotes. *Canadian Journal of Fisheries and Aquatic Sciences* 55:397–400.
- Ward, A. J., J. E. Herbert-Read, D. J. Sumpter, and J. Krause. 2011. Fast and accurate decisions through collective vigilance in fish shoals. *Proceedings of the National Academy of Sciences* 108:2312–2315.
- Ward, A. J., D. J. Sumpter, I. D. Couzin, P. J. Hart, and J. Krause. 2008. Quorum decision-making facilitates information transfer in fish shoals. *Proceedings of the National Academy of Sciences* 105:6948–6953.

- Ware, D. M. 1975. Relation between egg size, growth, and natural mortality of larval fish. *Journal of the Fisheries Board of Canada* 32:2503–2512.
- Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist*:242–272.
- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548.
- Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology* 69:1352–1366.
- Werner, E. E., D. J. Hall, D. R. Laughlin, D. J. Wagner, L. A. Wilsmann, and F. C. Funk. 1977. Habitat partitioning in a freshwater fish community. *Journal of the Fisheries Research Board of Canada* 34:360–370.
- Werner, E., and J. Gilliam. 1984. The ontogenetic niche and species interactions in size structured populations. *Annual Review of Ecology and Systematics* 15:393–425.
- White, J. W. 2011. Can inverse density dependence at small spatial scales produce dynamic instability in animal populations? *Theoretical Ecology* 4:357–370.
- White, J. W., J. F. Samhuri, A. C. Stier, C. L. Wormald, S. L. Hamilton, and S. A. Sandin. 2010. Synthesizing mechanisms of density dependence in reef fishes: behavior, habitat configuration, and observational scale. *Ecology* 91:1949–1961.
- White, J. W., and R. R. Warner. 2007. Safety in numbers and the spatial scaling of density-dependent mortality in a coral reef fish. *Ecology* 88:3044–3054.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional ecology* 3:385–397.
- Wilks, S. S. 1938. The large-sample distribution of the likelihood ratio for testing composite hypotheses. *The Annals of Mathematical Statistics* 9:60–62.
- Williams, G. C. 1966. *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton University Press.
- Willis, D. W., and L. D. Jones. 1986. Fish standing crops in wooded and nonwooded coves of Kansas reservoirs. *North American Journal of Fisheries Management* 6:105–108.
- Wills, T. C., M. T. Bremigan, and D. B. Hayes. 2004. Variable effects of habitat enhancement structures across species and habitats in michigan reservoirs. *Transactions of the American Fisheries Society* 133:399–411.

BIOGRAPHICAL SKETCH

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