Quantitative methods for integrating instream biological monitoring data into aquatic natural resource management decision making

by

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Abstract

Freshwater aquatic resource management is fraught with challenges, as managers of multiple-use, highly diverse systems must frequently make management decisions with limitations including unclear management objectives and inadequate knowledge of system state and response. In this dissertation, I present three different freshwater aquatic resource management problems and examine the application of quantitative methods to address specific limitations in each.

The first management context was a small wildlife refuge faced with making land use decisions that consider impacts to aquatic resource objectives. I examined hypotheses relating fish species occupancy to land use using multiple model comparison. Four species – striped shiner *Luxilus chrysocephalus*, redbreast sunfish *Lepomis auritus*, orangespotted sunfish *L. humilis*, and longear sunfish *L. megalotis* – had strong support for land use as a predictor of occupancy. However, only orangespotted sunfish had an estimated occupancy probability that was predicted to decrease with increasing urban and agricultural land use. Results suggest both the dominance of a mainstem reservoir in defining patterns of fish species distribution and the tolerance to urban and agricultural land use of most encountered species.

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The second management context was a hydropower-regulated river in which an adaptive management program has been initiated. Also using multiple model comparison, I examined patterns of fish species occupancy to evaluate the potential response to an implemented management action and to inform the next adaptive management iteration. Nine of 13 fish

species had distributions that reflected downstream impacts of the hydropower dam. Model results for three species – two minnows and one darter – indicated a potential positive response to management action, whereas up to five species – largescale stoneroller *Campostoma oligolepis*, Alabama hogsucker *Hypentelium etowanum*, speckled madtom *Noturus leptacanthus*, redbreast sunfish *Lepomis auritus*, and muscadine darter *Percina smithvanizi* – demonstrated potential negative responses. I hypothesize that an altered thermal regime may be inhibiting occupancy of several fish species, and recommend that the next iteration of adaptive management focus on thermal restoration.

The final management context considered statewide management of aquatic resources. In many states, established biomonitoring programs are expected to inform decision making. However, use of these data is often restricted to site classification decisions. To facilitate broader use, I provide a general framework to incorporate the index of biotic integrity (IBI), a widely used multi-metric index, into aquatic resource management decision making. I demonstrate use of the framework for a specific decision context wherein the IBI provides a basis for informing the selection of instream flow management alternatives that meet defined objectives of a state resource agency.

Data collected as part of a freshwater monitoring program may be used to inform and support management decision making by adding to our knowledge of system state and of system response to management actions. However, the most successful freshwater aquatic resource management program will include explicit definition of management objectives and hypotheses of system response, a monitoring plan linked directly these objectives and hypotheses, and a flexible management framework, such as adaptive management, that allows for the integration of monitoring data to update hypotheses and improve future management decision making.

Acknowledgments

Power has been incredibly influential in my current path and my optimistic outlook on management of regulated rivers.

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Finally, this dissertation was not an isolated trial. It has been accompanied by difficulties few people know or understand. Those who do know have expressed wonderment at how anyone could possibly endure and persist in the midst of such difficulty. What is true is this: I can do all things through Christ who strengthens me; when I am weak, He is strong; He has lifted me from the mire and set me on solid ground; He has guided me through the darkness with a light that never fades. Simply put, faith in my God and Savior and the strength and power that He imparts is what has allowed my family to endure and survive the past several years: Thanks be to Him for His indescribable gift.

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List of Abbreviations

7Q10	the annual minimum 7-day mean flow that occurs on average once every 10 years
ADCNR	Alabama Department of Conservation and Natural Resources
ADEM	Alabama Department of Environmental Management
AIC	Akaike's information criterion
AUC	area under the receiver operating characteristic curve
AWAWG	Alabama Water Agencies Working Group
CCHMC	Chamber of Commerce of Huntsville/Madison County
DELT	deformities, eroded fins, lesions, and tumors
DO	dissolved oxygen
ELOHA	ecological limits of hydrologic alteration
FERC	Federal Energy Regulatory Commission
GSA	Geological Survey of Alabama
IBI	index of biotic integrity
MAF	mean annual flow
NLCD	national land cover dataset
NWR	National Wildlife Refuge
PAE	prepositioned area electrofisher
SDM	structured decision making
SMF	September median flow

USCB	United States Census Bureau
USEPA	United States Environmental Protection Agency
USFWS	United States Fish and Wildlife Service
USGS	United States Geological Survey

Chapter 1. Introduction

Freshwater natural resource managers and conservation practitioners are faced with

daunting challenges as they seek to improve and maintain the condition of freshwater species and

communities and the ecosystems upon which they depend. Frequently, decisions must be made

in the face of substantial limitations including unclear management objectives (Yoccoz et al.

2001; Wilson 2002; Peterman 2004; Acheson 2006), inadequate knowledge of system state

(Ludwig et al. 1993, Gunderson 2000, Newmark and Hough 2000, Peterman 2004, Acheson

2006), and inadequate knowledge of system response to management actions and natural

perturbations (Ludwig et al. 1993, Newmark and Hough 2000, Peterman 2004, Acheson 2006,

Nagendra 2007). In some regions, effective management may be additionally complicated by

high faunal diversity; for example, the southeastern United States harbors one of the most

diverse assemblages of aquatic species in the world (Lydeard and Mayden 1995). Furthermore,

the consequences of these management limitations may be compounded by rigid policy

structures with limited options to reconfigure management actions once they are deemed

ineffective. For example, under the U.S. Federal Power Act, hydropower operating licenses

issued by the Federal Energy Regulatory Commission (FERC) may include operational

conditions intended to support biological and ecological objectives, but opportunities to change

the 30- to 50-year licenses are limited once they are issued.

Making sound and defensible management decisions is imperative to maintaining and

restoring valued natural resources. Therefore, managers and practitioners will require means to

overcome these challenges – to develop clear conservation objectives and explicit hypotheses describing system response to any potential management actions, to distinguish and choose from among various management options, and to reduce system uncertainty and apply new knowledge to improve management and approach attainment of conservation goals. The tools available within the frameworks of structured decision making (SDM) and adaptive management have potential to assist managers in meeting the challenges of aquatic resource management and providing the means to manage these systems effectively.

Structured decision making has its roots in the field of business management, and was developed to handle highly complex and uncertain decision problems (Keeney 1982). Given the highly complex and uncertain nature of ecological systems, SDM has obvious potential for application in the field of natural resource management (e.g., Gregory and Keeney 2002; Blomquist et al. 2010; Gregory et al. 2012; Conroy and Peterson 2013; McGowan 2013). The SDM framework ensures that a chosen decision is the best possible one, given what is known (and unknown) about the system. The SDM process is objective-based, meaning that identified management objectives drive the decision making. The best decision is determined through evaluation of the extent to which each potential alternative meets stated objectives. Structured decision making also ensures that the decision is transparent, explicit, and replicable, and therefore understood by and justifiable to others outside of the decision process.

Adaptive management is essentially an iterative structured decision making process. Data that are gathered through monitoring protocols that directly measure defined objectives and evaluate system hypotheses are incorporated into the decision making process, thereby continually improving the quality of management decisions (Holling 1978; Walters 1986; Lee 1993; Williams et al. 2009; Allen et al. 2011). Adaptive management has become a ubiquitous

component of state, regional, and federal management plans because of its acknowledgement of the uncertainty inherent in natural resource decision making and because of its flexible and comprehensive nature (Williams et al. 2009; Williams and Brown 2012).

Monitoring programs to support structured decision making and adaptive management are critical for evaluating the achievement of management objectives and updating hypotheses of system dynamics (Yoccoz et al. 2001; Nichols and Williams 2006; Lindenmayer and Likens 2009). They should be designed to collect data on state variables as defined by management objectives, and on any pertinent influencing variables as defined by system hypotheses (Yoccoz et al. 2001, Nichols and Williams 2006). Management decisions will be informed as hypotheses are evaluated and compared in light of monitoring data (Holling 1978, Walters 1986, Williams et al. 2009).

In the field of fisheries management, monitoring has often utilized such measures as diversity (e.g., Kushlan 1976; Pearsons et al. 1992; Cianfrani et al. 2009), richness (e.g., Bowen and Freeman 1998; Patton et al. 2000; Meador et al. 2005), or a composite metric such as the index of biotic integrity (IBI; e.g., Karr 1981; Roth et al. 1998; Rowe et al. 2009). Other approaches classify species into guilds based on resource use (Leonard and Orth 1988; Austen et al. 1994; Aarts and Nienhuis 2003), evaluate systems by species traits (Dolédec et al. 1999; Goldstein and Meador 2004, 2005), or manage for key habitats (Bain 1995; Freeman et al. 1997; Bowen et al. 1998). Alternatively, measured parameters may be direct measures of biological units such as population abundance or species occurrence (occupancy) probability. Perhaps the most common direct measure is relative abundance, which is typically measured as the number of animals collected (or catch) per unit of effort and is assumed to be directly proportional to the total population size (Ney 1999). Use of occupancy as a state variable in fisheries management

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has been comparatively limited, but is gaining greater attention (e.g., Wenger et al. 2008; Hagler et al. 2011; Anderson et al. 2012; Falke et al. 2012; Albanese et al. 2013; Jensen and Vokoun 2013). Occupancy is estimated using presence-absence data at multiple independent sites in a study area, and may be interpreted as the proportion of the study area that is occupied by a species of interest or the probability that a site in the study area is occupied (MacKenzie et al. 2002; 2006). Whatever parameter is selected for a monitoring program, the most critical characteristic is that it may be tied directly to identified management or conservation objectives.

Among the many problems that freshwater resource managers face as they seek to meet management objectives, loss of habitat often poses the greatest threat to instream biota and the greatest challenge (Allan and Flecker 1993; Richter et al. 1997; Dudgeon et al. 2006). Alteration of habitat may be caused directly by changes instream (e.g., impoundment) or indirectly by changes in surrounding land use. Impoundments reduce habitat connectivity, change the natural flow and temperature regimes, and alter the availability of nutrients and sediments (Poff et al. 1997; Ward 1998; Bunn and Arthington 2002; Vörösmarty et al. 2003; Bosch 2008; Olden and Naiman 2010). Land uses such as agriculture and urbanization may increase erosion and sedimentation and contribute point and non-point pollution from agricultural, residential, and industrial chemicals and waste (Clapham et al. 1999; Walsh 2000; Paul and Meyer 2001).

In this dissertation, I present three separate freshwater aquatic resource management problems associated with impacts to instream habitat and examine the potential application of quantitative methods to address existing management limitations in each case. Chapter 2 focuses on a management decision making problem in which aquatic resource objectives are considered in the context of land use decisions. Managers are frequently faced with making decisions related to land use activities, but information linking land use to aquatic resource objectives is

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often limited. To integrate aquatic resource goals into such decisions, managers can benefit from the development of empirically-supported hypotheses that describe the effects of land use perturbations on measured parameters representing aquatic resource objectives (Yoccoz et al. 2001; Nichols and Williams 2006; Lyons et al 2008). In this chapter, I compare hypotheses relating fish species occupancy to land use for a small National Wildlife Refuge in north-central Alabama to support land use decision making in the context of aquatic resource management.

State and federal resource agencies are also required to make decisions with regard to management of flows from hydropower facilities in the context of FERC relicensing. In the hydropower-regulated Tallapoosa River in east-central Alabama, an adaptive management program has been initiated ahead of relicensing to better inform the process once it begins (Irwin and Freeman 2002; Kennedy et al. 2006; Irwin and Kennedy 2008; Williams and Brown 2012; Williams and Brown 2014). In Chapter 3, I evaluate data collected in support of adaptive management with the purpose of determining effects of flow regulation on patterns of species occupancy, evaluating the response of species to an implemented change in management, and providing insight for the next adaptive management iteration.

On a larger scale, managers are often expected to make decisions about policies that influence how aquatic resources are managed across an entire jurisdiction. In many states, established biomonitoring programs are expected to inform such management decisions. Many of these biomonitoring programs collect data to support evaluation of multi-metric indices (USEPA 2002) such as the index of biotic integrity (IBI; Karr 1981). However, there is little evidence that such monitoring data assist decisions beyond those used to classify the level of impairment of a particular site (e.g., Yoder and Rankin 1998; USEPA 2002; Volstad et al. 2003). Chapter 4 presents a framework for incorporating an index of biotic integrity (IBI) into a broader

context of management decision making, using a statewide water resource management initiative as a case study.

Overall, the work presented herein demonstrates how data collected as part of a freshwater monitoring program may be used to inform and support management decision making, by adding to our knowledge of system state and of system response to management actions. It also brings to light the importance of clear management objectives and of a flexible management framework such as adaptive management to maximizing the value of these collected data.

Chapter 2. Using models of species occupancy to assess impacts
to aquatic resources in managed multiple-use systems

Abstract. – Managers of multiple-use management areas are often responsible for a

diverse resource base that must be managed in the context of broad-scope actions such as those

involving land use. However, information linking land use to aquatic resource objectives is often

limited. We compared hypotheses relating fish species occupancy to land use for a small but

intensively managed wildlife refuge in north-central Alabama to support land use decision

making in the context of aquatic resource management. Using a multiple model comparison

approach, we compared models that described species occupancy as a function of urban and

agricultural land use, ranked and identified those models that best described the collected data,

and incorporated model uncertainty into parameter estimates using model-averaging. Because of

the dominance of a large impoundment in the refuge, most sampled sites were lentic and most

fish species encountered were lentic-tolerant. Land cover was included in the best model for six

of 14 captured species; however, uncertainty among models in each set was high. Four of the six

species – striped shiner *Luxilus chrysocephalus*, redbreast sunfish *Lepomis auritus*,

orangespotted sunfish *L. humilis*, and longear sunfish *L. megalotis* – had strong support for land

use as a predictor of occupancy. Of these four species, only orangespotted sunfish had an

estimated occupancy probability that was predicted to decrease with increasing urban and

agricultural land use. Results suggest both the dominance of the reservoir in defining patterns of

fish species distribution and the tolerance to urban and agricultural land use of most encountered

species.

Introduction

Freshwater aquatic resource managers are often tasked with maintaining the ecological health, diversity, and integrity of managed resources within multiple-use systems. Among the many impacts associated with these systems, loss of habitat often poses the greatest threat to instream biota and the greatest challenge (Allan and Flecker 1993; Richter et al. 1997; Dudgeon et al. 2006). Alteration of habitat may be caused directly by changes instream (e.g., impoundment) or indirectly by changes in surrounding land use. The fundamental ecological consequence of changes to habitat is an altered aquatic community – the result of local species extinctions and colonizations (Bunn and Arthington 2002; Herbert and Gelwick 2003; Mims and Olden 2013).

Managers of multiple-use management areas such as those in the United States National Wildlife Refuge system are frequently faced with making decisions related to land use activities. However, information linking land use to aquatic resource objectives is often limited. To integrate aquatic resource goals into such decisions, managers require empirically-supported hypotheses of the effects of land use perturbations on measured parameters representing aquatic resource objectives (Yoccoz et al. 2001; Nichols and Williams 2006; Lyons et al 2008). In freshwater fisheries management, measured parameters may include indices of the total fish species pool, such as the index of biotic integrity (e.g., Karr 1981; Roth et al. 1998; Rowe et al. 2009) or species diversity (e.g., Kushlan 1976; Pearsons et al. 1992; Cianfrani et al. 2009), or direct measures of biological units such as population abundance or species occurrence (occupancy) probability.

Perhaps the most common direct biological measure is relative abundance, which is typically measured as the number of animals collected (or catch) per unit of effort and is

assumed to be directly proportional to the total population size (Ney 1999). Use of occupancy as a state variable in fisheries management has been comparatively limited, but is gaining greater attention (e.g., Wenger et al. 2008; Hagler et al. 2011; Anderson et al. 2012; Falke et al. 2012; Albanese et al. 2013; Jensen and Vokoun 2013). Occupancy is estimated using presence-absence data at multiple independent sites in a study area, and may be interpreted as the proportion of the study area that is occupied by a species of interest or the probability that a site in the study area is occupied (MacKenzie et al. 2002; 2006). In instances where assumptions for estimating relative abundance are greatly violated and the effort necessary to estimate absolute abundance cannot be supported fiscally (e.g., using distance sampling or mark-recapture methods; Seber 1982; Williams et al. 2002), occupancy may be regarded as an appropriate replacement measure for monitoring species and populations (MacKenzie and Nichols 2004; MacKenzie et al. 2006).

To support land use decision making in the context of aquatic resource management, we compared hypotheses relating fish species occupancy to land use for a small National Wildlife Refuge in north-central Alabama. Our specific objectives were to estimate occupancy probabilities of resident fish species and compare models of occupancy to evaluate the potential impact of land use on the distribution of fish species.

Methods

Study Site. – Wheeler National Wildlife Refuge (NWR) is a small (150 km^2) management area located in the Tennessee River basin of north-central Alabama (Figure 2-1). For 200 years agriculture has been and remains the dominant feature of the landscape surrounding Wheeler NWR, although urbanization and industry have been steadily increasing over the past 50 years

(USCB 1995, USCB 2009, CCHMC 2011). At the center of the refuge is Wheeler Reservoir, an impoundment of the Tennessee River that inundates most of the refuge's aquatic habitat (USFWS 2007). Depending on water levels of the reservoir, between 45 and 60 km^2 – from 30 to 40 percent – of the refuge is covered by surface water (USFWS 2007).

Managers of Wheeler NWR are concerned with the impacts of refuge land use on aquatic biota, and are faced with decisions such as whether to lease refuge lands to farmers, regulate the use of pesticides, convert former agricultural land to forest, or provide right-of-way access for public roads and utility lines (USFWS 2007). Understanding the impacts of agricultural and urban land use on aquatic biota will enable refuge managers to include aquatic resource objectives into management decisions.

Field Methods. – In July 2008, seven watersheds were sampled for fish community composition within the boundaries of Wheeler NWR: Flint Creek, Beaverdam Creek, Cotaco Creek, Indian Creek, Limestone Creek, Piney Creek, and Ginhouse Branch (Figure 2-1). Watersheds were chosen to include sites with known land use impact (Flint, Cotaco, and Indian Creeks are listed on Alabama's 303(d) list of impaired streams on account of siltation, pesticides, heavy metals, or pathogens; ADEM 2008) and those with no known land use impact (Beaverdam, Limestone, and Piney creeks, and Ginhouse Branch). To select sample sites, we employed a stratified random sampling design, where strata were defined by watershed, and the number of randomly-selected sites within each watershed was based on available sampling area of each watershed within the boundaries of Wheeler NWR. In total, there were 43 sampled sites: nine sites in Flint Creek, seven in Beaverdam Creek, six each in Cotaco and Indian creeks, and five each in Piney Creek, Limestone Creek, and Ginhouse Branch. See Appendix 1 for additional details on the methods for site selection.

Fish were collected using prepositioned area electrofishers (PAEs; Bain et al. 1985; Fisher and Brown 1993; Freeman et al. 2001) following methods described by Freeman et al. (2001). At each site, five spatially-replicated PAEs were sampled to later estimate detection probability of captured fish species (see *Data Analysis*). All collected fish were identified to species when possible; however, because of similar habitats and morphological characters (Echelle and Schnell 1976; Mettee et al. 1996; Boschung and Mayden 2004), blackstripe topminnow (*Fundulus notatus*) and blackspotted topminnow (*Fundulus olivaceus*) were evaluated as a single taxon, topminnows (*Fundulus* spp.). Within each PAE, habitat variables were measured including depth (cm), velocity (cm/s), percent areal vegetation cover, presence of large cover, and substratum type. For additional detail on field methods, see Appendix 1.

Data Analysis. – To estimate fish species occupancy, we used the modeling framework described in MacKenzie et al. (2002; 2006). All analyses were conducted using R (R 2.13.0; R Foundation for Statistical Computing, Vienna) statistical software; occupancy estimation was conducted using the R package "unmarked" (Fiske and Chandler 2011). Because fish species often go undetected even when present, we collected spatially repeated samples at each site to estimate species detection probability, which is the probability that a species is detected in a sample given that it is present at a site (MacKenzie et al. 2002; 2006). Failure to estimate detection probability may lead to underestimation of occupancy and biased estimates of covariate effects (Tyre et al. 2003, Gu and Swihart 2004, MacKenzie et al. 2006). As initially proposed by MacKenzie et al. (2002; 2003), sample replicates for estimating detection probability are to be gathered by repeated visits to a site over a relatively short period of time; however, MacKenzie et al. (2006) extended this conceptual framework to include randomly sampled spatial replicates.

Spatial replicates have been used to estimate occupancy for several taxa, including large carnivores (Hines et al. 2010; Karanth et al. 2011; Thorn et al. 2011), birds (Pavlacky et al. 2012), and fish (Albanese et al. 2007; Hagler et al. 2011; Anderson et al. 2012). However, though consistent with the published literature, occupancy estimation methods using spatial replicates may require a slightly different interpretation of detection probability than is used for temporal replicates. In this instance, we considered each PAE sample an independent spatial replicate for calculating detection probability (see *Field Methods*), where the inference for occupancy is at the site (50 m stream or shoreline reach) scale, and each independent PAE (9 m^2) sample is considered representative of the whole site. Therefore "detection" represents the probability of encountering a species in a single spatial sample of the site (that is, a single PAE), given that the species is present at the site.

For unbiased parameter estimates, models of occupancy assume that 1) sampled sites are closed to changes in occupancy during the sampling period; 2) occupancy probability is constant among sites and detection probability is constant among samples, or any parameter heterogeneity is accounted for by modeled covariates; 3) sites and samples are respectively independent of each other; and 4) species are not falsely detected (MacKenzie et al. 2006). To prevent violations of model assumptions, spatial replicates should be sampled randomly and within a short span of time (MacKenzie et al. 2006). MacKenzie et al. (2006) also suggested that spatial replicates should be sampled with replacement to ensure independence, as sampling without replacement can lead to positively biased occupancy estimates when species distribution is static and non-random (Kendall and White 2009). However, Guillera-Arriota (2011) demonstrated that the decision to sample with replacement should take into account the patterns of distribution and movement of the taxa under study, as sampling with replacement when local species

distribution is random can lead to a negative bias in occupancy (Guillera-Arriota 2011). The PAE samples taken within sites at Wheeler NWR were selected randomly and were collected over the course of a few hours at each site; however, disturbance caused by the method of sampling precluded the incorporation of replacement into the sampling design. Therefore, we assumed that after accounting for detection heterogeneity due to differences in depth among sample replicates, species distribution was random and detection probability was constant across replicates.

Detection histories were developed for each fish species at a total of 43 sites in seven watersheds within Wheeler NWR; a detection was a positively identified occurrence of a species in a sample. We used maximum-likelihood methods and modeled parameters as functions of measured covariates by means of the logit-link function as described by MacKenzie et al. (2002, 2006). To ensure robust models of detection probability for this limited data set, parameter estimation was limited only to those species that had high detection (i.e., were detected in a minimum of 4 replicates) for at least one of the 43 sites. Ensuring that models of detection are robust reduces the probability of a false absence, allowing for stronger inference of occupancy patterns (MacKenzie and Royle 2005; MacKenzie et al. 2006).

In addition, to avoid model overparameterization, we limited the covariates of detection and occupancy included in each model. Covariates of detection were limited to PAE depth, as PAE and user efficiency are strongly influenced by this variable (Bain et al. 1985; Larimore and Garrels 1985; Portt et al. 2006). Covariates of occupancy were limited to average depth (m) and velocity (m/s) at each site, as well as proportional values of land cover in a site watershed. Land cover was included as a covariate to evaluate the hypothesis that occupancy was a function of watershed land use. We used proportional land cover to represent management actions identified

by refuge managers, such as leasing refuge lands to farmers (increasing agricultural land cover), converting agricultural land to forest (decreasing agricultural land cover), and allowing right-of-way access for public roads and utility lines (increasing urban land cover) (USFWS 2007). Land cover data were taken from the 2001 national land cover dataset (NLCD) accessed from the Alabama Gap Analysis Project (Kleiner et al. 2007). U.S. Geological Survey 12-digit hydrologic units were used as the classification unit for all watersheds except Ginhouse Branch, which was manually delineated. We used three land cover classes for data analysis: pasture (NLCD class 81), row crop (class 82), and urban (classes 21, 22, 23, and 24), each expressed as a proportion of total area for each watershed.

Correlations among covariates were evaluated with pairwise Pearson correlation values, but no covariates were eliminated due to collinearity (all r values were < 0.6); furthermore, when correlations are low to moderate, an AIC model averaging approach is generally robust to the effects of collinearity (Freckleton 2011). We examined two models of detection (p) and seven models of occupancy (Ψ; Table 2-1). All three land cover types were included as individual covariates in each model of land cover (i.e., land cover = urban + row crop + pasture); this allowed for both the independent assessment of each land cover type and for an explicit accounting of any confounding effects of the proportional values. Two models of detection and seven models of occupancy resulted in a model set of fourteen models per species.

Following methods described in Burnham and Anderson (2010), competing models for each species were compared by means of Akaike's information criterion (AIC; Akaike 1973). Because an AIC approach assumes that at least one model in each set fits the data adequately, it is necessary to perform some type of goodness-of-fit test (Burnham and Anderson 2010). To evaluate model fit, we followed methods as described in MacKenzie and Bailey (2004) and

MacKenzie et al. (2006), wherein the fit of the global model for each set, p(depth) Ψ(depth + velocity + land cover) is assessed using parametric bootstrapping. This method generates alternative data sets based on the global model; if the observed data are similar to the generated data, the fit of the global model may be considered adequate (MacKenzie and Bailey 2004). We simulated 1000 bootstrapped datasets from the global model and refit the model to the simulated datasets. We compared the distribution of a Pearson chi-square statistic from the simulated datasets to the observed statistic to determine how well the global model fit the observed data (i.e., whether the observed statistic could be considered a random outcome of the sampling distribution). We considered the model a reasonable fit if the observed statistic fit the sampling distribution at α level of 0.10.

Models in each set were then further evaluated with multimodel inference (Burnham and Anderson 2010). Multimodel inference uses Akaike weights to calculate additive weights of modeled covariates and model-averaged parameter estimates. We calculated additive weights, model-averaged parameter estimates, and unconditional standard errors of parameter estimates following methods reported in Burnham and Anderson (2010). The additive weight of a modeled covariate represents its relative importance, and may be interpreted as the probability that the covariate is included in the best model of the model set. We used additive weights to compare the relative importance of depth as a predictor of detection over the null model, and of land cover as a predictor of occupancy over habitat alone. Model-averaged parameter estimates incorporate the strength of evidence of each model, and therefore any uncertainty among models, into parameter estimates. We focused primarily on model-averaged estimates of detection and occupancy, whereby parameter estimates were derived from each model and then averaged (however, see Appendix 2 for details regarding model-averaged regression coefficients). For

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each species, model-averaged detection was estimated for every sample, and model-averaged occupancy was estimated for every site. For species that had strong associations with land cover, we examined model-averaged occupancy estimates across a gradient of land cover types while holding other modeled covariates constant at their mean values. We also examined model-averaged occupancy estimates of two lotic species across a gradient of habitat conditions to illustrate further application of these models.

In addition, we evaluated the predictive performance of the averaged models for each set by calculating the area under the receiver operating characteristic curve (AUROC or AUC; Hanley and McNeil 1982; Fielding and Bell 1997; Pearce and Ferrier 2000) using the R package "ROCR" (Sing et al. 2005). The AUC measures the ability of the averaged model set to correctly determine site occupancy and species detection. A value of 0.5 indicates performance that is no better than random; a value of 1.0 indicates perfect prediction. Predictive performance of detection was based on estimates of unconditional detection probability; that is, detection given occupancy at a site ($d = \Psi p$).

Results

With the exception of Ginhouse Branch, sites were primarily lentic, with measured velocities of 0.00 m/s, substrates primarily of silt and sand, and some vegetation and large cover present. Indian Creek was absent of vegetation likely because of channelization that occurred to remove contaminated sediments (USEPA 2009). Habitat characteristics and land cover values for each sampled watershed are provided in Appendix 3.

Twenty-seven species of fish from eight families, most of which were lentic-tolerant taxa, were captured among sites sampled in Wheeler NWR (see Appendix 3). The taxonomic family

with the most detections (that is, recorded presence of individual species; see *Methods*) across all

samples and sites was Centrarchidae (sunfishes; 379 total detections), followed by Cyprinidae

(minnows), Fundulidae (topminnows), and Atherinopsidae (silversides). The species that was

detected on the most occasions was bluegill (*Lepomis macrochirus*; 131 total detections). Of the

27 fish species captured, 14 had high detection (i.e., were detected in a minimum of 4 replicates)

in at least one of the 43 sampled sites; these species were the focus of further analyses.

For the 14 modeled species, parametric bootstrapping demonstrated an adequate fit ($P >$

0.10) of the global model p(depth) Ψ(depth + velocity + land cover) to the observed data in each

case; that is, for each species, the observed data could be considered a random outcome of the

global model (MacKenzie and Bailey 2004; MacKenzie et al. 2006). Based on a comparison of

competing models using AIC, uncertainty among models in each set was high for all species,

with no one model clearly better than the others in most cases (Table 2-2). The top model with

the greatest support among all species was that for longear sunfish, *Lepomis megalotis*, p(depth)

Ψ(depth + land cover), which had an AIC weight of 0.60 (Table 2-2).

Depth was included in the best model of detection for eight of the 14 species (Table 2-2).

Of these eight taxa, four (topminnows; mosquitofish, *Gambusia affinis*; longear sunfish; and

redear sunfish, *Lepomis microlophus*) had strong support ($w_+ > 0.8$) for depth as a predictor of

detection over the constant model (Table 2-3). However, AUC values of the detection models

for topminnows and redear sunfish indicated relatively low predictive performance, suggesting

that there are likely additional factors influencing detection for these species (Table 2-4).

As a predictor of occupancy, habitat (depth and/or velocity) was included in the best

model for nine species (Table 2-2). Additionally, the constant model, which estimated

occupancy as constant across all conditions in the study area, had low to no support among

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models for each of these nine species (Table 2-3). Land cover was included along with habitat in the best model for six species (Table 2-2). Of these six taxa, four (striped shiner, *Luxilus chrysocephalus*; redbreast sunfish, *Lepomis auritus*; orangespotted sunfish, *Lepomis humilis*; and longear sunfish) had strong ($w_+ > 0.8$) support for land cover as a predictor of occupancy over models with habitat alone (Table 2-3). The AUC values of the occupancy models for these species indicated good to excellent predictive performance, ranging from 0.77 for redbreast sunfish and longear sunfish to 0.97 for striped shiner (Table 2-4). All species for which the constant occupancy model had relatively strong support were lentic-tolerant taxa (Table 2-3). For full model results, see Appendix 4.

Model-averaged estimates of detection ($\hat{\bar{p}}$) and occupancy ($\hat{\bar{\Psi}}$) varied widely both inter- and intraspecifically across sampled replicates and sites (Table 2-4). A wide range in model-averaged detection or occupancy was indicative of strong support for modeled covariates. For example, striped shiner, redbreast sunfish, and longear sunfish had both strong support for modeled occupancy covariates (Tables 2-2 and 2-3) and some of the largest ranges in occupancy estimates (Table 2-4). Conversely, bluegill had among the smallest ranges of estimated parameters (Table 2-4) and strong support for the constant models of detection and occupancy (Table 2-2). Detection probabilities were estimated to be substantially lower than 1 for all species, with an overall mean of 0.38 (0.13 sd; Table 2-4). For individual species, mean detection ranged from 0.18 (0.12 sd) for mosquitofish to 0.63 (0.00 sd) for bluegill, the most commonly encountered species in Wheeler NWR (Table 2-4).

The overall predictive performance of detection models was relatively low, with half of averaged model sets with AUC values < 0.60 (Table 2-4). However, several model sets also demonstrated high predictive performance (AUC > 0.85), specifically for largescale stoneroller

(*Campostoma oligolepis*), striped shiner, redbreast sunfish, and blackside snubnose darter (*Etheostoma duryi*). The overall predictive performance of occupancy models was much better than that of detection models, with all averaged model sets with AUC values > 0.60, and most with values > 0.70. Those model sets with the greatest predictive performance for occupancy (near or > 0.90) were those for largescale stoneroller, striped shiner, and blackside snubnose darter. These species, all lotic habitat specialists, also had high predictive performance for detection (Table 2-4).

Figure 2-2 displays model-averaged occupancy estimates for the four species with strong land cover associations across a gradient of land cover types. Of the four species, only orangespotted sunfish had estimated occupancy probabilities that were predicted to decrease with increasing proportions of agricultural and urban land use. Figure 2-3 provides model-averaged occupancy estimates for two lotic species, largescale stoneroller and blackside snubnose darter, across gradients of depth and velocity. For both of these species, the highest-ranked model estimated occupancy as a function of habitat alone, but model uncertainty was still considerable (Tables 2-2 and 2-3). As demonstrated in Figure 2-3, model-averaging incorporates this model uncertainty into parameter estimates.

Model-averaged regression coefficient estimates and suggestions for their interpretation are provided in Appendix 2.

Discussion

Management areas with many species and multiple possible sources of anthropogenic disturbance present major challenges for managers, even when the systems are relatively small. Such is the case for Wheeler National Wildlife Refuge, where the dominance of lentic habitat

and lentic-tolerant taxa implicates long-term impoundment as a primary driver of fish community composition, but intensive agricultural practices and urban development have likely had additional ecological influence on aquatic biota. For Wheeler NWR, we related patterns of fish species occupancy to patterns of agricultural and urban land use using a multiple model comparison framework. Hypotheses describing the functional relations between land use and occupancy were compared, their strength of evidence evaluated, and their uncertainty incorporated into parameter estimates. With this framework, we were able to identify those species that had strong associations with current land use, determine and rank the models that best described the collected data, and examine the uncertainty of each modeled association. Results demonstrated that four species collected in Wheeler NWR had patterns of occupancy that were best explained by land use, and these patterns generally reflected tolerance to agricultural or urban land use or both.

However, in spite of the primarily lentic and largely uniform aquatic habitat in Wheeler NWR, each evaluated species demonstrated unique patterns of occupancy and different estimated effects of modeled covariates. Some species, such as bluegill and largemouth bass (*Micropterus salmoides*), had little to no estimated response to land cover, whereas others, such as orangespotted sunfish and longear sunfish, had strong estimated effects. Of those species with relatively strong support for land cover as a predictor of occupancy, most associations were positive: three of four species were estimated to occur more often when urban or agricultural land use was proportionally high. Although a relatively small sample size precludes strong conclusions, one possibility is that some positive responses were due to advantageous conditions provided by an increase in available resources, resulting either directly from land use (e.g., from an increase in nutrients from agricultural or urban runoff) or indirectly from local extirpation of

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more sensitive species. For example, Miranda and Lucas (2004) also reported longear sunfish in large, moderately turbid lakes, and suggested the role of turbidity in decreasing abundance of visual piscivores (e.g., largemouth bass) thereby increasing abundances of potential prey. In addition, longear sunfish are known to maintain their homing ability when deprived of sight (Gunning 1959), potentially increasing their chances of survival in a system impacted by land use.

In management systems with varying sources of impact, multiple model comparison can support decision making by explicitly accounting for uncertainty among hypotheses and providing unbiased predictions of the consequences of management actions. The framework also lends itself to the testing of hypotheses, and to the incorporation of new data to improve models and support future decision making. Although uncertainty was relatively high among hypotheses of species occupancy in Wheeler NWR, model averaging took this uncertainty into account, and across all models, there was little support for strong negative impacts of agricultural and urban land use on species occupancy. These results may be due in part to historical impacts of impoundment and land use and consequent elimination of sensitive species, as the assemblage in the refuge was largely characterized by lentic or generalist species. Given the lack of support for negative effects of land use, managers might decide to allow some limited agricultural leases and right-of-way access permissions for public utilities in selected areas of the refuge; or, depending on the urgency of the decision, they might choose to collect additional data to reduce some of the current model uncertainty. However decisions are made, hypotheses should be continually updated with any newly acquired data to further improve future management decisions.

Model results of fish species occupancy in Wheeler NWR also give some perspective on the potential effects of changes to instream habitat. Whereas alternative management of water levels and flow in Wheeler Reservoir may not presently be under consideration by managers, results could inform potential future decision making as well as assist in current decisions regarding aquatic habitat protection. For example, occupancy estimates of both largescale stoneroller and blackside snubnose darter were predicted to be influenced primarily by habitat (depth and/or velocity), but with relatively high model uncertainty, as models including land use also had substantial weight. Because these are lotic species, it is likely that their distribution patterns are predominantly influenced by Wheeler Reservoir, and model uncertainty could be reduced by sampling additional lotic habitat. Yet even with high uncertainty, the models may still be useful for management decision making. By examining the slopes of predicted response curves, managers can develop preliminary targeted thresholds for instream habitat management. In this case, managers might use the curves to hypothesize that both species are unlikely to occupy refuge habitats with velocities less than 1 cm/s, largescale stoneroller is unlikely to occupy depths greater than 25 cm, and blackside snubnose darter is unlikely to occupy any depth without adequate velocities. Because of the limited habitat available in the refuge that support these species, managers could use this information to both identify additional locations of potentially valuable habitat on the refuge and to develop possible management actions for habitat restoration.

A simple spatial sampling effort can provide valuable information to support aquatic resource management; however, the ideal circumstance would include continued sampling over time. A regular sampling routine would provide new information to update system hypotheses, thereby reducing uncertainty regarding the impacts of management actions on aquatic resources

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and potentially improving future management decisions. With temporal sampling, managers may also estimate and compare hypotheses describing patterns of local species extinction or colonization, that is, changes in occupancy over time (MacKenzie et al. 2003; MacKenzie et al. 2006). Using occupancy as a state variable for monitoring can be advantageous as it allows direct estimation of a biologically-relevant parameter with relatively little effort. Given limited time and resources, occupancy may be preferable to the more intensive requirements of abundance estimation, especially when estimates of detection are included to minimize parameter bias.

When time and resources are especially limited, spatial replicates may provide the most efficient method of sampling for occupancy and detection estimation, as they require only one visit to a site. However, occupancy estimation methods using spatial replicates may require a different interpretation of detection probability than is used for methods with temporal replicates, as "detection" represents the probability of encountering a species in a single spatial sample of the site (that is, a single PAE), given that the species is present at the site. Kendall and White (2009) caution that spatial replicates can introduce a positive bias to occupancy estimates by violating the closure assumption in cases where species distribution is static and non-random. The closure assumption stipulates that a species must be available for detection on each sampling occasion; if a species has a static distribution, it would be available in a fixed proportion of samples, and therefore not available for detection in each replicate. The solution to this circumstance, as advocated by Kendall and White (2009), would be to sample with replacement, such that the species would be available for detection equally for all replicate samples.

However, in cases where a species is randomly available for detection at a site, such that each replicate has an equal probability of species availability, sampling with replacement could

instead incur a negative bias and violate the assumption of sample independence (Guillera-Arriota 2011). Therefore, the behavior and distribution of species at the site scale must be taken into consideration when developing a study design for estimating occupancy with spatial replication. Because PAE samples cause substantial local disturbance, sampling with replacement with this type of gear (or any other electrofishing method) is not a viable option, and would certainly violate the assumption of independence among replicates. In these cases, it must be reasonable to assume that the availability of a species for detection is random or is adequately described by modeled covariates. If this is not a reasonable assumption in a given context, a positive bias on occupancy estimates will be incurred. However, another solution is to expand the spatial extent of a defined site. A site that is large in comparison to the number of spatial replicates will reduce the chance and need for replacement as the ratio of sampled replicates to total replicate space decreases (Guillera-Arriota 2011).

We suggest that a multiple-model comparison approach to evaluate land use impacts, such as described here for Wheeler National Wildlife Refuge, may be applied to any management area with similar management contexts and high uncertainty associated with the sources of impact to the aquatic community. A relatively simple but carefully designed sampling effort and a basic set of hypotheses of system response can together provide a foundation on which to build a justifiable basis for management action in multiple-use systems. In many circumstances an occupancy-based assessment of species distribution patterns can simply and effectively provide the necessary information for such a foundation. Whereas PAEs may be useful in sampling for occupancy as they are a consistent and quantifiable sampling method, any replicate sample that includes measures of associated habitat would suffice. However, it is imperative that habitat measures are included, as even in systems with largely homogeneous

habitat, detection and occupancy probability of many species are likely dependent on local habitat conditions, as was evidenced in Wheeler NWR. Evaluating system hypotheses based on collected data in a multiple model comparison framework may then provide an explicit accounting of system uncertainty. In this way, managers may build a plan of action based on the strength of evidence of different hypotheses and make strides toward meeting their goals of maintaining the ecological health, diversity, and integrity of aquatic resource systems.

Table 2-1. Models of detection and occupancy used to evaluate the effects of management alternatives on fish species occupancy in Wheeler National Wildlife Refuge, Alabama. The $p(.)$ and $\Psi(.)$ models represent constant detection and occupancy, respectively. The remaining models estimate parameters as a function of habitat or both habitat and land cover covariates. In the models with land cover, three land cover types were included as individual covariates, such that land cover = urban + row crop + pasture.

Models
Detection (p)
$\quad p(.)$
$\quad p$(depth)
Occupancy (Ψ)
$\quad \Psi(.)$
$\quad \Psi$(depth)
$\quad \Psi$(velocity)
$\quad \Psi$(depth + velocity)
$\quad \Psi$(depth + land cover)
$\quad \Psi$(velocity + land cover)
$\quad \Psi$(depth + velocity + land cover)

Table 2-2. Model selection results for occupancy models of 14 fish species detected in Wheeler National Wildlife Refuge, Alabama. Number of parameters in each model (K), negative log likelihood (-log$L$), AIC, ΔAIC, AIC model weights (w_i), and cumulative model weights (cum w_i) are reported. Model results for each species are ranked in terms of AIC and w_i. Only the top 2 models are reported; full model results are provided in Appendix 4. Occupancy models estimated detection (p) as constant [$p(.)$] or as a function of depth [$p(depth)$], and occupancy (Ψ) as constant [Ψ(.)] or as a function of habitat [Ψ(depth), Ψ(velocity), Ψ(depth + velocity)] or habitat and land cover [Ψ(depth + lc), Ψ(velocity + lc), Ψ(depth + velocity + lc)]. Here land cover represents three covariates: urban + row crop + pasture (see text for more details).

Model	K	-log$L$	AIC	ΔAIC	w_i	cum w_i	Model	K	-log$L$	AIC	ΔAIC	w_i	cum w_i
Largescale Stoneroller							**Green Sunfish**						
p(.) Ψ(depth + velocity)	4	35.09	78.18	0.00	0.33	0.33	p(.) Ψ(velocity + lc)	6	75.95	163.91	0.00	0.22	0.22
p(depth) Ψ(depth + velocity)	5	34.72	79.44	1.26	0.18	0.51	p(depth) Ψ(velocity + lc)	7	74.96	163.92	0.01	0.22	0.45
Striped Shiner							**Orangespotted Sunfish**						
p(.) Ψ(depth + lc)	6	24.71	61.41	0.00	0.36	0.36	p(depth) Ψ(depth + lc)	7	77.75	169.50	0.00	0.22	0.22
p(depth) Ψ(depth + lc)	7	24.27	62.54	1.13	0.21	0.57	p(.) Ψ(depth + lc)	6	78.80	169.60	0.10	0.21	0.43
Bullhead Minnow							**Bluegill**						
p(.) Ψ(.)	2	72.89	149.78	0.00	0.20	0.20	p(.) Ψ(.)	2	141.89	287.79	0.00	0.36	0.36
p(.) Ψ(velocity)	3	72.02	150.03	0.25	0.17	0.37	p(.) Ψ(depth)	3	141.76	289.52	1.73	0.15	0.51
Inland Silverside							**Longear Sunfish**						
p(depth) Ψ(depth + lc)	7	94.81	203.63	0.00	0.16	0.16	p(depth) Ψ(depth + lc)	7	76.68	167.36	0.00	0.60	0.60
p(.) Ψ(depth + lc)	6	95.85	203.70	0.07	0.16	0.32	p(depth) Ψ(depth + velocity + lc)	8	76.74	169.48	2.12	0.21	0.81
Topminnows							**Redear Sunfish**						
p(depth) Ψ(.)	3	111.32	228.65	0.00	0.28	0.28	p(depth) Ψ(velocity)	4	95.83	199.67	0.00	0.39	0.39
p(depth) Ψ(velocity + lc)	7	107.71	229.42	0.78	0.19	0.46	p(depth) Ψ(velocity + lc)	7	93.41	200.82	1.16	0.22	0.60
Mosquitofish							**Largemouth Bass**						
p(depth) Ψ(.)	3	64.41	134.82	0.00	0.30	0.30	p(depth) Ψ(.)	3	110.70	227.40	0.00	0.26	0.26
p(depth) Ψ(velocity)	4	63.58	135.16	0.35	0.25	0.54	p(.) Ψ(.)	2	111.84	227.68	0.28	0.23	0.49
Redbreast Sunfish							**Blackside Snubnose Darter**						
p(depth) Ψ(depth + lc)	7	73.06	160.12	0.00	0.25	0.25	p(.) Ψ(velocity)	3	31.11	68.23	0.00	0.26	0.26
p(depth) Ψ(velocity + lc)	7	73.12	160.25	0.13	0.23	0.47	p(.) Ψ(velocity + lc)	6	28.52	69.04	0.82	0.17	0.44

Table 2-3. Additive weights (w_+) of detection (p) and occupancy (Ψ) covariates for 14 fish species detected in Wheeler National Wildlife Refuge, Alabama. Here additive weights represent the relative strength of evidence for depth as a predictor of detection, and of land cover as a predictor of occupancy over habitat alone. The notation Ψ(land cover) represents all occupancy models including land cover [Ψ(depth + land cover), Ψ(velocity + land cover), Ψ(depth + velocity + land cover)], where land cover represents three covariates: urban + row crop + pasture. The notation Ψ(habitat) represents all occupancy models with habitat covariates alone [Ψ(depth), Ψ(velocity), Ψ(depth + velocity)]. The null occupancy model Ψ(.) is given for reference.

Species	p(depth)	Ψ(land cover)	Ψ(habitat)	Ψ(.)
Largescale Stoneroller	0.31	0.34	0.66	0.00
Striped Shiner	0.35	0.97	0.03	0.00
Bullhead Minnow	0.28	0.16	0.57	0.27
Inland Silverside	0.54	0.65	0.30	0.05
Topminnows	0.93	0.42	0.28	0.30
Mosquitofish	0.95	0.11	0.59	0.30
Redbreast Sunfish	0.58	0.97	0.03	0.00
Green Sunfish	0.47	0.72	0.19	0.09
Orangespotted Sunfish	0.56	0.88	0.07	0.05
Bluegill	0.27	0.03	0.47	0.50
Longear Sunfish	0.83	0.97	0.03	0.00
Redear Sunfish	0.99	0.39	0.54	0.07
Largemouth Bass	0.53	0.07	0.44	0.51
Blackside Snubnose Darter	0.32	0.49	0.51	0.00

Table 2-4. Mean (sd) and range of model-averaged detection and occupancy estimates and predictive performance of averaged model sets for 14 species detected in Wheeler National Wildlife Refuge, Alabama. Predictive performance was evaluated with the area under the receiver operating curve (AUC). For each species, model-averaged detection was estimated for each of 215 samples; model-averaged occupancy was estimated for each of 43 sites. A large range in parameter estimates was generally indicative of strong support for modeled covariates.

Taxa	Model-averaged detection estimates			Model-averaged occupancy estimates		
	mean (sd)	min (se) - max (se)	AUC	mean (sd)	min (se) - max (se)	AUC
Largescale Stoneroller	0.48 (0.01)	0.46 (0.11) - 0.50 (0.15)	0.9467	0.15 (0.20)	0.02 (0.03) - 0.99 (0.04)	0.8968
Striped Shiner	0.59 (0.03)	0.52 (0.18) - 0.64 (0.12)	0.9746	0.14 (0.30)	0.00 (0.01) - 0.99 (0.03)	0.9730
Bullhead Minnow	0.36 (0.00)	0.35 (0.09) - 0.36 (0.09)	0.5894	0.37 (0.06)	0.17 (0.18) - 0.46 (0.16)	0.6921
Inland Silverside	0.36 (0.04)	0.28 (0.12) - 0.45 (0.12)	0.4839	0.57 (0.18)	0.09 (0.15) - 0.87 (0.17)	0.8009
Topminnows	0.37 (0.10)	0.15 (0.08) - 0.60 (0.11)	0.4720	0.68 (0.09)	0.43 (0.31) - 0.79 (0.17)	0.7161
Mosquitofish	0.18 (0.12)	0.03 (0.03) - 0.52 (0.16)	0.6088	0.57 (0.08)	0.40 (0.29) - 0.81 (0.22)	0.7655
Redbreast Sunfish	0.49 (0.05)	0.36 (0.16) - 0.60 (0.13)	0.8519	0.38 (0.29)	0.13 (0.09) – 1.00 (0.01)	0.7685
Green Sunfish	0.29 (0.03)	0.22 (0.11) - 0.37 (0.12)	0.7641	0.48 (0.19)	0.14 (0.19) - 0.85 (0.23)	0.7557
Orangespotted Sunfish	0.30 (0.06)	0.19 (0.13) - 0.44 (0.17)	0.5389	0.50 (0.25)	0.16 (0.18) - 0.91 (0.12)	0.7889
Bluegill	0.63 (0.00)	0.63 (0.05) - 0.64 (0.05)	0.5579	0.96 (0.01)	0.94 (0.09) - 0.97 (0.06)	0.7359
Longear Sunfish	0.22 (0.06)	0.10 (0.06) - 0.38 (0.12)	0.7338	0.71 (0.42)	0.02 (0.04) - 1.00 (0.01)	0.7664
Redear Sunfish	0.31 (0.15)	0.06 (0.04) - 0.68 (0.10)	0.5876	0.68 (0.17)	0.09 (0.16) - 0.82 (0.16)	0.6341
Largemouth Bass	0.32 (0.03)	0.25 (0.10) - 0.40 (0.11)	0.5751	0.71 (0.01)	0.69 (0.12) - 0.72 (0.12)	0.6357
Blackside Snubnose Darter	0.41 (0.02)	0.36 (0.15) - 0.45 (0.13)	0.9414	0.15 (0.23)	0.03 (0.05) - 0.98 (0.05)	0.9189
Mean across all species	0.38 (0.13)			0.50 (0.25)		
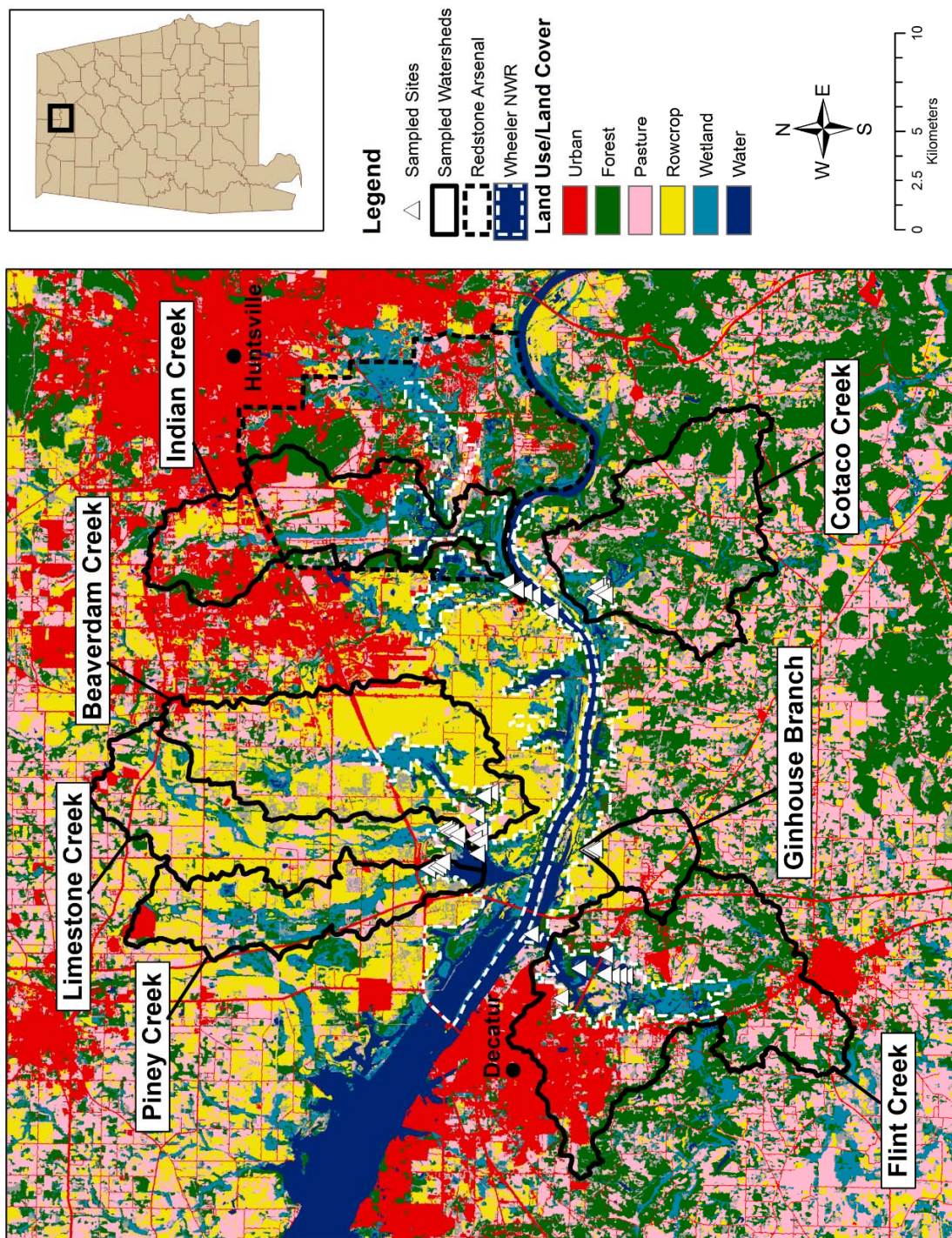
Figure 2-1. Map of the area surrounding Wheeler National Wildlife Refuge, Alabama, including land cover, sampled sites, and delineations of sampled watersheds.
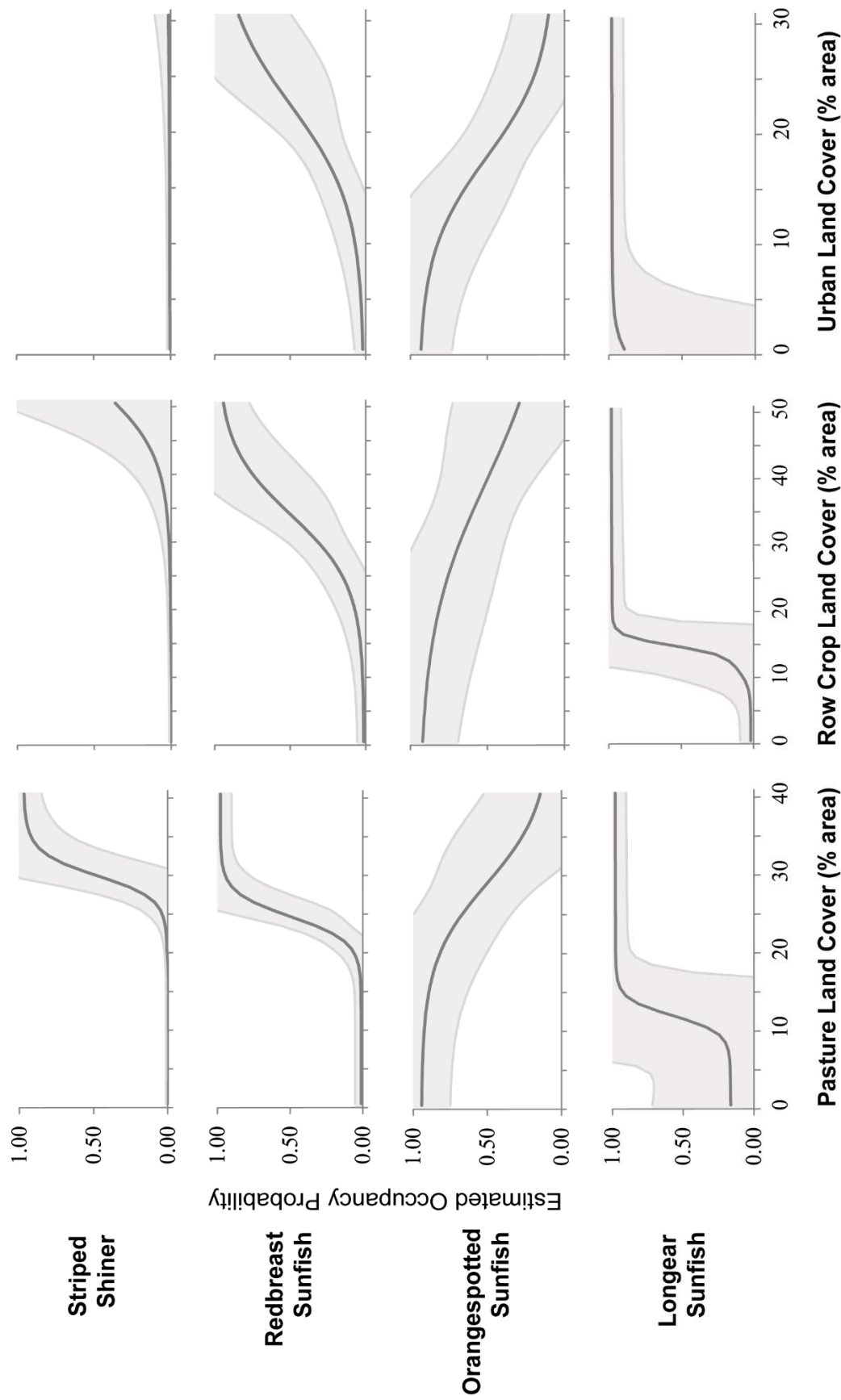
Figure 2-2. Estimated model-averaged occupancy probabilities for the four fish species detected in Wheeler National Wildlife Refuge, Alabama that had strong estimated associations with land cover. Values are shown across a gradient of pasture, row crop, and urban land covers. Estimates are given under average conditions for all other modeled covariates. The shaded area represents the 95% confidence interval.
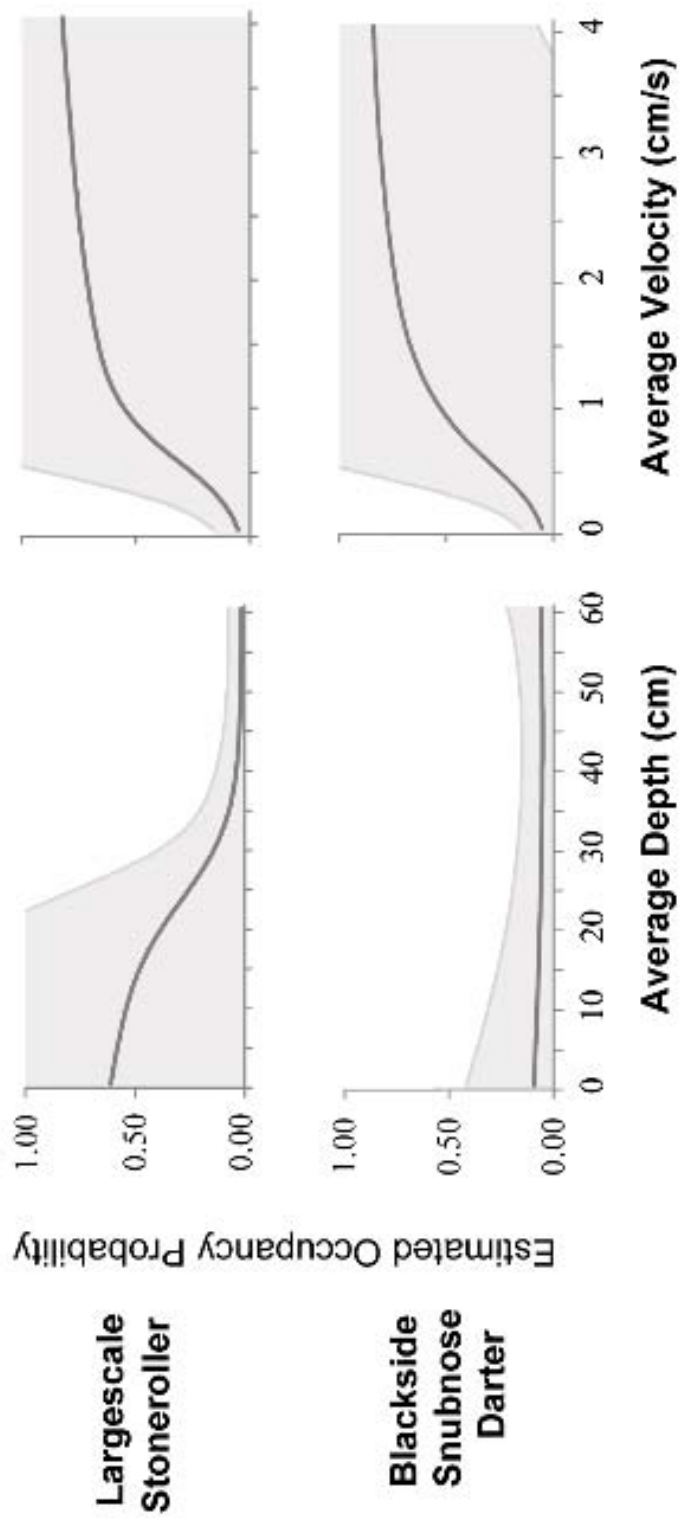
Figure 2-3. Estimated model-averaged occupancy probabilities for two lotic fish species detected in Wheeler National Wildlife Refuge, Alabama. Values are shown across a gradient of depth (cm) and velocity (cm/s). Estimates are given under average conditions for all other modeled covariates. The shaded area represents the 95% confidence interval.

Chapter 3. Using extinction-colonization models to assess impacts of a large hydropower dam on fish species occupancy dynamics in the Tallapoosa River, Alabama

Abstract. – Effective management aimed at reversing or mitigating the negative impacts of an altered flow regime is generally hindered by high faunal diversity and a lack of knowledge of specific flow requirements. Adaptive management provides a potential solution to this challenge by explicitly incorporating uncertainty into an iterative decision process where decisions are continually improved as new data are collected. In 2005, a change in flow management at a large hydropower dam was initiated as part of an adaptive management strategy on the Tallapoosa River in east-central Alabama. We examined patterns of species occupancy for a suite of fish species to evaluate potential response to the change in flow regime and to inform recommendations for the next iteration of adaptive management. Using a multiple model comparison approach, we compared models that described fish species occupancy, colonization, and local extinction rates as a function of measured downstream distance from the dam, ranked and identified those models that best described the collected data, and incorporated model uncertainty into parameter estimates using model-averaging. Downstream distance was included in the best model for nine of 13 captured fish species. The four species with models that demonstrated little to no support for dam effects were blacktail shiner *Cyprinella venusta*, speckled darter *Etheostoma stigmaeum*, Tallapoosa darter *E. tallapoosae*, and bronze darter *Percina palmaris*. Model results for three species – Alabama shiner *Cyprinella callistia*, Tallapoosa shiner *C. gibbsi*, and lipstick darter *Etheostoma chuckwachatte* – indicated a potential positive response to the change in flow management, whereas up to five species demonstrated

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potential negative responses. These five species were largescale stoneroller *Campostoma oligolepis*, Alabama hogsucker *Hypentelium etowanum*, speckled madtom *Noturus leptacanthus*, redbreast sunfish *Lepomis auritus*, and muscadine darter *Percina smithvanizi*. Based on these results, life history traits of the evaluated species, and current research in the field of regulated river ecology, we hypothesize that an altered thermal regime may be inhibiting occupancy of several fish species, and recommend that the next iteration of adaptive management focus on management alternatives that aim to restore more natural thermal patterns in the Tallapoosa River below Harris Dam.

Introduction

The southeastern United States harbors one of the most diverse assemblages of aquatic species in the world (Lydeard and Mayden 1995). This diversity is attributed in part to the diverse physiography, topography, and geology that defines the Southeast landscape, as well as by millions of years without the glaciation that influenced much of the northern portion of the continent (Lydeard and Mayden 1995; Boschung and Mayden 2004). This wealth of habitat and time has provided conditions for extensive speciation, resulting in the high diversity and endemism of the region. Because the Southeast escaped the carving and scraping of Pleistocene glaciers, it is also a landscape dominated by rivers and streams. This extensive network of flowing water that provided for the Southeast's high aquatic diversity also made hydropower a logical source of energy for the growing South in the early part of the 20th century. Since the 1920s, hydropower has become a dominant feature of the riverine landscape of the Southeast. The impact of hydroelectric dams on the river ecosystem has been profound, and the negative ecological consequences of altered flow regimes have been well-documented (Stanford et al.

1996; Poff et al. 1997; Bunn and Arthington 2002; Poff and Zimmerman 2010). Perhaps one of the most dramatic examples of the impacts of river impoundment has been the Coosa River, Alabama, where impoundment of the river by seven hydroelectric dams resulted in the extirpation of 34 species of gastropods, including at least three endemic genera (Neves et al. 1997; Johnson et al. 2013).

The neighboring river to the east, the Tallapoosa River, has been impounded by four dams along its length – Martin (1926), Yates (1928), Thurlow (1930), and Harris (1983) dams. Species have also been lost from the Tallapoosa system, as the dams along the Alabama and Tallapoosa Rivers have prevented migratory fish – Alabama shad, Alabama sturgeon, and possibly Gulf sturgeon – from ascending the river to spawn (Freeman et al. 2005). However, the rates of extirpation in the Tallapoosa River have been less severe compared to the Coosa River system. Between Harris Dam, the furthest dam upstream on the Tallapoosa, and the headwaters of the next impoundment downstream, Martin Dam, flows 78 km of unimpounded river, one the longest unimpounded sections of Piedmont river in the Southeast (Irwin and Freeman 2002). The greatest observed impact of altered flows in the Piedmont reach of the Tallapoosa has been declines in abundances and diversity of fish species downstream from Harris Dam (Pierson et al. 1986, Travnichek and Maceina 1994, Freeman et al. 2001). Among all aquatic biota in the Piedmont section of the Tallapoosa River system, only one is federally-listed, the mussel species finelined pocketbook *Hamiota altilis*; because this species generally favors sand and gravel substrata (Williams et al. 2008), it may not have occurred historically in much of the mainstem Tallapoosa River, which primarily flows over exposed bedrock.

Effective management aimed at reversing or mitigating the negative impacts of an altered flow regime is generally hindered by high faunal diversity and a lack of knowledge of specific

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flow requirements for native fauna (Bowen et al. 1998). Managers are often forced to make

decisions based on inadequate information available for only a few species. In many cases the

ineffectiveness of weakly-supported management decisions is compounded by a rigid policy

structure with no option to reconfigure management actions once they are deemed ineffective.

The framework of adaptive management provides a potential solution to such management

challenges by explicitly incorporating system uncertainty into an iterative decision process,

where decisions are continually improved as new data are collected (Holling 1978; Walters

1986; Lee 1993; Williams et al. 2009; Allen et al. 2011). In 2005, a change in management was

initiated as part of an adaptive management strategy on the Tallapoosa River below Harris Dam,

and a monitoring program was established to evaluate the response of fish species to the change

in flow regime downstream from the dam (Irwin and Freeman 2002; Kennedy et al. 2006; Irwin

and Kennedy 2008; Williams and Brown 2012; Williams and Brown 2014). Because of the long

stretch of free-flowing river, the lack of federally listed species, and the persistence of native

species within the Tallapoosa River below Harris Dam, this river reach provides an ideal

laboratory for managing adaptively with experimental flows.

A monitoring program to support adaptive management must be based on clear

management objectives and on some explicit hypotheses of the main drivers of system state

and/or proposed management actions (Yoccoz et al. 2001; Nichols and Williams 2006;

Lindenmayer and Likens 2009). In a regulated river, the main drivers of system state are

associated with the flow regime (Poff et al. 1997; Bunn and Arthington 2002), and management

actions in the Piedmont portion of the Tallapoosa River will inevitably involve manipulating

flows from Harris Dam (Irwin and Freeman 2002; Kennedy et al. 2006). However, additional

management strategies may need to be employed to address other important aspects of river

ecosystem function such as temperature, sediment, and nutrient regimes (Palmer and Bernhardt 2006; Beechie et al. 2010; Olden and Naiman 2010; Wohl et al. 2015). Management objectives in the system are many and vary among stakeholders (Irwin and Freeman 2002; Kennedy et al. 2006). In terms of the river biota, managers are especially concerned with conserving native fish assemblages, both sport and non-game fishes (Irwin and Freeman 2002; Kennedy et al. 2006).

Biomonitoring in fisheries management has often utilized such measures as diversity (e.g., Kushlan 1976; Pearsons et al. 1992; Cianfrani et al. 2009), richness (e.g., Bowen and Freeman 1998; Patton et al. 2000; Meador et al. 2005), or a composite metric such as the index of biotic integrity (IBI; e.g., Karr 1981; Roth et al. 1998; Rowe et al. 2009). However, in the diverse systems of the Southeast in which species have experienced millions of years of evolutionary specialization, these additive measures may not provide the information necessary for building effective hypotheses to inform specific management decisions. Other possible approaches are to classify species into guilds based on resource use (Leonard and Orth 1988; Austen et al. 1994; Aarts and Nienhuis 2003), to evaluate systems by species traits (Dolédec et al. 1999; Goldstein and Meador 2004, 2005), or to manage for key habitats (Bain 1995; Freeman et al. 1997; Bowen et al. 1998). Whereas these approaches may be more effective than whole-assemblage additive metrics, there still may be species that are mis- or under-managed because of assumed generalizations in resource or habitat use. Ideally, effective whole-assemblage management will be supported by knowledge of optimal flows required for the persistence of each species that is targeted for management.

In support of the adaptive management strategy on the Tallapoosa River, the purpose of this study was to examine patterns of species occupancy for a suite of fish species in the Piedmont reach of the Tallapoosa River to determine potential effects of flow regulation,

evaluate the response of species to the change in management, and identify hypotheses of response that may be evaluated in the next adaptive management iteration. Specifically, we aimed to 1) calculate species occupancy, colonization, and local extinction estimates for a suite of fish species in the Tallapoosa River; 2) compare models that relate these parameters to spatial differences in the flow regime; 3) determine which species have occupancy patterns that are potentially impacted by the dam; and 4) make recommendations for the next iteration of adaptive management of the Tallapoosa River below R.L. Harris Dam.

Methods

Study Site. – R.L. Harris Dam is a 150-foot, 135-megawatt dual-turbine hydropower peaking facility located on the Tallapoosa River in Alabama (Figure 3-1). Construction of Harris Dam was completed in 1982; it is owned and operated by Alabama Power, a subsidiary of Southern Company. Prior to 2005, Harris Dam operated strictly as a peaking hydropower generation facility, such that one or both turbines operated at capacity (226 m^3/second each) for approximately 4 to 6 hours, once or twice per day, five days per week (Freeman et al. 2001; Irwin and Freeman 2002). The operating license for the facility (FERC Project No. P-2628) requires a minimum flow that is equivalent to the pre-dam historic low flow measured 22 km downstream, which is 1.27 m^3/second. In 2003, as part of the first iteration of adaptive management, stakeholders from the Tallapoosa River basin participated in a structured decision making process to identify solutions for improving management of the river below Harris Dam (Kennedy et al. 2006; Irwin and Kennedy 2008). In 2005, based on the results of the stakeholder-based decision process, Alabama Power agreed to implement a change in management that provided additional flows during periods of non-generation as well as extended

periods of reduced generation in spring and summer to support spawning, conditional on water

availability and power generation needs (Kennedy et al. 2006).

To evaluate the changes in operation at Harris Dam, fish collections have been conducted

at 22 sites throughout the Piedmont region of the basin since 2005. Twelve of these sites are

located in the regulated river below Harris Dam, with five between Harris Dam and Malone,

Alabama; five between Malone and Wadley, Alabama; and two near Horseshoe Bend (Figure 3-

1). Ten additional sites are located in the unregulated Tallapoosa basin, with five in the

mainstem upstream from Harris Dam near Heflin, Alabama, and five in Hillabee Creek, a large

unregulated tributary of the Tallapoosa River (Figure 3-1). Each of the 22 sites is located on a

high-gradient shoal that was selected in a stratified random fashion from all known shoals sites

in the sampled reaches. High-gradient shoal habitats are features of large and medium-sized

rivers which are generally known to support high diversity and abundances of fish species on

account of the diversity of habitat types within the shoal as well as the high rates of productivity

due to the prevalence of shallow water habitats and stable substrates (Nelson and Scott 1962;

Grubaugh and Wallace 1995; Irwin and Freeman 2002).

Field Methods. – Fish were collected at each shoal site using prepositioned area

electrofishers (PAEs; Bain et al. 1985; Fisher and Brown 1993; Freeman et al. 2001) following

methods described by Freeman et al. (2001). From 2005-2007, 20 spatially-replicated PAE

samples were taken at each site in both summer and fall, with weather and flows permitting;

from 2008-2010, sample sizes were reduced to 10 samples at each site. All collected fish were

identified to species. For each PAE sample, habitat variables were measured including depth

(cm), velocity (cm/s), percent areal vegetation cover, presence of large cover, and substratum

type. For additional details on field methods, see Methods for Chapter 2 and Appendix 1.

Data Analysis. – To estimate fish species occupancy, colonization, and local extinction rates, we used the modeling framework described in MacKenzie et al. (2003; 2006). All analyses were conducted using R (R 3.1.2; R Foundation for Statistical Computing, Vienna) statistical software and the R package "unmarked" (Fiske and Chandler 2011). Because fish species often go undetected even when present, we used the spatially-replicated PAE samples at each site to estimate species detection probability, which in this case is the probability that a fish species is detected in a PAE sample given that it is present at the site (MacKenzie et al. 2002; 2003; 2006). As initially proposed by MacKenzie et al. (2002; 2003), sample replicates for estimating detection probability are to be gathered by repeated visits to a site over a relatively short period of time; however, MacKenzie et al. (2006) extended this conceptual framework to include randomly sampled spatial replicates. However, parameter estimation using spatial replicates rather than temporal replicates may require a different interpretation of detection probability. Here, we considered each PAE sample an independent spatial replicate for calculating the probability of capturing a fish species in a sample, where the inference for occupancy is at the site (shoal) scale, and each independent PAE (9 m^2) sample is considered representative of the whole site. Therefore, "detection" represents the probability of encountering a species in a single spatial sample of the site (that is, a single PAE), given that the species is present at the site.

Detection histories were developed for each fish species at a total of 22 shoal sites throughout the Tallapoosa River; a detection was a positively identified occurrence of a species in a sample. We used maximum-likelihood methods and modeled parameters as functions of measured covariates by means of the logit-link function as described by MacKenzie et al. (2002; 2003; 2006). Parameter estimation was limited to those species that had high detection (i.e.,

were detected in at least 40 replicates across all 6 years, which was the 75th percentile of total encounters) for at least one of the 22 sites.

For unbiased parameter estimates, extinction-colonization models assume that 1) sampled sites are closed to changes in occupancy within a single sampling period; 2) there is no unmodeled heterogeneity of occupancy, colonization, extinction, or detection; 3) sites and samples are respectively independent of each other; and 4) species are not falsely detected (MacKenzie et al. 2006). With spatial replicates, we also assume that after accounting for detection heterogeneity due to differences in depth and velocity among sample replicates, fish species distribution was random across each shoal and probability of detection of each species was constant across replicates. See Chapter 2 for an additional discussion on special considerations for spatially-replicated estimation of detection probability.

Covariates of detection were limited to measured PAE depth and velocity, as PAE and user efficiency are both strongly influenced by depth (Bain et al. 1985; Larimore and Garrels 1985; Portt et al. 2006), and user efficiency is likely to decrease with increases in velocity. Furthermore, most fish species have differential affinities to various depths and velocities (Boschung and Mayden 2004). Covariates of the remaining parameters were limited to measured downstream distance from the dam to evaluate the hypothesis that patterns in occupancy, colonization, and local extinction rates were a function of operations at Harris Dam. Effects of operations on river flows are generally diminished along a downstream longitudinal gradient due to the addition of unregulated tributary and other intervening flows to the mainstem river channel (Ward and Stanford 1983; Ward and Stanford 1995; Stanford and Ward 2001). Therefore, any corresponding impacts of dam operations on patterns of species occupancy, colonization, or local extinction should also follow a similar longitudinal gradient. The closest

site to the dam was approximately 2 river km downstream; the furthest was 70 river km. "Distance" of all unregulated sites was given an arbitrarily high value of 160 river km. We examined four models of detection (p) and two models each of occupancy (ψ), colonization (γ), and extinction (ε), for a total of 32 models in each set per evaluated species (Table 3-1).

Following methods described in Burnham and Anderson (2010), competing models for each species were compared by means of Akaike's information criterion (AIC; Akaike 1973). Models in each set were then further evaluated with multimodel inference (Burnham and Anderson 2010). Multimodel inference uses Akaike weights to calculate additive weights of modeled covariates and model-averaged parameter estimates. We calculated additive weights, model-averaged parameter estimates, and unconditional standard errors of parameter estimates following methods reported in Burnham and Anderson (2010). The additive weight of a modeled covariate represents its relative importance, and may be interpreted as the probability that the covariate is included in the best model of the model set. We used additive weights to compare the relative importance of depth and velocity as predictors of detection, and of distance as a predictor of occupancy, colonization, and local extinction over the null model. Model-averaged parameter estimates incorporate the strength of evidence of each model, and therefore any uncertainty among models, into parameter estimates. Only ranked models with AIC model weights that added to a cumulative weight of 1.00000 were used for calculating model-averaged estimates (that is, models with negligible weights were not included). For each species, model-averaged occupancy in 2005, colonization, and local extinction were estimated for each site. Estimates of site occupancy for each year following 2005 (i.e., 2006-2010) were derived from the averaged models using the equation:

$$\psi_{t+1} = \psi_t (1 - \varepsilon) + (1 - \psi_t)\, \gamma,$$

where ψ_t is occupancy at time t, with the model-averaged estimate of occupancy used for the

initial value, ψ_{t+1} is occupancy at time $t+1$, ε is the model-averaged estimate of local extinction,

and γ is the model-averaged estimate of colonization.

<div align="center">Results</div>

Fifty species of fish from nine families were captured among the 22 sites sampled in the

Piedmont region of the Tallapoosa River basin between 2005 and 2010 (Table 3-2). The

taxonomic family with the most detections (that is, recorded presence of individual species; see

Methods) across all samples was Percidae (perches; 5790 total detections), followed by

Cyprinidae (minnows), Centrarchidae (sunfishes), Catostomidae (suckers), and Ictaluridae

(catfishes). The species that was detected on the most occasions was bronze darter (*Percina*

palmaris; 1947 total detections), followed by Alabama shiner (*Cyprinella callistia*), lipstick

darter (*Etheostoma chuckwachatte*), muscadine darter (*Percina smithvanizi*), and speckled darter

(*Etheostoma stigmaeum*). Of the 50 fish species captured, 13 had high detection (i.e., were

detected in a minimum of 40 replicates across all years) in at least one of the 22 sampled sites;

these species were the focus of further analyses.

Depth was included in the best model of detection for ten of the 13 species (Table 3-3),

with nine of the ten (all but blacktail shiner, *Cyprinella venusta*) having very strong support (w_+

> 0.95) for depth as a predictor of detection (Table 3-4). Blacktail shiner was a species with

relatively high uncertainty among models, including models of detection (Table 3-3; Appendix

5). Velocity was included in the best model of all but one species, Tallapoosa shiner (*Cyprinella*

gibbsi; Table 3-3). Of those species with velocity in the best model, all but speckled darter had

very strong ($w_+ > 0.95$) support for velocity as a predictor of detection. Speckled darter still had

relatively strong (w_+ = 0.878) support for velocity as a predictor (Table 3-4), but this species also had relatively high uncertainty among models (Table 3-3; Appendix 5).

As a predictor of occupancy, distance from the dam was included in the best model for eight species (Table 3-3). Of these eight species, Tallapoosa shiner and redbreast sunfish (*Lepomis auritus*) had the strongest support among models for distance as a predictor of occupancy (w_+ = 1.000 and 0.992, respectively; Table 3-4). Speckled madtom (*Noturus leptacanthus*), lipstick darter, and muscadine darter also had relatively strong, though less support (w_+ > 0.85) for distance as a predictor of occupancy (Table 3-4). Strength of support for distance as a predictor of occupancy among models for the remaining three of the eight species – largescale stoneroller (*Campostoma oligolepis*), Alabama shiner, and Alabama hogsucker (*Hypentelium etowanum*) – was more moderate (w_+ = 0.670-0.769; Table 3-4). Distance was predicted to have a positive effect on occupancy for six of the eight species, such that occupancy increased with increasing distance from Harris Dam. For two species – redbreast sunfish and muscadine darter – models predicted that distance had a negative effect on occupancy, such that sites closer to Harris Dam had higher rates of occupancy than unregulated sites and those further from the dam (Table 3-5).

As a predictor of colonization and local extinction, distance was included in the best model for 4 species in each case (Table 3-3). Distance was included as a predictor of colonization in the best model for Alabama shiner, bullhead minnow *Pimephales vigilax*, Alabama hogsucker, and muscadine darter (Table 3-3). Alabama hogsucker had strong support (w_+ = 0.905) for distance as a predictor of species colonization; the other three species had very strong (w_+ > 0.95) support for this covariate (Table 3-4). For all four species, distance was predicted to have a positive effect on colonization, such that rates of colonization increased with

increasing distance from the dam (Table 3-6). Distance was included as a predictor of local

extinction in the best model for largescale stoneroller, Alabama hogsucker, speckled madtom,

and redbreast sunfish (Table 3-3). Similar to the colonization parameter, Alabama hogsucker

had relatively strong support ($w_+ = 0.893$) for distance as a predictor of local species extinction,

whereas the other three species had very strong support ($w_+ > 0.95$) for this covariate (Table 3-4).

For all four species, distance was predicted to have a negative effect on local extinction, with

extinction rates decreasing with increasing distance from the dam (Table 3-7).

Based on a comparison of competing models using AIC, there was considerable model

uncertainty for many of the species evaluated (Table 3-3; Appendix 5). For some species –

specifically blacktail shiner, speckled darter, and bronze darter – this uncertainty was coupled

with model-averaged parameter estimates that demonstrated little to no effect of dam operations

on occupancy patterns (Figures 3-2, 3-3, and 3-4, respectively). Tallapoosa darter also had

relatively high uncertainty among models (Table 3-3; Appendix 5) and low support for distance

as a covariate of modeled parameters (Table 3-4), though model-averaged estimates

demonstrated a slight increase in initial occupancy with increasing distance from Harris Dam

(Table 3-5). Unregulated sites and sites 60-70 km downstream had estimated rates of Tallapoosa

darter occupancy near 0.80 across the sampling period, with occupancy for all other sites

reaching near 0.80 by 2007 and remaining at that rate for the duration of the sampling period

(Figure 3-5).

Strong support for distance as a covariate of occupancy, colonization, or local extinction

among nine of the evaluated species (Table 3-4) resulted in distinct patterns of estimated species

occupancy over the sampling period. Among these species, only bullhead minnow had

occupancy rates estimated as relatively constant in the regulated reaches of the river, with

occupancy at all but the unregulated sites estimated near zero for the entire sampling period (Figure 3-6). For the unregulated sites, bullhead minnow occupancy was estimated to increase sharply from 2005 to 2006, with estimates consistently near 0.80 for the duration of the sampling period (Figure 3-6). Unconditional standard errors around estimates of local extinction were particularly high for this species (Table 3-7) due to the low initial occupancy estimates at most sites (Table 3-5; that is, rates of local extinction are difficult to estimate when a species is already absent).

Four species – largescale stoneroller, Alabama hogsucker, redbreast sunfish, and muscadine darter – had modeled occupancy rates that were estimated to decline in the regulated reaches of the Tallapoosa River during the sampling period. However, both redbreast sunfish and muscadine darter had initial estimates of occupancy that were negatively associated with distance from Harris Dam; that is, initial occupancy rates for these species were estimated to be higher at sites closer to the dam. An estimated colonization rate for redbreast sunfish of 0.67 across sites (Table 3-6) and greater extinction estimates at sites closer to Harris Dam (Table 3-7) resulted in a complex pattern of occupancy for this species, with increasing rates at the furthest-downstream and unregulated sites and a short period of decline (2005-2006) at the sites 12 km and closer to the dam, with stable estimates of occupancy from 2006 through 2010 (Figure 3-7).

For muscadine darter, colonization rates were positively associated with distance from Harris Dam, though unconditional standard errors were relatively high for estimates at sites 20 km and nearer (Table 3-6). With local extinction rates that were constant across all sites, a pattern of occupancy resulted wherein occupancy at sites closest to the dam (2-12 km) was estimated to decrease across the sampling period, and unregulated sites and those furthest from the dam (60-70 km) had a sharp increase in occupancy from 2005 to 2006, a slight decrease from

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2006 to 2007, and rates that stabilized near 0.85 for the duration of the sampling period (Figure 3-8).

Largescale stoneroller and Alabama hogsucker were the only species for which occupancy rates were estimated to both decrease with increasing distance from the dam, and decrease over time in the regulated reach. Model-averaged occupancy for largescale stoneroller was estimated to decline at all but the unregulated sites, with the greatest decreases occurring at sites 8-20 km downstream from Harris Dam (Figure 3-9). Unconditional standard errors were relatively high for occupancy estimates of this species at the 2 km site (Table 3-5), as well as for colonization estimates at the unregulated sites and sites 60-70 km downstream of the dam (Table 3-6).

Alabama hogsucker occupancy was characterized by consistently high rates of occupancy for unregulated sites and sites 60-70 km downstream and declines in occupancy at sites 20 km and closer to the dam (Figure 3-10). At the 16 km and 20 km sites, a decrease in occupancy was estimated for 2005 to 2006, but estimates remained consistent (near 0.80) for the duration of the sampling period (Figure 3-10). At the remaining sites, particularly sites 2-10 km from Harris Dam, occupancy was estimated to decrease during the sampling period, to less than 0.10 at the 2 km site (Figure 3-10). However, unconditional standard errors around estimates of occupancy and local extinction were also relatively high for this species at sites closest to Harris Dam (Tables 3-5 and 3-6, respectively).

The remaining four species – Alabama shiner, Tallapoosa shiner, speckled madtom, and lipstick darter – each had estimated patterns of occupancy characterized by a positive response to dam operations over the course of the sampling period. For both Alabama shiner and lipstick darter, occupancy was estimated to be consistently high during the sampling period at the

unregulated sites and sites furthest from Harris Dam. Specifically, Alabama shiner occupancy was characterized by consistently high rates of occupancy at the unregulated sites and sites 16 km and further, and increasing occupancy among sites 12 km and nearer, with all but the 2 km site reaching occupancy rates consistent with those throughout the rest of the basin by 2006 (Figure 3-11). At the 2 km site, estimated occupancy also increased substantially over the sampling period (Figure 3-11), but the unconditional standard error around the initial occupancy estimate for this site was relatively high (Table 3-5).

Lipstick darter had a similar pattern of estimated occupancy, with high model-averaged occupancy estimates for all sites except the 2 km site, which also had a relatively high unconditional standard error (Table 3-5). Colonization rates were estimated to be consistently high across the basin (Table 3-6), and local extinction rates were estimated to be consistently low (Table 3-7), resulting in a pattern of occupancy with estimates near 1.00 across the entire sampling period for all but the 2 km site (Figure 3-12). The 2 km site was estimated to have a sharp increase in occupancy from 2005 to 2006, with estimates increasing from near 0.20 to near 1.00 (Figure 3-12).

Occupancy patterns of Tallapoosa shiner and speckled madtom were also characterized by a positive response to dam operations; however, in contrast to the occupancy patterns of Alabama shiner and lipstick darter, occupancy of these species was estimated to decline in the unregulated reaches of the river and at sites furthest from the dam, as occupancy increased at sites closer to the dam. For Tallapoosa shiner, the model set for this species was unique among those evaluated, as it had a single model that outranked all others ($w = 1.000$; Table 3-3); this model described occupancy as a function of distance from Harris Dam with all other parameters constant. Estimated occupancy for Tallapoosa shiner was 0.00 (se = 0.00) at the site closest to

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the dam, increased sharply at 10 km, and reached values near and at 1.00 at sites 12-70 km

downstream of the dam (Table 3-5; Figure 3-13). Colonization and local extinction rates that

were estimated as constant across all sites (Tables 3-6 and 3-7, respectively) resulted in a pattern

of decreasing occupancy in the unregulated and furthest-downstream sites, and increasing

occupancy at sites 10 km and closer to Harris Dam (Figure 3-13).

Speckled madtom had high local extinction estimates for all but the unregulated sites

(Table 3-7), initial occupancy estimates that were low for all but the unregulated and furthest-

downstream (60-70 km) sites, and colonization rates that increased only slightly with increasing

distance from the dam (Table 3-5). These estimates resulted in a dynamic pattern of occupancy,

with occupancy at sites 2-12 km increasing from near 0.00 to near 0.20 between 2005 and 2006

and remaining near 0.20 for the duration of the sampling period, and with sites 60-70 km

experiencing a large decrease in occupancy, from near 0.90 to near 0.00 between 2005 and 2006.

These sites saw an increase in occupancy between 2006 and 2007, and another slight decrease

from 2007 to 2008, with estimates stabilizing near 0.20 for the duration of the sampling period.

The unregulated sites also had an estimated decrease in occupancy during the sampling period,

though not as severe, with rates decreasing from near 0.90 in 2005 to near 0.70 in 2010 (Figure

3-14).

Discussion

Calculated estimates of fish species occupancy at locations throughout the Piedmont

region of the Tallapoosa River were indicative of a downstream gradient of impact below R.L.

Harris Dam, consistent with the serial discontinuity concept of regulated rivers (Ward and

Stanford 1983; Ward and Stanford 1995; Stanford and Ward 2001) and with what has been

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observed for various taxa downstream of hydropower peaking facilities elsewhere (e.g., Bain et al. 1988; Voelz and Ward 1991; Kinsolving and Bain 1993; Vaughn and Taylor 1999; Bond and Jones 2013). Presence-absence data for most of the examined species (eight of 13), representing five taxonomic families, supported the hypotheses that species occupancy probabilities change with increasing distance from the dam. With the exception of blacktail shiner, which is one of the most widespread and ubiquitous minnows in Alabama (Boschung and Mayden 2004), those species that did not exhibit a strong pattern of occupancy related to longitudinal distance were darters – speckled darter, Tallapoosa darter, and bronze darter – all benthic fluvial specialists (Boschung and Mayden 2004).

Previous studies in the Tallapoosa River, both in the Piedmont reach below Harris Dam and in the Coastal Plain below Thurlow Dam, have also documented a downstream longitudinal gradient of impact (Kinsolving and Bain 1993; Travnichek and Maceina 1994). In both cases, the researchers attributed the change primarily to a loss of fluvial specialists near each dam, with generalist species showing little to no response to flow regulation throughout the regulated reaches. Although we found that several species had estimated occupancy trends that support this hypothesis, the trends of the darter species in the Tallapoosa River below Harris Dam suggest otherwise. Bowen et al. (1998) and Freeman et al. (2001) also documented resilience of darter species to flow regulation in the Piedmont Tallapoosa River. Freeman et al. (2001) looked specifically at juvenile abundance, and suggested that a prolonged reproductive season that extended at least into mid-summer was the trait most clearly associated with high abundance. Because inflows to Harris Reservoir are typically lower during the summer months, extended periods of non-generation are more likely; therefore, an extended reproductive season would allow species more opportunity to take advantage of these periods of stable flows without

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peaking operations. Freeman et al. (2001) also suggested that species with spring spawning seasons could potentially experience a shift in reproductive timing caused by altered thermal regimes in the regulated river. This may be the case for speckled darter and Tallapoosa darter, which are reportedly spring spawners (Freeman et al. 2001; Boschung and Mayden 2004), but continue to persist in the highly-regulated reaches of the Tallapoosa River.

An alternative or additional hypothesis to explain the occupancy patterns of darters in the regulated Tallapoosa River is that the high gradient shoals that characterize the river below Harris Dam provide the necessary shallow habitat and stable substrata that allow benthic fluvial specialists to persist under even the most flow-altered conditions. These Piedmont shoals are complex river features that include extensive shallow habitats, bedrock ledges, boulders, and other coarse substrata. The shallow habitats on these shoals may provide adequate darter habitat during non-generation events, while the bedrock ledges and larger coarse substrata may provide flow refuges that protect benthic species from the shear of high flow generation events and also provide stable habitat substrate that remains relatively unchanged between generation events.

Prior to 2005, peaking operations at Harris Dam usually entailed 4- to 6-hour flow releases once or twice per day, five days per week, followed by long periods of non-generation on weekends (Freeman et al. 2001; Irwin and Freeman 2002). Because the minimum flow requirement was to meet the historic low flow at a streamflow gauge 22 km downstream (Freeman et al. 2001; Irwin and Freeman 2002), and because intervening flows and surface water usually amounted to more than this minimum flow, periods of non-generation were generally associated with a lack of flow from the dam. Based on evidence from previous studies (Pierson et al. 1986; Travnichek and Maceina 1994; Bowen et al. 1998; Costley 1998; Nash 1999; Freeman et al. 2001), Irwin and Freeman (2002) hypothesized that these extended periods of low

flows limited habitat suitability for many riverine species, resulting in changes to the faunal assemblage. As distance downstream increased, channel storage and intervening flows from tributaries, groundwater, and surface water increasingly maintained habitat suitability, allowing species that were unable to occupy the more altered locations upstream to persist. When hydropower operations were adjusted to provide additional flows in the river downstream of Harris Dam in 2005, this change in operation provided more persistent base flows in the regulated river, especially at the shoal areas in closest proximity to the dam that had limited augmentation from intervening flows. Following the hypothesis of Irwin and Freeman (2002), it is likely that this change contributed to the estimated increase in occupancy that was documented for several species in the regulated Tallapoosa River. That is, as baseflows increased downstream from Harris Dam, there was an increase in the persistence of higher-velocity habitats between power generation events, supporting an increase in occupancy for species with affinities for these habitats.

For example, similar to the speckled, Tallapoosa, and bronze darters, the lipstick darter is a benthic fluvial percid that has persisted in most of the regulated Tallapoosa River. However, unlike the other darters, at the start of the sampling period, lipstick darter had a much lower estimated occupancy (albeit with a relatively high error) at the site closest to the dam. In 2006 and years following, estimated occupancy for this species increased to near 1, consistent with estimates at sites throughout the rest of the Tallapoosa Piedmont. The habitat preference for lipstick darter is shallow, fast habitat with coarse substrates (Wood and Mayden 1993; Freeman et al. 1997; Boschung and Mayden 2004); relative to other darter species, it may also have a lower tolerance for the slower, deeper habitats that would have been available between generation events prior to 2005 (Freeman et al. 1997). Thus, it is feasible that occupancy of this

species increased when preferred habitat conditions were more consistently provided with augmentation of baseflows in 2005. Similarly, Alabama shiner occupancy was estimated to increase in the regulated Tallapoosa River during the sampling period. Adults of this mid-column species typically prefer deep, swift flowing habitats (Freeman et al. 1997; Boschung and Mayden 2004), conditions that also would not have been persistent at the shoals closest to Harris Dam prior to 2005. When flows were provided more consistently below the dam, the increase in availability of persistent deep, fast habitat likely allowed for an increase in occupancy of Alabama shiner as well. Both Alabama shiner and lipstick darter are endemic species – Alabama shiner to the Mobile River basin and lipstick darter to the Piedmont Tallapoosa River (Boshung and Mayden 2004). However, lipstick darter is the only fish species in the study reach that is protected under Alabama's nongame species regulations. Adequate provision of persistent swift-flowing shallow water habitat with stable coarse substrate will likely remain critical for the long-term success of this protected species.

One species that might have been expected to thrive under the new flow management regime was largescale stoneroller, a species that has demonstrated affinities for fast-flowing water (Freeman et al. 2001; Boshung and Mayden 2004). Freeman et al. (2001) hypothesized that reduced fast-habitat availability and persistence in the regulated Tallapoosa River was a key limiting factor in the reproductive success of this species; thus, an increase in shallow- and deep-fast habitats could be expected to result in an increase in occupancy. However, both this species and Alabama hogsucker had occupancy probabilities that were estimated to decline in the regulated Tallapoosa River while remaining relatively constant in the unregulated reaches over the course of the study. Both largescale stoneroller and Alabama hogsucker are spring spawners (Freeman et al. 2001; Boshung and Mayden 2004), a trait which Freeman et al. (2001)

hypothesized was linked to low abundance in the regulated river due to the lack of persistent habitat during the spring months. High flows associated with hydropower peaking operations may influence reproductive success and recruitment of many fish species by reducing the duration of stable flows during critical spawning periods (Irwin and Freeman 2002). However, peaking operations were not substantially altered as a part of the 2005 change in flow operations at Harris Dam. The only changes in operation were an increase in baseflows and the conditional provision of extended periods of reduced generation in spring and summer to support spawning (Kennedy et al. 2006); yet, these species declined nonetheless.

A potential confounding impact of augmented baseflows in the regulated Tallapoosa is that the temperature of the hypolimnetic water released from Harris Dam results in a substantial decrease in water temperatures (as much as 10°C) in the river downstream from the dam (Irwin et al. 1997; Irwin and Freeman 2002; Goar 2013). Prior to 2005, water temperatures in the river would have decreased during generation events, potentially limiting reproduction by a lack of thermal habitat persistence. With the implementation of augmented baseflows, it is possible that water temperatures are depressed to an even greater degree, thereby limiting thermal habitat availability and impacting reproductive success of spring-spawning species. Therefore, the peaking flows themselves may not be the primary limiting factor of reproductive and occupancy rates of these species, but rather the associated decrease in water temperature in the regulated river. Olden and Naiman (2010) purport that under-representation of the thermal regime in flow management assessments may inhibit river restoration efforts below dams; this critical component of the ecosystem must therefore be incorporated into any management effort that aims to improve instream conditions for riverine fauna.

Two other species that had estimated declines in occupancy during the sampling period were redbreast sunfish and muscadine darter. However, these species were quite different in their predicted response than either largescale stoneroller or Alabama hogsucker. Occupancy probabilities for these species were estimated to be greater near the dam in 2005, and to decrease with increasing distance downstream. For redbreast sunfish, this is consistent with the hypothesis that the extreme conditions that result from flow alteration allows for proliferation of generalist species (Kinsolving and Bain 1993; Poff and Allan 1995; Scheidegger and Bain 1995; Travnichek et al. 1995). However, this hypothesis does not explain the decline in occupancy of redbreast sunfish during the sampling period, nor does it explain the occupancy pattern of muscadine darter, a benthic fluvial percid. Muscadine darter juveniles in particular favor shallow, slow water habitats, perhaps more so than other darters in the Tallapoosa River Piedmont (Freeman et al. 1997). Redbreast sunfish also require periods of relatively shallow, stable flows for successful spawning (Irwin et al. 1997; Andress 2002; Martin 2008; Goar 2013). The increase in flows in the regulated Tallapoosa River could have reduced the available shallow, slower water habitats required by these species. Alternately or additionally, the corresponding decrease in temperature could have limited reproductive success; redbreast sunfish in particular are highly dependent on adequate temperatures for spawning, hatching success, and larval development (Davis 1971; Irwin et al. 1997; Andress 2002; Goar 2013). Together, changes in flow and therefore changes in available and persistent physical and thermal habitat could have contributed to decreases in occupancy for muscadine darter and redbreast sunfish in the regulated Tallapoosa River.

To explain the concurrent increase in occupancy probabilities in the unregulated river for these species, we can look to the natural hydrological conditions during the study period. Of

particular note is the substantial drought of 2007 and 2008 that impacted the Tallapoosa River as well as much of the Southeast U.S. (data from multiple USGS stream gages; http://waterwatch.usgs.gov/). During the drought there was a considerably higher base flow in the regulated river compared to the unregulated reaches, as Alabama Power was required to provide a certain volume of water to meet flow needs downstream, in particular for navigation and waste effluent dispersal on the Alabama River near Montgomery. However, the tributaries and unregulated upper Tallapoosa River experienced record low flows (and consequently, Harris Reservoir experienced record low water levels). It is possible that while the regulated river may have had less suitable conditions for redbreast sunfish and muscadine darter during this time, the unregulated river had an increase in shallow, slow, stable habitat because of the drought, leading to conditions that allowed for an increase in occupancy for these species. Bullhead minnow also exhibited an increase in occupancy in the unregulated river during the sampling period, possibly also related to the drought conditions, as this species prefers low-gradient, slow-water habitats and has relatively high temperature thresholds for reproductive success (Boshung and Mayden 20014). These temperature requirements may also be responsible for the persistent low occupancy probabilities of this species in the regulated Tallapoosa River.

In contrast, Tallapoosa shiner occupancy was estimated to increase in the regulated river during the study period while decreasing in the unregulated reaches of the river. The shallow, slow habitat prevalent in the unregulated Tallapoosa River during the drought may have negatively impacted populations of this species, whereas baseflow increases in the regulated river may have been beneficial, as this species likely has habitat preferences similar to Alabama shiner and other *Cyprinella* species (Boshung and Mayden 2004); however, these results could suggest an even stronger preference of this species for deep-fast habitats. Interestingly, models

estimated that occupancy probabilities of the Tallapoosa shiner were similar across all sites in the study area by the end of the sampling period in 2010. Another possibility to consider is the potential influence of tributaries on regulated river populations of Tallapoosa shiner and other fish species. The number and quality of tributaries supplementing flows are an important determinant of the extent of hydrological and ecological impact of a regulated river (Bruns et al. 1984; Minshall et al. 1985; Bain and Boltz 1989). Tributaries increase baseflows and attenuate the hydrological impacts of dams, and might also serve as refugia from extreme mainstem conditions, or as a source to supplement or recolonize mainstem populations of fish and invertebrates (Bruns et al. 1984; Bain and Boltz 1989; Kinsolving and Bain 1993). As a result, low flows in tributaries during a drought could result in an increase in occupancy in the mainstem as fish move to find suitable habitat. Additionally, or alternatively, if the tributaries typically serve as refugia or as a source population for some species, low flows and reductions in available tributary habitat could result in a decrease in species occupancy in the mainstem.

Whereas the drought likely had substantial impacts on the population dynamics of multiple species in the Tallapoosa River basin during the sampling period, other hydrological conditions could have had additional influence. Mean flows at several sites within the Tallapoosa River indicated that 2005 and 2009 were wet years, 2006 was average, and in 2010 there was a very wet spring accompanied by a very dry summer (data from USGS stream gages 02412000, 02413300, and 02415000; http://waterwatch.usgs.gov/). Therefore, it is also possible that additional hydrological variability could have influenced species occupancy dynamics during the sampling period. This variability may not be adequately captured with the models evaluated as part of this analysis; future analyses should include a yearly covariate that examines the hypothesis that species occupancy is a function of water year.

For our analyses, we chose to keep models simple to focus on overall patterns of occupancy that would identify general downstream impacts of Harris Dam and indicate potential patterns of species recovery. However, it would be valuable for future analyses to explore additional hypotheses to provide further insight into the occupancy patterns of some species. For example, estimated patterns of occupancy for speckled madtom are currently not easily explained. This species had estimated declines in part of the regulated river, as well as in the unregulated river, and had a dynamic pattern of estimated occupancy due to the strong influence of river regulation on spatial occupancy patterns and high extinction rates in the regulated reach. Speckled madtom generally prefers deeper, swift-flowing habitats (Meffe and Sheldon 1988; Freeman et al.2001; Boshung and Mayden 2004), which may explain the estimated declines in the unregulated river, as deep-fast habitat was limited by the drought. However, this does not explain the complex pattern of occupancy estimated in the regulated river. Some aspects of habitat preference and behavior of speckled madtom could be relevant to explaining these patterns. One important trait that may be influential is a preference by this species for substrata dominated by coarse sand and gravel (Meffe and Sheldon 1988; Boshung and Mayden 2004). In high-gradient Piedmont bedrock shoal habitats, sand and gravel bars are present, but are not a dominant feature. It is possible that they are even less dominant in the high-gradient river reach below Harris Dam than they are in the unregulated reaches of the river, perhaps in part due to reduced sediment inputs and channel scouring below Harris Dam. Furthermore, madtoms are generally nocturnal feeders; therefore, detection probabilities may be a function of the time of day of sampling. Additional models that evaluate the influence of substrata type on occupancy and time of day on detection could improve our understanding of the management needs and implications for this species in the Tallapoosa River Piedmont.

For this study, we focused our analyses on species with the highest detection probabilities throughout the study area. In a system where common species may be detrimentally influenced by management actions associated with hydropower generation, understanding impacts to common species is an important first step to long-term ecologically-sustainable flow management. However, it is likely that there are several additional species that are of concern to natural resource managers. For example, the state resource agency is interested and invested in managing and improving sport fish populations such as Alabama bass *Micropterus henshalli*, Tallapoosa bass *M. tallapoosae*, and channel catfish *Ictalurus punctatus* in the regulated Tallapoosa River (S. Cook, Alabama Department of Conservation and Natural Resources, personal communication). System monitoring and evaluation should be dictated by the specific resource objectives articulated by managers and other system stakeholders, and evaluation of sportfish occupancy dynamics or those of any other species of interest should be included in future analyses.   With regard to rare species, elucidation of the dynamics of common species may provide important insight into the management of those species for which unbiased population parameters are difficult to obtain. Additionally, multi-species hierarchical occupancy models may prove useful in this case, as these models have been shown to improve parameter estimates for rare species by drawing inference from the whole assemblage (Dorazio et al. 2006; Kéry and Royle 2008; Kéry et al. 2009; Zipkin et al. 2010).

In the initial stages of design for the adaptive flow management plan for R.L. Harris Dam, natural resource managers articulated an objective to maximize diversity and abundance of native fauna and flora in the Tallapoosa River (Irwin and Freeman 2002; Kennedy et al. 2006). Results of this study indicate that the implemented change in management at R.L. Harris Dam may have been beneficial for some species, but detrimental for others. Assuming that the

ultimate target for diversity and abundance is a species assemblage that is similar in characteristics to that of the unregulated reaches of the Tallapoosa River, there were four species in particular that may be used to guide the direction for the next adaptive management iteration: largescale stoneroller, Alabama hogsucker, redbreast sunfish, and muscadine darter. Each of these species demonstrated declines in occupancy in the regulated Tallapoosa during the study period. As discussed above, current understanding of the life history requirements of these species and current ecological theory of the dynamics of regulated rivers support the hypothesis that thermal impacts may be a major driver of the occupancy dynamics of these species. Therefore, we recommend that the next decision iteration for the adaptive management of R.L. Harris Dam should focus on alternatives that address the management of thermal impacts in the river downstream from the dam. Management alternatives that may be considered include artificial reservoir destratification, multi-level outlet structures, surface pumps, floating intakes, and submerged curtains (see Sherman 2000 for a thorough review of these technologies). The next adaptive management iteration should also follow the process of the first iteration, integrating the results of this study, other relevant empirical data (e.g., Martin 2008; Goar 2013), and stakeholder input into a visually explicit structured decision making framework to examine the consequences of alternatives on management objectives and the trade-offs that may occur among competing objectives (Kennedy et al. 2006; Irwin and Kennedy 2008).

In addition, we recommend that stakeholders revisit the management objectives that were articulated at the initiation of the adaptive management process. At its core, adaptive management is an iterative process (Holling 1978; Walters 1986; Lee 1993; Williams et al. 2009; Allen et al. 2011). Each stage of the process should be periodically revisited to ensure that the correct problem is being addressed, management objectives are representative of the current

goals of managers and stakeholders, alternatives reflect the latest technologies and creative

thinking, and the most recent scientific knowledge and empirical data are being used to inform

management decisions. For our recommendations we assumed that the target for diversity and

abundance was associated with measured conditions in the unregulated reaches, as this target had

not been established explicitly. The current management objective to "maximize" diversity and

abundance may be adequate to distinguish among alternatives in a decision analysis, but may not

be adequate to determine when management goals are ultimately reached and conservation

success is achieved. Therefore, we recommend that managers set explicit targets against which

management success may be measured. Targets should include both measurable goals as well as

a spatial component that specifies how these goals will be evaluated across the landscape. For

example, managers should articulate whether they have the same objective target for the shoal 2

km downstream from Harris Dam as they do for the shoal 70 km downstream from Harris Dam.

Targets may also be species-specific, such that species of particular management concern, for

example state-protected species or important sportfish, may have more stringent targets than

others.

Revisiting management objectives will also require revisiting the monitoring program

designed to evaluate system response. Monitoring should be directly related to measurement of

defined management objectives and to evaluation of the hypotheses that support the proposed

management actions (Yoccoz et al. 2001; Nichols and Williams 2006; Lindenmayer and Likens

2009). For example, if a management alternative is selected to alter the thermal regime in the

regulated river, and objective targets are related to reaching occupancy probabilities as measured

in the unregulated river, the monitoring plan should aim to collect both data that will allow for

estimation of occupancy and data that may be used to evaluate changes in the thermal regime and

the potential response of target organisms. In addition, hypolimnetic releases may have substantial impacts on the levels of dissolved oxygen (DO) downstream from the dam (Fridel and Wuest 2002). It may therefore also be prudent to incorporate measures of DO along with temperature to evaluate the potential impacts of this additional system variable. However, since temperature and DO are highly correlated (Webb 1996; Caissie 2006), it is also possible that the impacts of these variables may not be separated without laboratory experimentation.

Although we continue to add to our knowledge of ecological systems and the impacts and dynamics of regulated rivers, there is still much that remains unknown. Furthermore, given the certainty of future change – whether due to a changing climate, population growth, or other influences – it may ultimately be infeasible to ever fully understand a complex, dynamic system like a highly diverse regulated river. In any regard, we certainly cannot wait until we have filled our knowledge reservoir to make river flow management decisions. Because of this, adaptive management must be a critical component of any long-term ecologically-sustainable hydropower management plan. As an iterative process, adaptive management requires that management objectives and potential action alternatives remain flexible to accommodate accumulated system knowledge and data, as well as the accumulated experience of managers. However, the flexibility that is required for implementation of adaptive management may be a challenge for many hydropower facilities, as investors demand a level of certainty that hydropower projects will be economically profitable into the future (or at least for the duration of the 30-50 year operating license). Therefore, hydropower owners and operators must be integral participants in the development and implementation of any adaptive flow management plan. Economic viability of a hydropower project can certainly be incorporated as an additional objective in an adaptive management framework, as can any potential risk that companies may face with regard

to various management alternatives. It is in the best interest of both hydropower and the river

ecosystem to engage in a process that aims to improve our understanding of the dynamic

regulated river ecosystem and reach solutions that lead to a sustainable and responsible future –

both with regard to our energy future and to the future of the ecological system and the species

and communities it supports.

Table 3-1. Models used to evaluate the effects of dam operations on fish species occupancy, colonization, and local extinction in the Tallapoosa River, Alabama. The ψ (.), γ (.), ε (.), and p (.) represent constant models of occupancy, colonization, extinction, and detection, respectively. Models including distance estimate parameters as a function of longitudinal distance downstream from a hydropower dam.

Models
Occupancy (ψ)
$\quad$ ψ (.)
$\quad$ ψ (distance)
Colonization (γ)
$\quad$ γ (.)
$\quad$ γ (distance)
Extinction (ε)
$\quad$ ε (.)
$\quad$ ε (distance)
Detection (p)
$\quad$ p (.)
$\quad$ p (depth)
$\quad$ p (velocity)
$\quad$ p (depth+velocity)

Table 3-2. Fish species detected in the Piedmont region of the Tallapoosa River basin, Alabama, and total number of detections for each species and family (in bold) across all samples and sites. A detection was a positively identified occurrence of a species in a sample. Fish were collected using prepositioned area electrofisher samples at 22 sites between 2005 and 2010. Maximum number of species detections at a site is also reported. Species with a maximum detection > 40 are indicated by an asterisk; these species were included in the full analysis of species occupancy, colonization, and local extinction.

Taxa	Total detections	Maximum detections per site
Clupeidae: shads	**13**	
Threadfin shad *Dorosoma petenense*	13	10
Cyprinidae: minnows	**4218**	
Largescale stoneroller *Campostoma oligolepis*	756	73*
Alabama shiner *Cyprinella callistia*	1566	131*
Tallapoosa shiner *Cyprinella gibbsi*	442	71*
Blacktail shiner *Cyprinella venusta*	340	64*
Lined chub *Hybopsis lineapunctata*	7	3
Striped shiner *Luxilus chrysocephalus*	127	22
Pretty shiner *Lythrurus bellus*	2	1
Speckled chub *Macrhybopsis aestivalis*	57	28
Bluehead chub *Nocomis leptocephalus*	6	5
Golden shiner *Notemigonus crysoleucas*	1	1
Burrhead shiner *Notropis asperifrons*	5	2
Rough shiner *Notropis baileyi*	39	13
Silverstripe shiner *Notropis stilbius*	294	34
Weed shiner *Notropis texanus*	14	4
Coosa shiner *Notropis xaenocephalus*	1	1
Riffle minnow *Phenacobius catostomus*	188	28
Bullhead minnow *Pimephales vigilax*	362	71*
Creek chub *Semotilus atromaculatus*	11	3
Catostomidae: suckers	**801**	
Alabama hogsucker *Hypentelium etowanum*	658	75*
Black redhorse *Moxostoma duquesnei*	101	18
Golden redhorse *Moxostoma erythrurum*	3	1
Blacktail redhorse *Moxostoma poecilurum*	39	9
Ictaluridae: catfishes		
Yellow bullhead *Ameiurus natalis*	7	2
Channel catfish *Ictalurus punctatus*	192	30
Black madtom *Noturus funebris*	160	28
Speckled madtom *Noturus leptacanthus*	223	48*
Flathead catfish *Pylodictis olivaris*	27	7

Table 3-2. Continued.

Taxa	Total detections	Maximum detections per site
Fundulidae: topminnows	**99**	
Stippled studish *Fundulus bifax*	45	21
Blackspotted topminnow *Fundulus olivaceus*	54	14
Poeciliidae: livebearers	**35**	
Mosquitofish *Gambusia affinis*	35	20
Cottidae: sculpins	**49**	
Tallapoosa sculpin *Cottus tallapoosae*	49	13
Centrarchidae: sunfishes	**975**	
Shadow bass *Ambloplites ariommus*	82	31
Redbreast sunfish *Lepomis auritus*	502	84*
Green sunfish *Lepomis cyanellus*	23	10
Warmouth *Lepomis gulosus*	2	1
Bluegill *Lepomis macrochirus*	112	32
Longear sunfish *Lepomis megalotis*	2	1
Redear sunfish *Lepomis microlophus*	10	3
Tallapoosa bass *Micropterus tallapoosae*	103	14
Alabama bass *Micropterus henshalli*	126	16
Largemouth bass *Micropterus salmoides*	12	2
Black crappie *Pomoxis nigromaculatus*	1	1
Percidae: perches	**5790**	
Lipstick darter *Etheostoma chuckwachatte*	1520	131*
Speckled darter *Etheostoma stigmaeum*	804	94*
Tallapoosa darter *Etheostoma tallapoosae*	485	72*
Yellow perch *Perca flavescens*	2	2
Mobile logperch *Percina kathae*	51	14
Bronze darter *Percina palmaris*	1947	149*
Muscadine darter *Percina smithvanizi*	981	91*

Table 3-3. Model selection results for extinction-colonization models of 13 fish species detected in the Piedmont region of the Tallapoosa River basin, Alabama. Number of parameters in each model (K), AIC, ΔAIC, AIC model weights (w_i), and cumulative model weights (cum w_i) are reported. Model results for each species are ranked in terms of AIC and w_i. Only the top 2 models are reported; additional model results are provided in Appendix 5. Models estimated occupancy (ψ) as constant [ψ(.)] or as a function of downstream distance from a large hydropower dam [ψ(dist)], colonization (γ) as constant [γ(.)] or as a function of distance [γ(dist)], extinction (ε) as constant [ε(.)] or as a function of distance [ε(dist)], and detection (p) as constant [p(.)] or as a function of habitat [p(depth), p(velocity), p(depth+velocity)].

Model	K	AIC	ΔAIC	w_i	cum w_i
Largescale stoneroller					
ψ(dist) γ(.) ε(dist) p(depth+velocity)	8	2391	0.000	0.467	0.467
ψ(dist) γ(dist) ε(dist) p(depth+velocity)	9	2392	1.315	0.242	0.710
Alabama shiner					
ψ(dist) γ(dist) ε(.) p(depth+velocity)	8	2955	0.000	0.737	0.737
ψ(.) γ(dist) ε(.) p(depth+velocity)	7	2957	2.366	0.226	0.963
Tallapoosa shiner					
ψ(dist) γ(.) ε(.) p(.)	5	1548	0.000	1.000	1.000
ψ(dist) γ(.) ε(.) p(depth+velocity)	7	1639	91.70	0.000	1.000
Blacktail shiner					
ψ(.) γ(.) ε(.) p(depth+velocity)	6	1360	0.000	0.220	0.220
ψ(.) γ(.) ε(.) p(velocity)	5	1361	1.214	0.120	0.340
Bullhead minnow					
ψ(.) γ(dist) ε(.) p(depth+velocity)	7	872.3	0.000	0.558	0.558
ψ(.) γ(dist) ε(dist) p(depth+velocity)	8	874.3	2.002	0.205	0.763
Alabama hogsucker					
ψ(dist) γ(dist) ε(dist) p(velocity)	8	2283	0.000	0.359	0.359
ψ(dist) γ(dist) ε(dist) p(depth+velocity)	9	2285	1.547	0.166	0.525
Speckled madtom					
ψ(dist) γ(.) ε(dist) p(depth+velocity)	8	820.2	0.000	0.617	0.617
ψ(dist) γ(dist) ε(dist) p(depth+velocity)	9	821.7	1.594	0.278	0.895

Model	K	AIC	ΔAIC	w_i	cum w_i
Redbreast sunfish					
ψ(dist) γ(.) ε(dist) p(depth+velocity)	8	1781	0.000	0.931	0.931
ψ(dist) γ(.) ε(dist) p(velocity)	7	1787	6.767	0.032	0.962
Lipstick darter					
ψ(dist) γ(.) ε(.) p(depth+velocity)	7	2934	0.000	0.458	0.458
ψ(.) γ(dist) ε(.) p(depth+velocity)	8	2936	1.901	0.177	0.634
Speckled darter					
ψ(.) γ(.) ε(.) p(depth+velocity)	6	2421	0.000	0.168	0.168
ψ(.) γ(dist) ε(.) p(depth+velocity)	7	2421	0.158	0.155	0.323
Tallapoosa darter					
ψ(.) γ(.) ε(.) p(depth+velocity)	6	1809	0.000	0.291	0.291
ψ(.) γ(dist) ε(.) p(depth+velocity)	7	1810	0.537	0.222	0.513
Bronze darter					
ψ(.) γ(.) ε(.) p(depth+velocity)	6	3095	0.000	0.390	0.390
ψ(.) γ(dist) ε(.) p(depth+velocity)	7	3097	1.994	0.144	0.533
Muscadine darter					
ψ(dist) γ(dist) ε(.) p(velocity)	7	2775	0.000	0.344	0.344
ψ(dist) γ(dist) ε(.) p(depth+velocity)	8	2775	0.047	0.336	0.679

Table 3-4. Additive AIC model weights (w_+) of occupancy (ψ), colonization (γ), extinction (ε), and detection (p) covariates for 13 fish species detected in the Piedmont region of the Tallapoosa River basin, Alabama. Here additive weights represent the relative strength of evidence for distance as a predictor of species occupancy, colonization, and local extinction, and of depth and velocity as predictors of species detection. Distance refers to the downstream distance below a large hydropower dam on the Tallapoosa River.

Species	ψ(distance)	γ(distance)	ε(distance)	p(depth)	p(velocity)
Largescale Stoneroller	0.728	0.436	0.971	1.000	1.000
Alabama shiner	0.769	0.964	0.000	1.000	1.000
Tallapoosa shiner	1.000	0.000	0.000	0.000	0.000
Blacktail shiner	0.284	0.363	0.267	0.647	1.000
Bullhead minnow	0.237	0.998	0.270	1.000	1.000
Alabama hogsucker	0.670	0.905	0.893	0.485	0.987
Speckled madtom	0.895	0.381	1.000	1.000	1.000
Redbreast sunfish	0.992	0.005	0.968	0.966	1.000
Lipstick darter	0.872	0.279	0.273	1.000	1.000
Speckled darter	0.414	0.438	0.351	1.000	0.878
Tallapoosa darter	0.421	0.295	0.271	0.997	1.000
Bronze darter	0.269	0.269	0.269	0.998	1.000
Muscadine darter	0.890	0.969	0.201	0.394	1.000

Table 3-5. Model-averaged fish species occupancy estimates (and unconditional standard errors) for sites downstream of a large hydropower dam on the Tallapoosa River, Alabama. Occupancy estimates are for the first year of sampling (2005). Note that because Tallapoosa shiner had a single best model with an AIC model weight of 1.000, the estimates given for this species include results of this top model only.

Species	2 km	8 km	10 km	12 km	16 km	20 km	60 km	70 km	Unregulated
Largescale Stoneroller	0.413 (0.412)	0.739 (0.186)	0.802 (0.147)	0.875 (0.121)	0.931 (0.094)	0.946 (0.082)	0.955 (0.077)	0.955 (0.077)	0.955 (0.077)
Alabama shiner	0.221 (0.322)	0.689 (0.242)	0.815 (0.158)	0.915 (0.114)	0.949 (0.085)	0.951 (0.085)	0.952 (0.085)	0.952 (0.085)	0.952 (0.085)
Tallapoosa shiner	0.000 (0.000)	0.089 (0.156)	0.408 (0.261)	0.949 (0.140)	1.000 (0.002)	1.000 (0.000)	1.000 (0.000)	1.000 (0.000)	1.000 (0.000)
Blacktail shiner	0.500 (0.157)	0.498 (0.153)	0.498 (0.153)	0.497 (0.152)	0.496 (0.151)	0.495 (0.152)	0.483 (0.180)	0.476 (0.204)	0.466 (0.237)
Bullhead minnow	0.000 (0.001)	0.000 (0.001)	0.000 (0.001)	0.000 (0.001)	0.000 (0.001)	0.000 (0.001)	0.001 (0.033)	0.022 (0.536)	0.237 (0.362)
Alabama hogsucker	0.326 (0.386)	0.713 (0.215)	0.807 (0.153)	0.890 (0.125)	0.926 (0.109)	0.930 (0.108)	0.932 (0.107)	0.932 (0.107)	0.932 (0.107)
Speckled madtom	0.012 (0.026)	0.021 (0.048)	0.029 (0.061)	0.054 (0.091)	0.179 (0.174)	0.393 (0.389)	0.906 (0.169)	0.906 (0.169)	0.906 (0.169)
Redbreast sunfish	0.997 (0.006)	0.994 (0.015)	0.990 (0.029)	0.960 (0.097)	0.568 (0.300)	0.124 (0.217)	0.008 (0.016)	0.008 (0.016)	0.008 (0.016)
Lipstick darter	0.181 (0.337)	0.953 (0.120)	0.978 (0.053)	0.986 (0.029)	0.987 (0.028)	0.987 (0.028)	0.987 (0.028)	0.987 (0.028)	0.987 (0.028)
Speckled darter	0.612 (0.167)	0.623 (0.155)	0.626 (0.153)	0.630 (0.150)	0.638 (0.149)	0.643 (0.150)	0.710 (0.216)	0.742 (0.236)	0.778 (0.221)
Tallapoosa darter	0.487 (0.270)	0.566 (0.182)	0.586 (0.167)	0.618 (0.159)	0.665 (0.185)	0.695 (0.207)	0.775 (0.225)	0.775 (0.225)	0.775 (0.225)
Bronze darter	1.000 (0.005)	1.000 (0.005)	1.000 (0.005)	1.000 (0.005)	1.000 (0.005)	1.000 (0.005)	1.000 (0.005)	1.000 (0.005)	1.000 (0.005)
Muscadine darter	0.987 (0.028)	0.981 (0.040)	0.976 (0.051)	0.957 (0.083)	0.829 (0.176)	0.571 (0.401)	0.107 (0.189)	0.107 (0.189)	0.107 (0.189)

Table 3-6. Model-averaged fish species colonization estimates (and unconditional standard errors) for sites downstream of a large hydropower dam on the Tallapoosa River, Alabama. Note that because Tallapoosa shiner had a single best model with an AIC model weight of 1.000, the estimates given for this species include results of this top model only.

Species	2 km	8 km	10 km	12 km	16 km	20 km	60 km	70 km	Unregulated
Largescale Stoneroller	0.120 (0.106)	0.128 (0.108)	0.130 (0.109)	0.133 (0.110)	0.139 (0.113)	0.144 (0.116)	0.247 (0.236)	0.340 (0.357)	0.471 (0.438)
Alabama shiner	0.220 (0.190)	0.961 (0.128)	0.978 (0.061)	0.984 (0.032)	0.985 (0.029)	0.985 (0.029)	0.985 (0.029)	0.985 (0.029)	0.985 (0.029)
Tallapoosa shiner	0.238 (0.079)	0.238 (0.079)	0.238 (0.079)	0.238 (0.079)	0.238 (0.079)	0.238 (0.079)	0.238 (0.079)	0.238 (0.079)	0.238 (0.079)
Blacktail shiner	0.555 (0.154)	0.559 (0.150)	0.560 (0.149)	0.562 (0.148)	0.565 (0.145)	0.567 (0.144)	0.595 (0.133)	0.614 (0.139)	0.652 (0.170)
Bullhead minnow	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.001 (0.011)	0.895 (0.181)
Alabama hogsucker	0.012 (0.025)	0.078 (0.101)	0.154 (0.138)	0.412 (0.275)	0.822 (0.286)	0.898 (0.174)	0.915 (0.154)	0.915 (0.154)	0.915 (0.154)
Speckled madtom	0.182 (0.067)	0.185 (0.066)	0.185 (0.066)	0.187 (0.065)	0.189 (0.065)	0.191 (0.065)	0.220 (0.085)	0.245 (0.118)	0.298 (0.204)
Redbreast sunfish	0.669 (0.096)	0.669 (0.096)	0.669 (0.096)	0.670 (0.096)	0.670 (0.096)	0.670 (0.096)	0.670 (0.096)	0.671 (0.096)	0.671 (0.097)
Lipstick darter	1.000 (0.005)	1.000 (0.005)	1.000 (0.005)	1.000 (0.005)	1.000 (0.005)	1.000 (0.005)	1.000 (0.005)	1.000 (0.005)	1.000 (0.005)
Speckled darter	0.321 (0.151)	0.341 (0.136)	0.347 (0.132)	0.358 (0.127)	0.380 (0.133)	0.398 (0.146)	0.494 (0.206)	0.514 (0.215)	0.557 (0.256)
Tallapoosa darter	0.676 (0.137)	0.678 (0.134)	0.678 (0.134)	0.679 (0.133)	0.679 (0.132)	0.680 (0.131)	0.690 (0.125)	0.696 (0.129)	0.709 (0.148)
Bronze darter	0.884 (9.433)	0.886 (9.230)	0.887 (9.184)	0.887 (9.106)	0.889 (8.980)	0.890 (8.887)	0.901 (7.855)	0.908 (7.356)	0.917 (6.621)
Muscadine darter	0.116 (0.242)	0.334 (0.182)	0.416 (0.178)	0.563 (0.331)	0.772 (0.447)	0.868 (0.354)	0.986 (0.028)	0.986 (0.028)	0.986 (0.028)

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Table 3-7. Model-averaged fish species local extinction estimates (and unconditional standard errors) for sites downstream of a large hydropower dam on the Tallapoosa River, Alabama. Note that because Tallapoosa shiner had a single best model with an AIC model weight of 1.000, the estimates given for this species include results of this top model only.

Species	2 km	8 km	10 km	12 km	16 km	20 km	60 km	70 km	Unregulated
Largescale Stoneroller	0.249 (0.090)	0.227 (0.080)	0.222 (0.078)	0.214 (0.075)	0.201 (0.070)	0.191 (0.066)	0.091 (0.046)	0.052 (0.039)	0.015 (0.020)
Alabama shiner	0.053 (0.024)	0.053 (0.024)	0.053 (0.024)	0.053 (0.024)	0.053 (0.024)	0.053 (0.024)	0.053 (0.024)	0.053 (0.024)	0.053 (0.024)
Tallapoosa shiner	0.196 (0.055)	0.196 (0.055)	0.196 (0.055)	0.196 (0.055)	0.196 (0.055)	0.196 (0.055)	0.196 (0.055)	0.196 (0.055)	0.196 (0.055)
Blacktail shiner	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
Bullhead minnow	0.401 (1.387)	0.399 (1.512)	0.398 (1.543)	0.398 (1.597)	0.396 (1.689)	0.395 (1.761)	0.366 (2.720)	0.325 (2.733)	0.194 (0.084)
Alabama hogsucker	0.371 (0.259)	0.267 (0.117)	0.245 (0.095)	0.214 (0.097)	0.179 (0.109)	0.163 (0.107)	0.083 (0.079)	0.054 (0.069)	0.025 (0.043)
Speckled madtom	1.000 (0.001)	1.000 (0.001)	1.000 (0.001)	1.000 (0.001)	1.000 (0.001)	1.000 (0.001)	0.999 (0.005)	0.996 (0.069)	0.140 (0.070)
Redbreast sunfish	0.351 (0.103)	0.315 (0.088)	0.307 (0.085)	0.294 (0.082)	0.272 (0.079)	0.256 (0.080)	1.00 (0.101)	0.049 (0.078)	0.013 (0.029)
Lipstick darter	0.017 (0.016)	0.017 (0.016)	0.017 (0.016)	0.017 (0.016)	0.017 (0.016)	0.017 (0.016)	0.017 (0.016)	0.018 (0.014)	0.019 (0.016)
Speckled darter	0.130 (0.051)	0.128 (0.049)	0.128 (0.049)	0.128 (0.049)	0.127 (0.047)	0.126 (0.047)	0.119 (0.041)	0.115 (0.041)	0.106 (0.047)
Tallapoosa darter	0.199 (0.070)	0.199 (0.069)	0.199 (0.069)	0.199 (0.069)	0.199 (0.068)	0.199 (0.068)	0.198 (0.064)	0.197 (0.065)	0.196 (0.075)
Bronze darter	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
Muscadine darter	0.162 (0.049)	0.162 (0.049)	0.162 (0.049)	0.162 (0.048)	0.162 (0.048)	0.162 (0.048)	0.162 (0.045)	0.161 (0.045)	0.160 (0.050)

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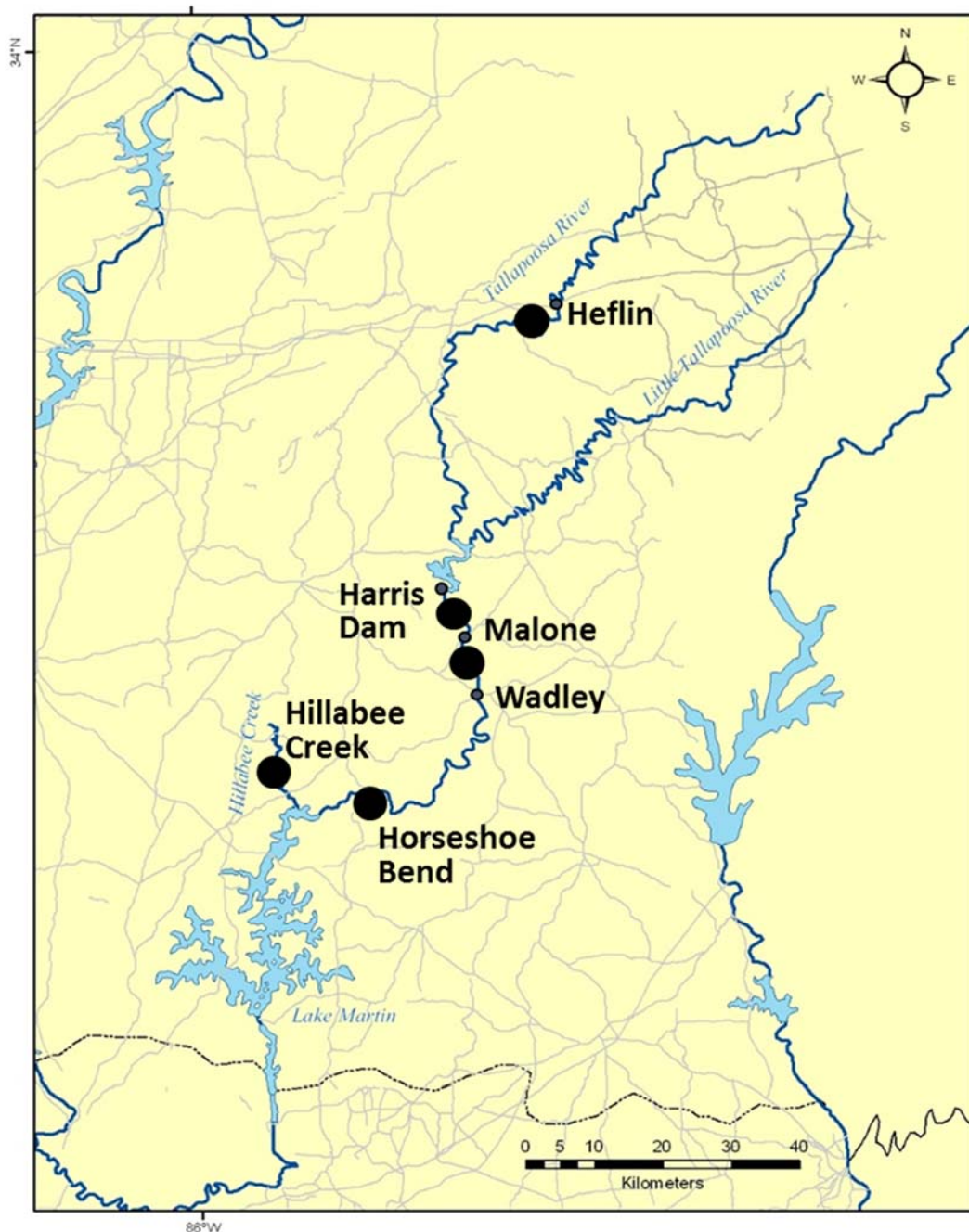
Figure 3-1. Locations of sites sampled as part of an adaptive management project to evaluate changes in operation from R. L. Harris Dam on the Tallapoosa River, Alabama. Fish collections have been conducted at 22 sites throughout the Piedmont region of the basin since 2005. Twelve of these sites are located in the regulated river below Harris Dam, with five between Harris Dam and Malone, Alabama; five between Malone and Wadley, Alabama; and two near Horseshoe Bend. Ten additional sites are located in the unregulated Tallapoosa basin – 5 in the mainstem upstream from Harris Dam near Heflin, Alabama, and 5 in Hillabee Creek.
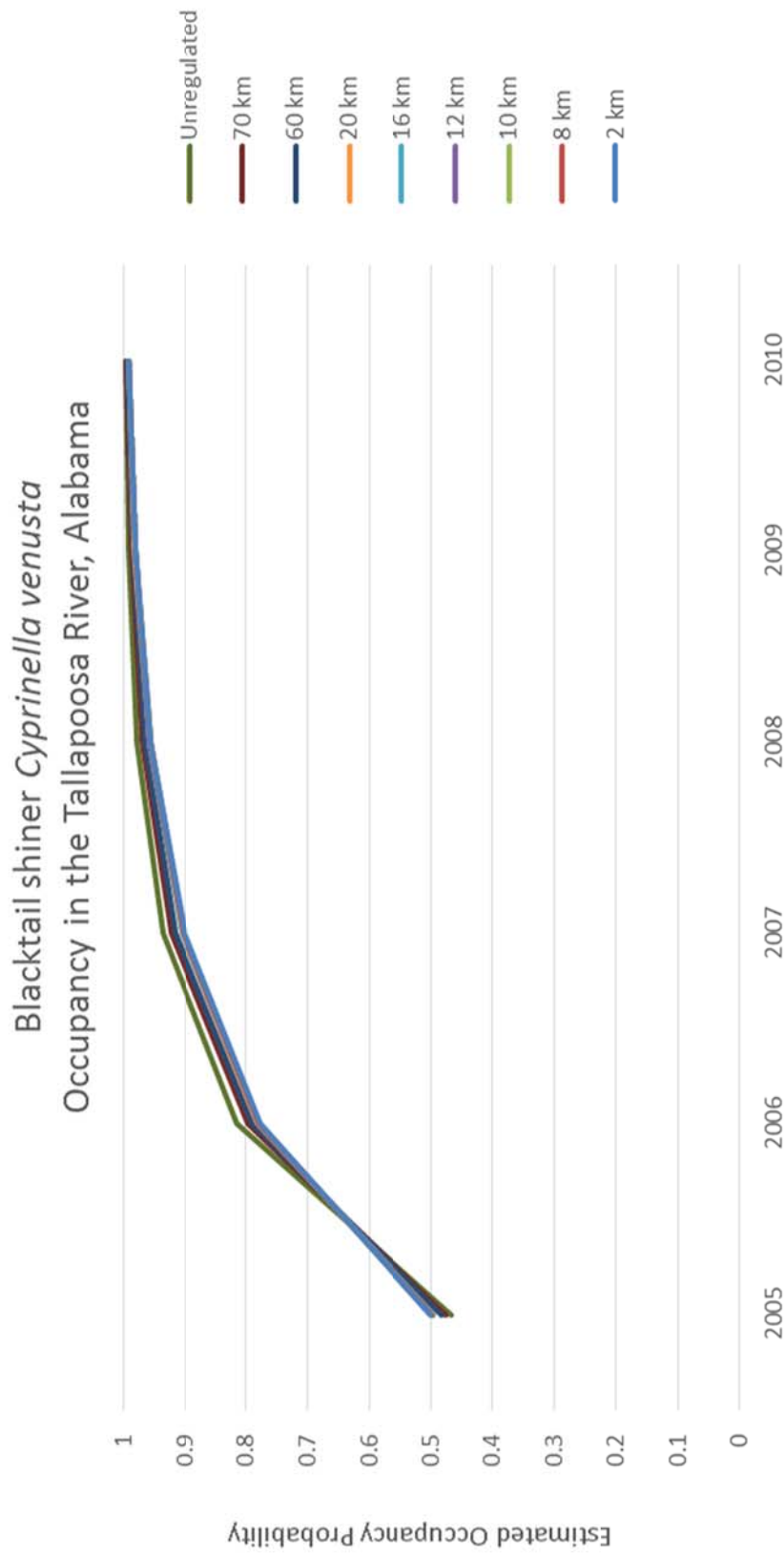
Figure 3-2. Estimated occupancy (ψ) of blacktail shiner (*Cyprinella venusta*) in the Piedmont reach of the Tallapoosa River, Alabama for 2005-2010. Occupancy for 2005 was a model-averaged estimate calculated from a set of extinction-colonization models evaluating the potential impacts of a large hydropower dam on species occupancy dynamics. Occupancy values for 2006-2010 were derived from model-averaged estimates of colonization (γ) and local extinction (ε) rates. Sites are identified as either those in the unregulated reaches of the Tallapoosa River basin or by a site's longitudinal distance downstream from the dam. Results demonstrated low to no impact of dam operations on occupancy dynamics of this species over the course of the study.

Speckled darter *Etheostoma stigmaeum*
Occupancy in the Tallapoosa River, Alabama

Figure 3-3. Estimated occupancy (ψ) of speckled darter (*Etheostoma stigmaeum*) in the Piedmont reach of the Tallapoosa River, Alabama for 2005-2010. Occupancy for 2005 was a model-averaged estimate calculated from a set of extinction-colonization models evaluating the potential impacts of a large hydropower dam on species occupancy dynamics. Occupancy values for 2006-2010 were derived from model-averaged estimates of colonization (γ) and local extinction (ε) rates. Sites are identified as either those in the unregulated reaches of the Tallapoosa River basin or by a site's longitudinal distance downstream from the dam. Results demonstrated low impact of dam operations on occupancy dynamics of this species over the course of the study.

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Figure 3-4. Estimated occupancy (ψ) of bronze darter (*Percina palmaris*) in the Piedmont reach of the Tallapoosa River, Alabama for 2005-2010. Occupancy for 2005 was a model-averaged estimate calculated from a set of extinction-colonization models evaluating the potential impacts of a large hydropower dam on species occupancy dynamics. Occupancy values for 2006-2010 were derived from model-averaged estimates of colonization (γ) and local extinction (ε) rates. Sites are identified as either those in the unregulated reaches of the Tallapoosa River basin or by a site's longitudinal distance downstream from the dam. Results demonstrated no effect of dam operations on occupancy dynamics of this species over the course of the study.

Figure 3-5. Estimated occupancy (ψ) of Tallapoosa darter (*Etheostoma tallapoosae*) in the Piedmont reach of the Tallapoosa River, Alabama for 2005-2010. Occupancy for 2005 was a model-averaged estimate calculated from a set of extinction-colonization models evaluating the potential impacts of a large hydropower dam on species occupancy dynamics. Occupancy values for 2006-2010 were derived from model-averaged estimates of colonization (γ) and local extinction (ε) rates. Sites are identified as either those in the unregulated reaches of the Tallapoosa River basin or by a site's longitudinal distance downstream from the dam. Results demonstrated only minimal effects of dam operations on occupancy dynamics of this species over the course of the study.

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Bullhead minnow *Pimephales vigilax*
Occupancy in the Tallapoosa River, Alabama

Figure 3-6. Estimated occupancy (ψ) of bullhead minnow (*Pimephales vigilax*) in the Piedmont reach of the Tallapoosa River, Alabama for 2005-2010. Occupancy for 2005 was a model-averaged estimate calculated from a set of extinction-colonization models evaluating the potential impacts of a large hydropower dam on species occupancy dynamics. Occupancy values for 2006-2010 were derived from model-averaged estimates of colonization (γ) and local extinction (ε) rates. Sites are identified as either those in the unregulated reaches of the Tallapoosa River basin or by a site's longitudinal distance downstream from the dam. Results demonstrated strong effects of dam operations on occupancy of this species that were constant over the course of the study.

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Figure 3-7. Estimated occupancy (ψ) of redbreast sunfish (*Lepomis auritus*) in the Piedmont reach of the Tallapoosa River, Alabama for 2005-2010. Occupancy for 2005 was a model-averaged estimate calculated from a set of extinction-colonization models evaluating the potential impacts of a large hydropower dam on species occupancy dynamics. Occupancy values for 2006-2010 were derived from model-averaged estimates of colonization (γ) and local extinction (ε) rates. Sites are identified as either those in the unregulated reaches of the Tallapoosa River basin or by a site's longitudinal distance downstream from the dam. Results demonstrated complex effects of dam operations on occupancy dynamics of this species over the course of the study.

Figure 3-8. Estimated occupancy (ψ) of muscadine darter (*Percina smithvanizi*) in the Piedmont reach of the Tallapoosa River, Alabama for 2005-2010. Occupancy for 2005 was a model-averaged estimate calculated from a set of extinction-colonization models evaluating the potential impacts of a large hydropower dam on species occupancy dynamics. Occupancy values for 2006-2010 were derived from model-averaged estimates of colonization (γ) and local extinction (ε) rates. Sites are identified as either those in the unregulated reaches of the Tallapoosa River basin or by a site's longitudinal distance downstream from the dam. Results demonstrated complex effects of dam operations on occupancy dynamics of this species over the course of the study.

Largescale stoneroller *Campostoma oligolepis*
Occupancy in the Tallapoosa River, Alabama

Figure 3-9. Estimated occupancy (ψ) of largescale stoneroller (*Campostoma oligolepis*) in the Piedmont reach of the Tallapoosa River, Alabama for 2005-2010. Occupancy for 2005 was a model-averaged estimate calculated from a set of extinction-colonization models evaluating the potential impacts of a large hydropower dam on species occupancy dynamics. Occupancy values for 2006-2010 were derived from model-averaged estimates of colonization (γ) and local extinction (ε) rates. Sites are identified as either those in the unregulated reaches of the Tallapoosa River basin or by a site's longitudinal distance downstream from the dam. Results demonstrated negative effects of dam operations on occupancy dynamics of this species over the course of the study.
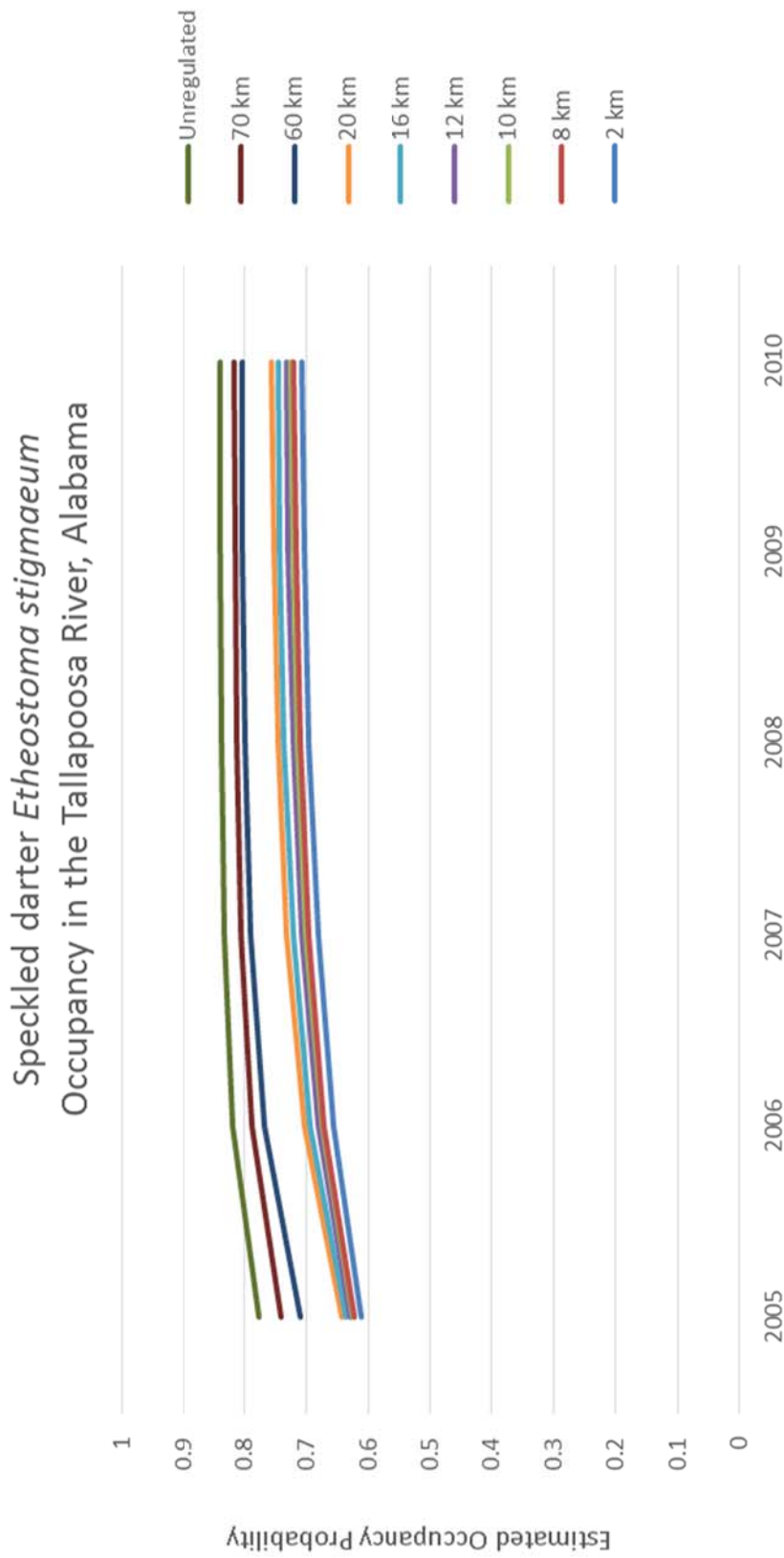
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Figure 3-10. Estimated occupancy (ψ) of Alabama hogsucker (*Hypentelium etowanum*) in the Piedmont reach of the Tallapoosa River, Alabama for 2005-2010. Occupancy for 2005 was a model-averaged estimate calculated from a set of extinction-colonization models evaluating the potential impacts of a large hydropower dam on species occupancy dynamics. Occupancy values for 2006-2010 were derived from model-averaged estimates of colonization (γ) and local extinction (ϵ) rates. Sites are identified as either those in the unregulated reaches of the Tallapoosa River basin or by a site's longitudinal distance downstream from the dam. Results demonstrated negative effects of dam operations on occupancy dynamics of this species over the course of the study.
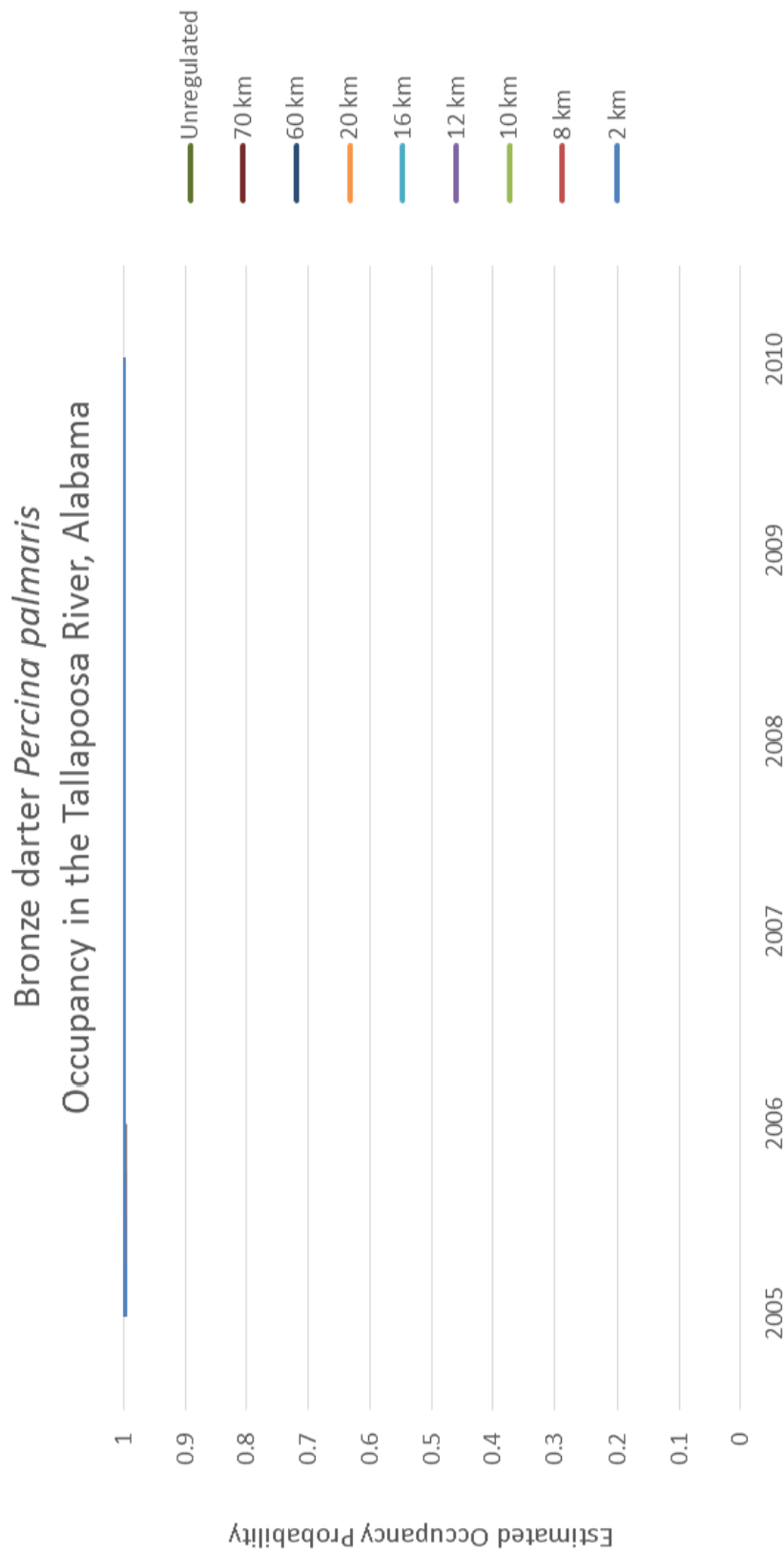
Figure 3-11. Estimated occupancy (ψ) of Alabama shiner (*Cyprinella callistia*) in the Piedmont reach of the Tallapoosa River, Alabama for 2005-2010. Occupancy for 2005 was a model-averaged estimate calculated from a set of extinction-colonization models evaluating the potential impacts of a large hydropower dam on species occupancy dynamics. Occupancy values for 2006-2010 were derived from model-averaged estimates of colonization (γ) and local extinction (ε) rates. Sites are identified as either those in the unregulated reaches of the Tallapoosa River basin or by a site's longitudinal distance downstream from the dam. Results demonstrated positive effects of dam operations on occupancy dynamics of this species over the course of the study.
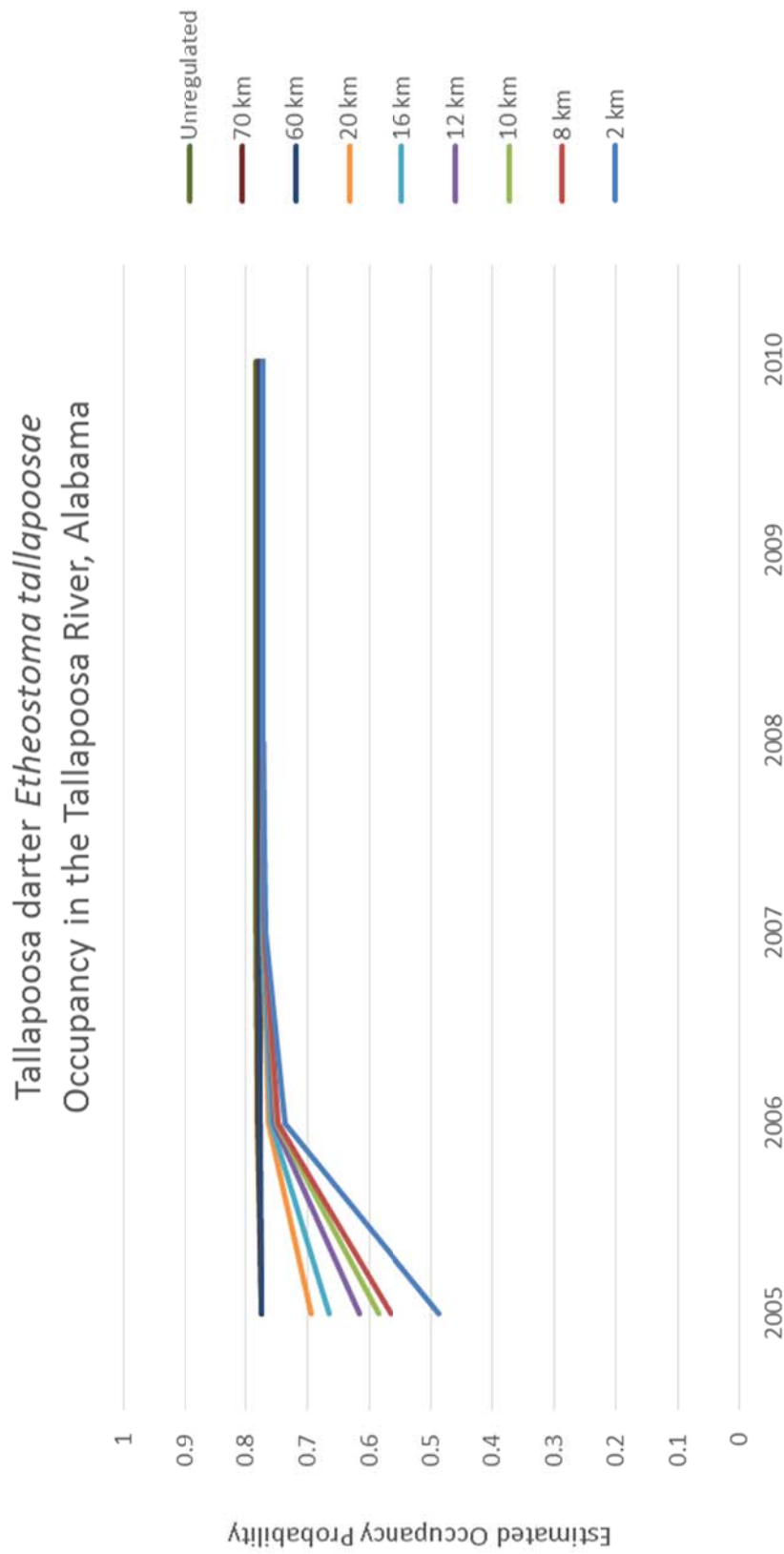
Figure 3-12. Estimated occupancy (ψ) of lipstick darter (*Etheostoma chuckwachatte*) in the Piedmont reach of the Tallapoosa River, Alabama for 2005-2010. Occupancy for 2005 was a model-averaged estimate calculated from a set of extinction-colonization models evaluating the potential impacts of a large hydropower dam on species occupancy dynamics. Occupancy values for 2006-2010 were derived from model-averaged estimates of colonization (γ) and local extinction (ϵ) rates. Sites are identified as either those in the unregulated reaches of the Tallapoosa River basin or by a site's longitudinal distance downstream from the dam. Results demonstrated positive effects of dam operations on occupancy dynamics of this species over the course of the study.
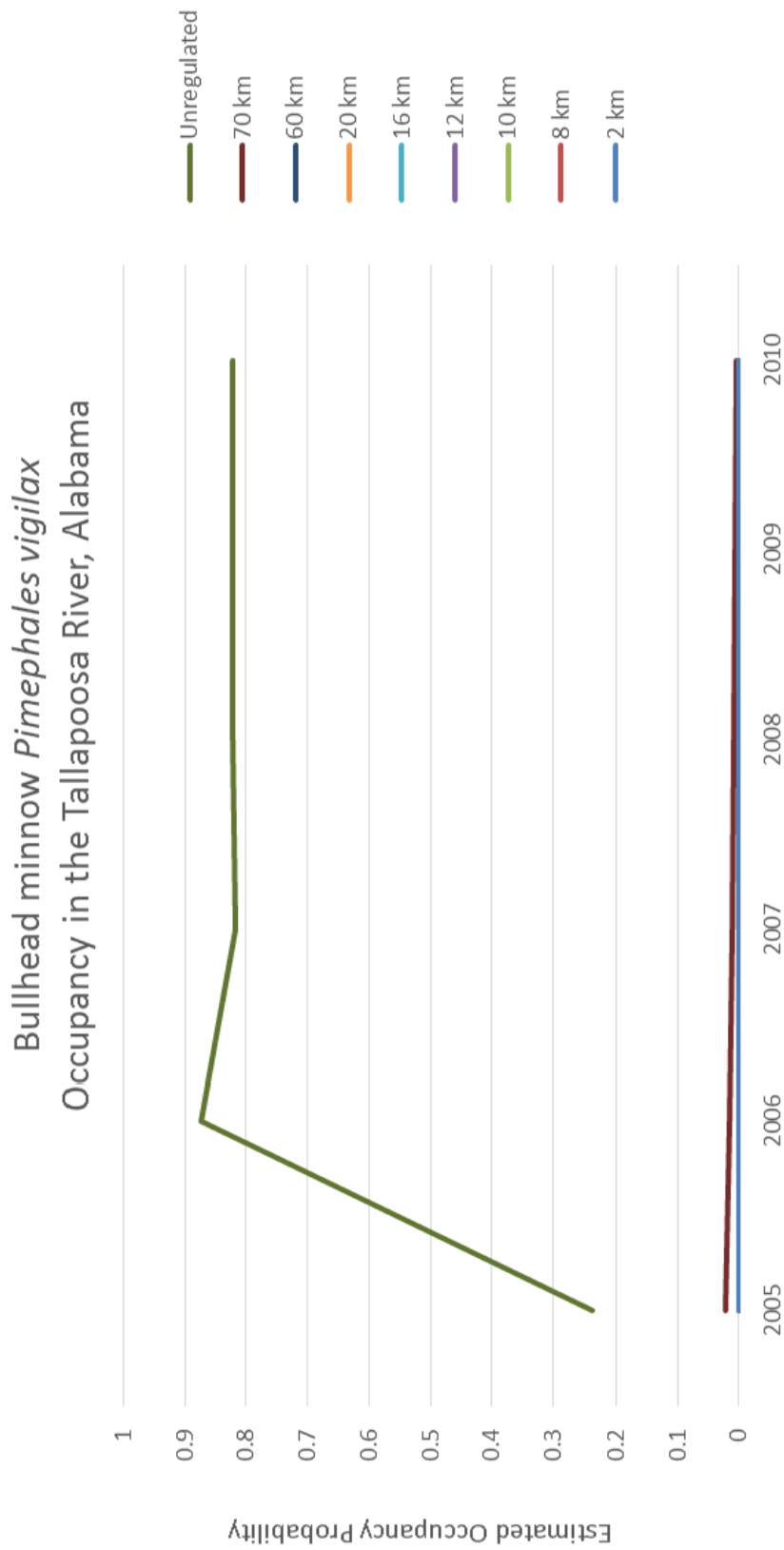
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Figure 3-13. Estimated occupancy (ψ) of Tallapoosa shiner (*Cyprinella gibbsi*) in the Piedmont reach of the Tallapoosa River, Alabama for 2005-2010. Occupancy for 2005 was a model-averaged estimate calculated from a set of extinction-colonization models evaluating the potential impacts of a large hydropower dam on species occupancy dynamics. Occupancy values for 2006-2010 were derived from model-averaged estimates of colonization (γ) and local extinction (ε) rates. Sites are identified as either those in the unregulated reaches of the Tallapoosa River basin or by a site's longitudinal distance downstream from the dam. Results demonstrated positive effects of dam operations on occupancy dynamics of this species over the course of the study.

Figure 3-14. Estimated occupancy (ψ) of speckled madtom (*Noturus leptacanthus*) in the Piedmont reach of the Tallapoosa River, Alabama for 2005-2010. Occupancy for 2005 was a model-averaged estimate calculated from a set of extinction-colonization models evaluating the potential impacts of a large hydropower dam on species occupancy dynamics. Occupancy values for 2006-2010 were derived from model-averaged estimates of colonization (γ) and local extinction (ε) rates. Sites are identified as either those in the unregulated reaches of the Tallapoosa River basin or by a site's longitudinal distance downstream from the dam. Results demonstrated complex effects of dam operations on occupancy dynamics of this species over the course of the study.
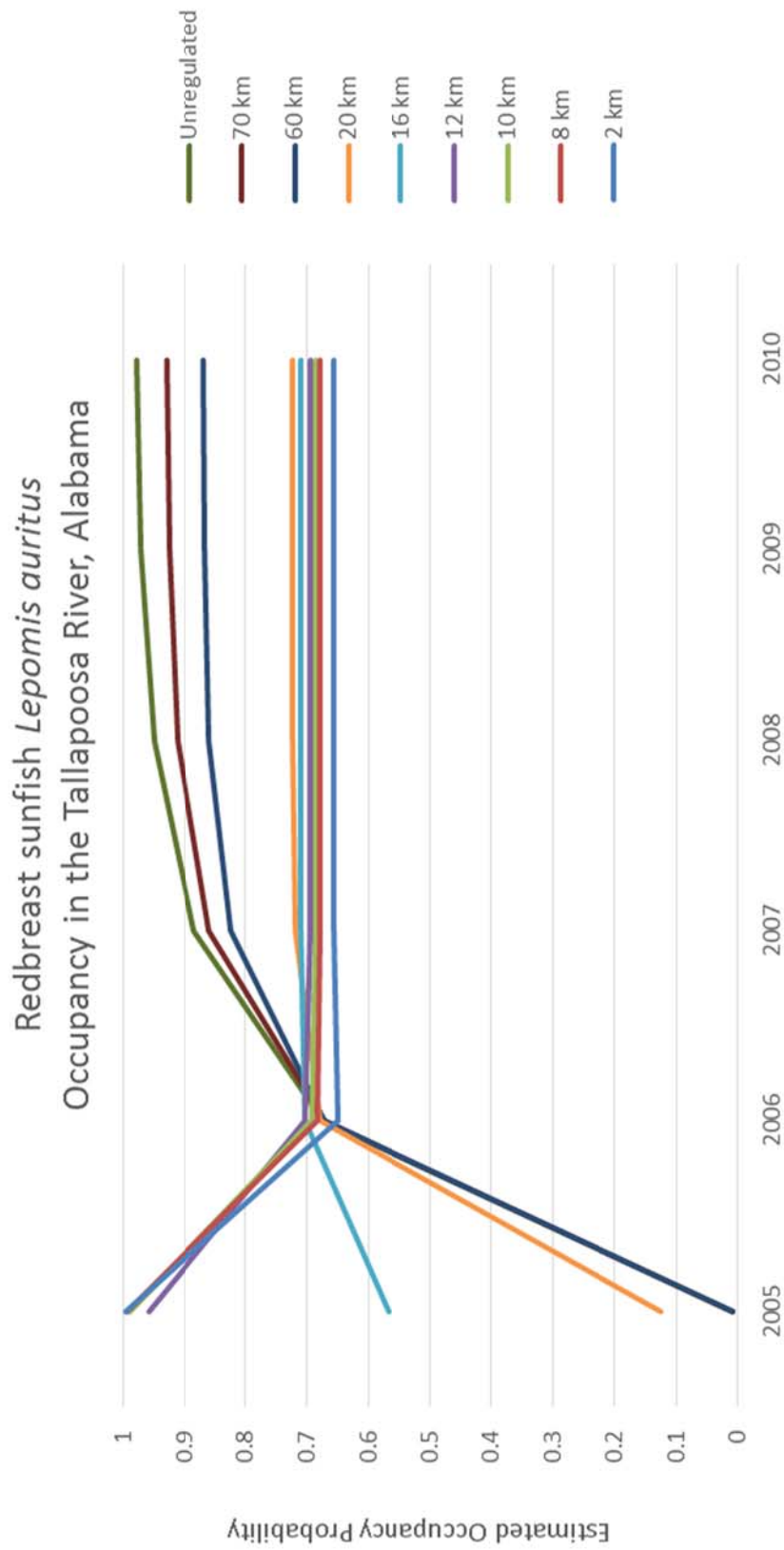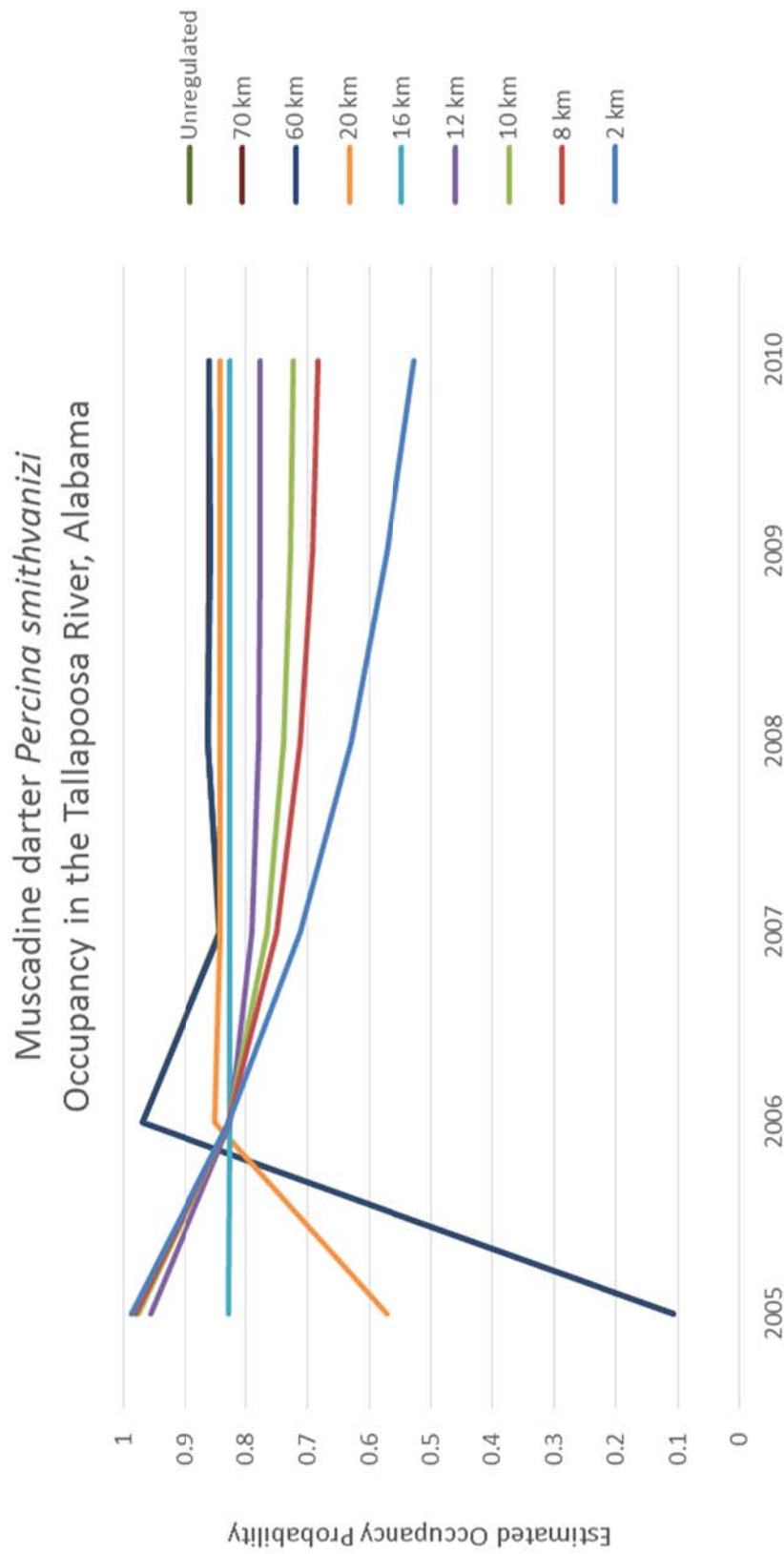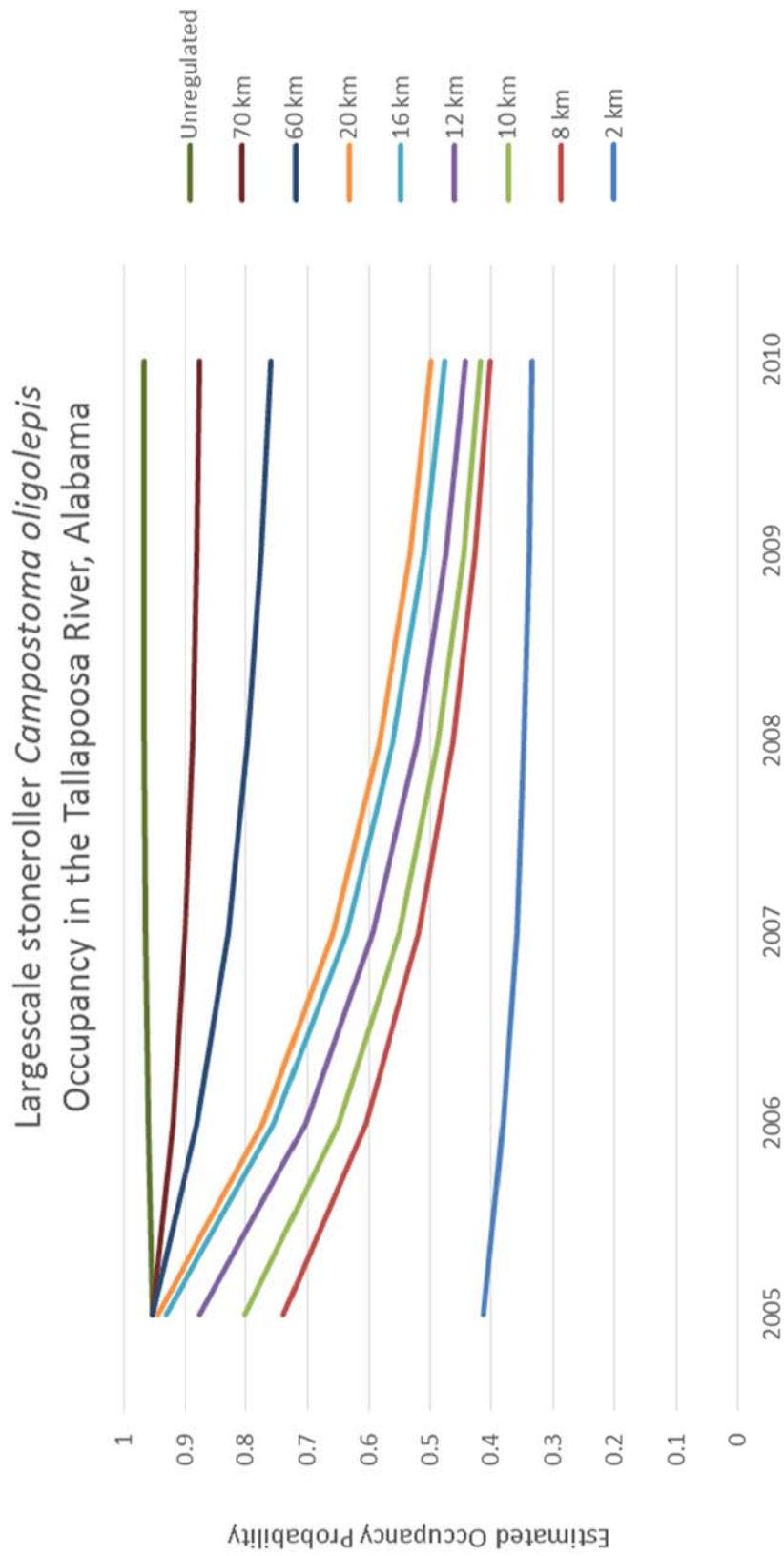
Chapter 4. Incorporating the index of biotic integrity into decision making
for aquatic natural resources management

Abstract. – The index of biotic integrity (IBI) is a multi-metric index used in the field of aquatic resource management to characterize the effects of anthropogenic impacts on the biological condition of water resources. Justification for development and use of an IBI by a natural resources agency often includes a stipulation that the index will help improve management decision making. However, use of the index in decision making has been primarily restricted to independent decisions based on IBI site classification; it has not been widely used to make decisions concerning direct management actions. To facilitate broader use, we provide a general framework to incorporate the IBI into aquatic resource management decision making. This framework takes a structured decision making approach, equating established IBI metrics to resource objectives, and linking these objectives to management actions with hypotheses of system response. We further demonstrate use of the framework for a specific decision context in the state of Alabama, where the IBI provides the basis for a statewide aquatic biomonitoring protocol. Data collected through this protocol is intended to improve resource management decisions, including those for managing instream flows. Using the outlined framework, we illustrate integration of the IBI into instream flow criteria decisions that may be applied to the development of Alabama's statewide water management plan. Within the described structured decision making framework, the IBI provides a basis for informing the selection of management actions that directly meet defined agency resource objectives.

Introduction

The index of biotic integrity (IBI) is a multi-metric index that was developed by Jim Karr in 1981 to assess the effects of anthropogenic impacts on the biological condition of water resources (Karr 1981). Prior to its development, most assessments had used water quality measures to determine impact, but recent studies had questioned the ability of these measures to successfully evaluate biological condition (Karr and Dudley 1981). An IBI is composed of several metrics that account for a wide range of important ecological factors, such as species composition and richness, trophic structure, and biotic health. A sum of the scaled values of each metric (the IBI "score") is intended to represent the "biotic integrity" of a water resource, generally defined as "the capability of supporting and maintaining a balanced, integrated adaptive community of organisms having a specific composition, diversity, and functional organization comparable to that of natural habitat in the region" (Karr and Dudley 1981).

Since the introduction of the IBI in 1981, there have been over 950 published documents that have cited Karr's seminal work, and many more that reference the index without specifically citing the original publication (Web of Science search, 5 October 2014, http://webofknowledge.com). Many of these studies are based on modifications of Karr's IBI, often using benthic macroinvertebrates or other taxa instead of or in addition to the fish taxa used in the original index (e.g., Roy et al. 2003; Diaz et al. 2004; Hering et al. 2006a). Some form of the IBI or other multi-metric index is now used in most states and by the Environmental Protection Agency (USEPA 2002), as well as in several regions around the world (e.g., Australia, Harris 1995; Africa, Toham and Teugels 1999; Europe, Uriarte and Borja 2009).

The primary utilities of an IBI or similar index are generally reported to be its ease of use (Karr 1981; Gergel et al. 2002; Coates et al. 2007) and the simplicity of the single resultant value

for communicating biological condition to managers, politicians, and the public (Diaz et al. 2004; Coates et al. 2007; Borja et al. 2008). Other purported benefits include the theoretical basis of the IBI, which is grounded in widely-accepted ecological theory and should therefore lead to an increase in scientific confidence of the index (Karr 1999; Borja et al. 2008; Korte 2010), and its inherent flexibility as metrics can be added, changed, and eliminated as users judge is necessary (Karr 1991; Hering et al. 2006b; Gabriels et al. 2010).

This latter point is viewed by some as a disadvantage rather than an advantage, as the IBI is not transferable among different geographic areas unless modified, and multiple separate indices have been developed as a result (Gergel et al. 2002; Hawkins 2006; Pinto et al. 2009). Additional shortcomings of the IBI identified in the literature include lack of information concerning the mechanism for degradation (Gergel et al. 2002; Angradi et al. 2009; Hawkins et al. 2010), the requirement of a relatively undisturbed "reference" site (Roset et al. 2007; Borja et al. 2009; Hawkins et al. 2010), correlation or overlap among composite metrics (Diaz et al. 2004; Feld et al. 2009), the subjectivity of some of the included metrics (Diaz et al. 2004), and unaccounted differences in detection probability among species (Dolph et al. 2010).

Justification for using an IBI often includes a stipulation that the index will help improve management decision making (Karr and Chu 1997; Karr 1999; Barbour et al. 2000; Ruaro and Guiani 2013). Most cases of decision making involving an IBI or other multi-metric index have been decisions to classify the impairment of a particular body of water (e.g., Yoder and Rankin 1998; USEPA 2002; Volstad et al. 2003). There are comparatively few cases in which an IBI was used to assist decisions about management actions aimed to change system state (Failing and Gregory 2003). However, if the primary objectives of aquatic resource management include protecting, conserving, or restoring resources, then the value of an IBI needs to extend past

describing the state of a resource to informing actions to meet these management objectives, especially if considerable fiscal and human resources are dedicated to ongoing IBI monitoring.

Because natural resource systems are complex and levels of uncertainty often high, using an IBI to inform decisions beyond descriptive classification can be challenging. Yet making sound and defensible management action decisions is imperative to maintaining and restoring valued natural resources amidst continuing population pressures and limited fiscal resources. In response to repeated failures and poorly documented natural resource decision processes, there has been a recent surge of interest to employ the framework of structured decision making (SDM) in the field of natural resource management (e.g., Gregory and Keeney 2002; Blomquist et al. 2010; Gregory et al. 2012; Conroy and Peterson 2013; McGowan 2013). Structured decision making is essentially the formalization of decision problems that are too complex for normal human cognition (i.e., common sense; Keeney 1982). It has its roots in the field of business management, and was developed to handle highly complex and uncertain decision problems (Keeney 1982). Given the highly complex and uncertain nature of ecological systems, it has obvious potential for application in the field of natural resource management. The SDM framework ensures that a chosen decision is the best possible one, given what is known (and unknown) about the system. The SDM process is objective-based, meaning that identified management objectives drive the decision making. The best decision is determined through evaluation of the extent to which each potential alternative meets stated objectives. Structured decision making also ensures that the decision is transparent, explicit, and replicable, and therefore understood by and justifiable to others outside of the decision process.

The overall objective of this paper is to provide a framework for managers to incorporate the index of biotic integrity into management decision making that is aimed directly toward

meeting management objectives. Specifically, we aim to 1) describe the theoretical basis for

using multi-metric indices in a structured decision making context, and how this theoretical basis

capitalizes on the strengths and minimizes the weaknesses of multi-metric indices; 2) outline a

specific process for managers to incorporate an index into decision making, and 3) provide an

example of how to use an IBI to inform decisions in a given management context.

Theoretical Basis

The index of biotic integrity was initially developed as a rapid assessment tool to describe

the level of impairment of a given water body. The impetus for its development was an

increasing awareness of the impact of human activities on aquatic systems and the inadequacy of

chemical measures to represent the effects of these activities on aquatic biota. Whereas

previously the condition of an aquatic resource had been determined almost exclusively by water

quality measures, the IBI shifted the focus of monitoring to also account for biological and

ecological components of an aquatic resource. This shift was largely supported by the Clean

Water Act, which was established "to restore and maintain the chemical, physical, and biological

integrity" of surface waters, recognizing that the integrity of a water resource was not solely

determined by its chemical and physical properties but by its biological and ecological properties

as well. The shift from chemical to biological measures was also a logical one, as successful

monitoring programs will focus on those parameters that are directly tied to management

objectives (Yoccoz et al. 2001; Nichols and Williams 2006; Lyons et al. 2008; Lindenmayer and

Likens 2009); if water resource managers cite biological integrity as an explicit management

objective, then successful monitoring schemes will incorporate relative biological measures.

Metrics included in an IBI generally draw on established ecological principles concerning the structure and function of aquatic ecosystems. In Karr's (1981) original IBI, 12 metrics based on fish collection data were used to measure biotic integrity (Table 4-1). Exclusive use of fish was justified based on availability of life-history data, inclusion of a large range of trophic levels, ease of identification, public familiarity, ubiquity, and direct applicability to the "fishable" waters goal of the Clean Water Act (Karr 1981). Metrics included total species richness, species richness within specific taxonomic groups, presence of intolerant species, sample abundance, and sample proportions of tolerant species, specific trophic groups, and diseased individuals. To select these metrics, Karr (1981) drew on the body of ecological literature, including evidence to support various tolerances of fishes to anthropogenic stressors and knowledge of the trophic relationships among fish species in aquatic systems.

Each of the metrics selected for inclusion in an IBI represents a particular component of the ecosystem considered by ecologists to be important for the biotic integrity of the water resource. If biotic integrity is an explicit management objective, the individual ecosystem components measured by the IBI metrics may be considered sub-objectives, forming an objectives hierarchy for aquatic resource management. (Figure 4-1).

However, if biotic integrity and its components are explicit management objectives, this implies that they have some associated value, whether assigned by managers, the public, or even by scientists. Objectives are in fact subjective; that is, they are dependent upon the values of those who set them. Indeed, if ecologists decide what ecosystem components are "important" for biotic integrity and ecosystem function, they are making value-based judgments, drawing on their own experience and expertise as well as on their personal values. It follows that whereas ecologists will likely agree on the value of biotic integrity, they will just as likely disagree on the

specific components used to define and measure it. In subsequent modifications of Karr's (1981) original IBI, authors have provided ecological justifications for using different taxa and for changing, adding, or removing specific metrics (Karr 1992; Simon and Lyons 1995; e.g., Steedman 1988; McCormick et al. 2001). Yet in spite of the most thorough and ecologically-sound justifications, disagreement persists as to the best metrics to use in a given aquatic system (Simon and Lyons 1995; Karr and Chu 2000; Norris and Hawkins 2000; Diaz et al. 2004; Hawkins 2006; Ruaro and Guiani 2013). This disagreement is fundamentally linked to the value-based nature of the IBI.

The subjectivity and flexibility of the index have been criticized by some ecologists as weaknesses of the IBI, purportedly because these traits prevent the index from being repeatable, defensible, and easily transferable from system to system (Norris and Hawkins 2000; Diaz et al. 2004; Doledec and Statzner 2010; Ruaro and Guiani 2013). However, in the context of structured decision making, the IBI's subjectivity and flexibility may instead be considered strengths of the index, as well-defined value-based objectives serve as the foundation for the structured decision making process (Gregory and Keeney 2002; Ohlson et al. 2005; Gregory and Long 2009; Gregory et al. 2012; Conroy and Peterson 2013). Furthermore, if biotic integrity is considered an objective, it must be context-dependent; that is, the definition of biotic integrity must change based on the system at hand and on the temporal and spatial management context of that system. Choosing IBI metrics that are specific to a management context will increase the likelihood of meeting management objectives, contribute knowledge and data to those areas where it is most needed, and decrease the risk of fiscal waste.

The flexibility of the IBI as it is used within the framework of structured decision making may also address other criticisms of the index cited in the literature, such as the tendency for

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correlation and overlap among metrics. In a structured decision making approach, this drawback may potentially be addressed by thoughtful and thorough objective setting. Although there is a general consensus among IBI practitioners that redundancy among metrics should be minimized (Karr 2006; Stoddard et al. 2008), correlated metrics are sometimes retained in an IBI because they are cited to independently represent some value or ecological function otherwise unrepresented in the index (e.g., Bowen et al. 1996; O'Neil and Shepard 2011; Carlisle et al. 2012). This seems to imply that minimizing redundancy is at odds with ensuring a complete accounting of all components of biological integrity. However, within a structured decision making framework, objectives should be both non-redundant and complete (Runge et al. 2011); that is, objectives should be distinct from each other and should account for all valued components of ecological integrity. In this context, redundancy should be defined by the extent to which each objective represents a similar component of biological integrity, and should not necessarily be determined by statistical correlation (Karr and Chu 1999; Karr 2006; Stoddard et al. 2008). Furthermore, some redundancy among metrics may be reduced by adding structure to the objectives hierarchy. For example, to minimize redundancy among taxa-specific richness and total native species richness, a hierarchical level may be added so that taxa-specific richness becomes a subordinate objective to total richness (Figure 4-2).

Another commonly cited weakness of the IBI is the requirement of reference sites to which the biotic integrity of all other sites is compared, and on which the extent of integrity at each site is dependent (Gergel et al. 2002; Roset et al. 2007; Borja et al. 2009; Pinto et al. 2009; Hawkins et al. 2010). In the framework of structured decision making, reference sites may serve as a source for justifiable objective targets, but because objectives are value-based, managers and decision makers have the flexibility to alter these targets as needed. For example, managers

might decide to increase an objective target above levels at a reference site if the target would be less than what managers believed was desirable or attainable. On the other hand, if a reference site were pristine, managers might decide to set lower targets to make them more realistic in terms of project scope and available resources. Furthermore, in cases where a reference site is unavailable, managers could reasonably set objective targets with historical data or with data from different systems. In the framework of structured decision making, a reference site is essentially optional, as long as managers are able to set satisfactory objective targets without it.

As it was designed, the IBI was intended to measure the effects of multiple anthropogenic impacts without directly addressing specific mechanisms. This lack of information concerning mechanism is another oft-cited disadvantage to using the IBI for conservation management, and many cite the inadequacy of continuing to measure impact without examining cause and potential actions for change (Gergel et al. 2002; Suter et al. 2002; Angradi et al. 2009; Pinto et al. 2009; Hawkins et al. 2010). In order to apply management actions that will preserve, conserve, or restore biotic integrity, hypotheses must be developed that link management actions (or no action) to index components. In structured decision making, these hypotheses are represented as potential *consequences* of management actions on defined management objectives. Depending on the desired level of complexity, managers may choose to focus on a single, well-developed hypothesis that describes the effect of management action *a* on management objective *x*; or if there is substantial disagreement among experts as to the hypothesized effect, more than one competing hypothesis may be represented. In the case of multiple competing hypotheses or where there is considerable uncertainty in the mechanism hypothesis, monitoring programs would include a data collection component aimed at reducing this uncertainty (Yoccoz et al. 2001; Nichols and Williams 2006; Lyons et al. 2008; Lindenmayer and Likens 2009).

Connecting the objective hierarchy given in an IBI to potential consequences of management actions provides the necessary step that takes information concerning aquatic systems from mere description to conservation action.

Using the IBI in a structured decision making framework addresses many of the cited weaknesses of multi-metric indices, and may also maintain many of their cited advantages, such as their ease of use and single-value simplicity. In a structured decision making framework, managers and decision makers choose the level of process complexity, including the spatial and temporal scope of the decision (e.g., single site or watershed, this year or the next 30 years), the number of objectives (IBI components), how to measure those objectives (e.g., simple counts or mathematical estimation), and what models will be used to describe the impact of management actions on defined objectives (e.g., conceptual or mathematical, single or multiple competing). With regard to the simplicity of a single value, structured decision making includes a process for evaluating management alternatives that often entails summing valuation scores across objectives (IBI components) and evaluating alternatives based on the highest score. This process is very similar to Karr's (1981) original IBI scoring method and retains the clarity of a single value while also explicitly incorporating hypotheses that describe mechanistic relationships between management actions and system response. The ecological theory that serves as the basis for the metrics may also be maintained; managers and involved scientists determine what information will be used to set objective targets and to develop models that describe action consequences. Additionally, the potential to include multiple hypotheses that describe impact can both increase the robustness of management decisions and account for any contention among scientists with differing views of system process.

As originally developed, the IBI had a purely descriptive role: to describe the state of an aquatic system relative to some known reference state. Metrics used to quantify system state were chosen by ecologists as ecosystem components that were necessary or important for maintenance of biotic integrity. Yet because of inherent differences among sites and differences in expert opinion, much disagreement has persisted as to the best methodologies for effective use of multi-metric indices. The subjective nature of the IBI, however, lends itself well to serving as the basis for an objective hierarchy in structured decision making. Much of the criticism of multi-metric indices has been associated with a lack of action, with management agencies doing well to describe the extent of biotic integrity across their management areas, but falling short in acting to make changes for maintenance or improvement of system state. Structured decision making provides the framework to use descriptive information of system state to make management actions that meet the objective of biotic integrity. Viewing the IBI as an objectives hierarchy establishes a framework for incorporating biotic integrity into the structured decision making process, which involves identifying alternatives and consequences of those alternatives on defined objectives, considering trade-offs of alternatives among objectives that are potentially competing, and finally making a decision to select an alternative that best meets established objectives. The structured decision making approach also provides a framework for incorporating system uncertainties, perceived risk, and linked decisions, that is, decisions that are dependent upon one another, as in the case of the iterative decision making of an adaptive management approach. To facilitate application of the index of biotic integrity in a structured decision making framework, we provide an outline to guide managers through the steps of structured decision making using the IBI, and then use an example decision problem to demonstrate how the IBI may be incorporated into the SDM process.

Steps to Incorporate an IBI into Structured Decision Making

Structured decision making involves a deliberate set of steps proven to help lead decision makers to selecting better decision options given available data. Here we outline steps for managers to incorporate an index of biotic integrity into a structured decision making framework based on methods described by Hammond et al. (1999) and Gregory and Keeney (2002), applied by Blomquist et al. (2010) and McGowan (2013), and used as the basis for the U.S. Fish and Wildlife National Conservation Training Center's course on structured decision making (Runge et al. 2011). These methods deconstruct a decision into five distinct components: the problem, objectives, alternatives, consequences, and trade-offs, and is sometimes described as the "PrOACT" process (Hammond et al. 1999). The approach is described as follows:

1. *Identify the problem.* To begin, managers and decision makers must think carefully about the problem at hand. They should ask questions such as: Why was this water body chosen among others for an IBI? What makes it unique? What are the perceived threats to biotic integrity? Was there a particular trigger for this decision context? Who has the authority to make a decision for action? What is the role of the manager? What is the temporal and spatial scope of the problem? What are the key uncertainties in the system? Are there any perceived risks associated with taking action? Is this decision a linked decision; that is, is this decision dependent on any other decisions or are other decisions dependent on it? Carefully describing the problem will assist managers in focusing the remainder of the decision making steps on the problem at hand without getting distracted by peripheral elements and problems beyond the scope of the decision.

2. *Define the objectives.* To incorporate an index of biotic integrity into structured decision making, managers should first consider each component of the IBI as a management

objective in an objectives hierarchy (Figure 1). However, it is imperative that managers

carefully evaluate these objectives to ensure they are appropriate for the specific study system,

management context, and decision problem being considered. Managers should eliminate

objectives that are not of interest or that are outside of the problem scope, but should especially

evaluate whether established IBI components cover all objectives of the management agency and

its partners or stakeholders. It is also important that redundancy among objectives is minimized;

this may be accomplished by eliminating objectives or by adding additional levels to the

objectives hierarchy (Figure 2). Inclusion of a full complement of distinct management

objectives is necessary for successful implementation of structured decision making.

    3. *Develop potential alternatives.* All considered alternative management actions

should be hypothesized to directly influence stated objectives. Alternatives may be considered

singly or as "portfolios" of several alternatives that each addresses different objectives or sets of

objectives. At least during the initial phases of alternatives development, managers should allow

themselves to be as creative as possible, with the judgment of possibility or practicality being left

for later stages. Creative thinking and a wide range of potential management alternatives will

lead to better decision making by increasing the chances that the best management alternative is

among those considered.

    4. *Describe the consequences.* At this step, managers will use the ecological literature,

collected data, expert opinion, and their own experience to describe how proposed management

alternatives will alter defined management objectives. These hypothesized links, or models, may

be simple and conceptual or complex and mathematical. The kind of models used will depend

on the degree of system uncertainty, desired model precision, and the values selected to measure

management objectives. It should be noted that decision making in even the most basic sense

involves use of models; we use conceptual models to make decisions every day. When decisions are complex and associated with high uncertainty or risk, models must be explicit to ensure the decision process is transparent and defensible.

5. *Evaluate trade-offs with optimization.* Once the consequences have been described, in some cases the best alternative is a clear choice, out-performing all others in meeting management objectives. However, because each alternative may have different impacts on different objectives, the best alternative is not always obvious. Optimization tools provide managers some assistance in making these difficult decisions by evaluating the trade-offs among the consequences of each management alternative. Many optimization tools are available, ranging in complexity from simple consequence tables to Bayesian decision networks to adaptive stochastic dynamic programming. The optimization tool that managers use will depend on personal preference, available resources, the degree of system uncertainty, and the type of models used to describe the consequences of each alternative.

6. *Repeat as necessary.* For successful application of structured decision making, managers should first strive to work through these five steps within a relatively short time frame (e.g., hours to days) as a form of rapid prototyping (e.g., see Blomquist et al. 2010). Once trade-offs of each alternative have been evaluated and the best alternatives become clear, managers should then re-assess each step in light of the best alternatives. In general, if managers do not feel that the selected alternatives are valid or appropriate, it is likely that one or more important factors have been overlooked. Does the problem need to be re-defined? Have managers missed any key uncertainties? Is there a level of risk that has not been accounted for? Have any objectives been missed? Were the evaluated alternatives too narrow; are there other possible alternatives that have not been considered? Do managers need to use different models to better

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describe the consequences? Would a different form of optimization have been more appropriate? Steps should be repeated and re-evaluated until managers and decision makers are satisfied with the structure of the process and with the resulting best alternatives. Ensuring all steps have been carefully followed will ensure the best possible decision.

7. *Make a decision.* Managers must also realize that not making a decision or waiting to make a decision are decisions in themselves and have their own associated consequences; unless these are included as valid options for management, managers should strive to complete the structured decision making process as quickly as possible. Once sufficient effort has been contributed to the process and trade-offs have been adequately assessed, managers should implement their best alternative. If the decision is part of a series of linked decisions, such as in the case of adaptive management, managers will continue to collect data after decision implementation to assess whether objectives were met and to improve modeled hypotheses for the next iteration of decision making.

It should be noted that although structured decision making successfully guides quality decision making, it does not always lead to the correct decision. Without perfect knowledge and foresight, even the best decision can sometimes lead to an undesirable result. Including risk in decision making can help mitigate negative outcomes by making appropriate modifications to the weights of alternatives and consequences. On the other hand, in cases where risk is low, negative results can add valuable information to the pool of knowledge, improving the next management decision that is made.

To demonstrate the application of these methods for incorporating the index of biotic integrity into structured decision making, here we provide an example of a specific decision problem in aquatic natural resource management.

Application

The index of biotic integrity provides the basis for a statewide aquatic biomonitoring protocol in the state of Alabama, with the overarching goal of gathering data to improve management of aquatic natural resources by the state's Department of Conservation and Natural Resources (ADCNR), the agency responsible for protecting and enhancing the state's fish and wildlife resources (ADCNR 2009; O'Neil and Shepard 2011). An IBI has been used partly because it is the established standard protocol for several other agencies across the state, including the Tennessee Valley Authority, the Geological Survey of Alabama (GSA), and the Alabama Department of Environmental Management (O'Neil et al. 2006). In addition, the state cites strengths and advantages of an IBI that include time efficiency, low cost, widespread and tested use by management agencies, scientific credibility, and simplicity (O'Neil et al. 2006; O'Neil and Shepard 2011).

In 2012, the governor of Alabama directed the Alabama Water Agencies Working Group (AWAWG) to recommend a statewide water management action plan to equitably manage the state's water resources (AWAWG 2013). The working group is comprised of five agencies with jurisdiction over water and water-related resources across the state, including the ADCNR. In 2013, the working group submitted a water resources management policy report to the governor, which proposed a process to develop and implement an initial water management plan and outlined potential policy options and recommendations (AWAWG 2013). As part of this proposed process, the working group acknowledged the need to develop adequate instream flow criteria for aquatic ecosystems and other uses such as recreation, navigation, power generation, waste removal, and consumption (AWAWG 2013). Because of the investment that has been made in collecting IBI data across the state, it would be desirable for the ADCNR to use the IBI

to assist their decisions and recommendations concerning ecological instream flow needs. Furthermore, potential to incorporate the IBI into instream flow decision making was identified as a specific benefit to justify the development of a state-wide IBI (O'Neil and Shepard 2011). However, a process for doing so has not yet been developed.

Using the framework outlined in the previous section, we illustrate how the state agency could integrate the IBI into their instream flow criteria for Alabama's future water management plan.

Identify the problem – The first step in applying an SDM approach is to clearly define the problem at hand. In this example, the agency is looking to make instream flow recommendations for Alabama's rivers and streams that meet the agency's goals of ecological integrity. While the ADCNR may have recognized the need to develop instream flow criteria long before now, the issuance of the governor's directive and the working group's process for water plan development has increased the urgency to make these recommendations. The governor's directive and the process for plan development established the timeframe for action (within 1-2 years of the formation of the "Instream Flow Focus Panel," if the recommendation to form the panel is adopted; AWAWG 2013) and the initial spatial scope of the problem (the entire state of Alabama). However, for the purposes of this exercise, we will limit the scope of the decision to Alabama's Valley and Ridge/Piedmont "ichthyoregion" (an ichthyoregion is a region with a unique ecology and fish community; O'Neil and Shepard 2011), for which an IBI has been developed by the GSA (O'Neil and Shepard 2011). In practice, the resource agency may choose to develop separate recommendations for different regions of the state or classes of streams; this same process would be applied to any region or stream class.

As noted by the AWAWG (2013), instream flow criteria will need to take into account the natural inter- and intra-annual flow variability that is necessary to support a functioning ecosystem (Poff et al. 1997; Bunn and Arthington 2002; Annear et al. 2004). However, much uncertainty remains with regard to the specific instream flow needs and requirements of individual species, and data to support hypotheses of the connection between flow and ecological variables are limited. This uncertainty is compounded by Alabama's high levels of aquatic biodiversity, which are among the highest in the world (Lydeard and Mayden 1995). The agency risks threatening an already largely imperiled aquatic fauna if resulting instream flows are too low, but risks threatening the state's potential for economic growth if recommended flows are too high.

The agency's recommendations for instream flows to support ecological integrity will eventually be connected to broader policy decisions that will take into account multiple competing water uses, such as municipal water supply, power generation, and recreation. If the guidance is eventually accepted, there still remains uncertainty with regard to implementation, as a legal and regulatory structure would need to be established before recommendations could be carried out. Furthermore, there is no guarantee that the guidance will be accepted – either in part or in full. This will be up to the ultimate decision makers – the lawmakers and citizens of Alabama.

Objectives – In this example, we assume that the resource agency is primarily interested in increasing or maintaining the biological integrity of Alabama's streams and rivers. The next step is to identify how "biological integrity" will be defined and measured. The IBI, composed of individual metrics that together represent biological integrity, provides both definition and measurement of this fundamental objective. As stated previously, to incorporate the IBI into an

SDM approach, the individual metrics of an IBI should be considered sub-objectives of biotic integrity, so that together they form an objectives hierarchy (Figure 4-1). The IBI developed by the GSA for Alabama's Valley and Ridge/Piedmont ichthyoregion consists of twelve individual metrics, which we will consider our twelve initial sub-objectives (Table 4-2). For each of these sub-objectives, the desired direction of movement (increase or decrease) and the aspired target value for each should be clearly identified (Table 4-2). The aspired target could be a specific function, threshold, degree of change, or simply a goal to minimize or maximize the objective. In this case, the desired targets for the GSA's IBI metrics are defined either by logarithmic functions that describe species richness in terms of watershed area, or simple threshold values (O'Neil and Shepard 2011; Table 4-2). Managers should carefully evaluate these targets to ensure that they accurately represent their management goals. In some cases, targets may need to be adjusted; for example, managers may consider adding a lower threshold to represent acceptable minimum values for the number of tolerant species, the % *Lepomis* species, or the percent omnivores and herbivores. Without minimum thresholds for these objectives, managers would be effectively valuing the absence of certain native species.

Because objectives are the criteria against which the decision or recommendation will be evaluated, the final set of objectives should also be specific to the decision context at hand. Managers should carefully evaluate the set of objectives derived from the IBI to determine if there are any additional objectives that should be added to the hierarchy, or if there are any that are not pertinent to this particular decision context. One objective that may need to be closely evaluated is the "number of intolerant species" objective. For the GSA's Valley and Ridge/ Piedmont IBI, intolerant species are those that are known to be sensitive to multiple stressors, including siltation, low dissolved oxygen, and chemical contamination (O'Neil and Shepard

2011). However, in the current example, the primary stressor is an altered flow regime; therefore, managers should think carefully about those species that may need to be added or even removed from this metric. For example, in an IBI developed for the flow-regulated Tallapoosa River, Bowen et al. (1996) included Tallapoosa shiner *Cyprinella gibbsi*, riffle minnow *Phenocobius catostomus*, and Tallapoosa darter *Etheostoma tallapoosae* among those species considered "intolerant" to altered flows. Bowen et al. (1996) also excluded lipstick darter *Etheostoma chuckwachatte* from the "intolerant" list; this decision may be supported by observations of relatively high abundance of lipstick darters in the flow-regulated Piedmont reach of the Tallapoosa River (E. Irwin, unpublished data).

Before proceeding to the next steps, managers should also examine potential relationships among objectives to determine if it would be useful or necessary to include additional levels in the hierarchy. Redundant objectives effectively weight the corresponding biological integrity component higher in the final decision or recommendation. Although giving more weight to one component over another may be desired in some cases, minimizing redundancy ensures that weights are given transparently and in a way that is easy to track and modify. Here, the objectives that aim to maintain or increase the number of shiner, *Lepomis*, and darter + madtom species are really subordinate under the objective to maintain or increase the number of native species, and could be structured in such a way to represent this relationship (Figure 4-2). Further structure could be added to the hierarchy by thinking of the rationale for including some of the metrics. For example, three of the objectives – percent omnivores and herbivores, percent insectivorous cyprinids, and percent top carnivores – are all part of a higher-level objective to account for the trophic integrity of a particular site. In addition, the two objectives that consider the "tolerance" of species, as well as the percent *Lepomis* objective, may be part of a higher-level

objective to ensure that species that are sensitive or insensitive to particular impacts are considered explicitly (Figure 4-2).

Alternatives – Once objectives are established, managers need to consider what alternative actions (or in this case, recommendations) will serve to meet these objectives. It is important that alternatives are always developed with an aim to meet objectives. Furthermore, in this case, because the decision context is specific to instream flows, alternatives will consist of actions specifically related to management of the flow regime. Initial stages of alternatives development should allow for as much creativity as possible to ensure a broad spectrum of actions and thus inclusion of a best alternative. However, it is helpful to have a starting point on which to build creative solutions. In this example, managers could begin by considering the flow management policies for Alabama's neighboring states, and use these policies as a basis for developing alternatives more specific to the decision context. Additionally, the scientific literature is rich with evidence describing the effects of different aspects of the flow regime on many ecological variables and processes. Hypotheses that link ecological objectives to specific flow components can also provide a sound basis for development of management alternatives.

For this example, we have selected a suite of potential recommendations that consists of five alternatives based on the policies of neighboring states and three alternatives based on a percentage of unregulated flow, for a total of 8 considered recommendation alternatives (Table 4-3). Brief descriptions of the instream flow policies of Alabama's neighboring states were provided in the AWAWG's (2013) water resources management policy report. The percentage of unregulated flow alternatives are based on the premise that an instream flow regime that follows an unregulated hydrograph will contain the elements of the natural hydrograph necessary to support a functioning river ecosystem (Poff et al. 1997; Bunn and Arthington 2002; Poff et al.

2010). Unregulated flows for a managed site are assumed to be proportionally equivalent by drainage area to streamflows at one or more nearby unregulated U.S. Geological Survey (USGS) stream gages. Whereas the alternatives presented here may be useful in practice, they are primarily meant to serve as examples. The most creative and applicable set of alternatives will be developed by the managers and decision makers directly associated with the decision context.

One important component of the structured decision making framework is the necessity to continually re-assess earlier steps of the process. At this point, it might become clear that some objectives cannot be achieved within the scope of the current decision. As stated above, alternatives should directly influence defined management objectives. However, because in this case alternatives are constrained to those tied to instream flow decisions, it is possible that not all management objectives can be addressed. If indeed there are any objectives that are not related to instream flow, they should be removed or set to the side for consideration under a different management context.

Consequences – The next step of SDM is to determine the consequences of each alternative on the defined set of management objectives. To do so, we must use models to define relationships between actions and objectives, and to make predictions regarding the outcome of each alternative. Ideally, we would have local empirical data linking each alternative to the defined management objectives. However, it is likely that such empirical data are limited, and it will therefore be necessary to develop hypothesized relationships based on the literature and the experience of resource managers. Decision makers should also enlist the expertise of scientists with knowledge in regional ecology to develop and refine hypotheses so that they are specific to the decision context at hand. Poff et al. (2010) present a thorough overview of key principles and methods for development of hypotheses that link instream flows to ecological objectives.

For this example, we use some basic flow-ecology hypotheses to establish a set of flow metrics that serve as means objectives to connect management alternatives to the fundamental ecological objectives (Table 4-4). The links between these flow objectives and the ecological objectives are represented by empirical models derived conceptually from the literature (Figure 4-3). For each of these models, we applied the basic assumption that ecological objectives are met when the median values of associated flow metrics are between the 25th and 75th percentile of unaltered, or run-of-river, conditions. Each model then predicts the deviation from desired ecological conditions that would occur as a result of deviations from run-of-river flow conditions.

To predict consequences at the scale of the Valley and Ridge/Piedmont ichthyoregion, we calculated flow metrics from USGS stream gage data from 13 sites within this geographic area that had at least 20 years of unregulated hydrologic data (Table 4-5; Figure 4-4). Hydrographs for each gage were modified to reflect each flow management alternative, and the deviation from run-of-river conditions was determined for each flow objective at each gage site. Predicted deviations from desired ecological conditions were then estimated from the empirical models, and for each ecological objective, consequence values were averaged across model results for all associated flow metrics (see Table 4-4). Consequence values were then averaged across gage sites to obtain a single value to represent the average consequence of each alternative on each ecological objective across the Valley and Ridge/Piedmont ichthyoregion (Table 4-6). See Table 4-7 for a sequential accounting of the steps taken to evaluate consequences for this example. Note that not all of the original established objectives (Figures 4-1 and 4-2) are represented at this stage. We have simplified the objectives hierarchy to include only those objectives tied to the flow-ecology hypotheses identified in Table 4-4 (Figure 4-5). In practice, managers and

regional scientists may develop other hypotheses that provide for inclusion of additional management objectives.

Trade-Offs – To evaluate how well each alternative performs with respect to the defined management objectives, managers need to examine the trade-offs among objectives that result when different alternatives are selected. When there are many objectives and alternatives and the relationships among them are complex, optimization tools provide the necessary structure to make such an evaluation possible. These tools range from simple to complex, and which tool is utilized depends on the complexity of the decision, the amount of uncertainty that is present, and on the personal preference of managers and decision makers (see Conroy and Peterson 2013 for an overview of various optimization methods). For this example we demonstrate the use of two different optimization tools: a simple consequence table and a more complex Bayesian decision network that allows for explicit incorporation of system uncertainty.

A consequence table provides a concise way for managers to compare alternatives in terms of defined management objectives. Raw consequence values are normalized and then added across objectives to determine the performance of each alternative. In this decision context, the consequence table has identified the "Unregulated 90" alternative as the best management recommendation given the objectives and the modeled hypotheses (Table 4-8). Although consequence tables do not explicitly incorporate uncertainty, the sensitivity of the result may be evaluated to determine whether the best alternative would change if decision components were altered. In this example, there is considerable uncertainty associated with the empirical models that are used to describe the links between flow metrics and ecological objectives. This uncertainty lies primarily in the shape and strength of each relationship, as the direction (positive or negative) of each response is generally supported by the literature. In this

example, if we increase or decrease the strength of the relationships among ecological metrics and the flow metrics associated with baseflows and small floods, for example, the consequence values of each alternative change, but the ranked best alternative and the rankings of the other alternatives do not change from the initial results (Tables 4-9 and 4-10).

Another tool useful for evaluating the performance of alternatives in terms of management objectives is a Bayesian decision network, or Bayes net. A Bayes net links action alternatives, means objectives, and fundamental objectives by way of conditional probability tables that incorporate uncertainty associated with each defined relationship (Figure 4-6). The best decision is determined by calculating which decision alternative optimizes identified objectives, based on defined conditional probabilities. For this example, conditional probabilities describing the link between alternatives and flow metrics were developed by evaluating how often calculated flow metrics fell within a given percentile range of the corresponding run-of-river flow metric; those describing the link between flow metrics and ecological objectives were developed based on the established flow-ecology models (Table 4-4; Figure 4-3). For both the flow and ecological metrics, conditional probabilities represent the probability of achieving objective targets; the value of each alternative represents how well it meets biotic integrity as defined by the ecological objectives. Similar to the consequence table described previously, the resulting best management alternative of the Bayes net in this example is the "Unregulated 90" alternative. The results of a Bayes net may also be evaluated with a sensitivity analysis to determine whether the results would change under various scenarios. For example, if the conditional probability tables are modified to ignore the uncertainty in the flow-ecology relationships, the best alternative is not different from the original result, but the

rankings of the "Unregulated 85/80" and "Seasonally-variable % of MAF" alternatives change (Figure 4-7).

So far in this example, each of the ecological objectives have been weighted equally; however, managers could decide that one or more objectives have more bearing on the decision than others. Such weighting would consequently have an impact on the value of each decision alternative. For example, increasing the weight of the species richness objective so that it is twice as important as other objectives changes the ranking of some of the management alternatives (the "Unregulated 85/80" and "Seasonally-variable % of MAF" alternatives), though it does not change the overall best decision (Figure 4-8). In addition, there has yet been no accounting of potential risk in this decision process. Risk of a negative outcome should be incorporated especially when there are threatened and endangered species or other high-risk factors impacted by the decision. To incorporate risk into decision making, managers could simply examine the uncertainty in the result of each management alternative, or an additional node may be added to the network that is directly related to risk attitudes of the managers and decision makers (Figure 4-9). For example, to incorporate the risk of species loss in the current context, managers could aim to maximize the chance of minimum loss (90-100% native species), minimize the chance of maximum loss (0-10% native species), or maximize the chance of a minimum performance for this objective (e.g., at least 75% native species), depending on the risk attitudes of the decision makers. When risk of species loss is incorporated in the current decision context by maximizing the chance of minimum loss, the best alternative remains the same, though it increases in differential value compared to other alternatives, and the rankings of the "Unregulated 80/70/75" and "Seasonally-variable % of MAF" alternatives shift (Figure 4-9).

Repeat as Necessary – Before making a decision, managers should review each step of the decision making process to ensure that no important detail was overlooked. This is particularly important if there is a lack of satisfaction with the resulting best alternative. Managers and decision makers should confirm that all pertinent objectives, any new creative alternatives, or missed sources of data that would reduce model uncertainty are included. In the current example, managers might decide that there are additional objectives relative to the decision context that should be considered. For example, it might be desirable to include objectives for other important taxa groups, such as freshwater mussels or riparian plant communities, or for other relevant fish guilds, such as benthic fluvial specialists. Whereas the IBI may be a valuable starting point for decision making, it should not limit the scope of management objectives or decision making. Managers must be aware that objectives that are not identified will have no assurance of achievement. Therefore, the suite of objectives included in any decision process should be representative of the full complement of context-specific management goals.

Make a Decision – Once trade-offs are examined, the best alternative (or alternatives) determined, and managers and decision makers are satisfied with the SDM results, a decision should be implemented. Especially in cases where there is substantial uncertainty in the relationships among decision components, a monitoring protocol that evaluates the decision against defined objectives is essential (Yoccoz et al. 2001; Nichols and Williams 2006; Lyons et al. 2008; Lindenmayer and Likens 2009). Fortunately, the state of Alabama already has a framework for collecting IBI data, but this framework may need to be adjusted slightly so that information tied directly to reducing decision-specific uncertainty may be collected.

Furthermore, if additional objectives are included in the decision making, these measures should also be incorporated into the monitoring protocol.

Because monitoring will provide new information and may result in a reduction of uncertainty that could lead to a different best alternative, there should also be a framework for re-visiting the decision making process to ensure that the best management actions are being pursued. This flexibility can be difficult to incorporate into policy decisions, but it may be possible to establish a periodic review, for example every 10 to 15 years, into the policy itself. In effect, this would be equivalent to a type of formalized adaptive management, where new information is incorporated into the decision process for iterative decision making over a long time frame. With the uncertainty of a changing climate, population demographics, and associated impacts on society's goals and values, inclusion of some kind of flexibility into water management policy may be necessary to ensure continued attainment of resource goals. Our world is constantly changing, and we must accept that what is a best decision today may not be the best decision in the future.

For the SDM example given here, we only considered objectives associated with finding a best water management recommendation to maintain ecological integrity. There is of course another decision linked to this recommendation, wherein a water management policy will be chosen that will take into account multiple additional objectives including recreation, navigation, power generation, waste assimilation, and water supply (AWAWG 2013). The recommendation made based on ecological objectives will also need to be evaluated against these other objectives. The framework presented here can certainly be used for these broader decisions by including additional water users and stakeholders, thereby incorporating additional objectives and ideas for creative decision alternatives. There would also be a different decision maker – state legislators

and ultimately the citizens of Alabama – as well as additional water management risks, such as those associated with municipal water supply security. By considering this broader decision, the levels of complexity and uncertainty no doubt increase in magnitude. However, this should be all the more reason to enlist tools and frameworks to provide the structure and transparency necessary to make good decisions, such as is provided by the structured decision making process described here.

Discussion

Environmental flow management is a topic covered intensively in the literature, with a large focus on methods to determine the flows necessary to support ecological structure and function of rivers and streams (Poff et al. 1997; Bunn and Arthington 2002; Annear et al. 2004; Tharme 2010; Zimmerman and Poff 2010). Drawing on the wealth of literature of the past decades, Poff et al. (2010) outlined a comprehensive framework for developing regional flow standards, known as the ecological limits of hydrologic alteration, or ELOHA. Part of this framework includes a social component that involves incorporation of goals and objectives, integration of environmental flow standards, and implementation of flow management actions; however, the authors clearly articulate that the focus of their presentation of the ELOHA framework was specifically on the science and the challenges of determining the ecological consequences of flow management (Poff et al. 2010). In the language of structured decision making, the ELOHA framework discussed by Poff et al. (2010) focused on the *consequences* of flow management *alternatives* on ecological *objectives*.

It follows that the framework presented herein for integrating the index of biotic integrity into structured decision making, and the example provided for applying this framework in the

context of flow management, is strongly compatible with the ELOHA framework. The hydrologic data, ecologically-relevant flow metrics, and flow-ecology hypotheses that are integral parts of ELOHA were also central to the SDM process in our example. A structured decision making process also provides the link for incorporating these environmental flow standards into a rigorous social process by addressing the important elements of objective setting, alternatives development, and trade-offs comparison. The ELOHA framework and the SDM framework can work in concert to ensure successful environmental flow management, whereby the ELOHA process aims to articulate the consequences of flow management and alteration on ecological objectives, and the SDM process aims to use these linkages to ensure that the best decisions are made to meet the ecological needs that environmental flows are intended to serve.

Instream flow management decisions are of course just one application of the described structured decision making framework for IBIs; additional contexts in which this framework may be applied include stream channel restoration, dam siting and removal, and riparian and watershed land use and protection. However, note that these contexts are not focused directly on management objectives, but rather on different types of management actions. To most effectively meet aquatic resource management objectives, a set of alternatives will encompass multiple types of management actions reflecting various hypotheses of impact, including but not limited to instream flow modifications, riparian land use practices, species reintroduction, and public policy.

Critical to the development of a comprehensive set of alternatives is clear definition of the specific problem at hand. This problem may or may not be ecologically-based. In the example of making instream flow recommendations for the state of Alabama, the identified

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problem was less about ecology and more about policy. The state needed to make a policy

decision aimed toward protecting and enhancing the resource, but there was no specific

ecological problem identified (e.g., declining species or loss of functional groups). Rather, the

IBI served to provide the ecological objectives necessary to give direction to this policy problem.

Yet because an IBI is often pre-determined, it will likely not be adequate to represent the

objectives of all aquatic resource management decisions. For example, the Valley and

Ridge/Piedmont IBI developed by O'Neil and Shepard (2011) was not created specifically for

flow-specific stressors, and therefore did not include resource objectives directly tied to flow

impacts, such as the percent of benthic fluvial specialists, a metric that was included in a flow-

specific IBI developed for the Tallapoosa River, Alabama (Bowen et al. 1996). On the other

hand, there were several IBI metrics that were not incorporated into the Alabama flow

management decision process because of a lack of direct connection to the decision context.

Because the IBI and other multimetric indices like it are touted for their flexibility to

adjust to various geographical areas (Karr 1991; Hering et al. 2006b; Gabriels et al. 2010), they

should also be flexible to adjust to various decision contexts. Ensuring that IBI metrics are

specific to a decision context will increase the likelihood of making a decision that will meet

identified management objectives. This required specificity for each decision context may bring

into question the value of continued collection of IBI data without identification of the decision

contexts for which the data will be used. However, if a resource agency ensures that an IBI fully

represents the agency's resource objectives for the spatial scale and extent at which the IBI was

created, it will also ensure that the collected data will be applicable to any decision context

aimed at protecting and enhancing the resources to which the agency is entrusted. It follows that

in some decision contexts, some objectives may not be addressed (as in the flow management

scenario), but under the described framework, there will also be additional management strategies being pursued that aim to achieve the full suite of resource objectives.

Choosing IBI metrics based on how closely they are linked to resource agency objectives could be a major shift from how metrics are often currently selected. In many cases, IBI metrics are chosen based on how well they characterize identified "disturbed" sites, and how correlated they are to various indicators of habitat degradation (e.g., local population density, phosphorus load, and percent urban land cover) rather than on their value for characterizing ecological integrity alone (e.g., Karr and Chu 1997; Karr 1999; Hering et al. 2006b, O'Neil and Shepard 2011). This logic is based on the original development of the IBI as an index to assess anthropogenic impacts on the biological "condition" of water resources. Choosing metrics based on degradation ensures that the IBI accurately detects anthropogenic disturbance. This method of IBI metric selection is fundamentally different from selecting metrics based on established objectives. The former is focused on measuring anthropogenic disturbance; the latter is focused on measuring specific ecological components of identified importance. In each case, the fundamental management objectives are different, and will have bearing on how decisions are made.

It could be argued that selecting ecological metrics based on identified indicators of anthropogenic disturbance is not materially better than using those indicators of disturbance alone, since defining ecological metrics based on disturbance metrics requires the assumption that the characteristics of disturbance are fully known. If we fully know what characterizes disturbance, it should not be necessary to collect biological data to support a known pattern. We should simply be able to use the disturbance metrics to find disturbed sites and make decisions based on that information alone. This reiterates the importance of establishing objectives that are

tied directly to values, and monitoring metrics that are directly related to these objectives. If the fundamental goal is ecological integrity, then metrics that strictly and directly measure ecological integrity should be included and monitored. Managers can then link these ecological metrics to identified metrics of anthropogenic disturbance to develop hypotheses of response, as well as to develop alternatives for meeting the defined objectives.

In all cases, linking management objectives to action alternatives with hypotheses of impact both ensures that management actions are directly aimed at achieving identified objectives, and also importantly connects resource objectives to a hypothesized mechanism of response. Ideally, to develop action alternatives most likely to achieve objectives, a full exploration of the hypotheses of impact and response should be conducted. In our example of flow management decision making, hypotheses were relatively limited both for the sake of the decision context (establishing instream flow standards) and for the sake of example. However, in practice the hypotheses of response could be expanded to include those linked to sub-daily flows and flow management practices such as hydropeaking power generation. In a broader decision context for achieving management objectives, additional hypotheses related to nutrient and sediment inputs, stream connectivity, and habitat availability, for example, could be included to find management alternatives directly aimed at achieving biotic integrity.

Thus far, we have been considering the IBI in decision contexts exclusively controlled by the aquatic resource agency. However, in most water management scenarios, decisions are not made in a vacuum; multiple other stakeholders, including other agencies, organizations, municipalities, industries, and citizens groups, play important roles in defining competing objectives (e.g., water supply, power generation, and recreation) and helping to develop creative management alternatives. In the example of making decisions for Alabama's instream flow

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policy, understanding how each alternative impacts other competing interests will be critical to determining which alternative is truly the best decision in the broader water resources context. Incorporating competing objectives will also help to further distinguish some of those alternatives that were similarly ranked in their ability to meet defined objectives. Independent of competing objectives, it was unsurprising that the best alternative for instream flow policy was the alternative that provided flows most closely resembling natural conditions, as the incorporated flow-ecology hypotheses were largely dependent on the natural flow regime paradigm (Poff et al.1997; Bunn and Arthington 2002; Annear et al. 2004; Poff and Zimmerman 2010). When additional management objectives are considered, it is likely that some of the other highly-ranked alternatives that have more potential flexibility for other water uses will rank even higher in their ability to meet multiple competing objectives.

Because of the widespread use of the index of biotic integrity and other multimetric indices and the availability of associated long-term monitoring datasets, there is a critical need for its integration into the decision making and policy recommendations of resource managers. With its established and scientifically-supported ecological metrics, the IBI is ideally suited for incorporation into a formal structured decision making process to support aquatic resource management. An SDM approach links identified IBI resource objectives to management actions designed to achieve these objectives, providing a framework to ensure that collected IBI data are used to the benefit of the aquatic resources they represent. Furthermore, when SDM is repeated in an iterative manner to support an adaptive approach to management, information gathered through monitoring can improve future decisions by evaluating management success and updating hypotheses of system response. In this way, managers have the means to continue to

make defensible, informed decisions, ensuring the continued protection and enhancement of managed aquatic resources into the future.

Table 4-1. The 12 metrics that comprised the original index of biotic integrity (IBI) as described by Karr (1981). Karr's IBI was based exclusively on fish collection data.

IBI Metrics
Species composition and richness
Number of species
Presence of intolerant species
Species richness and composition of darters
Species richness and composition of suckers
Species richness and composition of sunfish (except green sunfish)
Proportion of green sunfish
Proportion of hybrid individuals
Ecological factors
Number of individuals in a sample
Proportion of omnivores
Proportion of insectivorous cyprinids
Proportion of top carnivores
Proportion with disease, tumors, fin damage, and other anomalies

Table 4-2. The 12 metrics of the Geological Survey of Alabama's index of biotic integrity (IBI) for Alabama's Valley and Ridge/Piedmont ichthyoregion. These 12 metrics were considered initial sub-objectives in an objectives hierarchy used within a structured decision making framework for incorporating the IBI into natural resource management decision making. For each sub-objective, the desired direction of movement and target values are given. Objective targets are defined either by logarithmic functions that describe species richness in terms of watershed area or by simple threshold values as defined by O'Neil and Shepard (2011). DELT = deformities, eroded fins, lesions, and tumors.

IBI Metric	Direction	Target Values
1. Number of native species	$\geq$	$12\log(\text{area})+10$
2. Number of shiner species	$\geq$	$2\log(\text{area})+3$
3. Number of *Lepomis* species	$\geq$	$2\log(\text{area})+2$
4. Number of darter + madtom species	$\geq$	$2\log(\text{area})+2$
5. Number of intolerant species	$\geq$	2
6. Percent individuals as tolerant species	$\leq$	15
7. Percent individuals as *Lepomis*	$\leq$	10
8. Percent individuals as omnivores and herbivores	$\leq$	15
9. Percent individuals as insectivorous cyprinids	$\geq$	60
10. Percent individuals as top carnivores	$\geq$	2
11. Percent individuals with DELT + hybrids	$\leq$	0.2
12. Percent individuals as simple nonlithophilic spawners	$\geq$	35

Table 4-3. Decision alternatives evaluated in an example structured decision making framework designed to inform instream flow recommendations for Alabama's water resource planning process. State policy-based alternatives are based on current state instream flow policies; brief descriptions are provided in the Alabama Water Agency Working Group's policy report (AWAWG 2013). For the unregulated percentage-of-flow alternatives, unregulated flows are assumed to be proportionally equivalent by drainage area to streamflows at one or more nearby unregulated USGS stream gages.

Alternative Instream Flow Recommendations	Description
≥ 7Q10 (Mississippi)	Instream flows will be greater than or equal to the historical 7Q10, that is the annual minimum 7-day mean flow that occurs on average once every 10 years
Monthly 7Q10 (Georgia)	Instream flows will be greater than or equal to the monthly 7Q10, that is the monthly minimum 7-day mean flow that has a recurrence interval of once every 10 years
Seasonally-variable % of MAF (Georgia)	Instream flows will be greater than or equal to 30% mean annual flow (MAF) Jul-Nov, 60% MAF Jan-Apr, and 40% MAF May-June, Dec
≥ 20% above SMF (Tennessee)	Instream flows will be greater than or equal to 20% of the available flow above the historical September median flow
≥ 50% above SMF (Tennessee)	Instream flows will be greater than or equal to 50% of the available flow above the historical September median flow
Unregulated 90	Instream flows will be greater than or equal to 90% of unregulated flows.
Unregulated 85/80	Instream flows will be greater than or equal to 85% of unregulated flows Aug-Nov, and 80% of unregulated flows Dec-July
Unregulated 80/70/75	Instream flows will be greater than or equal to 80% of unregulated flows Aug-Nov, 70% of unregulated flows Dec-Jan, and 75% of unregulated flows Feb-Jul

Table 4-4. A set of basic hypotheses relating streamflow metrics to ecological metrics that serve as objectives within a structured decision making framework developed to incorporate the index of biotic integrity into management decision making. Identified flow metrics serve as means objectives to relate management alternatives to identified ecological objectives. The links between flow objectives and ecological objectives are represented by empirical models derived conceptually from the literature; see Figure 4-3.

Direction	Streamflow Metric	Direction	Ecological Metric	Empirical Model in Figure 4-3	Supporting References
A decrease in	Baseflows	will result in a decrease in	Native species richness Percent insectivorous cyprinids Percent non-lithophilic spawners Percent top carnivores	c b b b	Travnichek et al. 1995; Bunn and Arthington 2002; Freeman and Marcinek 2006
A decrease in	Baseflows	will result in an increase in	Percent habitat generalists Percent unhealthy individuals	a a	Freeman and Marcinek 2006
An increase in	Baseflows	will result in a decrease in	Native species richness Percent insectivorous cyprinids Percent non-lithophilic spawners	e d d	Poff et al. 1997; Bunn and Arthington 2002; Poff and Zimmerman 2010
An increase in	Low Flow Duration	will result in a decrease in	Native species richness Percent insectivorous cyprinids Percent non-lithophilic spawners Percent top carnivores	g g g g	Travnichek et al. 1995; Bunn and Arthington 2002; Freeman and Marcinek 2006
An increase in	Low Flow Duration	will result in an increase in	Percent habitat generalists Percent trophic generalists Percent unhealthy individuals	f f f	Freeman and Marcinek 2006
An increase in	High Flow Pulse Frequency	will result in a decrease in	Native species richness Percent insectivorous cyprinids	j i	Kinsolving and Bain 1993; Scheidegger and Bain 1995; Poff et al. 1997; Bunn and Arthington 2002
An increase in	High Flow Pulse Frequency	will result in an increase in	Percent habitat generalists Percent trophic generalists	h h	Kinsolving and Bain 1993; Poff and Allan 1995; Poff and Zimmerman 2010
A decrease in	Small Flood Duration, Frequency, and Magnitude	will result in a decrease in	Native species richness Percent insectivorous cyprinids Percent top carnivores	l k k	Junk et al. 1989; Poff et al. 1997; Bunn and Arthington 2002; Poff and Zimmerman 2010

Table 4-5. Thirteen U.S. Geological Survey streamflow gages located within the Valley and Ridge/Piedmont ichthyoregion of Alabama. All gages have at least 20 years of recorded unregulated streamflow. Data from these gages were used to evaluate decision alternatives for an example structured decision making process to provide instream flow recommendations for Alabama's state-wide water resource planning process.

Gage Number	Gage Name	River basin	Contributing drainage area (km^2)	Unregulated Years of Record
2398300	Chattooga River above Gaylesville, AL	Coosa	948	1959-1967 1985-2014
2399200	Little River near Blue Pond, AL	Coosa	515	1959-1967 1971-2014
2400100	Terrapin Creek at Ellisville, AL	Coosa	653	1963-1967 1981-2014
2400500	Coosa River at Gadsden, AL	Coosa	15,035	1927-1947
2401000	Big Wills Creek near Reece City	Coosa	471	1944-1970 1987-2014
2404400	Choccolocco Creek at Jackson Shoal near Lincoln, AL	Coosa	1,246	1961-1967 1985-2014
2405500	Kelly Creek near Vincent, AL	Coosa	500	1952-1970 1987-2014
2406500	Talladega Creek at Alpine, AL	Coosa	388	1900-1905 1940-1951 1988-2014
2408540	Hatchet Creek below Rockford, AL	Coosa	674	1981-2014
2412000	Tallapoosa River near Heflin, AL	Tallapoosa	1,160	1952-2014
2413300	Little Tallapoosa River near Newell, AL	Tallapoosa	1,052	1976-2014
2414500	Tallapoosa River at Wadley, AL	Tallapoosa	4,338	1924-1974
2415000	Hillabee Creek near Hackneyville, AL	Tallapoosa	492	1952-1970 1986-2014

Table 4-6. Consequences of various flow management alternatives on a selected suite of ecological objectives evaluated within a structured decision making framework for incorporating the index of biotic integrity into management decision making. Run-of-river conditions represent the maximum desired value of ecological objectives; values under each other management alternative represent proportional deviations from desired ecological conditions. See text for details concerning each management alternative. Values were determined based on empirical models that predicted consequences of management alternatives on ecological objectives using flow-ecology hypotheses derived from the scientific literature.

Ecological Objective	Desired Direction	Run-of-River	Annual 7Q10	Monthly 7Q10	MAF	SMF 20	SMF 50	Unreg 80-70-75	Unreg 85-80	Unreg 90
					Management Alternatives					
Native Species Richness	max	1.00	0.46	0.51	0.61	0.62	0.76	0.86	0.88	0.90
Percent Insectivorous Cyprinids	max	1.00	0.64	0.68	0.81	0.81	0.88	0.93	0.94	0.95
Percent Top Carnivores	max	1.00	0.64	0.68	0.80	0.81	0.88	0.93	0.94	0.95
Percent Non-Lithophilic Spawners	max	1.00	0.48	0.56	0.95	0.93	0.97	0.98	0.99	1.00
Percent Trophic Generalists	min	1.00	4.14	2.48	1.00	1.00	1.00	1.00	1.00	1.00
Percent Habitat Generalists	min	1.00	2.67	1.80	1.02	1.07	1.03	1.02	1.01	1.00
Percent Unhealthy Individuals	min	1.00	2.67	1.80	1.02	1.07	1.03	1.02	1.01	1.00

Table 4-7. Steps taken to evaluate the consequences of alternative flow management scenarios on ecological metrics representing components of an index of biotic integrity (IBI) for Alabama's Valley and Ridge/Piedmont ichthyoregion. Resulting consequence values were used within an example decision making process to provide instream flow recommendations for Alabama's state-wide water resource planning process.

Step	Description
1	Modify streamflow data from 13 USGS gage sites (Table 4-5) to reflect streamflow patterns of 8 flow management alternatives (Table 4-3).
2	Calculate identified streamflow metrics (Table 4-4) for each altered hydrograph created in Step 1.
3	Calculate identified streamflow metrics (Table 4-4) for each of the 13 original unaltered run-of-river hydrographs (Table 4-5).
4	Determine the deviation of each streamflow metric calculated in Step 2 from its corresponding run-of-river value calculated in Step 3.
5	Based on the values determined in Step 4, estimate the predicted deviation of the ecological metric in each of the identified flow-ecology hypotheses in Table 4-4 using the corresponding models in Figure 4-3.
6	For each individual ecological metric (i.e., native species richness, percent habitat generalists, etc.), calculate the average deviation value from Step 5 across all models for that metric. The resulting values are the consequence values of each flow alternative on each streamflow metric for each of the 13 gage sites.
7	For each individual ecological metric, average consequence values calculated in Step 6 across all 13 gage sites under each flow alternative. *The resulting values are the consequences of each flow alternative on each streamflow metric.* Normalized values are given in Table 4-8.

Table 4-8. Consequence table with normalized values comparing management alternatives in terms of defined ecological objectives. The sum of the normalized values represents the relative performance of each alternative. In this case, the highest performing alternative is the "Unreg 90" alternative, which represents a management scenario in which instream flows are greater than or equal to 90% of unregulated flows. See text for additional details regarding the various management alternatives.

Ecological Objective	Desired Direction	Run-of-River	Management Alternatives							
			Annual 7Q10	Monthly 7Q10	MAF	SMF 20	SMF 50	Unreg 80-70-75	Unreg 85-80	Unreg 90
Native Species Richness	max	1.00	0.00	0.10	0.29	0.30	0.55	0.74	0.79	0.81
Percent Insectivorous Cyprinids	max	1.00	0.00	0.10	0.46	0.47	0.66	0.80	0.84	0.85
Percent Top Carnivores	max	1.00	0.00	0.10	0.44	0.47	0.66	0.80	0.84	0.85
Percent Non-Lithophilic Spawners	max	1.00	0.00	0.15	0.90	0.86	0.93	0.97	0.98	1.00
Percent Trophic Generalists	min	1.00	0.00	0.53	1.00	1.00	1.00	1.00	1.00	1.00
Percent Habitat Generalists	min	1.00	0.00	0.52	0.99	0.96	0.98	0.99	0.99	1.00
Percent Unhealthy Individuals	min	1.00	0.00	0.52	0.99	0.96	0.98	0.99	0.99	1.00
Sum			0.00	1.20	5.05	4.99	5.74	6.29	6.42	6.51

Table 4-9. Consequence table to evaluate the sensitivity of the best flow management alternative when modeled relationships among ecological metrics and the flow metrics associated with baseflows and small floods are decreased so that the effect size is reduced by half. The consequence values of each alternative change accordingly, but the ranked best alternative ("Unreg 90") and the rankings of the other alternatives do not change compared to the initial results presented in Table 4-8. See text for additional details regarding the various management alternatives.

Ecological Objective	Desired Direction	Run-of-River	Annual 7Q10	Monthly 7Q10	MAF	SMF 20	SMF 50	Unreg 80-70-75	Unreg 85-80	Unreg 90
						Management Alternatives				
Native Species Richness	max	1.00	0.00	0.10	0.46	0.47	0.66	0.80	0.84	0.85
Percent Insectivorous Cyprinids	max	1.00	0.00	0.10	0.63	0.64	0.77	0.87	0.89	0.90
Percent Top Carnivores	max	1.00	0.00	0.10	0.62	0.64	0.77	0.87	0.89	0.90
Percent Non-Lithophilic Spawners	max	1.00	0.00	0.12	0.95	0.92	0.96	0.98	0.99	1.00
Percent Trophic Generalists	min	1.00	0.00	0.53	1.00	1.00	1.00	1.00	1.00	1.00
Percent Habitat Generalists	min	1.00	0.00	0.53	0.99	0.98	0.99	0.99	1.00	1.00
Percent Unhealthy Individuals	min	1.00	0.00	0.53	0.99	0.98	0.99	0.99	1.00	1.00
Sum			0.00	1.99	5.64	5.63	6.13	6.51	6.60	6.65

Table 4-10. Consequence table to evaluate the sensitivity of the best flow management alternative when modeled relationships among ecological metrics and the flow metrics associated with baseflows and small floods are increased so that the effect size is doubled. The consequence values of each alternative change accordingly, but the ranked best alternative ("Unreg 90") and the rankings of the other alternatives do not change compared to the initial results presented in Table 4-8. See text for additional details regarding the various management alternatives.

| Ecological Objective	Desired Direction	Management Alternatives								
		Run-of-River	Annual 7Q10	Monthly 7Q10	MAF	SMF 20	SMF 50	Unreg 80-70-75	Unreg 85-80	Unreg 90
Native Species Richness	max	1.00	0.00	0.10	0.18	0.18	0.47	0.69	0.75	0.77
Percent Insectivorous Cyprinids	max	1.00	0.00	0.10	0.31	0.30	0.55	0.74	0.79	0.81
Percent Top Carnivores	max	1.00	0.00	0.10	0.26	0.30	0.55	0.74	0.79	0.81
Percent Non-Lithophilic Spawners	max	1.00	0.00	0.20	0.90	0.76	0.89	0.94	0.96	1.00
Percent Trophic Generalists	min	1.00	0.00	0.53	1.00	1.00	1.00	1.00	1.00	1.00
Percent Habitat Generalists	min	1.00	0.00	0.52	0.97	0.92	0.96	0.98	0.99	1.00
Percent Unhealthy Individuals	min	1.00	0.00	0.52	0.97	0.92	0.96	0.98	0.99	1.00
Sum			0.00	2.07	4.60	4.38	5.38	6.08	6.25	6.39
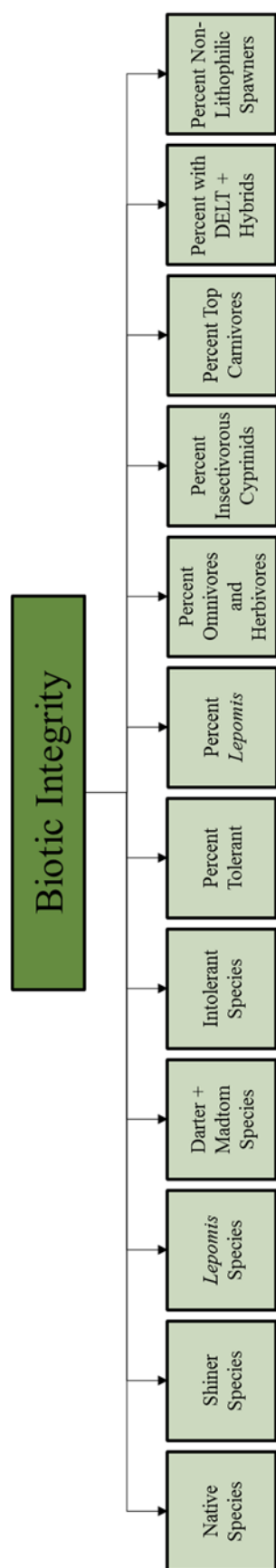
Figure 4-1. An objectives hierarchy developed to incorporate the index of biotic integrity (IBI) into a structured decision making framework, where each IBI component is considered a sub-objective of the fundamental objective of biotic integrity. Objectives here are based on the IBI developed for Alabama's Ridge and Valley/Piedmont ichthyoregion by O'Neil and Shepard (2011). DELT = deformities, eroded fins, lesions, and tumors.
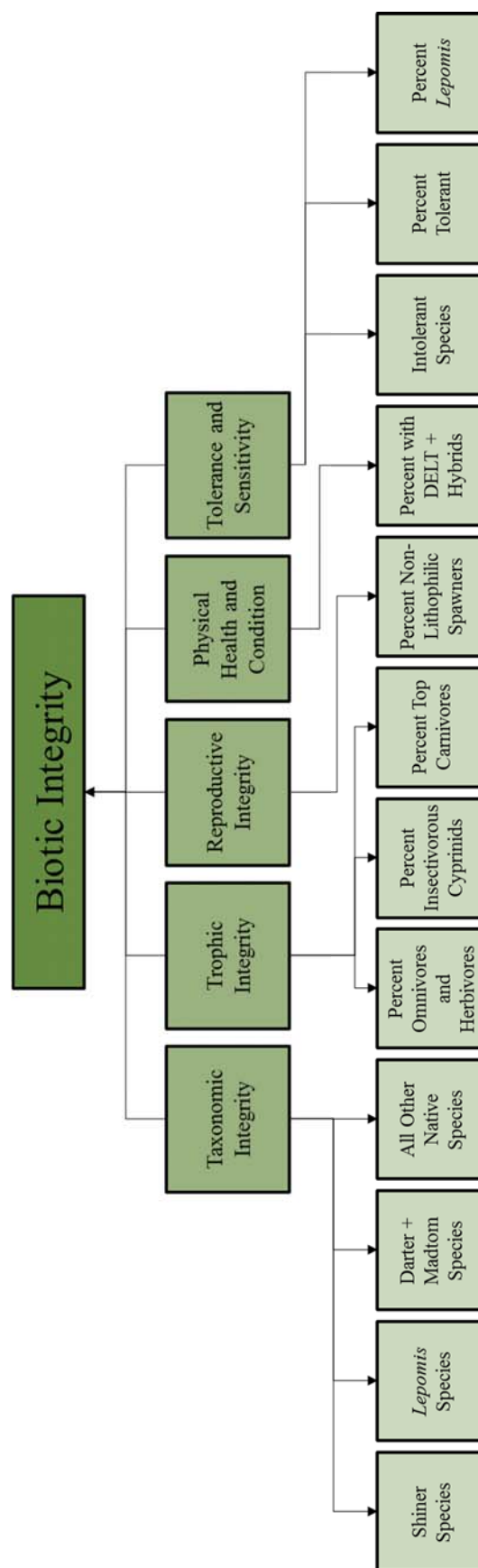

Figure 4-2. An index of biotic integrity (IBI) objectives hierarchy with multiple hierarchical levels aimed to organize and reduce redundancy among objectives. Objectives are based on an IBI developed for Alabama's Ridge and Valley/Piedmont ichthyoregion by O'Neil and Shepard (2011). DELT = deformities, eroded fins, lesions, and tumors.

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Figure 4-3. Empirical models describing the links between flow metrics and ecological objectives derived from an index of biotic integrity for the Valley and Ridge/Piedmont ichthyoregion of Alabama. Flow metrics are represented on a relative scale as a deviation from values under run-of-river conditions. In each case, desired attainment of objectives is represented by a value of 1. Models are primarily conceptual and were derived from empirical data gathered from the literature (see Table 4-4). Letters correspond to the hypotheses represented by each model, as described in Table 4-4. Note that the scale for deviation from run-of-river low flow duration (upper right panel) is larger to account for the greater deviations that are typical under various flow management alternatives.

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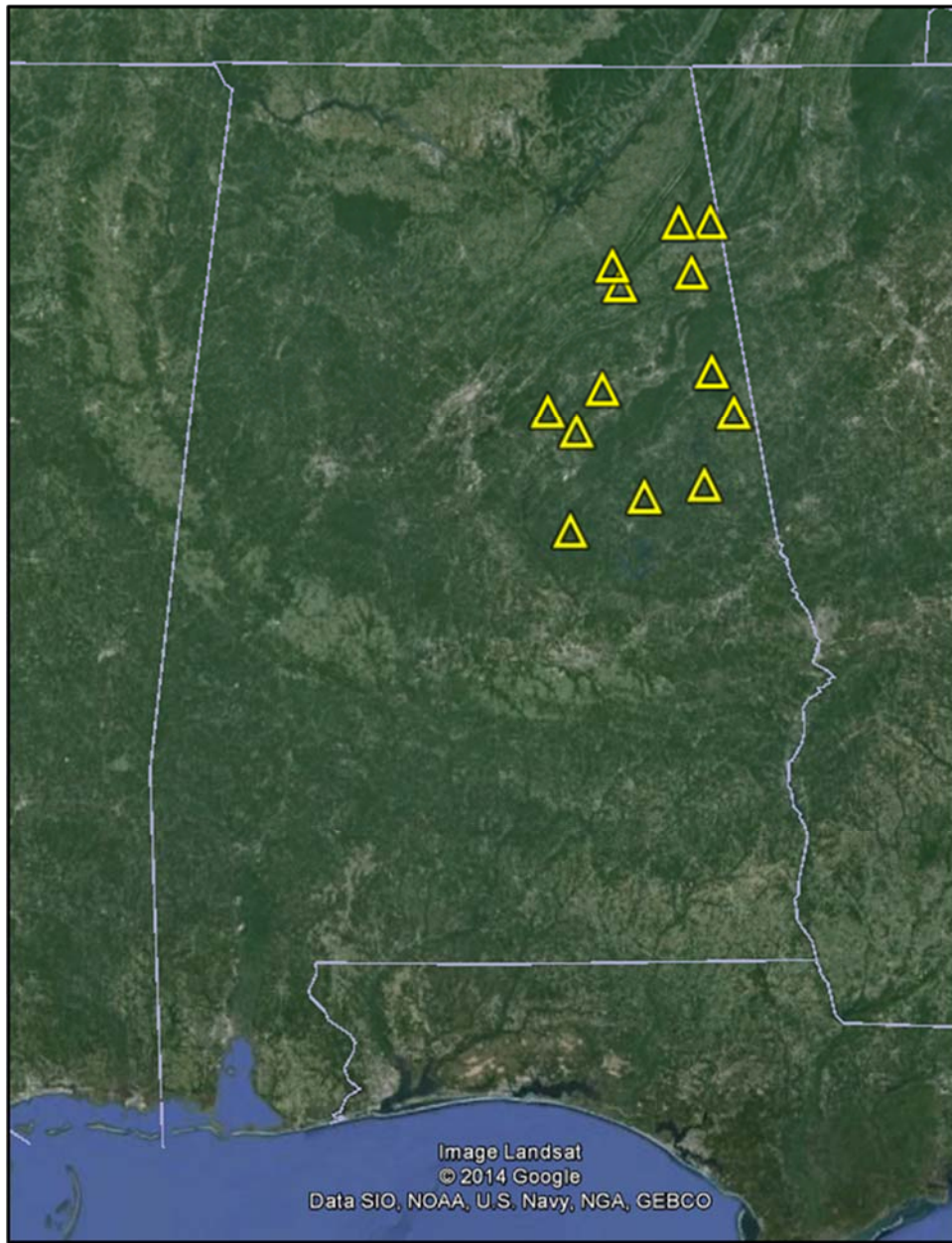
Figure 4-4. Location of 13 USGS stream gages in Alabama's Valley and
Ridge/Piedmont ichthyoregion. Hydrologic data from these gages were
used to predict consequences of various flow management alternatives on
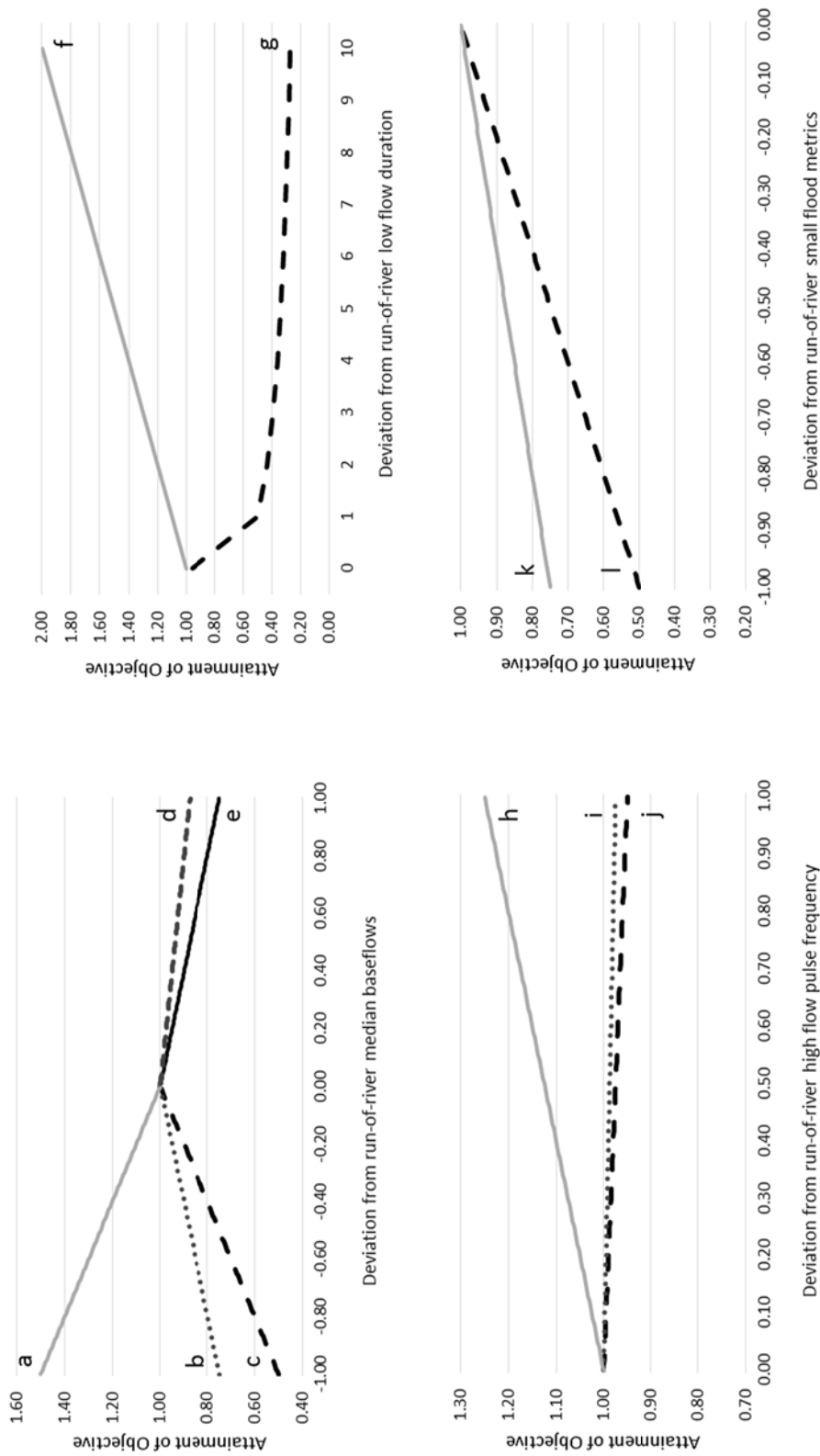identified ecological objectives.
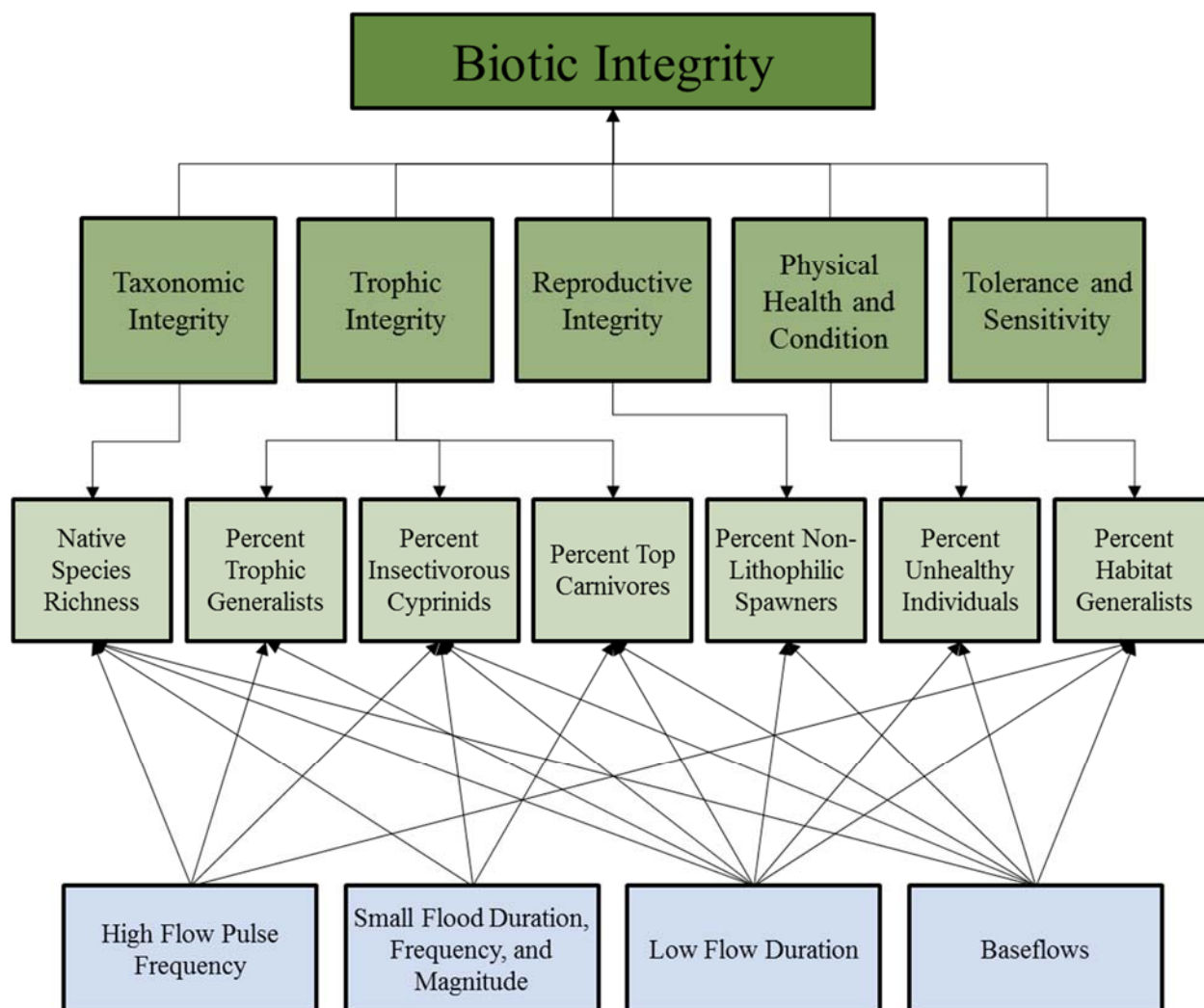
Figure 4-5. Influence diagram representing the linkages between flow metrics and ecological objectives derived from an index of biotic integrity for Alabama's Ridge and Valley/Piedmont ichthyoregion (O'Neil and Shepard 2011).
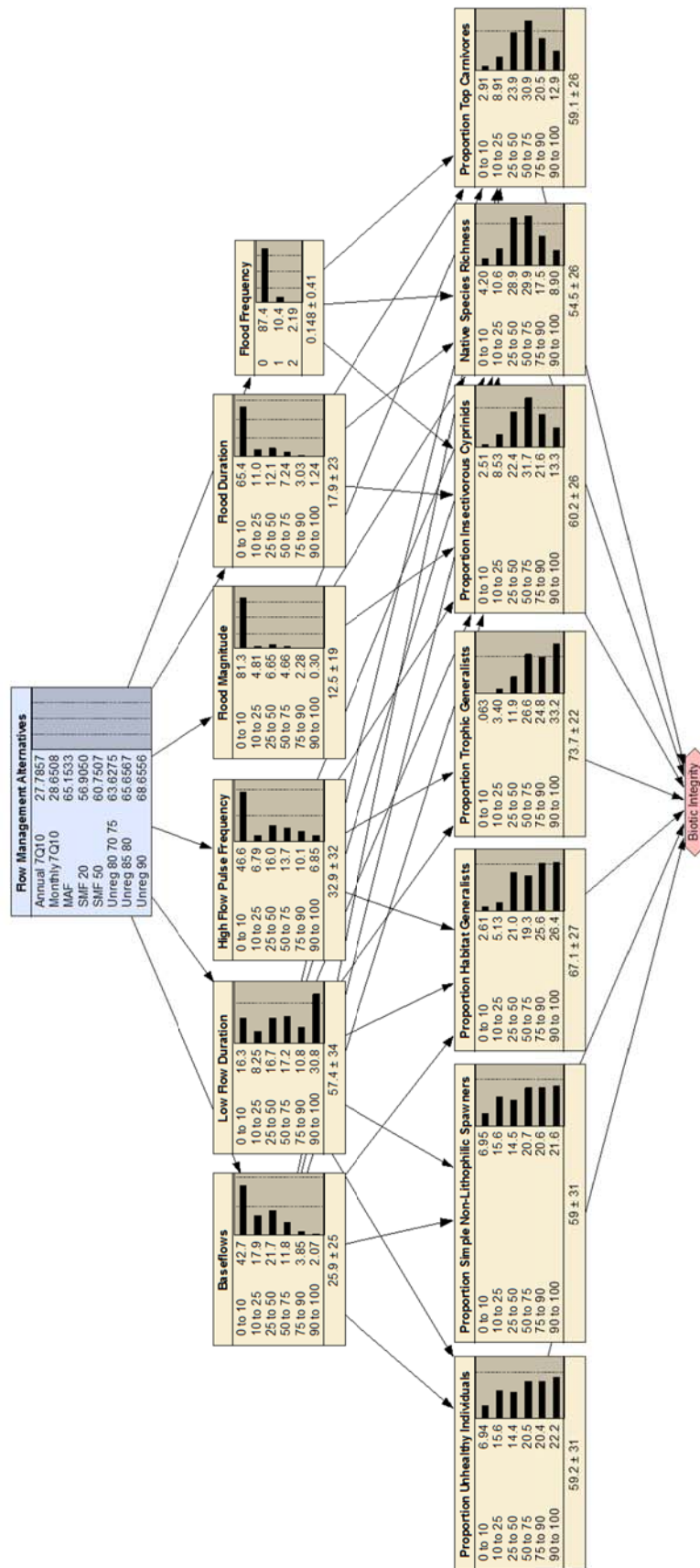
Figure 4-6. A Bayesian decision network for flow management decision making that incorporates ecological objectives based on an index of biotic integrity for Alabama's Valley and Ridge/Piedmont ichthyoregion (O'Neil and Shepard 2011). Relationships among nodes are defined by conditional probability tables based on empirical models derived from the literature. For both the flow and ecological metrics, values represent the probability of achieving objective targets. The value of each flow management decision alternative is an average weighted utility value based on the defined conditional probabilities in the network with equal weights among ecological objectives. A higher value represents greater biotic integrity as defined by the ecological objectives. See Table 4-3 for a description of each of the flow management alternatives evaluated in this decision network.

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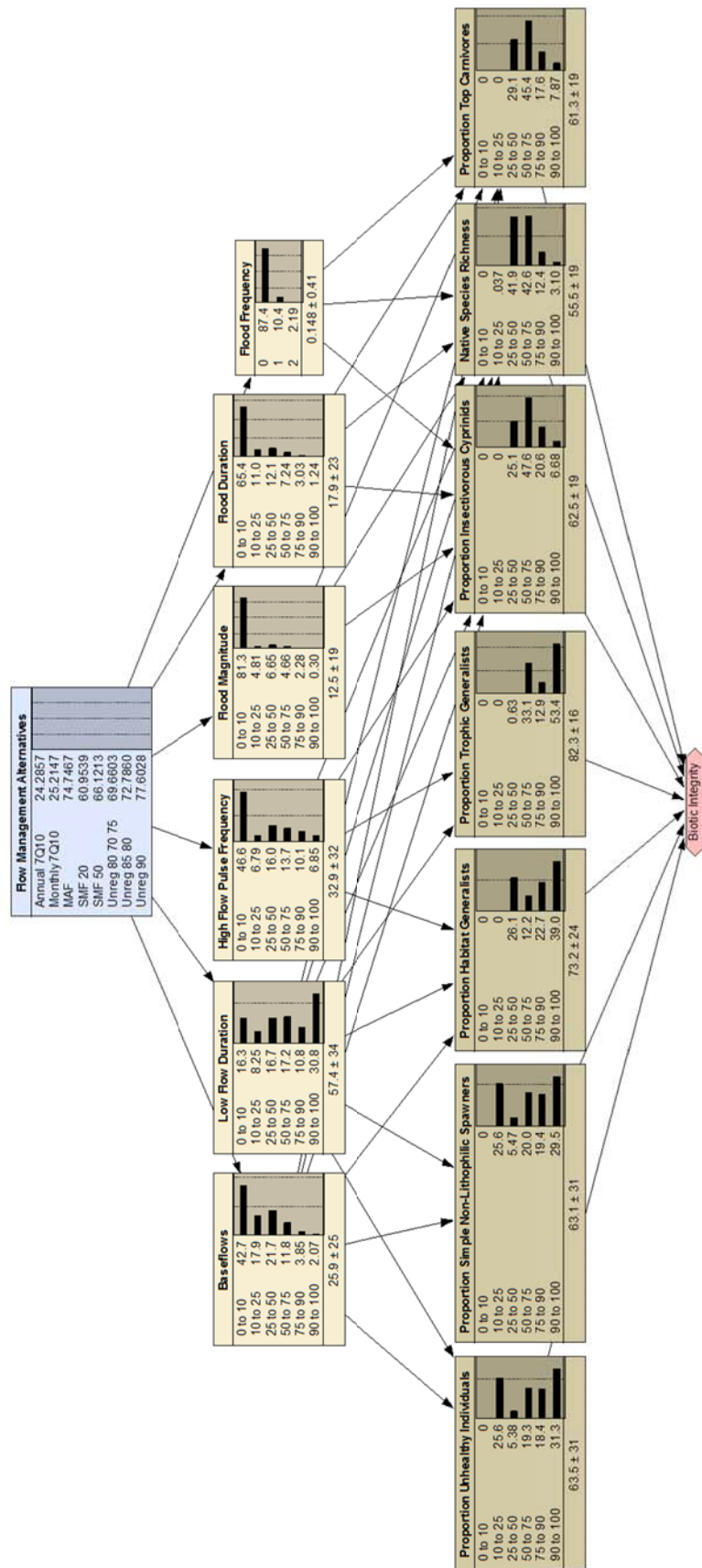
Figure 4-7. A Bayesian decision network for flow management decision making wherein links among flow metrics and ecological objectives are deterministic (i.e., without uncertainty) instead of probabilistic, as in Figure 4-6. Ignoring the uncertainty in these relationships did not alter the best decision ("Unreg 90"), but did change the ranking of the "Unreg 85 80" and "MAF" alternatives evaluated in this decision network. See Table 4-3 for a description of each of the flow management alternatives evaluated in this decision network.

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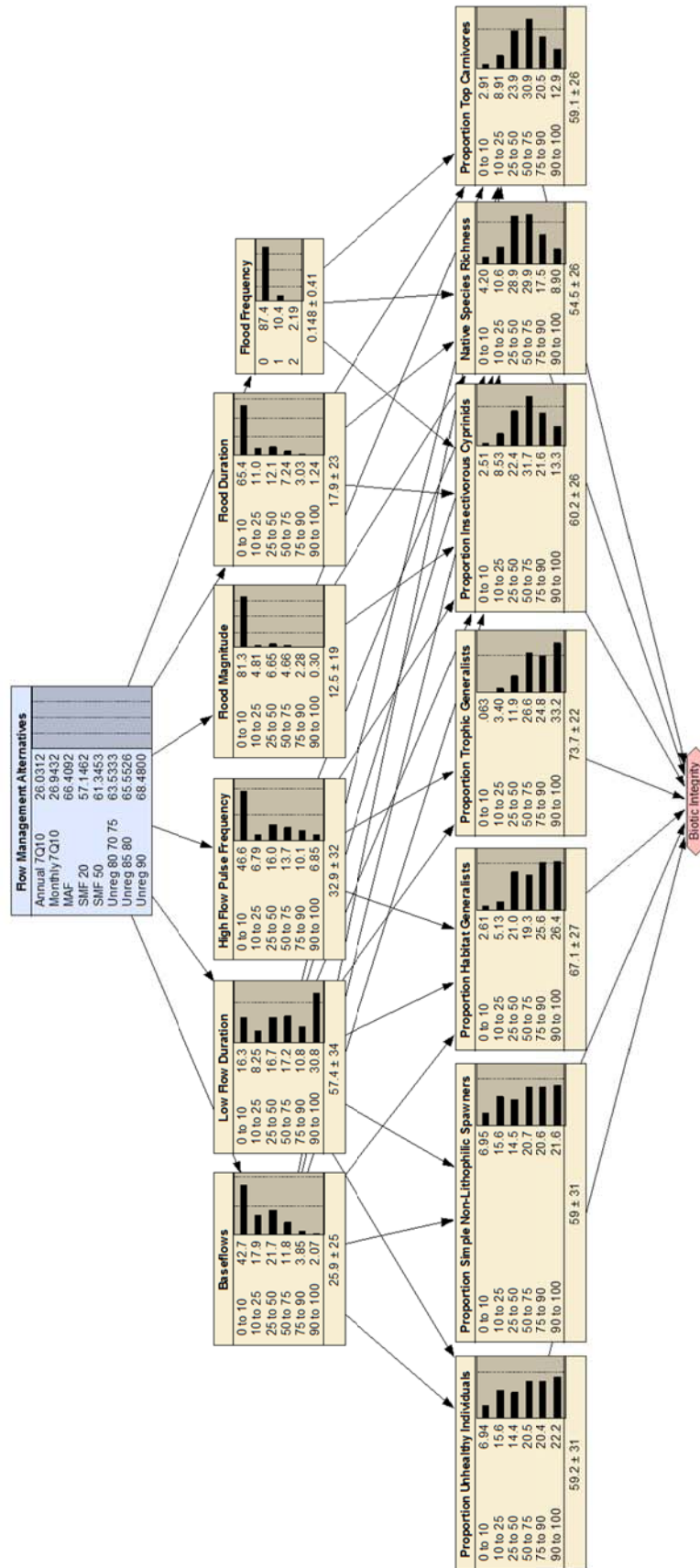
Figure 4-8. A Bayesian decision network for flow management decision making wherein the "Native Species Richness" objective is given twice as much weight as the other ecological objectives. Changing these weights did not alter the best decision ("Unreg 90"), but did change the ranking of the "Unreg 85 80" and "MAF" alternatives. See Table 4-3 for a description of each of the flow management alternatives evaluated in this decision network.

Figure 4-9. A Bayesian decision network for flow management decision making wherein a utility node is incorporated to represent the risk attitudes of managers toward species loss. Incorporating risk into this network did not alter the best decision ("Unreg 90"), but did increase the differential value of the best alternative, and change the ranking of the "Unreg 80 70 75" and "MAF" alternatives. See Table 4-3 for a description of each of the flow management alternatives evaluated in this decision network.

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Chapter 5. Summary and Conclusions
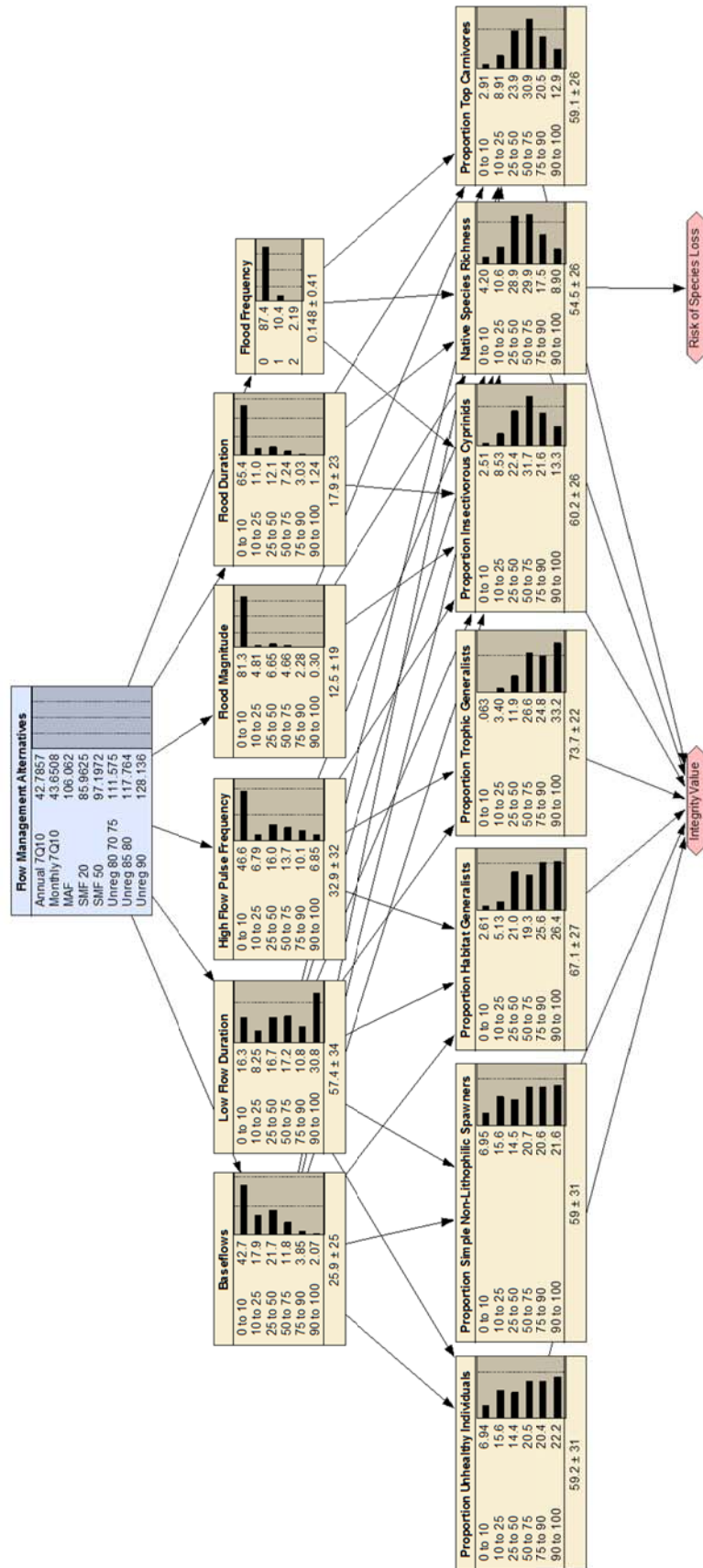
Empirical evidence demonstrating the detrimental impacts of anthropogenic activities on freshwater aquatic ecosystems is in no short supply (e.g., Allan and Flecker 1993; Richter et al. 1997; Ward 1998; Henley et al. 2000; Bunn and Arthington 2002; Dudgeon et al. 2006). The results presented from the data gathered in Wheeler National Wildlife Refuge (NWR) and on the Tallapoosa River have certainly added to this pool of evidence. The fish community in Wheeler NWR has been clearly influenced by the effects of impoundment, as most encountered species were lentic-tolerant and also exhibited evidence of tolerance to the impacts of urban and agricultural land use. In the Tallapoosa River, collected data strongly supported the effects of an altered flow regime downstream of a large hydropower facility. Such data are necessary to establish a context for the state of the ecosystem and provide a frame for resource managers and conservation practitioners to define potential problems that must be addressed (Ludwig et al. 1993, Gunderson 2000, Newmark and Hough 2000, Peterman 2004, Acheson 2006).

However, data that describe community composition and distribution patterns do not in themselves demand a call to action, nor do they prescribe a particular course of action that must be taken. What provides an impetus for action is not science or the data or theories it produces, but the conservation and other values established by individuals, organizations, and society. Values define the mission statements of resource agencies and conservation organizations and propel individuals, agencies, and organizations to act. In turn, measurable, value-based objectives serve an important link between science and management. Resource managers (likely

guided in large part by policy) establish conservation objectives, whereas science helps to elucidate the state of the system and how actions and system perturbations influence the achievement of objectives.

Chapter 1 introduced three limitations to effective freshwater aquatic natural resource management: unclear management objectives, inadequate knowledge of system state, and inadequate knowledge of system response to management actions and perturbations. The first limitation must be addressed primarily by resource managers and conservation practitioners, who will define management objectives that are reflective of the values that they represent. The latter two limitations, both of which reflect a lack of system knowledge, must be addressed by science that is informed by the objectives defined by managers and practitioners.

Each chapter of this dissertation contributed to either improving an understanding of system state, improving an understanding of the relationships among actions and objectives, or both. For Wheeler NWR, species occupancy models were used to relate patterns of fish distribution to urban and agricultural land use, resulting in information that suggested the current species assemblage (already impacted by impoundment) may not respond negatively to land use changes. In the Tallapoosa River, models of fish species occupancy dynamics demonstrated improvements in occupancy for some species after a change in flow management, but declines in occupancy for others, leading to the formation of additional hypotheses for testing in the next iteration of adaptive management. Finally, in Chapter 4, the framework developed for integrating an index of biotic integrity into a structured decision making process provided a means to link management actions and objectives in a variety of freshwater management contexts.

Limited knowledge and high system uncertainty can make freshwater aquatic resource management an overwhelming responsibility that in some cases may lead to delayed or even avoided decisions. However, system uncertainty need not be a limitation to making informed management decisions. In both Wheeler NWR and the Tallapoosa River, results demonstrated relatively high model uncertainty; in only one case (for models describing Tallapoosa shiner occupancy dynamics in the Tallapoosa River) was there a single strong model that described the data better than all other models evaluated. Such uncertainty is not unusual or unexpected, as multiple-use freshwater systems with highly diverse assemblages are very complex and dynamic. In circumstances when there is no one clear model describing the data, multiple-model comparison can provide the means to employ several models at once, each according to its own strength of evidence, thereby adding value to management decision making by explicitly accounting for uncertainty among hypotheses and providing unbiased predictions of the consequences of management actions.

However, whereas incorporating model uncertainty into management decision making can improve the quality of decisions that are made, it does not in any way ensure a positive outcome. Because of this, it is imperative that new information is continually used to update system hypotheses, improving future management decisions and the potential for meeting conservation objectives. This framework – making decisions by incorporating system uncertainty, monitoring system response, and updating hypotheses for the next decision iteration – is essentially the framework of adaptive management (Holling 1978; Walters 1986; Lee 1993; Williams et al. 2009; Allen et al. 2011). Adaptive management therefore must be a central component of any successful long-term freshwater aquatic resources management plan.

In turn, critical to the success of the adaptive management of any freshwater aquatic system is clear definition of management objectives. Among the limitations to effective freshwater aquatic resource management identified in Chapter 1, unclear management objectives is the one limitation that was not directly addressed in this dissertation. In each chapter, the importance of clear objectives for making sound management decisions and achieving conservation success was emphasized, yet lack of clarity regarding management objectives still remained a prominent limitation in each case. For Wheeler NWR, objectives were drawn from a conservation plan and were not associated with explicit measures; for Alabama's IBI, monitoring metrics were chosen by how well they distinguished anthropogenic disturbance rather than by how well they reflected the overall objective of biotic integrity; and the Tallapoosa River objectives to maximize diversity may lack specificity for adequately measuring long-term management success.

As stated previously, management and conservation objectives ultimately need to be identified by managers and conservation practitioners, that is, those who are in the position to initiate conservation actions and are the decision makers. Therefore, improvement in this arena will require partnerships among managers and scientists, with managers making deliberate efforts to define objectives and scientists making deliberate efforts to elicit them. Freshwater aquatic resource management will continue to be ineffective if management objectives are absent or vague, as it is not possible to achieve success if success has not been clearly defined (Yoccoz et al. 2001; Wilson 2002; Peterman 2004; Acheson 2006). Furthermore, any monitoring plan to support freshwater aquatic resource management should be directly tied to measurement of established objectives and to those parameters that represent pertinent hypotheses of impact (Yoccoz et al. 2001; Nichols and Williams 2006; Lindenmayer and Likens 2009), as it is not

possible to claim success (or failure) if objectives are not adequately measured. In addition, an adaptive framework will be imperative to provide the flexibility necessary to allow incorporation of new information, as well as to update other management components, such as objectives and action alternatives (Holling 1978; Walters 1986; Lee 1993; Williams et al. 2009; Allen et al. 2011).

The most successful freshwater aquatic resource management program will be that which is clear on its desired result, which can make the best possible decision given the information it has at the present, and which is adaptable to change in the future – whether due to new information, new patterns of climate, new political regimes, or even new social values. With clear management objectives, explicit hypotheses of system response, a monitoring plan directly linked to these objectives and hypotheses, and a flexible management framework, freshwater aquatic resource managers will have the means to make sound decisions and approach attainment of their explicit conservation goals.

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Appendix 1. Detailed methods for site selection and collection of fish species data in Wheeler National Wildlife Refuge, Alabama (Chapter 2)

Site Selection: In July 2008, seven watersheds were sampled for fish community composition within the boundaries of Wheeler National Wildlife Refuge (NWR), Alabama: Flint Creek, Beaverdam Creek, Cotaco Creek, Indian Creek, Limestone Creek, Piney Creek, and Ginhouse Branch. To select sample sites, we employed a stratified random sampling design, where strata were defined by watershed, and the number of randomly-selected sites within each watershed was based on available sampling area of each watershed within the boundaries of Wheeler NWR. For each watershed, we delineated the within-refuge shoreline (most of the refuge's stream habitat has been inundated) or stream length (when channel width was <10 m) of each body of water into 50 m segments. We assigned each delineated segment a unique number, and randomly selected sites in each watershed from the numbered segments using a random number generator (Microsoft Excel 2002). The minimum number of sites sampled was arbitrarily set at five; the maximum number of sites sampled (n = 9) was determined by sampling as many sites as possible in Flint Creek (the watershed with the most available sampling area: 50,000 m of shoreline) during daylight hours on the first day of sampling. The number of sites sampled in the remaining watersheds was proportional to the total shoreline (or stream length) available for sampling within each: seven sites in Beaverdam Creek (27,750 m), six sites each in Cotaco (12,500 m) and Indian (6,250 m) creeks, and five sites each in Piney Creek (2,350 m), Limestone Creek (2,250 m), and Ginhouse Branch (750 m), for a total of 43 sites. When a site was inaccessible to sampling gear, the next closest accessible site was sampled.

Fish Data Collection: Fish were collected using prepositioned area electrofishers (PAEs; Bain et al. 1985; Fisher and Brown 1993; Freeman et al. 2001); methods of collection closely followed those described by Freeman et al. (2001). The PAEs were each composed of two 6-m electrodes separated by two 1.5-m lengths of polyvinyl chloride tubing, and were powered remotely with alternating current by a 3500 W generator and pulsator unit (Smith-Root 3.5 GPP; Smith-Root, Vancouver, Washington). At each randomly selected site, we collected five spatially-replicated PAE samples to later estimate detection probability of captured fish species (see Data Analysis). The five PAEs were placed semi-randomly, such that sample locations were not pre-determined but were set at least 2 m apart and at a depth of no more than 1 m. Once all five PAEs were set, they were left undisturbed for at least 15 min. To collect each sample, a PAE was powered for 20 s while two field crew members held a seine at the downstream end (in lotic habitat) or pulled a seine through the sample (in lentic habitat) to collect stunned fish; each field crew member holding the seine also held a dip net to assist in collection. An additional field crew member walked through the sample to disturb the substrate, facilitate movement of stunned fish into the seine, and assist in collection with an additional small dip net. Stunned fish were measured, euthanized with MS-222 (tricaine methanesulfonate), and preserved in the field. When possible, large fish (>100 mm) were identified, measured, retained in a live well, and released in the field after all samples at a site were completed. Once a single sample was completed, the next PAE was powered and processed; each sample took approximately 10 min to process.

All preserved collection samples were returned to the laboratory for identification; fish were identified to species when possible. If the identity of an individual fish was uncertain, the sample was taken to the Auburn University Natural History Museum Fish Collection for

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verification. Because of similar habitats and morphological characters (Echelle and Schnell 1976; Mettee et al. 1996; Boschung and Mayden 2004), blackstripe topminnow (Fundulus notatus) and blackspotted topminnow (Fundulus olivaceus) were evaluated as a single taxon, topminnows (Fundulus spp.).

Habitat Data Collection: Habitat variables were measured within each PAE, including depth (cm), velocity (cm/s), percent areal vegetation cover (primarily emergent vegetation, e.g., waterwillow, Justicia americana; smartweed, Polygonum spp.; and alligatorweed, Alternanthera phyloxeroides), presence of large cover (large woody debris, submerged bushes, undercut banks, roots, boulders, other large submerged debris, e.g., discarded rubber tires), and substratum type. Depth and velocity were measured at a representative location within each PAE, generally near the center of the sample. Depth was measured with a top-setting wading rod, and velocity with a flow meter (Marsh-McBirney; Model 2000 Flo-Mate). Presence of large cover within a PAE was noted and percent vegetation was estimated visually. Visual estimation of vegetation was conducted by the same observer at each location to maintain consistency; recorded estimates were based on proportion of PAE area covered, and were between 5 and 100%, with estimates above 5% limited to increments of 10 (e.g., 10%, 20%, 30%, etc.). For substratum, types were classified by particle size based on a modified Wentworth scale (Wentworth 1922; Cummins 1962). Assigned types were approximated based on visual and tactile observation within each PAE; multiple types were recorded sequentially by decreasing proportion of area covered (e.g., "gravel-cobble-sand" described a PAE dominated by gravel, with some cobble, and less sand). A constructed scale was then developed, where 0 was assigned to those samples dominated by silt, 5 to those dominated by gravel, and 10 to those dominated by boulder. Each PAE sample

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was assigned a relative value; values for samples with multiple substratum classes were approximated such that an increase in value corresponded to a relative increase in average particle size.

Appendix 2. Model-averaged regression coefficient estimates for 14 fish species detected in Wheeler National Wildlife Refuge, Alabama, and suggestions for interpretation (Chapter 2)

Model-averaged coefficient estimates for the 14 species in Wheeler National Wildlife Refuge that had high detection (i.e., were detected in a minimum of 4 replicates) in at least one of the 43 sampled sites are presented in Tables A2-1 and A2-2. For each species, parameters (detection and occupancy) were modeled as functions of measured covariates by means of the logit-link function, as described in MacKenzie et al. (2006:72):

$$\text{logit}(\theta_q) = \ln\left(\frac{\theta_q}{1-\theta_q}\right) = \beta_0 + \beta_1 x_{q1} + \beta_2 x_{q2} + \cdots + \beta_J x_{qJ}, \tag{1}$$

where θ_q is the parameter of interest (detection or occupancy) for the unit q (a sample for detection or a site for occupancy), and $x_{q1}, x_{q2}, \ldots, x_{qJ}$ are the values for the J model covariates associated with unit q. Under this framework, modeled parameters may vary across sampling units, but the regression coefficients (β) are effectively modeled as constant across samples (for detection) or sites (for occupancy).

Model-averaged regression coefficients were calculated as

$$\hat{\bar{\beta}}_J = \sum_{i=1}^{R} w_i \hat{\beta}_{ji}, \tag{2}$$

where $\hat{\beta}_{ji}$ is the regression coefficient associated with covariate x_j in model i, and w_i is the Akaike weight for model i. Unconditional standard errors of coefficient estimates were calculated as:

$$SE\left(\hat{\bar{\beta}}_J\right) = \sum_{i=1}^{R} w_i \sqrt{var(\hat{\beta}_{ji}|g_i) + (\hat{\beta}_{ji} - \hat{\bar{\beta}}_J)^2}, \tag{3}$$

where $var(\hat{\beta}_{ji}|g_i)$ is the variance of the coefficient estimate from model i (Burnham and Anderson 2010).

By rearranging Equation 1, parameter (detection or occupancy) values may be calculated from covariates and model-averaged coefficient estimates per the following equation:

$$\theta = \frac{\exp\left(\widehat{\overline{\beta_0}}+\widehat{\overline{\beta_1}}x_1+\widehat{\overline{\beta_2}}x_2+\cdots+\widehat{\overline{\beta_J}}x_J\right)}{1+\exp\left(\widehat{\overline{\beta_0}}+\widehat{\overline{\beta_1}}x_1+\widehat{\overline{\beta_2}}x_2+\cdots+\widehat{\overline{\beta_J}}x_J\right)}, \tag{4}$$

where $\widehat{\overline{\beta_1}}, \widehat{\overline{\beta_2}}, \dots, \widehat{\overline{\beta_J}}$ are the model-averaged coefficients associated with the J model covariates, and $\widehat{\overline{\beta_0}}$ is the model-averaged regression intercept.

Coefficient estimates may also be interpreted as the odds of success; that is, the odds of detection or occupancy:

$$odds\ of\ success = \frac{\theta}{1-\theta} = \exp\left(\widehat{\overline{\beta_0}} + \widehat{\overline{\beta_1}}x_1 + \widehat{\overline{\beta_2}}x_2 + \cdots + \widehat{\overline{\beta_J}}x_J\right) \tag{5}$$

$$= \exp\left(\widehat{\overline{\beta_0}}\right)\exp\left(\widehat{\overline{\beta_1}}x_1\right)\exp\left(\widehat{\overline{\beta_2}}x_2\right)\dots\exp\left(\widehat{\overline{\beta_J}}x_J\right). \tag{6}$$

In these terms, $\exp\left(\widehat{\overline{\beta_0}}\right)$ is the odds of success in a sampling unit when all other covariate values are zero, and $\exp\left(\widehat{\overline{\beta_0}}\right)\exp\left(\widehat{\overline{\beta_J}}\right)$ is the odds of success in a sampling unit with a one-unit change in the covariate x_j. The associated probability of success (detection or occupancy) may be calculated as:

$$\Theta = \frac{odds\ of\ success}{1+odds\ of\ success}. \tag{7}$$

See MacKenzie et al. (2006:71-73) for additional explanation.

Interpretation of regression coefficient estimates requires knowledge of the units of covariate measures. Units for covariates presented in Tables A2-1 and A2-2 are as follows: depth (m), velocity (m/s), and land cover (proportion). As a covariate of detection, depth was the

measured depth in each sample; as covariates of occupancy, depth and velocity were averaged measures across all samples taken at a site.

Coefficient estimates with large values and large errors are generally those associated with parameter estimates of detection or occupancy that are close to or equal to either 0 or 1, as the precision of maximum likelihood estimators decreases as true parameter values approach these bounds. In addition, because regression coefficients are based on single units of each covariate, large errors may also be associated with coefficients that have unit values that are far from measured values (e.g., 1 m/s velocity or proportional values of "1" for land cover covariates). For these reasons, we chose to focus our efforts and analysis on model-averaged estimates of detection and occupancy, after they had been estimated for each model.

Table A2-1. Model-averaged detection coefficient estimates (and unconditional standard errors) of occupancy models for 14 fish species detected in Wheeler National Wildlife Refuge, Alabama. As a covariate of detection, depth represents specific depth measures taken on each sampling occasion. See text in Appendix 2 for details on interpretation of coefficient estimates.

Species	Intercept	Depth
Largescale stoneroller (*Campostoma oligolepis*)	-0.22 (0.60)	0.33 (1.22)
Striped shiner (*Luxilus chrysocephalus*)	0.76 (0.81)	-1.05 (2.00)
Bullhead minnow (*Pimephales vigilax*)	-0.62 (0.49)	0.07 (0.72)
Inland silverside (*Menidia beryllina*)	0.02 (0.76)	-1.61 (2.05)
Topminnows (*Fundulus* spp.)	1.08 (0.76)	-4.40 (2.00)
Mosquitofish (*Gambusia affinis*)	1.33 (1.11)	-8.22 (3.33)
Redbreast sunfish (*Lepomis auritus*)	0.76 (0.91)	-2.12 (2.48)
Green sunfish (*Lepomis cyanellus*)	-0.33 (0.83)	-1.52 (2.21)
Orangespotted sunfish (*Lepomis humilis*)	0.12 (1.15)	-2.62 (3.20)
Bluegill (*Lepomis macrochirus*)	0.57 (0.26)	-0.04 (0.42)
Longear sunfish (*Lepomis megalotis*)	0.05 (0.85)	-3.61 (2.29)
Redear sunfish (*Lepomis microlophus*)	1.88 (0.80)	-7.39 (2.24)
Largemouth bass (*Macrochirus salmoides*)	-0.19 (0.73)	-1.48 (1.89)
Blackside snubnose darter (*Etheostoma duryi*)	-0.06 (0.76)	-0.86 (1.80)

Table A2-2. Model-averaged occupancy coefficient estimates (and unconditional standard errors) of occupancy models for 14 fish species detected in Wheeler National Wildlife Refuge, Alabama. As a covariate of occupancy, depth and velocity represent measures averaged across all occasions at a site. See text in Appendix 2 for details on interpretation of coefficient estimates.

Species	Intercept	Depth	Velocity	Pasture	Rowcrop	Urban
Largescale Stoneroller	-3.27 (11.59)	-12.61 (12.48)	333.82 (358.64)	12.56 (20.83)	6.08 (11.60)	8.76 (18.46)
Striped Shiner	-31.18 (19.55)	19.93 (20.31)	46.46 (190.24)	64.65 (34.47)	18.83 (12.35)	8.76 (17.98)
Bullhead Minnow	-1.24 (1.78)	1.84 (3.28)	-49.50 (108.45)	-0.34 (2.03)	0.46 (1.16)	0.04 (1.06)
Inland Silverside	10.06 (9.02)	-4.91 (5.88)	-95.51 (192.94)	-15.97 (16.03)	-9.41 (9.29)	-14.86 (15.08)
Topminnows	4.38 (5.82)	-0.97 (3.06)	24.03 (60.55)	-11.54 (17.44)	-1.14 (3.02)	-2.80 (5.44)
Mosquitofish	1.80 (3.78)	-3.69 (6.47)	42.15 (102.73)	0.43 (4.39)	-0.28 (2.33)	-1.39 (4.67)
Redbreast Sunfish	-20.96 (9.60)	0.95 (3.71)	7.69 (544.20)	60.89 (28.66)	18.74 (8.69)	21.30 (10.81)
Green Sunfish	-3.83 (6.81)	-0.14 (3.18)	93.17 (106.86)	1.10 (10.75)	7.92 (9.13)	10.83 (13.76)
Orangespotted Sunfish	10.19 (6.87)	-3.76 (6.31)	-11.63 (49.41)	-17.83 (13.28)	-8.10 (6.39)	-20.83 (12.02)
Bluegill	3.54 (2.69)	-1.59 (4.54)	2.14 (50.26)	0.83 (2.96)	0.23 (0.88)	0.19 (0.94)
Longear Sunfish	-81.41 (168.84)	119.34 (296.76)	8.99 (997.24)	76.88 (202.28)	123.12 (277.91)	47.02 (102.84)
Redear Sunfish	3.45 (4.50)	-0.41 (3.12)	-162.09 (242.99)	-6.95 (11.63)	0.56 (4.17)	-5.07 (8.46)
Largemouth Bass	0.51 (1.58)	0.15 (1.92)	-4.40 (24.60)	1.15 (2.85)	0.24 (0.77)	0.08 (0.73)
Blackside Snubnose Darter	-7.68 (7.87)	1.11 (5.17)	328.49 (405.71)	15.28 (18.76)	5.69 (7.66)	-0.83 (10.07)

Appendix 3: Land cover, habitat, and fish species collection data from Wheeler National Wildlife Refuge, Alabama (Chapter 2)

Table A3-1. Total area and percent area of each land cover type in sampled watersheds of Wheeler National Wildlife Refuge, Alabama, as well as mean (sd) habitat measures for each watershed sampled. Total watershed area includes watershed area outside of the refuge boundary. Standard deviations are not reported for large cover means because the mean is the proportion of sites with large cover present; standard deviations are reported when proportions were averaged among watersheds.

Watershed	Total area (km^2)	Urban (%)	Pasture (%)	Rowcrop (%)	Depth (cm)	Velocity (cm/s)	Vegetation (%)	Large cover (0/1)	Substratum (0 to 10)
Flint	135.03	26.15	22.36	4.41	40.37 (9.08)	0.00 (0.00)	26.44 (22.78)	0.73	0.38 (1.11)
Beaverdam	99.98	8.18	13.49	50.69	38.06 (9.48)	0.00 (0.00)	0.14 (0.85)	0.43	1.26 (1.46)
Cotaco	87.66	4.21	28.07	4.93	37.08 (8.70)	0.00 (0.00)	5.00 (5.09)	0.60	0.00 (0.00)
Indian	80.19	28.61	18.77	8.09	36.17 (13.70)	0.00 (0.00)	0.00 (0.00)	0.73	0.30 (0.53)
Limestone	70.62	7.52	21.25	39.07	34.02 (9.86)	0.00 (0.00)	2.20 (3.84)	0.40	1.56 (1.45)
Piney	52.72	8.42	17.11	34.60	43.40 (7.83)	0.00 (0.00)	10.20 (18.11)	0.16	0.84 (1.37)
Ginhouse	16.44	10.22	36.37	18.86	31.09 (11.02)	0.96 (1.70)	0.60 (2.20)	0.76	2.52 (2.22)
Among all samples					37.48 (10.52)	0.11 (0.65)	7.77 (15.87)	0.56	0.90 (1.49)
Among watersheds					37.17 (4.04)	0.14 (0.36)	6.37 (9.57)	0.54 (0.22)	0.98 (0.87)

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Table A3-2. Fish species detected in Wheeler National Wildlife Refuge, Alabama, and total number of detections for each species and family (in bold) across all samples and sites. A detection was a positively identified occurrence of a species in a sample. Maximum number of species detections at a site is also reported. Fish were collected using five pre-positioned area electrofisher samples at each of 43 sites in July 2008.

Taxa	Total detections	Maximum detections per site
Clupeidae: shads	**13**	
Gizzard Shad *Dorosoma cepedianum*	5	2
Threadfin Shad *Dorosoma petenense*	8	2
Cyprinidae: minnows	**98**	
Largescale Stoneroller *Campostoma oligolepis*	17	4
Striped Shiner *Luxilus chrysocephalus*	18	5
Golden Shiner *Notemigonus crysoleucas*	19	3
Mimic Shiner *Notropis vollucellus*	3	3
Pugnose Minnow *Opsopoeodus emiliae*	5	1
Bluntnose Minnow *Pimephales notatus*	8	3
Bullhead Minnow *Pimephales vigilax*	28	4
Catostomidae: suckers	**7**	
Smallmouth Buffalo *Ictiobus bubalus*	1	1
Spotted Sucker *Minytrema melanops*	6	3
Atherinopsidae: silversides	**50**	
Brook Silverside *Labidesthes sicculus*	6	2
Inland Silverside *Menidia beryllina*	44	4
Fundulidae: topminnows	**54**	
Topminnows *Fundulus* spp.	54	5
Poeciliidae: livebearers	**23**	
Mosquitofish *Gambusia affinis*	23	4
Centrarchidae: sunfishes	**379**	
Redbreast Sunfish *Lepomis auritus*	41	5
Green Sunfish *Lepomis cyanellus*	30	4
Warmouth *Lepomis gulosus*	15	2
Orangespotted Sunfish *Lepomis humilis*	32	4
Bluegill *Lepomis macrochirus*	131	5
Longear Sunfish *Lepomis megalotis*	32	4
Redear Sunfish *Lepomis microlophus*	45	5
Spotted Bass *Micropterus punctulatus*	3	1
Largemouth Bass *Micropterus salmoides*	49	5
Black Crappie *Pomoxis nigromaculatus*	1	1
Percidae: perches	**21**	
Blackside Snubnose Darter *Etheostoma duryi*	13	4
Logperch *Percina caprodes*	8	2

Appendix 4: Full model comparison results for occupancy models of 14 fish species detected in Wheeler National Wildlife Refuge, Alabama (Chapter 2)

This appendix includes model selection results for occupancy models of 14 species detected in Wheeler National Wildlife Refuge, Alabama. Number of parameters in each model (K), negative log likelihood (-log$L$), AIC, ΔAIC, AIC model weights (w_i), and cumulative model weights (cum w_i) are reported. Model results for each species are ranked in terms of AIC and w_i. Occupancy models estimated detection (p) as constant [$p(.)$] or as a function of depth [p(depth)], and occupancy (Ψ) as constant [Ψ(.)] or as a function of habitat [Ψ(depth), Ψ(velocity), Ψ(depth + velocity)] or habitat and land cover [Ψ(depth + land cover), Ψ(velocity + land cover), Ψ(depth + velocity + land cover)]. Here land cover represents three covariates: urban + row crop + pasture (see Chapter 2 for more details).

Table A4-1. Model selection results for largescale stoneroller (*Campostoma oligolepis*) in Wheeler National Wildlife Refuge, Alabama.

Model	K	-logL	AIC	ΔAIC	w_i	cum w_i
p(.) Ψ(depth + velocity)	4	35.09	78.18	0.00	0.33	0.33
p(depth) Ψ(depth + velocity)	5	34.72	79.44	1.26	0.18	0.51
p(.) Ψ(velocity)	3	37.23	80.47	2.29	0.11	0.62
p(.) Ψ(depth + land cover)	6	34.38	80.77	2.59	0.09	0.71
p(.) Ψ(velocity + land cover)	6	34.49	80.98	2.80	0.08	0.79
p(.) Ψ(depth + velocity + land cover)	7	33.64	81.28	3.10	0.07	0.86
p(depth) Ψ(depth + land cover)	7	34.31	82.63	4.45	0.04	0.90
p(depth) Ψ(velocity)	4	37.40	82.79	4.61	0.03	0.93
p(depth) Ψ(velocity + land cover)	7	34.42	82.85	4.67	0.03	0.96
p(depth) Ψ(depth + velocity + land cover)	8	33.55	83.10	4.92	0.03	0.99
p(.) Ψ(depth)	3	40.28	86.57	8.39	0.01	1.00
p(depth) Ψ(depth)	4	40.22	88.45	10.27	0.00	1.00
p(.) Ψ(.)	2	43.07	90.13	11.95	0.00	1.00
p(depth) Ψ(.)	3	43.04	92.09	13.91	0.00	1.00

Table A4-2. Model selection results for striped shiner (*Luxilus chrysocephalus*) in Wheeler National Wildlife Refuge, Alabama.

Model	K	-logL	AIC	ΔAIC	w_i	cum w_i
p(.) Ψ(depth + land cover)	6	24.71	61.41	0.00	0.36	0.36
p(depth) Ψ(depth + land cover)	7	24.27	62.54	1.13	0.21	0.57
p(.) Ψ(depth + velocity + land cover)	7	24.68	63.35	1.94	0.14	0.71
p(.) Ψ(velocity + land cover)	6	25.81	63.61	2.20	0.12	0.83
p(depth) Ψ(depth + velocity + land cover)	8	24.21	64.42	3.01	0.08	0.91
p(depth) Ψ(velocity + land cover)	7	25.54	65.09	3.67	0.06	0.97
p(.) Ψ(velocity)	3	30.98	67.97	6.55	0.01	0.99
p(depth) Ψ(velocity)	4	30.76	69.52	8.11	0.01	0.99
p(.) Ψ(depth + velocity)	4	30.85	69.71	8.30	0.01	1.00
p(depth) Ψ(depth + velocity)	5	30.62	71.24	9.82	0.00	1.00
p(.) Ψ(.)	2	37.50	79.01	17.59	0.00	1.00
p(.) Ψ(depth)	3	36.78	79.56	18.15	0.00	1.00
p(depth) Ψ(.)	3	37.05	80.11	18.70	0.00	1.00
p(depth) Ψ(depth)	4	36.36	80.73	19.32	0.00	1.00

Table A4-3. Model selection results for bullhead minnow (*Pimephales vigilax*) in Wheeler National Wildlife Refuge, Alabama.

Model	K	-log$L$	AIC	ΔAIC	w_i	cum w_i
$p(.)$ Ψ(.)	2	72.89	149.78	0.00	0.20	0.20
$p(.)$ Ψ(velocity)	3	72.02	150.03	0.25	0.17	0.37
$p(.)$ Ψ(depth)	3	72.32	150.65	0.86	0.13	0.50
$p(.)$ Ψ(depth + velocity)	4	71.55	151.11	1.33	0.10	0.60
p(depth) Ψ(velocity)	4	71.83	151.66	1.87	0.08	0.68
p(depth) Ψ(.)	3	72.87	151.75	1.97	0.07	0.76
p(depth) Ψ(depth)	4	72.32	152.65	2.86	0.05	0.80
$p(.)$ Ψ(velocity + land cover)	6	70.35	152.70	2.92	0.05	0.85
p(depth) Ψ(depth + velocity)	5	71.46	152.92	3.14	0.04	0.89
$p(.)$ Ψ(depth + land cover)	6	70.50	153.00	3.22	0.04	0.93
$p(.)$ Ψ(depth + velocity + land cover)	7	69.85	153.71	3.93	0.03	0.96
p(depth) Ψ(velocity + land cover)	7	70.34	154.68	4.90	0.02	0.98
p(depth) Ψ(depth + land cover)	7	70.50	155.00	5.22	0.01	0.99
p(depth) Ψ(depth + velocity + land cover)	8	69.90	155.80	6.02	0.01	1.00

Table A4-4. Model selection results for inland silverside (*Menidia beryllina*) in Wheeler National Wildlife Refuge, Alabama.

Model	K	-log$L$	AIC	ΔAIC	w_i	cum w_i
p(depth) Ψ(depth + land cover)	7	94.81	203.63	0.00	0.16	0.16
$p(.)$ Ψ(depth + land cover)	6	95.85	203.70	0.07	0.16	0.32
p(depth) Ψ(velocity)	4	98.26	204.52	0.89	0.10	0.42
p(depth) Ψ(velocity + land cover)	7	95.36	204.71	1.09	0.09	0.51
$p(.)$ Ψ(depth + velocity + land cover)	7	95.40	204.80	1.17	0.09	0.60
p(depth) Ψ(depth + velocity + land cover)	8	94.41	204.83	1.20	0.09	0.69
$p(.)$ Ψ(velocity)	3	99.59	205.19	1.56	0.07	0.76
$p(.)$ Ψ(velocity + land cover)	6	96.80	205.60	1.97	0.06	0.82
p(depth) Ψ(depth + velocity)	5	98.04	206.08	2.45	0.05	0.87
$p(.)$ Ψ(depth + velocity)	4	99.06	206.13	2.50	0.05	0.92
p(depth) Ψ(.)	3	100.48	206.96	3.34	0.03	0.95
$p(.)$ Ψ(.)	2	101.70	207.40	3.77	0.02	0.97
$p(.)$ Ψ(depth)	3	101.28	208.55	4.92	0.01	0.99
p(depth) Ψ(depth)	4	100.29	208.58	4.96	0.01	1.00

Table A4-5. Model selection results for topminnows (*Fundulus* spp.) in Wheeler National Wildlife Refuge, Alabama.

Model	K	-log$L$	AIC	ΔAIC	w_i	cum w_i
p(depth) Ψ(.)	3	111.32	228.65	0.00	0.28	0.28
p(depth) Ψ(velocity + land cover)	7	107.71	229.42	0.78	0.19	0.46
p(depth) Ψ(velocity)	4	111.17	230.35	1.70	0.12	0.58
p(depth) Ψ(depth + land cover)	7	108.26	230.51	1.87	0.11	0.69
p(depth) Ψ(depth)	4	111.31	230.62	1.97	0.10	0.79
p(depth) Ψ(depth + velocity + land cover)	8	107.37	230.74	2.10	0.10	0.89
p(depth) Ψ(depth + velocity)	5	111.17	232.34	3.69	0.04	0.93
p(.) Ψ(.)	2	114.94	233.87	5.23	0.02	0.95
p(.) Ψ(velocity + land cover)	6	111.63	235.26	6.62	0.01	0.96
p(.) Ψ(depth + land cover)	6	111.75	235.51	6.86	0.01	0.97
p(.) Ψ(depth + velocity + land cover)	7	110.81	235.63	6.98	0.01	0.98
p(.) Ψ(velocity)	3	114.83	235.66	7.01	0.01	0.99
p(.) Ψ(depth)	3	114.90	235.81	7.16	0.01	1.00
p(.) Ψ(depth + velocity)	4	114.78	237.56	8.91	0.00	1.00

Table A4-6. Model selection results for mosquitofish (*Gambusia affinis*) in Wheeler National Wildlife Refuge, Alabama.

Model	K	-log$L$	AIC	ΔAIC	w_i	cum w_i
p(depth) Ψ(.)	3	64.41	134.82	0.00	0.30	0.30
p(depth) Ψ(velocity)	4	63.58	135.16	0.35	0.25	0.54
p(depth) Ψ(depth)	4	63.96	135.93	1.11	0.17	0.71
p(depth) Ψ(depth + velocity)	5	63.19	136.37	1.56	0.14	0.85
p(depth) Ψ(velocity + land cover)	7	62.28	138.56	3.74	0.05	0.89
p(depth) Ψ(depth + land cover)	7	62.51	139.03	4.21	0.04	0.93
p(depth) Ψ(depth + velocity + land cover)	8	61.99	139.98	5.17	0.02	0.95
p(.) Ψ(depth)	3	67.11	140.21	5.40	0.02	0.97
p(.) Ψ(depth + velocity)	4	66.52	141.05	6.23	0.01	0.99
p(.) Ψ(depth + land cover)	6	65.10	142.20	7.39	0.01	0.99
p(.) Ψ(depth + velocity + land cover)	7	65.13	144.26	9.45	0.00	1.00
p(.) Ψ(velocity)	3	69.25	144.51	9.69	0.00	1.00
p(.) Ψ(.)	2	70.44	144.88	10.07	0.00	1.00
p(.) Ψ(velocity + land cover)	6	67.91	147.81	13.00	0.00	1.00

Table A4-7. Model selection results for redbreast sunfish (*Lepomis auritus*) in Wheeler National Wildlife Refuge, Alabama.

Model	K	-log$L$	AIC	ΔAIC	w_i	cum w_i
p(depth) Ψ(depth + land cover)	7	73.06	160.12	0.00	0.25	0.25
p(depth) Ψ(velocity + land cover)	7	73.12	160.25	0.13	0.23	0.47
p(.) Ψ(depth + land cover)	6	74.41	160.82	0.70	0.17	0.65
p(.) Ψ(velocity + land cover)	6	74.44	160.88	0.76	0.17	0.82
p(depth) Ψ(depth + velocity + land cover)	8	73.06	162.12	2.00	0.09	0.91
p(.) Ψ(depth + velocity + land cover)	7	74.41	162.82	2.70	0.06	0.97
p(depth) Ψ(velocity)	4	79.31	166.61	6.49	0.01	0.98
p(.) Ψ(velocity)	3	80.51	167.03	6.91	0.01	0.99
p(depth) Ψ(depth + velocity)	5	79.00	168.00	7.88	0.00	0.99
p(.) Ψ(depth + velocity)	4	80.31	168.62	8.50	0.00	0.99
p(depth) Ψ(.)	3	81.87	169.74	9.63	0.00	1.00
p(depth) Ψ(depth)	4	81.32	170.64	10.52	0.00	1.00
p(.) Ψ(.)	2	83.32	170.65	10.53	0.00	1.00
p(.) Ψ(depth)	3	82.58	171.16	11.04	0.00	1.00

Table A4-8. Model selection results for green sunfish (*Lepomis cyanellus*) in Wheeler National Wildlife Refuge, Alabama.

Model	K	-log$L$	AIC	ΔAIC	w_i	cum w_i
p(.) Ψ(velocity + land cover)	6	75.95	163.91	0.00	0.22	0.22
p(depth) Ψ(velocity + land cover)	7	74.96	163.92	0.01	0.22	0.45
p(.) Ψ(depth + velocity + land cover)	7	75.83	165.67	1.76	0.09	0.54
p(depth) Ψ(depth + velocity + land cover)	8	75.07	166.15	2.24	0.07	0.61
p(.) Ψ(velocity)	3	80.29	166.58	2.67	0.06	0.67
p(.) Ψ(depth + land cover)	6	77.34	166.68	2.77	0.06	0.73
p(.) Ψ(.)	2	81.45	166.89	2.99	0.05	0.78
p(depth) Ψ(depth + land cover)	7	76.45	166.90	2.99	0.05	0.83
p(depth) Ψ(velocity)	4	79.47	166.95	3.04	0.05	0.88
p(depth) Ψ(.)	3	80.58	167.16	3.25	0.04	0.92
p(.) Ψ(depth + velocity)	4	80.22	168.44	4.53	0.02	0.94
p(.) Ψ(depth)	3	81.25	168.50	4.59	0.02	0.97
p(depth) Ψ(depth + velocity)	5	79.47	168.94	5.03	0.02	0.98
p(depth) Ψ(depth)	4	80.57	169.14	5.24	0.02	1.00

Table A4-9. Model selection results for orangespotted sunfish (*Lepomis humilis*) in Wheeler National Wildlife Refuge, Alabama.

Model	K	-log$L$	AIC	ΔAIC	w_i	cum w_i
p(depth) Ψ(depth + land cover)	7	77.75	169.50	0.00	0.22	0.22
p(.) Ψ(depth + land cover)	6	78.80	169.60	0.10	0.21	0.43
p(depth) Ψ(velocity + land cover)	7	77.84	169.68	0.18	0.20	0.62
p(.) Ψ(velocity + land cover)	6	79.56	171.12	1.62	0.10	0.72
p(depth) Ψ(depth + velocity + land cover)	8	77.71	171.43	1.93	0.08	0.80
p(.) Ψ(depth + velocity + land cover)	7	78.74	171.49	1.99	0.08	0.88
p(depth) Ψ(.)	3	83.92	173.83	4.33	0.02	0.91
p(depth) Ψ(velocity)	4	83.12	174.24	4.75	0.02	0.93
p(.) Ψ(.)	2	85.13	174.25	4.76	0.02	0.95
p(.) Ψ(velocity)	3	84.49	174.98	5.49	0.01	0.96
p(.) Ψ(depth)	3	84.77	175.55	6.05	0.01	0.97
p(depth) Ψ(depth)	4	83.92	175.83	6.33	0.01	0.98
p(.) Ψ(depth + velocity)	4	83.97	175.94	6.44	0.01	0.99
p(depth) Ψ(depth + velocity)	5	83.12	176.24	6.75	0.01	1.00

Table A4-10. Model selection results for bluegill (*Lepomis macrochirus*) in Wheeler National Wildlife Refuge, Alabama.

Model	K	-log$L$	AIC	ΔAIC	w_i	cum w_i
p(.) Ψ(.)	2	141.89	287.79	0.00	0.36	0.36
p(.) Ψ(depth)	3	141.76	289.52	1.73	0.15	0.51
p(depth) Ψ(.)	3	141.89	289.77	1.98	0.13	0.65
p(.) Ψ(velocity)	3	141.89	289.78	1.99	0.13	0.78
p(.) Ψ(depth + velocity)	8	141.76	291.51	3.72	0.06	0.84
p(depth) Ψ(depth)	7	141.76	291.51	3.72	0.06	0.89
p(depth) Ψ(velocity)	3	141.82	291.64	3.85	0.05	0.95
p(depth) Ψ(depth + velocity)	4	141.75	293.50	5.71	0.02	0.97
p(.) Ψ(depth + land cover)	2	141.46	294.93	7.14	0.01	0.98
p(.) Ψ(velocity + land cover)	3	141.51	295.02	7.23	0.01	0.99
p(depth) Ψ(depth + land cover)	3	141.47	296.94	9.15	0.00	0.99
p(.) Ψ(depth + velocity + land cover)	4	141.47	296.95	9.16	0.00	1.00
p(depth) Ψ(velocity + land cover)	5	141.52	297.04	9.25	0.00	1.00
p(depth) Ψ(depth + velocity + land cover)	8	141.47	298.95	11.16	0.00	1.00

Table A4-11. Model selection results for longear sunfish (*Lepomis megalotis*) in Wheeler National Wildlife Refuge, Alabama.

Model	K	-log*L*	AIC	ΔAIC	w_i	cum w_i
p(depth) Ψ(depth + land cover)	7	76.68	167.36	0.00	0.60	0.60
p(depth) Ψ(depth + velocity + land cover)	8	76.74	169.48	2.12	0.21	0.81
p(.) Ψ(depth + land cover)	6	79.41	170.81	3.45	0.11	0.92
p(.) Ψ(depth + velocity + land cover)	7	79.40	172.81	5.44	0.04	0.96
p(depth) Ψ(velocity)	4	83.86	175.73	8.36	0.01	0.96
p(.) Ψ(velocity)	3	85.10	176.21	8.85	0.01	0.97
p(depth) Ψ(velocity + land cover)	7	81.18	176.36	9.00	0.01	0.98
p(depth) Ψ(depth + velocity)	5	83.68	177.37	10.00	0.00	0.98
p(depth) Ψ(.)	3	85.70	177.39	10.03	0.00	0.99
p(.) Ψ(velocity + land cover)	6	82.71	177.42	10.06	0.00	0.99
p(.) Ψ(.)	2	86.82	177.64	10.28	0.00	0.99
p(.) Ψ(depth + velocity)	4	85.01	178.01	10.65	0.00	1.00
p(depth) Ψ(depth)	4	85.48	178.95	11.59	0.00	1.00
p(.) Ψ(depth)	3	86.78	179.55	12.19	0.00	1.00

Table A4-12. Model selection results for redear sunfish (*Lepomis microlophus*) in Wheeler National Wildlife Refuge, Alabama.

Model	K	-log*L*	AIC	ΔAIC	w_i	cum w_i
p(depth) Ψ(velocity)	4	95.83	199.67	0.00	0.39	0.39
p(depth) Ψ(velocity + land cover)	7	93.41	200.82	1.16	0.22	0.60
p(depth) Ψ(depth + velocity)	5	96.00	202.01	2.34	0.12	0.72
p(depth) Ψ(depth + land cover)	7	94.33	202.66	2.99	0.09	0.81
p(depth) Ψ(depth + velocity + land cover)	8	93.34	202.68	3.01	0.09	0.90
p(depth) Ψ(.)	3	98.56	203.13	3.46	0.07	0.97
p(depth) Ψ(depth)	4	98.53	205.06	5.39	0.03	0.99
p(.) Ψ(depth + velocity)	4	100.70	209.40	9.73	0.00	0.99
p(.) Ψ(velocity)	3	101.98	209.96	10.30	0.00	1.00
p(.) Ψ(depth + land cover)	6	99.95	211.91	12.24	0.00	1.00
p(.) Ψ(depth + velocity + land cover)	7	98.96	211.93	12.26	0.00	1.00
p(.) Ψ(.)	2	104.25	212.51	12.84	0.00	1.00
p(.) Ψ(depth)	3	103.27	212.55	12.88	0.00	1.00
p(.) Ψ(velocity + land cover)	6	100.35	212.69	13.02	0.00	1.00

Table A4-13. Model selection results for largemouth bass (*Micropterus salmoides*) in Wheeler National Wildlife Refuge, Alabama.

Model	K	-log$L$	AIC	ΔAIC	w_i	cum w_i
p(depth) Ψ(.)	3	110.70	227.40	0.00	0.26	0.26
p(.) Ψ(.)	2	111.84	227.68	0.28	0.23	0.49
p(depth) Ψ(depth)	4	110.67	229.34	1.94	0.10	0.59
p(depth) Ψ(velocity)	4	110.70	229.41	2.01	0.10	0.69
p(.) Ψ(depth)	3	111.81	229.62	2.22	0.09	0.78
p(.) Ψ(velocity)	3	111.83	229.67	2.27	0.08	0.86
p(depth) Ψ(depth + velocity)	5	110.67	231.33	3.93	0.04	0.90
p(.) Ψ(depth + velocity)	4	111.81	231.62	4.22	0.03	0.93
p(.) Ψ(velocity + land cover)	6	110.46	232.93	5.53	0.02	0.95
p(depth) Ψ(velocity + land cover)	7	109.47	232.95	5.55	0.02	0.96
p(depth) Ψ(depth + land cover)	7	109.82	233.63	6.23	0.01	0.98
p(.) Ψ(depth + land cover)	6	110.92	233.84	6.44	0.01	0.99
p(depth) Ψ(depth + velocity + land cover)	8	109.36	234.72	7.32	0.01	0.99
p(.) Ψ(depth + velocity + land cover)	7	110.46	234.92	7.52	0.01	1.00

Table A4-14. Model selection results for blackside snubnose darter (*Etheostoma duryi*) in Wheeler National Wildlife Refuge, Alabama.

Model	K	-log$L$	AIC	ΔAIC	w_i	cum w_i
p(.) Ψ(velocity)	3	31.11	68.23	0.00	0.26	0.26
p(.) Ψ(velocity + land cover)	6	28.52	69.04	0.82	0.17	0.44
p(depth) Ψ(velocity)	4	31.02	70.03	1.81	0.11	0.54
p(.) Ψ(depth + land cover)	6	29.12	70.25	2.02	0.10	0.64
p(.) Ψ(depth + velocity)	4	31.19	70.38	2.16	0.09	0.73
p(depth) Ψ(velocity + land cover)	7	28.31	70.61	2.39	0.08	0.80
p(.) Ψ(depth + velocity + land cover)	7	28.53	71.05	2.82	0.06	0.87
p(depth) Ψ(depth + velocity)	5	30.80	71.59	3.37	0.05	0.92
p(depth) Ψ(depth + land cover)	7	28.81	71.62	3.40	0.05	0.96
p(depth) Ψ(depth + velocity + land cover)	8	28.20	72.41	4.18	0.03	1.00
p(.) Ψ(.)	2	37.49	78.97	10.75	0.00	1.00
p(.) Ψ(depth)	3	36.81	79.63	11.40	0.00	1.00
p(depth) Ψ(.)	3	37.03	80.07	11.84	0.00	1.00
p(depth) Ψ(depth)	4	36.49	80.98	12.75	0.00	1.00

Appendix 5: Model comparison results for extinction-colonization models of 13 fish species detected in the Piedmont region of the Tallapoosa River basin, Alabama (Chapter 3)

This appendix includes model selection results for occupancy models of 13 species detected in the Piedmont region of the Tallapoosa River basin, Alabama. Number of parameters in each model (K), negative log likelihood (-log$L$), AIC, ΔAIC, AIC model weights (w_i), and cumulative model weights (cum w_i) are reported. Model results for each species are ranked in terms of AIC and w_i. Models estimated occupancy (ψ) as constant [$\psi(.)$] or as a function of downstream distance from a large hydropower dam [ψ(distance)], colonization (γ) as constant [$\gamma(.)$] or as a function of distance [γ(distance)], extinction (ϵ) as constant [$\epsilon(.)$] or as a function of distance [ϵ(distance)], and detection (p) as constant [$p(.)$] or as a function of habitat [p(depth), p(velocity), p(depth+velocity)]. Only ranked models with AIC model weights that add to a cumulative weight of 1.00000 are included (that is, those models with negligible weights are not included).

Table A5-1. Model selection results for largescale stoneroller (*Campostoma oligolepis*) in the Piedmont region of the Tallapoosa River, Alabama.

Model	K	-logL	AIC	ΔAIC	w_i	cum w_i
ψ(distance) γ(.) ε(distance) p(depth+velocity)	8	1187.56	2391.11	0.00000	0.46745	0.46745
ψ(distance) γ(distance) ε(distance) p(depth+velocity)	9	1187.22	2392.43	1.31462	0.24225	0.70971
ψ(.) γ(distance) ε(distance) p(depth+velocity)	8	1188.55	2393.10	1.98553	0.17321	0.88292
ψ(.) γ(.) ε(distance) p(depth+velocity)	7	1190.23	2394.45	3.33783	0.08809	0.97101
ψ(distance) γ(distance) ε(.) p(depth+velocity)	8	1191.35	2398.71	7.59397	0.01049	0.98150
ψ(.) γ(distance) ε(.) p(depth+velocity)	7	1192.43	2398.86	7.74653	0.00972	0.99122
ψ(distance) γ(.) ε(.) p(depth+velocity)	7	1192.71	2399.42	8.30553	0.00735	0.99857
ψ(.) γ(.) ε(.) p(depth+velocity)	6	1195.35	2402.70	11.5803	0.00143	1.00000

Table A5-2. Model selection results for Alabama shiner (*Cyprinella callistia*) in the Piedmont region of the Tallapoosa River, Alabama.

Model	K	-logL	AIC	ΔAIC	w_i	cum w_i
ψ(distance) γ(distance) ε(.) p(depth+velocity)	8	1469.47	2954.94	0.00000	0.73731	0.73731
ψ(.) γ(distance) ε(.) p(depth+velocity)	7	1471.65	2957.30	2.36582	0.22590	0.96322
ψ(distance) γ(.) ε(.) p(depth+velocity)	7	1473.63	2961.25	6.31312	0.03139	0.99461
ψ(.) γ(.) ε(.) p(depth+velocity)	6	1476.45	2964.90	9.95915	0.00507	0.99968
ψ(distance) γ(distance) ε(.) p(velocity)	7	1478.62	2971.24	16.2977	0.00021	0.99989
ψ(.) γ(distance) ε(.) p(velocity)	6	1480.73	2973.46	18.5205	0.00007	0.99996
ψ(.) γ(distance) ε(distance) p(velocity)	7	1480.74	2975.49	20.5500	0.00003	0.99999
ψ(distance) γ(.) ε(.) p(velocity)	6	1482.72	2977.43	22.4959	0.00001	0.99999
ψ(.) γ(.) ε(.) p(velocity)	5	1485.48	2980.96	26.0197	0.00000	1.00000

Table A5-3. Model selection results for Tallapoosa shiner (*Cyprinella gibbsi*) in the Piedmont region of the Tallapoosa River, Alabama.

Model	K	-logL	AIC	ΔAIC	w_i	cum w_i
ψ(distance) γ(.) ε(.) p(.)	5	768.816	1547.63	0.00000	1.00000	1.00000
ψ(distance) γ(.) ε(.) p(depth+velocity)	7	812.665	1639.33	91.6992	0.00000	1.00000

Table A5-4. Model selection results for blacktail shiner (*Cyprinella venusta*) in the Piedmont region of the Tallapoosa River, Alabama.

Model	K	-logL	AIC	ΔAIC	w_i	cum w_i
ψ(.) γ(.) ε(.) p(depth+velocity)	6	673.851	1359.70	0.00000	0.22005	0.22005
ψ(.) γ(.) ε(.) p(velocity)	5	675.458	1360.92	1.21371	0.11994	0.33999
ψ(.) γ(distance) ε(.) p(depth+velocity)	7	673.460	1360.92	1.21828	0.11967	0.45966
ψ(distance) γ(.) ε(.) p(depth+velocity)	7	673.838	1361.68	1.97433	0.08200	0.54166
ψ(.) γ(.) ε(distance) p(depth+velocity)	7	673.860	1361.72	2.01796	0.08023	0.62189
ψ(.) γ(distance) ε(.) p(velocity)	6	675.067	1362.13	2.43128	0.06525	0.68714
ψ(distance) γ(distance) ε(.) p(depth+velocity)	8	673.282	1362.57	2.86237	0.05260	0.73973
ψ(distance) γ(.) ε(.) p(velocity)	6	675.444	1362.89	3.18533	0.04475	0.78449
ψ(.) γ(.) ε(distance) p(velocity)	6	675.467	1362.93	3.23086	0.04375	0.82824
ψ(.) γ(distance) ε(distance) p(depth+velocity)	8	673.469	1362.94	3.23641	0.04363	0.87186
ψ(distance) γ(.) ε(distance) p(depth+velocity)	8	673.848	1363.70	3.99398	0.02987	0.90173
ψ(distance) γ(distance) ε(.) p(velocity)	7	674.893	1363.79	4.08401	0.02856	0.93029
ψ(.) γ(distance) ε(distance) p(velocity)	7	675.076	1364.15	4.44897	0.02379	0.95408
ψ(distance) γ(distance) ε(distance) p(depth+velocity)	9	673.292	1364.58	4.88147	0.01917	0.97325
ψ(distance) γ(.) ε(distance) p(velocity)	7	675.453	1364.91	5.20441	0.01631	0.98956
ψ(distance) γ(distance) ε(distance) p(velocity)	8	674.903	1365.81	6.10438	0.01040	0.99995
ψ(.) γ(.) ε(.) p(depth)	5	684.868	1379.74	20.0339	0.00001	0.99996
ψ(.) γ(.) ε(.) p(.)	4	686.351	1380.70	20.9989	0.00001	0.99997
ψ(.) γ(distance) ε(.) p(depth)	6	684.499	1381.00	21.2964	0.00001	0.99997
ψ(distance) γ(.) ε(.) p(depth)	6	684.860	1381.72	22.0167	0.00000	0.99998
ψ(.) γ(.) ε(distance) p(depth)	6	684.877	1381.75	22.0509	0.00000	0.99998
ψ(.) γ(distance) ε(.) p(.)	5	685.982	1381.96	22.2618	0.00000	0.99999
ψ(distance) γ(distance) ε(.) p(depth)	7	684.318	1382.64	22.9330	0.00000	0.99999
ψ(distance) γ(.) ε(.) p(.)	5	686.341	1382.68	22.9795	0.00000	0.99999
ψ(.) γ(.) ε(distance) p(.)	5	686.359	1382.72	23.0159	0.00000	0.99999
ψ(.) γ(distance) ε(distance) p(depth)	7	684.508	1383.02	23.3136	0.00000	0.99999
ψ(distance) γ(distance) ε(.) p(.)	6	685.805	1383.61	23.9075	0.00000	1.00000

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Table A5-5. Model selection results for bullhead minnow (*Pimephales vigilax*) in the Piedmont region of the Tallapoosa River, Alabama.

Model	K	-logL	AIC	ΔAIC	w_i	cum w_i
ψ(.) γ(distance) ε(.) p(depth+velocity)	7	429.149	872.298	0.00000	0.55785	0.55785
ψ(.) γ(distance) ε(distance) p(depth+velocity)	8	429.150	874.301	2.00226	0.20499	0.76284
ψ(distance) γ(distance) ε(.) p(depth+velocity)	8	429.331	874.661	2.36293	0.17116	0.93400
ψ(distance) γ(distance) ε(distance) p(depth+velocity)	9	429.314	876.629	4.33058	0.06399	0.99800
ψ(distance) γ(.) ε(.) p(depth+velocity)	7	435.117	884.234	11.9353	0.00143	0.99943
ψ(distance) γ(.) ε(distance) p(depth+velocity)	8	435.053	886.107	13.8086	0.00056	0.99999
ψ(.) γ(distance) ε(.) p(velocity)	6	441.605	895.209	22.9106	0.00001	0.99999
ψ(distance) γ(distance) ε(.) p(velocity)	7	441.165	896.330	24.0315	0.00000	1.00000

Table A5-6. Model selection results for Alabama hogsucker (*Hypentelium etowanum*) in the Piedmont region of the Tallapoosa River, Alabama.

Model	K	-logL	AIC	ΔAIC	w_i	cum w_i
ψ(distance) γ(distance) ε(distance) p(velocity)	8	1133.72	2283.44	0.00000	0.35896	0.35896
ψ(distance) γ(distance) ε(distance) p(depth+velocity)	9	1133.49	2284.99	1.54651	0.16566	0.52462
ψ(.) γ(distance) ε(distance) p(depth+velocity)	8	1134.52	2285.03	1.59433	0.16175	0.68637
ψ(.) γ(distance) ε(distance) p(velocity)	7	1135.88	2285.76	2.31713	0.11269	0.79906
ψ(distance) γ(.) ε(distance) p(depth+velocity)	8	1135.12	2286.25	2.81022	0.08807	0.88712
ψ(distance) γ(distance) ε(.) p(velocity)	7	1137.18	2288.37	4.92740	0.03055	0.91768
ψ(distance) γ(distance) ε(.) p(depth+velocity)	8	1136.34	2288.68	5.23918	0.02614	0.94382
ψ(.) γ(distance) ε(.) p(depth+velocity)	7	1137.46	2288.92	5.48505	0.02312	0.96694
ψ(.) γ(distance) ε(.) p(depth)	6	1139.02	2290.04	6.60537	0.01320	0.98015
ψ(.) γ(distance) ε(.) p(velocity)	6	1139.05	2290.09	6.65467	0.01288	0.99303
ψ(.) γ(.) ε(distance) p(depth+velocity)	7	1138.79	2291.58	8.13692	0.00614	0.99917
ψ(distance) γ(.) ε(.) p(depth+velocity)	7	1140.87	2295.73	12.2911	0.00077	0.99994
ψ(.) γ(.) ε(.) p(depth+velocity)	6	1144.36	2300.72	17.2788	0.00006	1.00000

Table A5-7. Model selection results for speckled madtom (*Noturus leptacanthus*) in the Piedmont region of the Tallapoosa River, Alabama.

Model	K	-logL	AIC	ΔAIC	w_i	cum w_i
ψ(distance) γ(.) ε(distance) p(depth+velocity)	8	402.077	820.153	0.00000	0.61679	0.61679
ψ(distance) γ(distance) ε(distance) p(depth+velocity)	9	401.873	821.747	1.59373	0.27801	0.89479
ψ(.) γ(distance) ε(distance) p(depth+velocity)	8	403.867	823.734	3.58060	0.10295	0.99774
ψ(.) γ(.) ε(distance) p(depth+velocity)	7	408.940	831.879	11.7261	0.00175	0.99950
ψ(.) γ(distance) ε(.) p(depth+velocity)	7	410.745	835.490	15.3370	0.00029	0.99978
ψ(distance) γ(distance) ε(.) p(depth+velocity)	8	410.712	837.425	17.2717	0.00011	0.99989
ψ(distance) γ(.) ε(.) p(depth+velocity)	7	411.827	837.654	17.5014	0.00010	0.99999
ψ(distance) γ(.) ε(distance) p(velocity)	7	414.880	843.760	23.6070	0.00000	1.00000

Table A5-8. Model selection results for redbreast sunfish (*Lepomis auritus*) in the Piedmont region of the Tallapoosa River, Alabama.

Model	K	-logL	AIC	ΔAIC	w_i	cum w_i
ψ(distance) γ(.) ε(distance) p(depth+velocity)	8	882.323	1780.65	0.00000	0.93075	0.93075
ψ(distance) γ(.) ε(distance) p(velocity)	7	886.707	1787.41	6.76699	0.03158	0.96233
ψ(distance) γ(.) ε(.) p(depth+velocity)	7	886.915	1787.83	7.18455	0.02563	0.98796
ψ(.) γ(.) ε(distance) p(depth+velocity)	7	889.086	1792.17	11.5259	0.00292	0.99088
ψ(.) γ(distance) ε(.) p(depth+velocity)	7	889.526	1793.05	12.4054	0.00188	0.99277
ψ(.) γ(.) ε(.) p(depth+velocity)	6	890.549	1793.10	12.4509	0.00184	0.99461
ψ(distance) γ(.) ε(.) p(velocity)	6	890.589	1793.18	12.5313	0.00177	0.99638
ψ(.) γ(distance) ε(distance) p(depth+velocity)	8	888.924	1793.85	13.2016	0.00127	0.99764
ψ(distance) γ(distance) ε(.) p(depth+velocity)	8	889.164	1794.33	13.6809	0.00100	0.99864
ψ(distance) γ(distance) ε(distance) p(depth+velocity)	9	888.526	1795.05	14.4056	0.00069	0.99933
ψ(.) γ(.) ε(distance) p(velocity)	6	892.877	1797.75	17.1076	0.00018	0.99951
ψ(.) γ(distance) ε(.) p(velocity)	6	893.124	1798.25	17.6018	0.00014	0.99965
ψ(.) γ(.) ε(.) p(velocity)	5	894.171	1798.34	17.6955	0.00013	0.99978
ψ(.) γ(distance) ε(distance) p(velocity)	7	892.551	1799.10	18.4558	0.00009	0.99988
ψ(distance) γ(distance) ε(.) p(velocity)	7	892.763	1799.53	18.8792	0.00007	0.99995
ψ(distance) γ(distance) ε(distance) p(velocity)	8	892.151	1800.30	19.6558	0.00005	1.00000

Table A5-9. Model selection results for lipstick darter (*Etheostoma chuckwachatte*) in the Piedmont region of the Tallapoosa River, Alabama.

Model	K	-log*L*	AIC	ΔAIC	w_i	cum w_i
ψ(distance) γ(.) ε(.) p(depth+velocity)	7	1460.05	2934.10	0.00000	0.45756	0.45756
ψ(distance) γ(distance) ε(.) p(depth+velocity)	8	1460.00	2936.00	1.90114	0.17686	0.63442
ψ(distance) γ(.) ε(distance) p(depth+velocity)	8	1460.04	2936.09	1.98582	0.16952	0.80394
ψ(.) γ(.) ε(.) p(depth+velocity)	6	1462.96	2937.92	3.81823	0.06782	0.87176
ψ(distance) γ(distance) ε(distance) p(depth+velocity)	9	1459.96	2937.92	3.82104	0.06772	0.93948
ψ(.) γ(.) ε(distance) p(depth+velocity)	7	1462.92	2939.84	5.73581	0.02600	0.96548
ψ(.) γ(distance) ε(.) p(depth+velocity)	7	1462.96	2939.92	5.81758	0.02496	0.99043
ψ(.) γ(distance) ε(distance) p(depth+velocity)	8	1462.92	2941.84	7.73505	0.00957	1.00000

Table A5-10. Model selection results for speckled darter (*Etheostoma stigmaeum*) in the Piedmont region of the Tallapoosa River, Alabama.

Model	K	-log*L*	AIC	ΔAIC	w_i	cum w_i
ψ(.) γ(.) ε(.) p(depth+velocity)	6	1204.62	2421.24	0.00000	0.16808	0.16808
ψ(.) γ(distance) ε(.) p(depth+velocity)	7	1203.70	2421.40	0.15775	0.15533	0.32342
ψ(distance) γ(.) ε(.) p(depth+velocity)	7	1203.72	2421.43	0.19360	0.15257	0.47599
ψ(.) γ(.) ε(distance) p(depth+velocity)	7	1204.17	2422.34	1.09612	0.09716	0.57316
ψ(.) γ(distance) ε(distance) p(depth+velocity)	8	1203.22	2422.44	1.20176	0.09216	0.66532
ψ(distance) γ(distance) ε(.) p(depth+velocity)	8	1203.23	2422.45	1.21346	0.09163	0.75695
ψ(distance) γ(.) ε(distance) p(depth+velocity)	8	1203.40	2422.79	1.55138	0.07738	0.83433
ψ(distance) γ(distance) ε(distance) p(depth+velocity)	9	1202.97	2423.94	2.70369	0.04349	0.87782
ψ(.) γ(distance) ε(.) p(depth)	6	1206.52	2425.05	3.80616	0.02506	0.90289
ψ(.) γ(.) ε(.) p(depth)	5	1207.61	2425.21	3.96966	0.02310	0.92598
ψ(distance) γ(.) ε(.) p(depth)	6	1206.70	2425.41	4.16547	0.02094	0.94692
ψ(.) γ(.) ε(distance) p(depth)	6	1207.20	2426.40	5.15566	0.01276	0.95969
ψ(distance) γ(distance) ε(.) p(depth)	7	1206.23	2426.46	5.21578	0.01239	0.97207
ψ(.) γ(distance) ε(distance) p(depth)	7	1206.27	2426.53	5.29004	0.01193	0.98401
ψ(distance) γ(.) ε(distance) p(depth)	7	1206.42	2426.83	5.59268	0.01026	0.99427
ψ(distance) γ(distance) ε(distance) p(depth)	8	1206.00	2428.00	6.75613	0.00573	1.00000

Table A5-11. Model selection results for Tallapoosa darter (*Etheostoma tallapoosae*) in the Piedmont region of the Tallapoosa River, Alabama.

Model	K	-logL	AIC	ΔAIC	w_i	cum w_i
ψ(.) γ(.) ε(.) p(depth+velocity)	6	898.648	1809.30	0.00000	0.29051	0.29051
ψ(distance) γ(.) ε(.) p(depth+velocity)	7	897.917	1809.83	0.53706	0.22210	0.51261
ψ(.) γ(distance) ε(.) p(depth+velocity)	7	898.444	1810.89	1.59148	0.13109	0.64370
ψ(.) γ(.) ε(distance) p(depth+velocity)	7	898.645	1811.29	1.99424	0.10718	0.75088
ψ(distance) γ(.) ε(distance) p(depth+velocity)	8	897.895	1811.79	2.49318	0.08352	0.83440
ψ(distance) γ(distance) ε(.) p(depth+velocity)	8	897.900	1811.80	2.50336	0.08309	0.91749
ψ(.) γ(distance) ε(distance) p(depth+velocity)	8	898.437	1812.87	3.57730	0.04857	0.96606
ψ(distance) γ(distance) ε(distance) p(depth+velocity)	9	897.885	1813.77	4.47307	0.03103	0.99709
ψ(.) γ(.) ε(.) p(velocity)	5	905.491	1820.98	11.6849	0.00084	0.99793
ψ(distance) γ(.) ε(.) p(velocity)	6	904.756	1821.51	12.2158	0.00065	0.99858
ψ(.) γ(distance) ε(.) p(velocity)	6	905.273	1822.55	13.2497	0.00039	0.99897
ψ(.) γ(.) ε(distance) p(velocity)	6	905.484	1822.97	13.6707	0.00031	0.99928
ψ(distance) γ(.) ε(distance) p(velocity)	7	904.728	1823.46	14.1592	0.00024	0.99952
ψ(distance) γ(distance) ε(.) p(velocity)	7	904.735	1823.47	14.1741	0.00024	0.99977
ψ(.) γ(distance) ε(distance) p(velocity)	7	905.270	1824.54	15.2429	0.00014	0.99991
ψ(distance) γ(distance) ε(distance) p(velocity)	8	904.715	1825.43	16.1335	0.00009	1.00000

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Table A5-12. Model selection results for bronze darter (*Percina palmaris*) in the Piedmont region of the Tallapoosa River, Alabama.

Model	K	-logL	AIC	ΔAIC	w_i	cum w_i
ψ(.) γ(.) ε(.) p(depth+velocity)	6	1541.65	3095.29	0.00000	0.38957	0.38957
ψ(.) γ(distance) ε(.) p(depth+velocity)	7	1541.64	3097.29	1.99408	0.14374	0.53331
ψ(distance) γ(.) ε(.) p(depth+velocity)	7	1541.64	3097.29	1.99423	0.14373	0.67704
ψ(.) γ(.) ε(distance) p(depth+velocity)	7	1541.65	3097.29	1.99797	0.14346	0.82050
ψ(distance) γ(distance) ε(.) p(depth+velocity)	8	1541.64	3099.29	3.99346	0.05290	0.87339
ψ(.) γ(distance) ε(distance) p(depth+velocity)	8	1541.65	3099.29	3.99682	0.05281	0.92620
ψ(distance) γ(.) ε(distance) p(depth+velocity)	8	1541.65	3099.29	3.99751	0.05279	0.97899
ψ(distance) γ(distance) ε(distance) p(depth+velocity)	9	1541.65	3101.29	5.99739	0.01942	0.99841
ψ(.) γ(.) ε(.) p(velocity)	5	1549.09	3108.18	12.8861	0.00062	0.99903
ψ(.) γ(distance) ε(.) p(velocity)	6	1549.08	3110.17	14.8750	0.00023	0.99926
ψ(distance) γ(.) ε(.) p(velocity)	6	1549.08	3110.17	14.8753	0.00023	0.99949
ψ(.) γ(.) ε(distance) p(velocity)	6	1549.09	3110.17	14.8786	0.00023	0.99972
ψ(distance) γ(distance) ε(.) p(velocity)	7	1549.08	3112.17	16.8733	0.00008	0.99980
ψ(.) γ(distance) ε(distance) p(velocity)	7	1549.09	3112.17	16.8769	0.00008	0.99988
ψ(distance) γ(.) ε(distance) p(velocity)	7	1549.09	3112.17	16.8777	0.00008	0.99997
ψ(distance) γ(distance) ε(distance) p(velocity)	8	1549.09	3114.17	18.8775	0.00003	1.00000

Table A5-13. Model selection results for muscadine darter (*Percina smithvanizi*) in the Piedmont region of the Tallapoosa River, Alabama.

Model	K	-log*L*	AIC	ΔAIC	w_i	cum w_i
ψ(distance) γ(distance) ε(.) *p*(velocity)	7	1380.35	2774.69	0.00000	0.34370	0.34370
ψ(distance) γ(distance) ε(.) *p*(depth+velocity)	8	1379.37	2774.74	0.04689	0.33573	0.67943
ψ(distance) γ(distance) ε(distance) *p*(velocity)	8	1379.88	2775.76	1.06985	0.20131	0.88074
ψ(.) γ(distance) ε(.) *p*(velocity)	6	1383.37	2778.74	4.04389	0.04550	0.92624
ψ(.) γ(distance) ε(.) *p*(depth+velocity)	7	1382.43	2778.86	4.16383	0.04286	0.96910
ψ(.) γ(.) ε(.) *p*(velocity)	5	1385.79	2781.57	6.87790	0.01103	0.98013
ψ(.) γ(.) ε(.) *p*(depth+velocity)	6	1384.84	2781.69	6.99534	0.01040	0.99053
ψ(distance) γ(.) ε(.) *p*(velocity)	6	1385.62	2783.24	8.54298	0.00480	0.99533
ψ(distance) γ(.) ε(.) *p*(depth+velocity)	7	1384.68	2783.35	8.65995	0.00453	0.99986
ψ(distance) γ(distance) ε(distance) *p*(depth+velocity)	9	1386.83	2791.65	16.9608	0.00007	0.99993
ψ(.) γ(distance) ε(distance) *p*(depth+velocity)	8	1389.17	2794.33	19.6372	0.00002	0.99995
ψ(.) γ(.) ε(distance) *p*(depth+velocity)	7	1390.34	2794.67	19.9809	0.00002	0.99996
ψ(.) γ(distance) ε(distance) *p*(velocity)	7	1390.55	2795.11	20.4113	0.00001	0.99998
ψ(.) γ(.) ε(distance) *p*(velocity)	6	1391.74	2795.48	20.7860	0.00001	0.99999
ψ(distance) γ(.) ε(distance) *p*(depth+velocity)	8	1390.07	2796.15	21.4542	0.00001	1.00000

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