

RESEARCH ARTICLE

Floods, drying, habitat connectivity, and fish occupancy dynamics in restored and unrestored oxbows of West Central Iowa, USA

Jesse R. Fischer¹ | Bryan D. Bakevich¹ | Colin P. Shea² | Clay L. Pierce³  | Michael C. Quist¹

¹Department of Natural Resource Ecology & Management, Iowa State University, Ames, Iowa, USA

²Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, Florida, USA

³US Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, Iowa State University, Ames, Iowa, USA

Correspondence

Clay L. Pierce, US Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, 2310 Pammel Drive, Ames, IA 50011, USA.
Email: cpierce@iastate.edu

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Abstract

1. In the agricultural landscape of the Midwestern USA, waterways are highly altered. Oxbows are among the few remaining off-channel habitats associated with streams, supporting fish assemblages that include the endangered Topeka shiners *Notropis topeka* in portions of their remaining range. Oxbow restorations seek to increase the number and quality of oxbows for Topeka shiners. For oxbows to provide optimal habitat, periods of isolation from streams and connection with streams during floods are necessary.
2. Water levels and patterns of drying and hydrological connectivity between 12 oxbows and their neighboring streams in West Central Iowa were continuously monitored from May to October 2011, and fish assemblages were assessed for responses to the differing hydrodynamics using dynamic occupancy modelling.
3. The 12 oxbows exhibited varied hydrodynamics and connectivity with streams. Two oxbows never contained fish; these oxbows never flooded and were among the three oxbows that were dry for the longest periods.
4. Occupancy modelling suggested that connection with the stream via floods significantly increased the probability of colonization, and low water level increased the probability of local extinction from oxbows. Thirteen of the 16 fish species encountered had detection probabilities over 60%, and eight had detection probabilities over 90%, including Topeka shiners.
5. None of the five previously restored oxbows flooded; all five contained fish, but only one contained Topeka shiners. Three of the four oxbows containing Topeka shiners flooded and all four dried at least once.
6. These results suggest that planning for future oxbow restorations should consider: (i) sites that flood frequently; and (ii) construction methods promoting alternating periods of isolation from and connection with streams.

KEYWORDS

agriculture, endangered species, flood plain, *Notropis topeka*, restoration, Topeka shiner

1 | INTRODUCTION

In the agriculture-dominated landscape of the Midwestern USA, streams and their associated habitats are highly altered from their pristine state (Blann, Anderson, Sands, & Vondracek, 2009; Hughes, Wang, & Seelbach, 2006; Waters, 1995). Streams that once meandered through a mosaic of natural prairie and savannah now flow between fields of highly cultivated row crops, often in artificially straightened channels (Gallant, Sadinski, Roth, & Rewa, 2011; Whitney, 1994). Prior to this conversion, meandering prairie streams were characterized by diverse habitats, both in-stream and off-channel, with many natural connections between habitats within the flowing stream and associated areas of standing or slow-flowing water (Matthews, 1988; Miller, Crumpton, & van der Valk, 2009; Prince, 1997). A variety of processes associated with this conversion have resulted in the reduced diversity and quality of in-stream habitats and the isolation of streams from off-channel habitats, which are increasingly rare and less diverse (Allan, 2004; Blann et al., 2009; Infante, Allan, Linke, & Norris, 2009; Rowe, Pierce, & Wilton, 2009a, b).

Oxbows, formed when looping stream meanders are cut off through bank erosion, leaving a standing water habitat in the remnant stream channel (Charlton, 2008; Ward, Tockner, Arscott, & Claret, 2002), or as the result of artificial straightening (Bishop, 1981), are among the few remaining slow- or standing-water habitats associated with many prairie streams (Menzel, 1983; Miller et al., 2009). Although some oxbows remain, holding water and supporting numerous fish and other aquatic life, many other oxbows have partially filled in with sediment, have become increasingly isolated from their associated streams as a result of the downcutting of the stream channel, and have even been cultivated in dry years (Blann et al., 2009). Where oxbows have become rare or eliminated, slow- and standing-water habitats are likewise rare or non-existent. In turn, some native fish species that require these slow- or standing-water habitats have become rare or have been extirpated (Gido, Dodds, & Eberle, 2010; Menzel, 1981).

Early accounts of habitat use by many fish species in prairie streams describe habitats such as slow pools, submerged and emergent vegetation, side channels, and backwaters that are rare or non-existent in those streams today (Meek, 1892; Menzel, 1981, 1983). The Topeka shiner *Notropis topeka*, native to prairie regions in six Midwestern and Great Plains states, and listed as endangered by the US Fish and Wildlife Service (Tabor, 1998), is a prime example. Prior to listing, habitats of Topeka shiners were typically described as pools and side- or off-channel areas of slow current, with sandy or gravel substrates, and with abundant vegetation (Loan-Wilsey, Pierce, Kane, Brown, & McNeely, 2005; Minckley & Cross, 1959; Pflieger, 1997; Wall & Berry, 2004). Although these types of habitats are no doubt still important where they exist, habitat studies in Midwestern streams suggest that they are rare or absent in many locales with predominantly agricultural land use (Hughes et al., 2006; Rowe et al., 2009b). Recent studies document Topeka shiners inhabiting streams lacking many of these features (Bakevich, Pierce, & Quist, 2013; Clark, 2000; Simpson, Pierce, Roe, & Weber, 2017; Zambory, Bybel, Pierce, Roe, & Weber, 2017), but occurrences are rare and abundances are typically low. Increasingly, oxbows appear to support the most prevalent and abundant populations of Topeka shiners (Bakevich et al., 2013; Clark,

2000; Hatch, 2001), at least in some portions of their remaining range, and the restoration of oxbows for the purpose of providing Topeka shiner habitat is now under way in Iowa (Kenney, 2013) and Minnesota (Utrup, 2015). In South Dakota, Topeka shiners are frequently found in analogous habitats termed dugouts, which were originally constructed to provide reliable water sources for cattle in floodplains near streams (Johnson, Higgins, Kjellsen, & Elliott, 1997), but now are also considered important Topeka shiner habitat (Natural Resource Conservation Service, 2010).

For oxbows to function optimally as habitats for the endangered Topeka shiner and other fish species, periods of isolation from and connection with associated streams are thought to be necessary (Bunn & Arthington, 2002; Environmental Protection Agency, 2015). Floods connect oxbows with nearby streams and the associated stream network, allowing the colonization of new habitats. Periods of isolation from streams may enable the persistence of species vulnerable to competition and predation (Magoulick & Kobza, 2003; Scheerer, 2002), especially for species such as Topeka shiners that have a relatively high tolerance to the increasing thermal and oxygen stress experienced in oxbows as the water levels drop between floods (Koehle & Adelman, 2007). Periodic complete drying could possibly serve as a 'reset button', whereby entire fish assemblages are eliminated, providing new opportunities for colonists during the next flood event, and enabling the re-establishment of rare species such as Topeka shiners where they were previously absent. Previous studies have documented considerable variation in fish assemblages among oxbows, including the presence and absence of Topeka shiners (Bakevich et al., 2013; Clark, 2000), and the differing degrees of connectivity to streams may be a determining factor. The goal of this study was to document patterns of hydrological connectivity between a series of oxbows and their nearby streams, and periodically monitor fish assemblages for evidence of responses to the differing patterns of connectivity. The occurrence of Topeka shiners was an important aspect of the fish assemblage response. A combination of graphical and occupancy modelling approaches was used to explore these relationships.

2 | METHODS

2.1 | Study area

The North Raccoon River Basin (NRRB), located on the Des Moines Lobe sub-ecoregion (Griffith, Omernik, Wilton, & Pierson, 1994) of West Central Iowa (Figure 1), is characterized by gently rolling terrain and predominantly row crop agriculture. Four oxbows were selected along each of three adjacent tributaries of the North Raccoon River: Buttrick Creek, Cedar Creek, and Hardin Creek (Figure 1). Fifty-five fish species have been collected in the NRRB over the last 6 years (Bakevich et al., 2013; Bakevich, Pierce, & Quist, 2015; Zambory et al., 2017), with 51 species in streams and 38 species in oxbows, including nine Species of Greatest Conservation Need (SGCN; Iowa Department of Natural Resources, 2015). As one of the remaining strongholds in Iowa and range-wide for endangered Topeka shiners, the NRRB has been a focus of concern for declining abundance and prevalence (Bakevich et al., 2015), and a centre for oxbow habitat

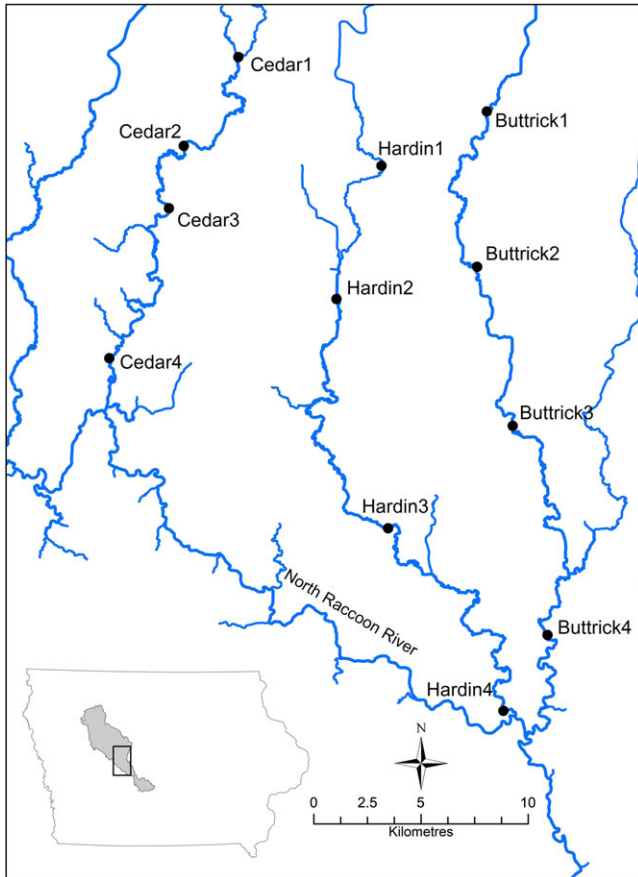


FIGURE 1 Oxbow locations in the North Raccoon River Basin of West Central Iowa, USA

restoration activity coordinated by the US Fish and Wildlife Service (Kenney, 2013). Five of the 12 oxbows were restored before this study (Table 1).

2.2 | Oxbow physical dimensions, water levels, and connection to streams

The physical dimensions of the oxbows were quantified in a concurrent study (Bakevich et al., 2013), and areas were calculated from these dimensional measurements. In each oxbow, an HOBO U20 Water Level Data Logger (Onset Computer Company, Pocasset, MA, USA) was installed in April 2011 to monitor stage height continuously (at 30-minute intervals) until October 2011. A data logger was placed in PVC housing, secured to a steel fence post that was driven into the deepest point of each oxbow (Figure 2). The flood stage for each oxbow was identified by using a laser transit to determine the minimum stage height of the oxbow during a flood event. Data were retrieved from the loggers and compiled using the HOBOWARE PRO software package. The 30-minute time series stage data were then converted to average daily time series for the entire study period. Because the stage measurements were specific to each oxbow, a direct comparison of stage measurements across oxbows was not possible; hence, the relative stage height was calculated by dividing each daily stage measurement by the flood stage height. An additional stage-related covariate, connection, was also calculated as a binary

TABLE 1 Physical dimensions, hydrological characteristics, restoration status, and presence of fish in 12 oxbow study sites, April–October 2011, along Buttrick Creek, Cedar Creek, and Hardin Creek in the North Raccoon River Basin in West Central Iowa, USA; restoration described in Kenney (2013)

Oxbow	Length (m)	Width (m)	Mean depth (m)	Maximum depth (m)	Area (m ²)	Restored?	Days wetted	Flood events	Drying events	Fish?	Topeka shiners?
Buttrick 1	54	6.1	0.13	0.2	249		42		1		
Buttrick 2	72	7.3	0.59	0.9	642	Yes	111		1	Yes	Yes
Buttrick 3	87	8.3	0.95	1.5	564	Yes	111		1	Yes	Yes
Buttrick 4	175	11.8	0.44	0.8	2076		170			Yes	Yes
Cedar 1	57	9.9	0.34	0.5	522		59	2	2	Yes	Yes
Cedar 2	105	11.3	0.77	1.6	1112	Yes	170			Yes	Yes
Cedar 3	24	6.9	0.57	0.9	173	Yes	134		1	Yes	Yes
Cedar 4	100	17.5	0.84	1.0	1259	Yes	172			Yes	Yes
Hardin 1	102	5.1	0.36	0.6	511		94	1	1	Yes	Yes
Hardin 2	80	8.4	0.33	0.5	521		132	1	1	Yes	Yes
Hardin 3	63	4.4	0.07	0.2	207		43	1	3	Yes	Yes
Hardin 4	91	12.0	0.16	0.25	961		49		2		



FIGURE 2 Oxbows, with water (top) and dried up (bottom), in the North Raccoon River Basin of West Central Iowa, USA. The data loggers that recorded stage height, mounted on steel fence posts, are visible

indicator variable that received a value of 1 if the maximum stage height during a given time interval (at any time) was greater than or equal to the flood stage (i.e. a connection event had occurred), and 0 otherwise.

2.3 | Fish sampling

From April to October 2011, fish were collected monthly in each oxbow using three-pass removal with a bag seine (6.0 m × 1.5 m or 10.0 m × 1.5 m, with 6-mm mesh). Prior to seining, each oxbow was divided into four equal sections with block nets. At the beginning of the study one of the four sections in each oxbow was randomly selected as a refuge, and was not sampled throughout the study to minimize potentially adverse sampling effects on endangered Topeka shiners and to provide a release location for catches from the three-pass removal method used in adjacent sections. Fish captured in each pass with the seine were identified to species level, counted, and released alive into the refuge section. Block nets were removed when sample processing was complete, allowing fish to redistribute throughout the oxbow between monthly sampling sessions.

Concurrent stream sampling was conducted in reaches adjacent to each oxbow to determine the occurrence of species readily

available to colonize the oxbows. Stream fish were sampled with single-pass electrofishing using a battery-powered backpack LR-20 electrofisher (Smith Root Inc., Vancouver, Washington, USA) or generator-powered, barge-mounted VVP-15B electrofishing unit (Smith-Root Inc., Vancouver, Washington, USA), with two netters (6-mm mesh dip nets). The stream reach length was approximately 35 times the mean wetted width of the stream, with a minimum of 50 m and a maximum of 300 m (average length 272 m). All fish captured were identified to species level, counted, and released alive back into the stream.

2.4 | Species traits and stream fish effects

One of our primary objectives was to use species traits to generalize how fishes respond to changing hydrological conditions in oxbows. To this end, each of the 16 fish species collected from oxbows over the course of this study were assigned traits representing their tolerance to environmental stressors (dissolved oxygen and temperature extremes), and their habitat preference (Table 2). Traits were assigned to each species based on published species accounts (Frimpong & Angermeier, 2009), and were binary coded, with tolerant and lacustrine species coded as 1 and otherwise coded 0 (i.e. intolerant and riverine species served as the statistical baselines).

Stream sampling data were used to assess whether the presence of each species in an adjacent stream reach during a given time interval influenced that species' probability of local extinction (i.e. a rescue effect) in oxbows. Note that this covariate was not included in the colonization model because in the event of a species colonizing an oxbow, the species was by definition present in the adjacent stream reach. Whether or not the presence of piscivorous species (flathead catfish *Pylodictis olivaris*, smallmouth bass *Micropterus dolomieu*, largemouth bass *Micropterus salmoides*, and walleye *Sander vitreus*) influenced local colonization rates was also of interest. For example, the presence of piscivores in an adjacent stream during a given time interval may promote the movement of species into oxbows. For simplicity, the four piscivore species were grouped into a single binary variable (1, piscivore present in stream; 0, piscivore not present in stream). Because some species could have gone undetected during the single-pass electrofishing surveys, these covariates were imperfect representations of the available species pool in the riverine habitat adjacent to each oxbow; however, they were included because they represented the best available information regarding the status of fish assemblages in each of the paired stream reaches.

2.5 | Occupancy modelling

A hierarchical representation of a dynamic multi-species occupancy model was used to estimate occupancy, local colonization, local extinction, and detection probabilities for 16 oxbow species (Royle & Kéry, 2007; Shea, Bettoli, Potoka, Saylor, & Shute, 2015). The model, which is particularly well suited for Midwestern and Great Plains species in dynamic environments prone to local colonization and extinction (Falke, Bailey, Fausch, & Bestgen, 2012), consisted of two linked submodels: a state process model (i.e. imperfectly observed

TABLE 2 Species collected and traits used in the dynamic multi-species occupancy models

Species	Tolerant	Lacustrine	Collections	Number of individuals
Bigmouth buffalo <i>Ictiobus cyprinellus</i>	0	1	5	16
Black bullhead <i>Ameiurus melas</i>	1	1	67	13426
Bluntnose minnow <i>Pimephales notatus</i>	1	1	2	5
Brassy minnow <i>Hybognathus hankinsoni</i>	0	0	22	112
Brook stickleback <i>Eucalia inconstans</i>	0	1	3	4
Common carp <i>Cyprinus carpio</i>	1	1	25	1034
Common shiner <i>Luxilus cornutus</i>	1	0	8	15
Creek chub <i>Semotilus atromaculatus</i>	1	0	13	30
Fathead minnow <i>Pimephales promelas</i>	1	1	72	7486
Green sunfish <i>Lepomis cyanellus</i>	1	1	21	94
Orangespotted sunfish <i>Lepomis humilis</i>	0	1	1	1
Sand shiner <i>Notropis stramineus</i>	0	0	1	1
Spotfin shiner <i>Cyprinella spiloptera</i>	0	0	1	3
Topeka shiner <i>Notropis topeka</i>	1	0	21	278
White sucker <i>Catostomus commersoni</i>	1	1	23	149
Yellow bullhead <i>Ameiurus natalis</i>	0	1	21	220

The Collections column indicates the number of collections (maximum possible was 120) in which each species was detected. Number of individuals is the total number in all collections.

temporal changes in occupancy) and an observation model (detection and non-detection data). The model produced four parameters of interest: initial occupancy probability, colonization probability, persistence probability, and detection probability.

For the state process model, the initial occupancy state for each species, z_{1ij} , was defined as a Bernoulli random variable, where $z_{1ij} = 1$ if species j occurred at site i during time 1 (and 0 otherwise), denoted by:

$$z_{1ij} \sim \text{Bernoulli}(\psi_{1ij}) \quad (1)$$

where ψ_{1ij} was the probability that species j occupied site i at time 1. For subsequent time periods, changes in occupancy were modelled explicitly in terms of local colonization and extinction processes. Local extinction (ϵ_{tij}) was defined as the probability that a site occupied by species j at site i and time t was unoccupied at time $t+1$ [i.e., $\epsilon_{tij} = \Pr(z_{t+1ij} = 0 \mid z_{tij} = 1)$]. Local colonization (γ_{tij}) was defined as the probability that a site unoccupied by species j at time t was occupied at time $t+1$ [i.e., $\gamma_{tij} = \Pr(z_{t+1ij} = 1 \mid z_{tij} = 0)$]. Oxbow fish occupancy dynamics were therefore modelled as:

$$z_{t+1ij} \mid z_{tij} \sim \text{Bernoulli}\left\{z_{tij}^* (1 - \epsilon_{tij}) + [1 - z_{tij}]^* \gamma_{tij}\right\} \quad (2)$$

Because patch dynamic rates potentially varied among species, locations, and years, a logit link function was used to model initial occupancy (ψ_{1ij}) and dynamic rates (γ_{tij} and ϵ_{tij}) as a function of site- and species-level characteristics.

As with most ecological surveys, we suspected that not all individuals and species were detected during sampling in this study (MacKenzie et al., 2002; Tyre et al., 2003). To estimate species detection probabilities, the three block-netted sections in each oxbow were considered spatially replicated samples (hereafter, replicates), which allowed for the development of an observation model for the

detection and nondetection data y_{tijk} . The observation model for time t , site i , species j and replicate k was defined as:

$$y_{tijk} \sim \text{Bernoulli}\left(z_{tij}^* p_{tijk}\right) \quad (3)$$

where y_{tijk} was the observed detection (1) or nondetection (0) of species j during replicate k at site i and time t , and p_{tijk} was the probability of detecting species j during replicate k at site i and time t , conditional on species j being present (i.e., $z_{tij} = 1$).

Lastly, occupancy, colonization, extinction, and detection probabilities also could have varied among species as a function of unmeasured covariates (Royle & Dorazio, 2008). Thus, species-level random intercepts were included in the occupancy, colonization, extinction, and detection models to account for unique effects associated with each of the 16 species that were unexplained by model covariates. All random effects were assumed to be normally distributed with a grand mean intercept and random effect-specific variance (Raudenbush & Bryk, 2002).

2.6 | Model fitting and selection

There is currently no consensus regarding appropriate model selection techniques for Bayesian hierarchical models (Hooten & Hobbs, 2015). Hence, methods described by King et al. (2016) were followed to identify the best-approximating dynamic multi-species occupancy model. First, a global model was constructed that contained all initial occupancy, detection, local colonization, and local extinction predictor variables: the global initial occupancy model included tolerant and lacustrine; the global colonization model included connection, tolerant species, riverine species, and the presence of a piscivore species in adjacent stream reaches during the previous time interval; the global extinction model included mean relative stage height, tolerant species, riverine species, and the presence/absence status of each species in

paired stream reaches during the previous time interval; and the global detection model did not include any species- or site-specific predictor variables (i.e. intercept-only model). Then the global model was fitted using 16 different error structures, each representing a different combination of species-level random intercepts in the initial occupancy, detection, local colonization, and local extinction models. Goodness-of-fit for each error structure was assessed by calculating Bayesian p -values, which vary from 0 to 1 and where p -values close to 0.5 indicating adequate model fit (Zipkin, Dewan, & Royle, 2009). The model with the simplest error structure (i.e. the fewest randomly varying intercepts) and acceptable p -value (i.e. close to 0.5) was considered the best-approximating model. Following identification of the best-approximating error structure, the global model was re-fitted and initial occupancy, local colonization, and local extinction parameter estimates were considered statistically significant if their 95% credible intervals did not overlap zero (i.e. the estimated effect was either positive or negative with 95% certainty). To facilitate model fitting the single continuous covariate, relative stage height, was standardized with a mean of 0 and a standard deviation of 1. All other predictors were included as binary variables as described above. To facilitate interpretation, odds ratios (OR) for each fixed effect parameter estimate (Hosmer & Lemeshow, 2000) were calculated. Markov Chain Monte Carlo (MCMC), as implemented in OpenBUGS software, version 3.2.1 (Lunn, Spiegelhalter, Thomas, & Best, 2009), was used to fit the dynamic multi-species occupancy models. All models were fitted using 1,000,000 MCMC iterations, with the first 300,000 samples discarded as burn-in. Lastly, site-level detection probabilities were evaluated by calculating the cumulative detection probability for each species, assuming that three independent replicate surveys were conducted, as:

$$P_{site_j} = 1 - (1 - p_j)^K \quad (4)$$

where K represented the number of replicate surveys (3 in this case) and p_j represented the probability of detecting species j during a single survey occasion, given the species was present.

3 | RESULTS

3.1 | Floods, drying, connection to streams, and fish collected

The 12 oxbows varied from 172 to 2076 m² in surface area, from 0.07 to 0.95 m in mean depth, and from 0.2 to 1.6 m in maximum depth (Table 1). Owing to variation in water levels throughout the study (Figure 2; Appendix S1) physical dimensions changed accordingly, and thus these values are only approximate.

When floods occurred in oxbows, water levels were sufficiently high for a connection to occur between the oxbow and the nearby stream. Floods occurred in four of the 12 oxbows, none of which had been restored (Table 1; Appendix S1). Three of the four oxbows that flooded only flooded once, whereas one (Cedar 1) flooded twice. Nine of the 12 oxbows dried up completely at least once during the study, with two of these drying up twice (Cedar 1 and Hardin 4) and one oxbow (Hardin 3) drying up three times. Of the

five restored oxbows, three dried up, and each of these only a single time. All of the four oxbows that flooded eventually dried up, and two of the oxbows that flooded had dried up previously, including the one (Cedar 1) that flooded twice. Three oxbows, Cedar 2, Cedar 4, and Buttrick 4, neither flooded nor dried up (Table 1; Appendix S1).

In total, 22 874 fish from 16 species were collected from 10 of the 12 oxbows (Table 2). Black bullheads *Ameiurus melas* and fathead minnows *Pimephales promelas* were the most abundant species, and each occurred in more than half of the collections (Table 2). Six other species, including Topeka shiners, were found in more than 20 collections. Three species were found in only one collection each, and two of these were represented by single individuals (Table 2).

Two oxbows (Buttrick 1 and Hardin 4) never contained fish; these two oxbows never flooded and were among the three oxbows that were dry for the longest period (Table 1; Appendix S1). The oxbow that was dry at the beginning of the study (Hardin 4) never flooded and had no fish. The other two oxbows (Cedar 1 and Hardin 3) that dried briefly early in the study flooded shortly after the drying event, and had fish on the next sampling date (Appendix S1). All five restored oxbows contained fish (Table 1).

Topeka shiners were found in four oxbows, only one of which (Buttrick 2) had been restored (Table 1). Three of the four oxbows containing Topeka shiners flooded, and Topeka shiners were present in every collection following a flood in these three oxbows (Table 1; Appendix S1). All of the four oxbows containing Topeka shiners dried up at least once (Table 1).

3.2 | Best-approximating occupancy model error structure and goodness-of-fit

The best-approximating global error structure included a fixed-effect intercept (i.e. a non-randomly varying intercept) in the initial occupancy, local extinction, and local colonization models, and a randomly varying intercept in the detection models. Estimates of among-species variability indicated that the cumulative (i.e. site-level across three surveys) detection probability varied substantially among species, averaging from less than 40% for bluntnose minnows *Pimephales notatus* to greater than 90% for eight species, including Topeka shiners (Figure 3). The assessment of model adequacy using the discrepancy measure method indicated that the global model provided an adequate description of the data, with a Bayesian P value of 0.46.

Parameter estimates from the best-approximating initial occupancy model indicated that lacustrine species and tolerant species were 2.7 and 3.5 times more likely, respectively, to initially occupy oxbows, compared with riverine species and intolerant species (Table 3).

Parameter estimates from the best-approximating initial occupancy model indicated that lacustrine species were approximately three times more likely to occupy oxbows compared with other species (Appendix S1); however, the 95% credible interval for this parameter estimate overlapped zero slightly, resulting in some uncertainty about the direction of its effect on occupancy (Table 3).

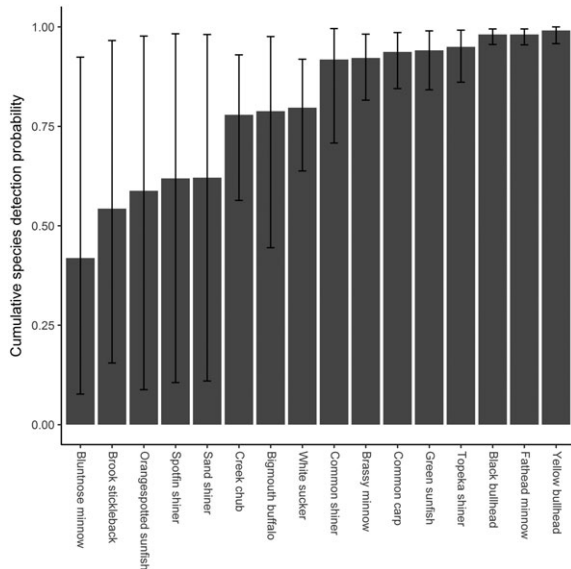


FIGURE 3 Mean cumulative detection probabilities (i.e. mean probability of detection given the species is present in an oxbow) across three replicated surveys (i.e. three-pass removals via seining) for each of the 16 species encountered during the study. Error bars represent 95% prediction intervals

Parameter estimates from the best-approximating local extinction model indicated that the probability of local extinction was strongly and negatively influenced by relative stage (Figure 4; Table 3). The odds ratio suggested that all species were 17.5 times more likely, on average, to become locally extinct from an oxbow for every 1-SD decrease in relative stage (0.28 or 28% of maximum stage height).

TABLE 3 Parameter estimates, standard deviations (SD), lower and upper 95% credible intervals, and odds ratios (OR) from the best-approximating dynamic multi-species occupancy model

Parameter	Mean	SD	Lower	Upper	OR
Initial occupancy (ψ)					
Intercept	-2.738	0.554	-3.877	-1.701	
Lacustrine	0.987	0.488	0.058	1.973	2.684
Tolerant	1.257	0.493	0.320	2.253	3.515
Detection (p)					
<i>Fixed effect</i>					
Intercept	-0.034	0.388	-0.869	0.657	
<i>Random effect</i>					
Intercept (species)	1.265	0.419	0.590	2.221	
Local extinction (ϵ)					
Intercept	-1.638	0.975	-3.668	0.153	
Relative stage	-2.863	0.680	-4.299	-1.650	0.057
Tolerant	-1.317	0.951	-3.214	0.532	0.268
Lacustrine	-0.822	0.869	-2.588	0.840	0.440
Species present in stream	0.944	0.829	-0.656	2.612	2.569
Local colonization (γ)					
Intercept	-4.190	0.685	-5.609	-2.914	
Connection	3.623	0.654	2.418	4.984	37.450
Tolerant	0.652	0.589	-0.506	1.810	1.918
Lacustrine	-1.069	0.594	-2.270	-0.117	0.343
Piscivore present in stream	-1.121	0.868	-2.969	0.442	0.326

The influence of the remaining predictors in the local extinction model – tolerant, lacustrine, and species present in adjacent stream reach – was considered uncertain because their 95% confidence intervals spanned zero (Table 3).

Parameter estimates from the best-approximating local colonization model indicated that the probability of local colonization was, on average, very low and positively related to connection events (Table 3). Odds ratios suggested that if a connection occurred during the previous time interval, oxbows were 37.5 times more likely to be colonized by at least one of the 16 species (Table 3). Parameter estimates also indicated that lacustrine species were 2.9 times less likely than riverine species to colonize oxbows (Table 3). The influence of the remaining predictors in the local colonization model, tolerant and presence of piscivores, was considered uncertain because their 95% credible intervals spanned zero (Table 3).

4 | DISCUSSION

4.1 | Detection probabilities

Although detection probabilities for the 16 species varied from 40% to well over 90%, 13 of the 16 species had detection probabilities over 60%, and eight, including Topeka shiners, had detection probabilities over 90%. Fathead minnows, which had among the highest detection probabilities, have been associated with the presence of Topeka shiners in other research in this region (Bakevich et al., 2013). It is noteworthy that a species thought to be a nest associate of Topeka shiners, orangespotted sunfish *Lepomis humilis* (Campbell, Szuwalski,

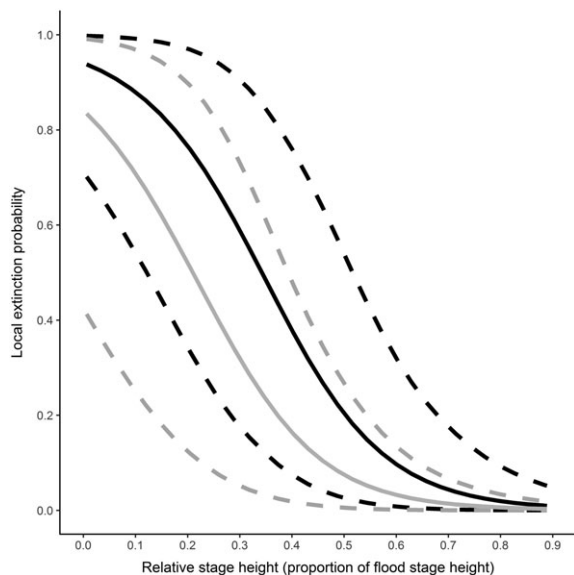


FIGURE 4 Mean probability of local extinction for tolerant (solid grey line) and intolerant (solid black line) species at different relative stage heights. Dashed lines represent 95% prediction intervals

Tabor, & DeNoyelles, 2016; Pflieger, 1997), had one of the lowest detection probabilities. The detection probability results suggest that sampling effort and intensity were adequate for most species, and this will be especially important in future status assessments and oxbow restoration evaluations for Topeka shiner conservation.

4.2 | Occupancy modelling – initial occupancy, local extinction, and local colonization

Lacustrine species (e.g. black bullheads, common carp *Cyprinus carpio*, fathead minnows, green sunfish *Lepomis cyanellus*, and white suckers *Catostomus commersoni*) were more likely than riverine species to be the initial occupants of oxbows, perhaps suggesting that they are better able to overwinter in oxbows. It is interesting that tolerant species, such as Topeka shiners that are known to be able to survive in relatively high temperatures and low oxygen concentrations (Falke et al., 2012; Falke, Bestgen, & Fausch, 2010; Koehle & Adelman, 2007), were also more likely to initially occupy oxbows.

Water levels (relative stage height) had the most pronounced effect on local extinctions, with a higher probability of extinction as water levels declined. As water levels decline in oxbows the habitat volume becomes smaller, the habitat complexity is reduced as vegetation is dewatered, the diel temperature variations increase, and the minimum O₂ concentrations are reduced (Magoulick & Kobza, 2003). In turn, these changes can lead to increased competition for food and space, increased predation risk, and physiological stress, any of which could result in local extinction (Magoulick & Kobza, 2003). The results also suggest, although with some degree of uncertainty, that tolerant species may be less likely to become locally extinct than intolerant species, suggesting that during the portion of the year that was studied, tolerant species are better than intolerant species at persisting once established in oxbows.

Floods, which provide connections to the stream, had the most pronounced effect on local colonization, with a higher probability of colonization as the number of floods increased. Riverine species such as brassy minnows and Topeka shiners were more likely than lacustrine species to colonize after floods, although one species classified as lacustrine, the fathead minnow, was also frequently found in oxbows after floods where it had been absent before the flood. Regardless of the identity or type of species, floods clearly provide opportunities for species present in streams to colonize oxbows during the time that the two habitats are connected.

The evidence for influence of species' presence in nearby streams was inconclusive. This suggests that floods and the resulting oxbow–stream habitat connections do not merely unite the local assemblages in close proximity before flooding. Floods probably facilitate the redistribution of species over a wider spatial extent than individual oxbows and their immediately adjacent stream reaches. Similarly, the presence of piscivores in the nearby stream reach also did not influence oxbow occupancy in the present study. Using different approaches, Knight and Gido (2005) and Bakevich et al. (2013) found similarly inconclusive evidence for piscivores influencing Topeka shiner presence. Earlier studies have implicated piscivores as influencing stream fish assemblages in general (Hoeinghaus & Pelicice, 2010), and Topeka shiners in particular (Mammoliti, 2002; Schrank Guy, While, & Brock, 2001; Winston, 2002). Although clearly at some spatial and temporal scale the fish assemblage of the adjacent stream network must influence oxbow assemblages, more research will be necessary to determine the scales at which these relationships are evident. Current research is addressing the need for more intensive sampling in streams adjacent to oxbows (Simpson et al., 2017; Zambory et al., 2017).

4.3 | Oxbows as variable off-channel habitats with variable connectivity to streams

Although their common fluvial geomorphic origins constrain oxbow characteristics and positioning relative to their nearby streams, as off-channel habitats of streams they exhibit high hydrodynamic variability. The results demonstrated that in a relatively small geographic area, and in response to similar seasonal rainfall, oxbows varied in physical dimensions, flooded or did not flood, dried or did not dry up, did so at different times, and varied almost four-fold in the amount of time that they held water during the study. Rather than responding to precipitation in relative unison, as would in-channel sites along a stream network (Sheldon et al., 2010), the oxbows studied exhibited widely variable hydrodynamics. In turn, these variable hydrodynamics presented fish assemblages and other aquatic biota with variable environmental conditions, which is a type of portfolio effect (Schindler, Armstrong, & Reed, 2015).

In the 14 years from 2002 until 2015, the study year (2011) was the second driest in the West Central Iowa reporting region (US Geological Survey, 2017), which includes the study area. Drying would probably be less frequent in wetter years, but we would expect differences among oxbows in hydrodynamics and connectivity with nearby streams, regardless of regional precipitation. A similar study conducted over multiple years with different precipitation magnitudes

and temporal distribution would be useful to explore the impacts of climatic variation. Modelling (Karim, Kinsey-Henderson, Wallace, Arthington, & Pearson, 2012) is another promising approach to a better understanding of connectivity dynamics, and is currently under way (Zambory et al., 2017).

Habitat connectivity is an important consideration for the conservation of many species, particularly as natural land cover and habitats continue to decline (Fischer & Lindenmayer, 2007). Connectivity among diverse habitats is important to the ecological functioning of river floodplains and the species that they support (Amoros & Bornette, 2002; Bunn & Arthington, 2002; Tockner & Stanford, 2002). The role of variable hydrodynamics among oxbows in determining connectivity with the adjacent river, and its relationship to the flood-pulse concept (Junk, Bailey, & Sparks, 1989), has been demonstrated elsewhere (Hudson, Heitmuller, & Leitch, 2012). The results of the present study support findings from other taxa and systems (Casanova & Brock, 2000) in suggesting that the extent of connectivity with nearby habitats may influence the presence of species, including Topeka shiners. Results from a similar study in floodplain dugouts in South Dakota are also in agreement with the notion that separation punctuated by frequent connections with the stream enhances the value of dugouts as Topeka shiner habitat (Natural Resource Conservation Service, 2010).

4.4 | Oxbows as important habitats for conservation of endangered Topeka shiners

Numerous studies have illustrated the importance of oxbows and analogous standing water bodies in floodplains as habitat for Topeka shiners in today's agriculturally dominated Midwestern landscape (Bakevich et al., 2013; Clark, 2000; Natural Resource Conservation Service, 2010; Simpson et al., 2017). The restoration of oxbows and similar water bodies is now an important part of the Topeka shiner conservation strategy (Kenney, 2013, 2014; Natural Resource Conservation Service, 2010), as well as a promising approach for the reduction of nutrient loading to streams and rivers (Jones, Kult, & Laubach, 2015; Schilling, Kult, Wilke, Streeter, & Vogelgesang, 2017). The results suggest that the hydrodynamics that affect connections with nearby streams should be an important consideration for future oxbow restorations, and efforts to predict the hydrodynamic characteristics of different oxbow locations, elevations relative to the stream, groundwater characteristics, and perhaps other considerations would be useful. Current research is addressing some of these considerations (Zambory et al., 2017). Because oxbow restoration primarily involves excavation, the depth of the resulting restored oxbow is the most readily controllable characteristic. A somewhat counterintuitive finding emerged from a recent study (Bakevich et al., 2013), suggesting that shallower oxbows more frequently harboured Topeka shiners than deeper oxbows. The present results provide further evidence that Topeka shiners tend to occur in shallower oxbows, both in terms of mean and maximum depth, but not in the shallowest oxbows. The mean and maximum depths of the restored oxbows in this study resembled deeper oxbows lacking Topeka shiners, whereas the shallower depths of unrestored oxbows were similar to the depths of oxbows that contained Topeka shiners.

This apparent trend should be viewed cautiously until supported by a larger sample size of oxbows, but it suggests that oxbow depth may correlate with multiple influences on Topeka shiners. At the shallow end of the depth continuum, oxbows need sufficient depth to retain water for significant lengths of time and provide the wetted habitat required by all fish. The two oxbows that never harboured fish of any species were dry for the longest periods of time, and were among the three shallowest oxbows. Drying up is currently not a goal of oxbow restoration for this reason (A. Kenney, pers. comm.); however, at the other end of the depth continuum, the deepest oxbows may be less than optimal for Topeka shiners. Deeper oxbows may contain more piscivores than shallower oxbows, and may result in local extinction by predation, as has been suggested in other studies (Mammoliti, 2002; Schrank et al., 2001; Winston, 2002). Compared with many other species, Topeka shiners are tolerant of the high temperatures and low oxygen concentrations that are characteristic of shallow water bodies (Koehle & Adelman, 2007), and thus may be able to exploit these habitats as refuges from predation (Magoulick & Kobza, 2003). Other factors yet to be elucidated may also play a role in shaping the relationships between Topeka shiners, hydrodynamics, and oxbow habitats in agriculturally dominated Midwestern USA landscapes.

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ORCID

Clay L. Pierce  <http://orcid.org/0000-0001-5088-5431>

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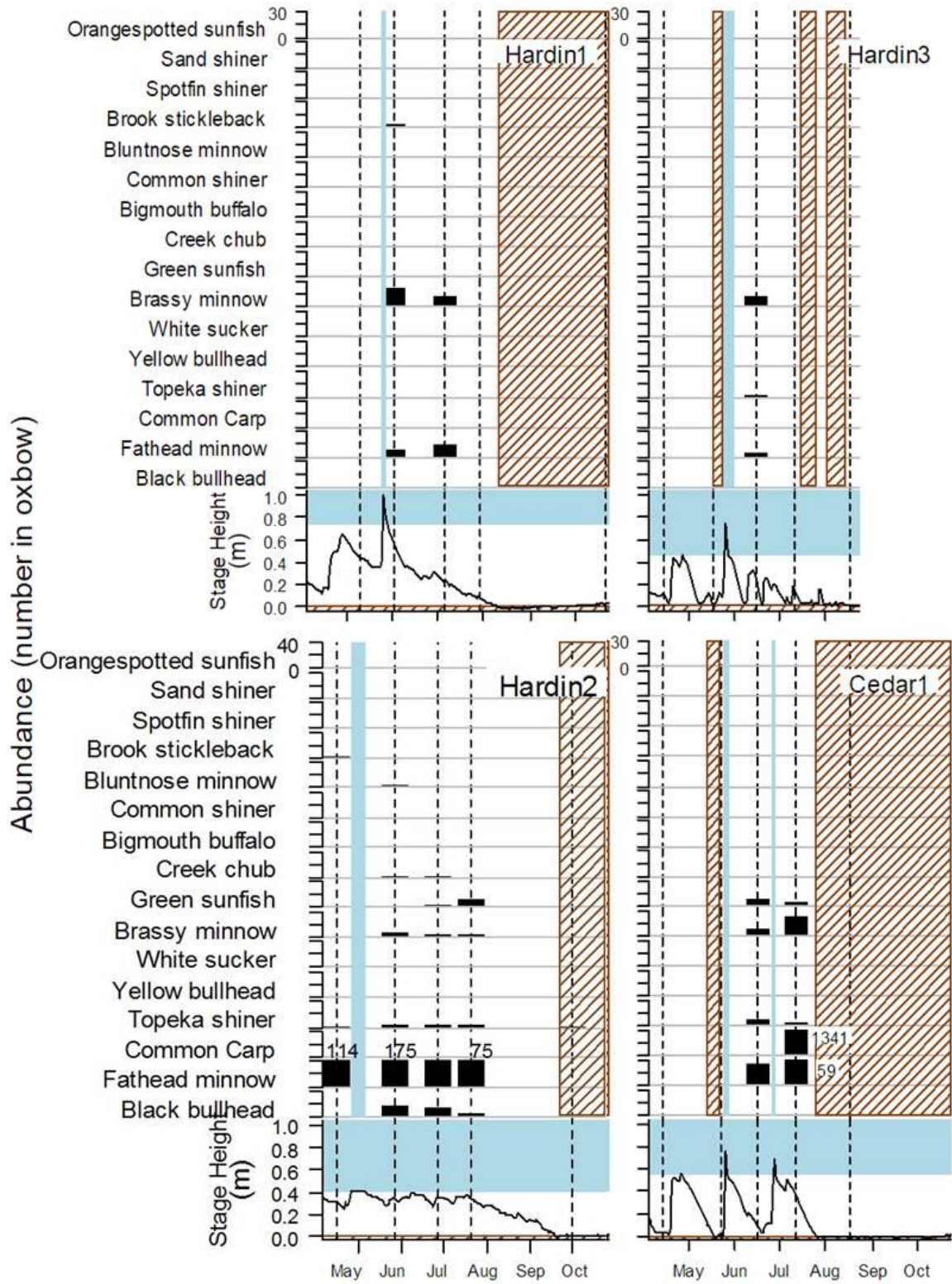
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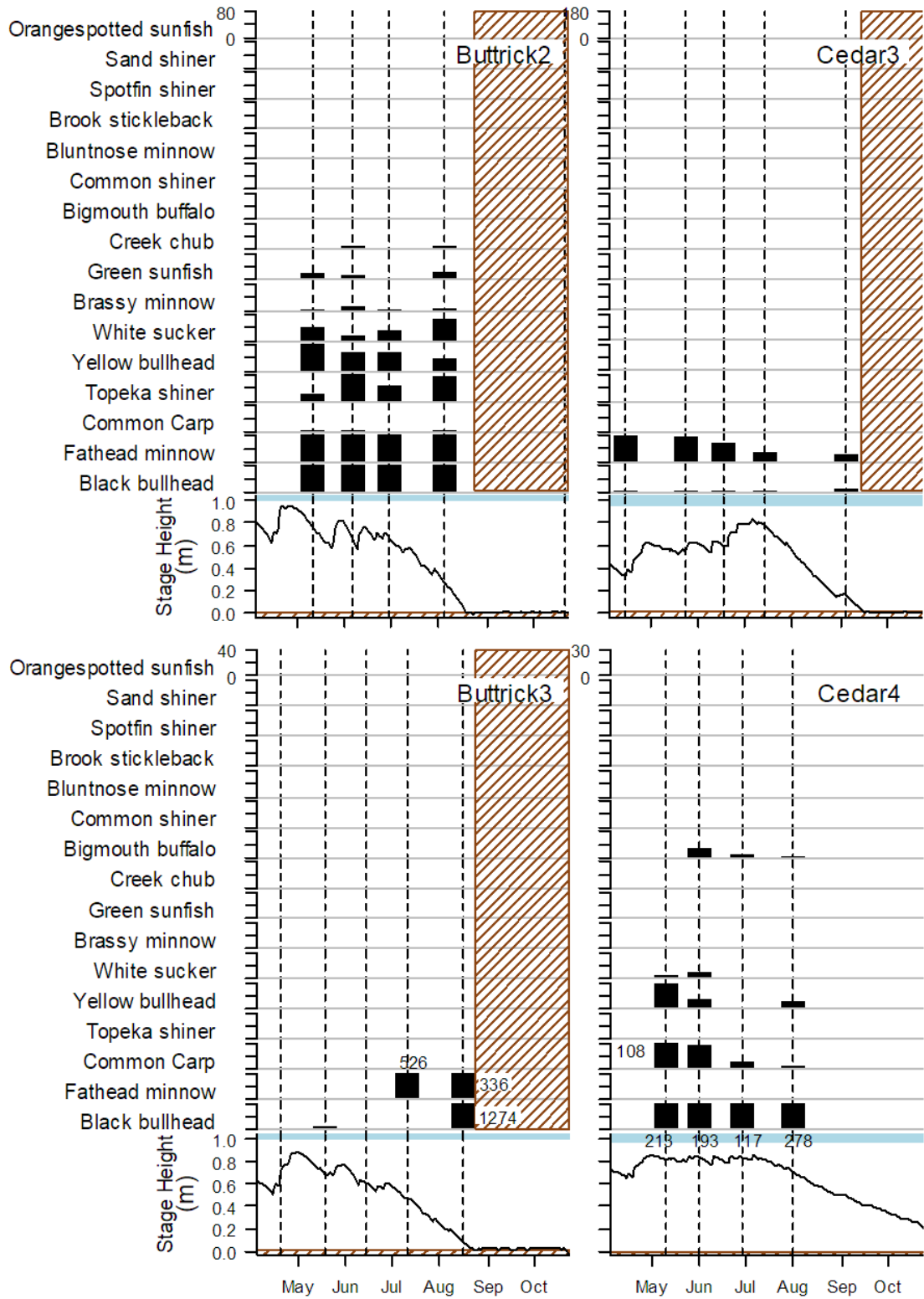
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SUPPORTING INFORMATION

FIGURE S1 Fish species abundance and water depths (stage height) in 12 oxbow study sites, April-October, 2011, along Buttrick Creek, Cedar Creek, and Hardin Creek in the North Raccoon River Basin in west-central Iowa, USA. Species abundances shown as histograms by sampling date. Sampling dates indicated as vertical dashed lines. Abundance scale shown at upper left corner of each panel. Number of fish shown next to histograms when abundance exceeded scale. Stage height shown as irregular solid line at bottom of panels. Light blue shading on stage height graphs indicates depths where flooding occurred and oxbows were connected to neighboring streams. Light blue shaded vertical bars indicate occurrence and duration of floods. Brown hatched bars indicate occurrence and duration of drying events.



Abundance (number in oxbow)



Abundance (number in oxbow)

