



Updated status of Bayou darter, a narrowly ranged endemic in a geomorphically active watershed

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ABSTRACT: Comparison of historical and current data are critical in establishing population trends for imperiled taxa. In this paper we revisit the status of the Bayou darter *Nothonotus rubrum*, an endemic fish restricted to the Bayou Pierre river system, Mississippi, USA. The Bayou Pierre has experienced substantial geomorphic change in the past century, leading to questions about persistence of this imperiled species. We employed historical field notes and museum records to identify collection localities, and we resampled 32 of these localities using methodologies comparable to the original samples. We further sampled an additional 10 sites with similar methodologies to fill in spatial data gaps. Rates of capture and numbers of individuals were similar between historical and contemporary samples; however, collections with multiple individuals in contemporary samples were largely restricted to the upstream periphery of their historical distribution. Qualitative comparisons of numbers of individuals caught over several decades using variable methodology suggest that declines in abundances have happened since the species was first described. Bayou darter occupancy was positively related to stream link magnitude (beta estimate = 3.07), and *N*-mixture modeling estimated contemporary abundance at 7.36 ± 3.83 individuals per site. Bayou darter counts were negatively related to variance in kilometer-scale stream elevation (beta estimate = -0.60). Our results suggest that this species remains imperiled and is experiencing a declining range, and that continued efforts to study and monitor this species, and to reduce geomorphic change in the system, are merited.

KEY WORDS: Bayou Pierre · Erosion · Occupancy · Distribution · Assemblage change

1. INTRODUCTION

Conservation efforts for freshwater fishes are rapidly reaching a critical turning point at which sufficient long-term monitoring of some endangered but neglected species has begun to enable robust assessments of their present status compared to their past status. A limited minority of fishes are well studied due to their cultural or economic importance, and considerable inferences have been made about how their ranges or abundances have changed over time (e.g. black basses, Taylor et al. 2019; salmonids, Quinn 2018). But for most freshwater fishes, data deficiencies on populations, distributions, and even basic life histories have historically been the norm

rather than the exception (Jelks et al. 2008, Matthews 2015). Detailed documentation of known species distributions, ecologies, and conservation statuses began to appear in the second half of the 20th century, and these works were heavily informed by regional surveys, status updates, museum specimens, and personal field notes (Cross 1967, Deacon et al. 1979, Williams et al. 1989, Etnier & Starnes 1993, Ross 2000, Robison & Buchanan 2020). The first few decades of the 21st century have seen researchers revisit these efforts and provide the beginnings of some quantitative estimates of changes to distributions and population statuses of neglected taxa (Jelks et al. 2008, Robison & Buchanan 2020). Yet the ability to make such assessments is critically dependent on

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continued collection of raw data sources, especially museum collections (Lister 2011) and status updates of individual endangered taxa conducted to be congruent with previous research efforts.

The Bayou darter *Nothonotus rubrum* was described in 1966 (Raney & Suttkus 1966) and is endemic to the Bayou Pierre system in southwestern Mississippi (Suttkus & Clemmer 1977). Given the small range and ongoing habitat degradation (Kuhajda et al. 2009), it is currently listed as threatened under the US Endangered Species Act and endangered by the state of Mississippi. *N. rubrum* occupy a fairly specific habitat, specializing in shallow riffles or runs with large substrate and fast current velocities in Bayou Pierre proper and the lower reaches of some of the larger Bayou Pierre tributaries (see Fig. 1). Spawning occurs in April and May over gravel and coarse sand substrate (Ross & Wilkins 1993, Slack et al. 2004). *N. rubrum* feed opportunistically on invertebrates found in faster-flowing habitats, with chironomids (midges), simuliids (blackflies), and Hydracarina (water mites) making up most of the stomach contents (Knight & Ross 1994). Previous surveys for the species have identified a number of healthy populations, primarily in middle/upper Bayou Pierre, Foster Creek, Turkey Creek, and White Oak Creek (Ross et al. 1992). There have been a small number of new localities reported over the last 10–15 yr, including a new locality below the confluence of Bayou Pierre and Little Bayou Pierre, and another in Tallahalla Creek. In general, these are collections with few individuals and suggest the distribution remains unknown or is changing. While portions of the range have been surveyed, there has not been a survey across the distribution of this species in nearly 30 years.

Given the close proximity and similar habitats, one might think *N. rubrum* could also occur in Little Bayou Pierre (see Fig. 1). Both Ross et al. (1990) and Slack et al. (2004) noted the lack of *N. rubrum* in what appeared to be suitable habitat in Little Bayou Pierre. Given the life history and potential for colonizing previously unoccupied areas, a more thorough survey of Little Bayou Pierre was conducted in 2010. That work documented similar habitat structure, but fish assemblages in Little Bayou Pierre were more distinct than expected, and there were no occurrences of *N. rubrum*. While the assemblages differed, there were no other species found to be exclusive to one area or the other in that study (Schaefer 2011).

Conservation research efforts to date have focused on surveys, population estimates, population genetics, life history and microhabitat assessments (Knight

& Ross 1992, Ross et al. 2001, Slack et al. 2010). Population genetic work on the 4 most robust populations (Foster Creek, upper Bayou Pierre, middle Bayou Pierre below Turkey Creek confluence, and Bayou Pierre near White Oak Creek confluence) found very little genetic structure or diversity, indicators of small population sizes and recent bottlenecks (Slack et al. 2010). The major threats to the species are erosion (directly removing viable habitat) resulting from extensive headcutting in the system coupled with the extremely limited range. Various activities in the Bayou Pierre system and downstream Mississippi River have dramatically altered the physical structure of the system (Slack et al. 2004, 2010). Substrate instability and rapid changes to river geomorphology have resulted in changes in fish assemblages, particularly for darters that have close ties to the benthos (Tipton et al. 2004). Conservation recommendations for Bayou Pierre include restricting gravel mining and other activities that accelerate headcutting and destabilize banks in the system (Kuhajda et al. 2009). There are some indications that populations have moved in response to erosion-facilitated habitat modifications. However, populations below assumed current active headcutting regions appear small, and have not been systematically sampled. Slack et al. (2004) hypothesized that larvae may drift downstream and later migrate upstream, indicating the species has the potential for colonizing favorable habitat in other tributaries. This would also result in populations being isolated around falls associated with migrating knickpoints. While Slack et al. (2004) could not definitively support this hypothesis, larvae are known to drift, and short-term colonization upstream is probable. The mobility of this species might also explain a changing distribution and new, and possibly sporadic, localities reported throughout the system.

The goals of the present project are to (1) survey historical localities of *N. rubrum* throughout the species' range to assess assemblage changes and verify if *N. rubrum* populations still persist at localities where they were previously documented, (2) survey areas where there have been anecdotal *N. rubrum* records, or where there may be suitable habitat but no historical collections, and (3) use hierarchical models to evaluate multiple working hypotheses to better understand patterns in Bayou darter occupancy and abundance at multiple spatial extents. For contemporary surveys, we utilized similar methods employed in previous surveys to contextualize our results and better inform future management decisions regarding *N. rubrum*.

2. MATERIALS AND METHODS

2.1. Site selection

We acknowledge that the history of ichthyological explorations in the Bayou Pierre includes a tremendous amount of research effort by multiple teams (Teels 1976, Matthews 1978, Ross et al. 1992, 2001, Slack et al. 2004). The differences in goals, spatial extent, sampling methods, and degree of data availability make comparisons across many of these datasets challenging and beyond the scope of our project. After thorough review of literature, museum records, and field notes, we selected a series of sites that had complete assemblage data (sampling all habitats without targeting any one) throughout the basin with documented effort and gear (detailed in Section 2.2) used during the relatively brief window in the late 1980s to early 1990s (Fig. 1, Table 1). The purpose of our study is not to review all historical sampling efforts, but to make direct comparisons of samples using known methods roughly 30 yr apart. We further supplemented these sites with a smaller number of sites spread throughout regions of the basin which

have historically been undersampled. Sampling occurred throughout the watershed including upper portions indicated by Ross et al. (2001) to be undergoing active erosion, and lower portions where Slack et al. (2004) demonstrated continued *Nothonotus rubrum* presence.

We identified 32 localities which were sampled with known effort 1 to 4 times (1987–1992) within a 1 km radius of an available access point and which had associated fish community data collected with standardized effort (Fig. 1). We further randomly selected 10 sites spread among Little Tallahalla Creek, White Oak Creek, the headwaters of the Little Bayou Pierre, and the mainstem Bayou Pierre below the confluence of the Little Bayou Pierre to fill in gaps for areas that were not historically sampled. The fish assemblage data from 1987–1992 includes 51 samples collected from 32 sites (hereinafter called historical data), which was combined with our 42 samples (hereinafter called contemporary data, see below).

The sampled sites covered most of the known distribution (highlighted river sections in Fig. 1) and include populations cited as being the most robust (Slack et al. 2010). There are many additional histor-

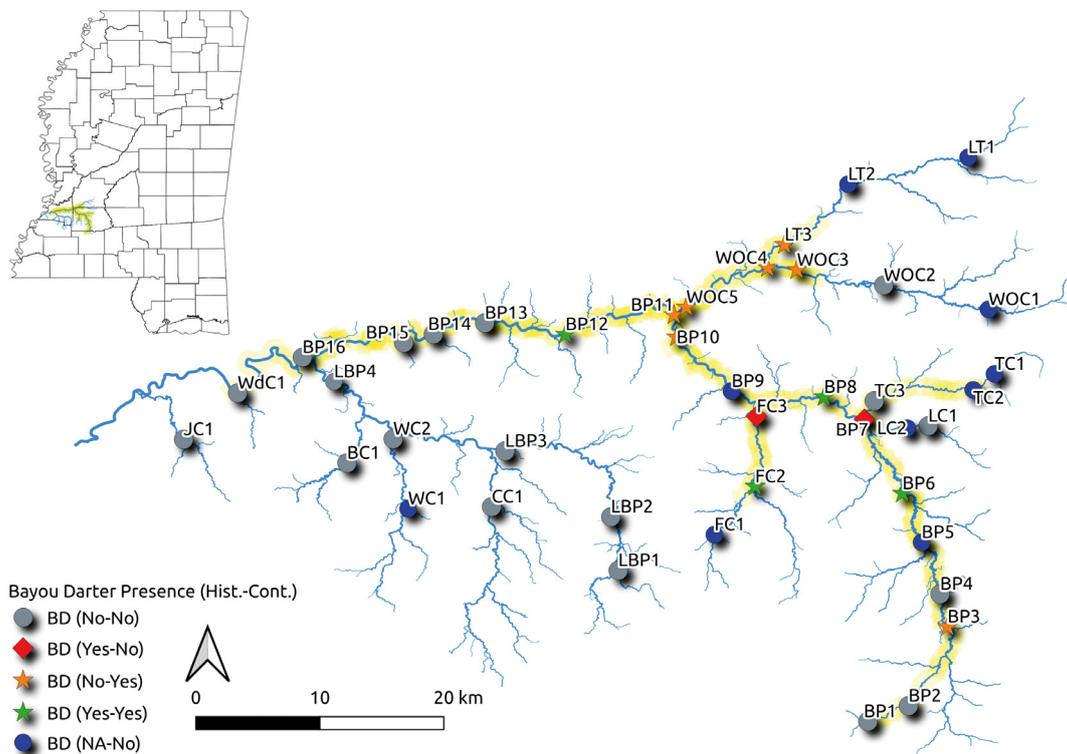


Fig. 1. All sampling locations from 2019 (see Table 1 for details of each site) within the Bayou Pierre system (inset: Mississippi, USA). Symbols represent the presence of assemblage data in the historical (Hist.) dataset (blue circles: no historical data available [NA]; all other symbols: historical data available) and the presence of Bayou darter (BD) *Nothonotus rubrum* in 2019 samples (Cont.: contemporary; stars: present; circles or diamonds: absent). Highlighted segments of river represent the entire known range of the species

Table 1. The 42 sites sampled, locality, county, GPS coordinates, and the presence or absence of Bayou darter ('BD Pres') *Nothonotus rubrum* in 2019–2020 samples (and number collected) and in historical collections from the Bayou Pierre river system, MS, USA. Site labels match those in Fig. 1. HWY: highway; SHWY: state highway

Site	Locality	County	Date (m/d/y)	Latitude (°N)	Longitude (°W)	BD Pres 2019–2020	Historical sample (BD Pres)
BC1	Bakers Creek at Gordon Road	Claiborne	03/23/19	31.89598	90.96961	No	Yes (No)
BP1	Bayou Pierre at Old Red Star Dive	Lincoln	03/22/19	31.67598	90.52711	No	Yes (No)
BP2	Bayou Pierre at Lott Smith Road	Lincoln	03/22/19	31.68924	90.49264	No	Yes (No)
BP3	Bayou Pierre at Cline Road	Copiah	03/22/19	31.75653	90.45947	Yes (13)	No (No)
BP4	Bayou Pierre at Tyson Road	Copiah	03/22/19	31.78443	90.46580	No	Yes (No)
BP5	Bayou Pierre at HWY 28	Copiah	07/11/19	31.82843	90.48147	No	No (No)
BP6	Bayou Pierre at Smyrna	Copiah	05/24/19	31.87004	90.49778	Yes (18)	Yes (Yes)
BP7	Bayou Pierre at Turkey Creek confluence	Copiah	08/21/19	31.93317	90.52994	No	Yes (Yes)
BP8	Bayou Pierre at bridge 2/3 mi S Dentville	Copiah	06/17/19	31.95206	90.56438	Yes (5)	Yes (Yes)
BP9	Bayou Pierre 2 km below Foster Creek	Copiah	08/16/19	31.95707	90.64292	No	No (No)
BP10	Bayou Pierre at HWY 18 upstream	Copiah	06/17/19	32.00312	90.68973	Yes (1)	Yes (No)
BP11	Bayou Pierre at White Oak Creek confluence	Copiah	08/21/19	32.02189	90.69181	Yes (4)	Yes (No)
BP12	Bayou Pierre at Carslile Lane	Claiborne	07/11/19	32.00537	90.78409	Yes (3)	Yes (Yes)
BP13	Bayou Pierre at Natchez Trace	Claiborne	07/20/20	32.01514	90.85259	No	Yes (No)
BP14	Bayou Pierre at Whiskey Branch Creek	Claiborne	07/24/20	32.00558	90.89623	No	Yes (No)
BP15	Bayou Pierre at Rapalje Creek	Claiborne	07/24/20	31.99834	90.92149	No	No (No)
BP16	Bayou Pierre at HWY 18 downstream	Claiborne	08/23/20	31.98592	91.00749	No	Yes (No)
CC1	Clarks Creek at SHWY 547	Claiborne	03/23/19	31.85868	90.84678	No	Yes (No)
FC1	Foster Creek at Barlow Road	Copiah	05/23/19	31.83499	90.65750	No	No (No)
FC2	Foster Creek at Smyrna Road	Copiah	05/24/19	31.87593	90.62291	Yes (4)	Yes (Yes)
FC3	Foster Creek 0.5 km above confluence	Copiah	08/16/19	31.93563	90.62166	No	Yes (Yes)
JC1	James Creek at Russum Westside Road	Claiborne	03/23/19	31.91606	91.10839	No	Yes (No)
LBP01	Little Bayou Pierre at SHWY 547	Claiborne	03/23/19	31.80452	90.73916	No	Yes (No)
LBP2	Little Bayou Pierre at Barland Road	Claiborne	06/18/19	31.85007	90.74545	No	Yes (No)
LBP3	Little Bayou Pierre at Pattison Road	Claiborne	06/18/19	31.90609	90.83539	No	Yes (No)
LBP4	Little Bayou Pierre, Little Bayou Pierre at HWY 65	Claiborne	09/21/19	31.96524	90.98067	No	Yes (No)
LC1	Long Creek at Rocky Fall Road	Copiah	03/07/19	31.92749	90.47587	No	Yes (No)
LC2	Long Creek at Dentville Road	Copiah	03/22/19	31.92566	90.49378	No	No (No)
LT1	Little Tallahalla Creek at Dry Grove Road	Hinds	06/18/19	32.15610	90.44192	No	No (No)
LT2	Little Tallahalla Creek at Chapel Hill Road	Hinds	06/18/19	32.13324	90.54396	No	No (No)
LT3	Little Tallahalla Creek at HW 27	Hinds	05/23/19	32.08173	90.59792	Yes (6)	Yes (No)
TC1	Turkey Creek at Tanyard Road	Copiah	03/07/19	31.97178	90.41954	No	No (No)
TC2	Turkey Creek at Milsaps Road	Copiah	03/07/19	31.95824	90.43762	No	No (No)
TC3	Turkey Creek at Dentville Road	Copiah	05/23/19	31.94882	90.52165	No	Yes (No)
WC1	Willis Creek at Tillman Road	Claiborne	08/01/19	31.85704	90.91770	No	No (No)
WC2	Willis Creek at HWY 547	Claiborne	08/01/19	31.91647	90.93034	No	Yes (No)
WdC1	Widows Creek at Rodney Road	Claiborne	09/21/19	31.95557	91.06260	No	Yes (No)
WOC1	White Oak Creek at Gallatin Road	Copiah	08/01/19	32.02675	90.42458	No	No (No)
WOC2	White Oak Creek at Bear Creek Road	Copiah	05/23/19	32.04732	90.51361	No	Yes (No)
WOC3	White Oak Creek at Low Water Bridge Road	Hinds	08/02/19	32.06027	90.58737	Yes (4)	Yes (No)
WOC4	White Oak Creek at Little Tallahalla Creek confluence	Hinds	08/02/19	32.06206	90.61230	Yes (5)	Yes (No)
WOC5	White Oak Creek at Bayou Pierre confluence	Copiah	08/02/19	32.02857	90.68138	Yes (2)	Yes (No)

ical sites of *N. rubrum* collection that do not appear to have full community data and/or information about collecting effort readily available. In particular, there are 56 lots containing 1050 individuals in the Tulane University collection taken primarily from lower White Oak Creek, the White Oak Creek confluence with Bayou Pierre, and Bayou Pierre below this confluence (Sites BP10, BP11, WOC5, and BP12 in Fig. 1). There are also over 350 individuals from mul-

tiple lots in the Mississippi Museum of Natural Science and University of Southern Mississippi (USM) collections from Foster Creek (FC1, FC2, and FC3) and areas near the Turkey Creek–Bayou Pierre confluence (BP7, BP8, TC3, LC2) (Knight & Ross 1994). Those locations without known standardized sampling effort are not part of our analyses. Other surveys of the basin were not included because sampling effort was not documented, sample count data

are not available, or *N. rubrum* were released and no records of counts are known. However, given the large numbers of individuals taken from these areas, we discuss qualitative patterns of abundance through time below (see Discussion). All sampling was conducted in summer 2019, with the exception of the 4 lowest points on the Bayou Pierre which were not accessible due to flooding. These sites were sampled in summer 2020.

2.2. Fish sampling

At each site, we selected a 100–250 m reach (based on estimated wetted width) that included at least 1 swift water mesohabitat unit (i.e. riffle, run, or fast glide). Each reach was divided into 3 equal-length subsample plots. Fish were sampled by seining (4 m × 1.5 m seine with 3 mm mesh) all available habitats with effort being in proportion to habitat availability. We employed kicksets within riffle habitats. With the exception of *N. rubrum* and crystal darters *Crystallaria asprella*, all fish were fixed in 10% buffered formalin, and later identified, transferred to 70% ethanol and deposited in the USM Ichthyological Collection. Prior to their release, individuals of *C. asprella* and *N. rubrum* were photographed with a reference ruler for later digital size measurement.

2.3. Habitat sampling

We measured habitat data using a point-transect method, with 3 transects per sample subplot (9 transects site⁻¹) and points taken at roughly every meter of stream width. For each transect, we recorded the bankfull and wetted stream width to the nearest meter measured with a Nikon Aculon 6×20 6.0° digital range finder, visually classified bank stability (low, medium, high based on bank angle and evidence of recent erosion via exposed alluvial material) of both banks, and visually estimated percent canopy cover at the center of the transect. At each point on a transect, we recorded water depth (cm), water velocity (m s⁻¹, Hach Flowmate 2000), dominant substrate on a rank Wentworth scale (1 = clay/silt, 2 = sand..., 6 = bedrock), embeddedness (percentage visually estimated), and the presence of any available cover elements (woody structure, boulder/cobble). We calculated means and the coefficient of variation (CV) for each of our reach-scale hydrogeomorphic variables (depth, current velocity, substrate size, wetted width, bankfull width, embeddedness, and woody structure).

2.4. Analyses

All analyses used contemporary and historical datasets with fish assemblage data at the same sites (except for the new sites added, see Section 2.1) and comparable methods and effort. We used traditional measures of diversity (Shannon's index, rarefied diversity) to describe patterns in historical and contemporary assemblages, and non-metric multidimensional scaling (NMDS) to summarize a Bray-Curtis similarity matrix of proportional abundance (McCune & Grace 2002, Legendre & Legendre 2012), and permutational MANOVA (Anderson 2001) to test for assemblage differences between historical and contemporary samples with and without *N. rubrum*. We plotted samples in NMDS space to qualitatively examine (1) similarity between historical and contemporary assemblages and (2) uniqueness of assemblage structure (historical and contemporary) associated with *N. rubrum*. For the first objective, we examined historical and contemporary patterns of abundance and occurrence of all taxa and qualitatively assessed if historical and contemporary samples overlapped in ordination space. For the second objective, we examined historical and contemporary assemblages associated with *N. rubrum* to assess if species associated with the presence of *N. rubrum* had changed over time. We tested for differences between historical and contemporary assemblages with and without *N. rubrum* with permutational MANOVA.

Network topology (link magnitude, Link-Mag) was extracted from stream attributes (watershed area and confluence-link) in the National Hydrography Dataset Plus (NHDPlus; www.horizon-systems.com/nhd-plus/). Link-Mag is the summation of the number of first-order segments upstream of a given locality in a stream network (Fairchild et al. 1998). We extracted land use data for 2016 from the national land cover dataset (NLCD, <https://www.mrlc.gov/data>). That year was used because it was the closest to when the contemporary sites were sampled. NLCD data includes 20 classes of land use that we reclassified into 5 broad land-use variables: forested, urban, wetland, open water, and agricultural. We then estimated the relative area of each land-use type associated with each site's upstream watershed area. A principal component analysis (PCA) of the land-use data explained 45.5% of the variation (with forested land having the highest loading) and was used (hereinafter: LC1) in analyses. We estimated means and SDs of elevation change using the US Geological Survey (USGS) national elevation dataset (<https://>

www.nrcs.usda.gov/wps/portal/nrcs/detail/national/). We established three 200 m cross-sections at 1 km intervals (upstream, site, downstream) at each site, reasoning that unstable stream reaches should be characterized by a greater magnitude of elevation change or greater variation in elevation change within a reach. Elevation data were collected every 10 m along a cross-section and then used to calculate the average change in elevation (CE Avg) and the SD of elevation change (CE SD) for each site. These variables were included as covariates within our occupancy models. We used PCA to reduce the dimensionality of hydrogeomorphic variables, followed by a broken-stick model to determine how many axes to retain. We saved PC1, PC2, and PC3 scores (henceforth Hab1, Hab2, and Hab3) as descriptors of environmental variation at the reach scale.

We used single-species occupancy models to characterize reach-scale and landscape-scale environmental variation associated with the probability of occurrence (Ψ) of *N. rubrum* (MacKenzie et al. 2002) using contemporary sites excluding Little Bayou Pierre. Because spatial replicates may not represent truly independent surveys and lead to the inflation of occupancy estimators (Kendall & White 2009), we also developed spatial dependence models (Hines et al. 2010). Spatial dependence models allow the probability that a spatial segment may or may not be occupied based upon whether the previous segment was occupied (θ') or not (θ) (Hines et al. 2010) where parameters are modeled as a first-order Markov process. We used the logit link transformation to model Ψ as a function of covariates. Due to our small sample size ($n = 32$), detection (p) was modeled as constant to reduce model complexity. Reach-scale habitat (Hab1, Hab2, and Hab3), elevational (CE Avg and CE SD), and landscape-scale (link magnitude, Link-Mag and LC1) variables were included as covariates to estimate Ψ . We used untransformed beta estimates to infer relationships (positive or negative) between covariates and occupancy. We standardized Link-Mag, CE Avg, and CE SD by subtracting the mean and dividing by twice the SD. Prior to modeling, we tested for the correlation between covariates. Any 2 covariates which had a Pearson correlation greater than the absolute value of 0.5 were not included in the same model. However, correlated variables were used as separate covariates for detection and occupancy within the same model. To assess the relative fit of our single-species occupancy models, we used the MacKenzie-Bailey goodness of fit test (MacKenzie & Bailey 2004), in which overdispersion (\hat{c}) is estimated by calculating the chi-squared goodness of fit statistic for a global

model and then dividing it by the mean test statistic of 10 000 bootstrap samples. To model *N. rubrum* abundance as a function of reach-scale and landscape-scale environmental variation, we used zero-inflated Poisson regression models (R package 'glmmTMB') (Brooks et al. 2017). Zero-inflated regression models allow the user to account for overdispersion in the response variable by modeling zeros in a dataset as a function of a 2-state process. One of the 2 states, the zero state, may be defined as the probability of an event being so low that it cannot be readily differentiated from zero. The second state, the normal state, includes both zeros and continuous values falling within the interval (0, 1) (Liu & Eugenio 2018). We modeled the zero state as a function of mean depth and current velocity. We included stream size as a random effect; stream size groupings were based on a site's Link-Mag (small = 0 to 30, 30 to 100 = medium, >100 = large; 10, 10, and 8 sites respectively).

We used Akaike's information criterion for small sample sizes (AIC_c) to assess the quality of competing models (Anderson & Burnham 2002). Models with small ΔAIC_c and large Akaike weights (w_i) indicate a more optimal balance of parsimony and fit (Anderson & Burnham 2002). We only interpreted models with $w_i > 0.10$. To prevent the inclusion of uninformative parameters, models which only differed in ΔAIC_c by 1–2 units from the best models and possessed similar log-likelihood values were removed (Anderson & Burnham 2002). As an alternative to using a single best-supported model, we applied model averaging to quantify unconditional model average estimates of Ψ and p , and associated standard errors (bounded between 0 and 1.0) for all occupancy and detection parameters within models with $w_i > 0.001$.

To estimate the mean abundance of *N. rubrum* per site, we modeled abundance using the N -mixture model as described by (Royle 2004). Often, count data is used to estimate abundance or population size, ignoring the fundamental detection process which generated these data. When modeling abundance, it is presumed that the population under study is closed with respect to mortality, recruitment, and movement so that the counts may be construed as binomial random variables. This model makes 2 distributional assumptions:

$$n_{ij} \text{ Binomial } (N_i, p) \quad (1)$$

$$N_i \text{ Pois } (\lambda_i) \quad (2)$$

where n_{ij} is the number of *N. rubrum* counted at site i in survey j , N_i is the number of *N. rubrum* present at site i , p is the probability of detection, and λ_i is the conditional mean abundance of *N. rubrum* at site i .

For our dataset, we assumed counts followed a Poisson (Pois) distribution and thus used the Poisson mixture. Due to time constraints, we substituted spatial replicates for temporal replicates to model N_i . While we recognize that our observed data do not represent true temporally, replicated counts, estimates of abundance are much preferred by state and federal agencies so that they can more effectively manage federally threatened species such as *N. rubrum*. We did not model N_i as a function of our environmental covariates; we only constructed a null model to obtain an estimate of N_i . All hierarchical models were constructed using the package 'unmarked' in R (version 0.13-1) (Fiske & Chandler 2011).

3. RESULTS

3.1. Fish assemblages

The 42 contemporary samples contained 20 855 individuals representing 71 species. The most abundant species were *Cyprinella venusta* (mean of 261 site⁻¹, collected at 33 sites), *Notropis volucellus* (100.4 site⁻¹ at 20 sites), *N. atherinoides* (81.4 site⁻¹ at 15 sites), *N. longirostris* (34.8 site⁻¹ at 34 sites), and *Percina vigil* (41.2 site⁻¹ at 25 sites). The most commonly occurring species were *Fundulus olivaceus* and *N. longirostris* (both 34 sites), and *C. venusta*, *C. camura*, and *Lepomis megalotis* (each 33 sites). The 51 historical samples contained 11 243 individuals representing 63 species. Notable changes in species rank abundance between historical and contemporary include increases in *N. atherinoides* (increase in rank from 38 to 3), *N. volucellus* (increase in rank from 25 to 2), and *P. vigil* (increase from 14 to 5), and declines in *C. lutrensis* (decrease in rank from 2 to 13) and *Etheostoma lynceum* (decrease from 4 to 17). All species present in 1 of the 2 datasets and absent from the other were rare, occurring in 4 or fewer samples. Measures of diversity were similar between contemporary (Shannon's index: 1.8 ± 0.08 SE, rarefied diversity: 11.3 ± 0.48 SE) and historical (Shannon's index: 1.8 ± 0.05 SE, rarefied diversity: 11.1 ± 0.32 SE) collections.

3.2. *Nothonotus rubrum* occurrence and abundance

We collected 65 *N. rubrum* at 11 sites (26 % of sites sampled), a similar rate of capture as in the historical samples (8 sites, 27.5%). Four of the 11 sites were localities where *N. rubrum* were sampled in histori-

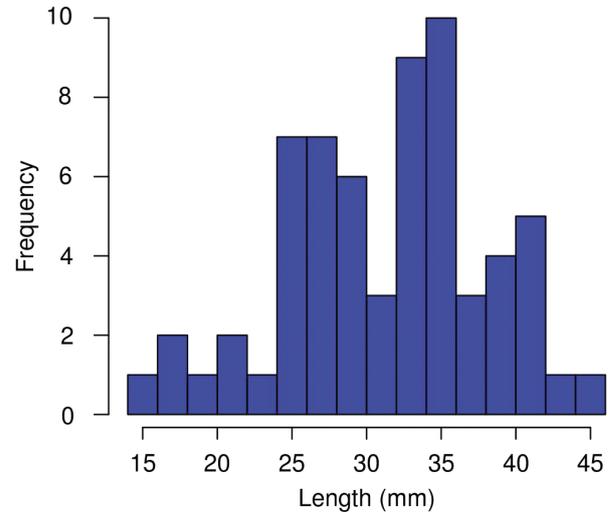


Fig. 2. Size distribution (standard length) of *Nothonotus rubrum* sampled in 2019

cal collections (green stars, Fig. 1). Seven of the sites with *N. rubrum* did not have any occurrences in historical data (orange stars), while 2 sites with *N. rubrum* historically did not have any in our collections (red diamonds). The mean (5.9 contemporary, 11.6 historical) and maximum (18 contemporary, 48 historical) number of *N. rubrum* captured at sites where present was similar between contemporary and historical samples. Note that in the historical dataset, sites with *N. rubrum* were often sampled multiple times, most likely to provide adequate sample size for life history, genetic, or diet study objectives. Some other sites are known to contain *N. rubrum*, but they were absent in collections from those sites in the historical dataset (see Section 2.1). There were 2 further localities sampled opportunistically while hiking to other sites. These sites contained habitat that appeared ideal, and both sites contained *N. rubrum*. We did not include data from these 2 occurrences in analyses because the same standard sampling protocol was not followed. These additional sites are also not represented on Fig. 1. Two of the 65 *N. rubrum* were taken as vouchers, while the remaining 63 were photographed to obtain standard length and estimate mass. The mean size of *N. rubrum* collected was 31.3 mm (6.6 SD), with a range from 15.1 to 44.9 mm (Fig. 2).

3.3. Synthesis of reach-scale environmental variation

The PCA of our hydrogeomorphic variables revealed physical habitat gradients associated with stream

slope and stream size. The strongest loadings on Hab1 (27.2% variance explained, Table 2) were substrate size (−1.13), embeddedness (1.03), and the CV of embeddedness (−1.02). Important loadings on Hab2 (17.1% variance explained, Table 2) included wetted width (−0.82), the bankfull width (−0.88), and canopy cover (−0.82). Finally, variables with the greatest loadings on Hab3 (12.2% variance explained, Table 2) included CV of wetted width and CV of bankfull width. Thus, Hab1 represented a depth and substrate gradient; sites with negative scores along Hab1 were characterized by more coarse sediments and shallower depths. Hab2 represented a stream size gradient; sites with positive scores along Hab2 were characterized by narrower active channel widths and a greater percentage of canopy cover. Hab3 represented an erosion gradient; sites with positive scores along Hab3 were characterized by greater variability in active channel and bankfull widths.

3.4. Hierarchical modeling of *N. rubrum* occurrence and abundance

N. rubrum were detected at 11 of the 32 sampled sites analyzed, yielding a naïve occupancy estimate of 0.34. When modeling detection as constant, we obtained an unconditional estimate for p of 0.33 ± 0.11 . Preliminary analyses indicated that the single-season null model was better supported ($w_i = 0.92$) than the spatial dependence null model, suggesting that detections were not spatially autocorrelated, jus-

Table 2. Variables and loadings for the first 6 axes from the principal component analysis. Percent variance explained is included for each axis. CV: coefficient of variation

Variable	PC1 27.2%	PC2 17.1%	PC3 12.2%
Depth	0.788	0.252	−0.305
Current velocity	−0.361	0.823	0.528
Substrate size	−1.128	0.024	−0.114
% Embeddedness	1.028	−0.024	−0.114
% Woody structure	0.848	−0.245	−0.416
% Canopy cover	−0.177	−0.816	−0.374
Wetted width	0.207	0.818	−0.374
Bankfull width	0.102	0.879	0.378
CV of depth	−0.019	−0.438	0.336
CV of current velocity	−0.310	−0.452	−0.318
CV of substrate size	−0.722	−0.068	−0.264
CV of % embeddedness	−1.018	0.107	−0.287
CV of % woody structure	0.228	0.433	−0.298
CV of % canopy cover	0.004	0.435	−0.140
CV of wetted width	0.041	−0.317	0.835
CV of bankfull width	−0.045	−0.001	0.851

tifying the use of spatial replicates for p . Our global model indicated no evidence of a lack of model fit ($p = 0.56, \hat{c} = 0.82$). Occupancy of *N. rubrum* was best modeled by Link-Mag and Hab2 (Table 3), with a positive relationship to Link-Mag (beta estimate, 3.07 ± 1.87 , Fig. 3) and negative relationship to Hab2 (beta estimate, $−0.73 \pm 0.79$, Fig. 3). Our null model of abundance estimated the N_i of *N. rubrum* at 7.36 ± 3.83 individuals site^{−1}. *N. rubrum* counts were best modeled as a function of the variation in elevation change at the kilometer scale (Table 4) with a significant, negative relationship (beta estimate = $−0.60$; $p < 0.001$) between CE SD and *N. rubrum* counts.

3.5. Fish assemblages

Historical and contemporary fish assemblages without *N. rubrum* were generally concordant and overlapped broadly in ordination space (light and dark gray polygons in Fig. 4), while historical and contemporary assemblage structure at sites with *N. rubrum* diverged in ordination space (blue and green polygons in Fig. 4). Non-parametric MANOVA indicated significant differences between historical and contemporary assemblages that were much more pronounced (more variance explained by time variable) in samples with *N. rubrum* ($F_{1,32} = 7.2, R^2 = 0.19, p < 0.001$) compared to samples without *N. rubrum* ($F_{1,32} = 3.2, R^2 = 0.05, p < 0.003$). The 2 species most

Table 3. Single-species occupancy models and intercept-only models for occurrence of Bayou darters sampled in the Bayou Pierre River system. K : number of parameters, AIC_c : Akaike's information criterion for small sample sizes; w_i : model weights; p : probability of detection; Ψ : probability of occurrence; Link-Mag: link magnitude; Hab1, Hab2, and Hab3: reach-scale habitat variables; CE SD: standard deviation of elevation change; CE Avg: average change in elevation. Intercept-only models are designated by periods in place of covariates. Models with parameters θ and θ' indicate spatial-dependence models with the probability that a spatial segment may or may not be occupied based on whether the previous segment was occupied (θ') or not (θ)

Model	K	AIC_c	ΔAIC_c	w_i
p (.), Ψ (Link-Mag)	3	80.41	0	0.70
p (.), Ψ (Hab2)	3	82.47	2.06	0.25
p (.), Ψ (.)	2	88.16	7.75	0.01
p (.), Ψ (Hab3)	3	88.98	8.57	0.01
p (.), Ψ (Land use)	3	89.17	8.76	0
p (.), Ψ (CE SD)	3	89.54	9.13	0
p (.), Ψ (Hab1)	3	89.83	9.42	0
Global	9	90.30	9.89	0
p (.), Ψ (CE Avg)	3	90.65	10.24	0
p (.), Ψ (.), θ (.) θ' (.)	5	95.05	15.28	0

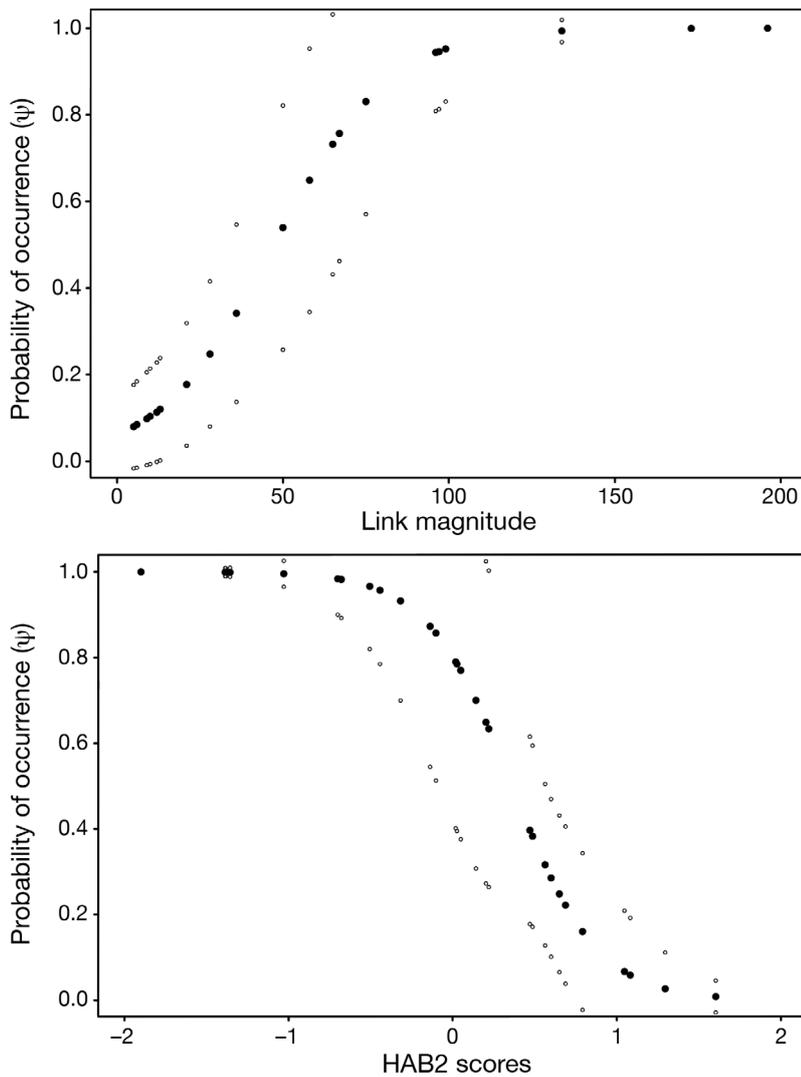


Fig. 3. Predicted values of Bayou darter occupancy plotted against link magnitude (upper panel) and Hab2 scores (lower panel) for the 28 surveyed sites. Black circles: predicted values; white circles: 95% confidence limits

Table 4. Zero-inflated Poisson mixed effects models of Bayou darter counts sampled in the Bayou Pierre River system. K : number of parameters; AIC_c : Akaike’s information criterion for small sample sizes; w_i : model weights; CE SD: standard deviation of elevation change; CE Avg: average change in elevation; Hab1, Hab2, and Hab3: reach-scale habitat variables

Model	K	AIC_c	ΔAIC_c	w_i
Abundance ~ CE SD + 1 Stream size	3	80.41	0	0.70
Abundance ~ Land use + 1 Stream size	3	82.47	5.08	0.05
Abundance ~ 1 + 1 Stream size	2	88.16	9.9	0.01
Abundance ~ CE Avg + 1 Stream size	3	88.98	11.2	0
Abundance ~ Hab1 + 1 Stream size	3	89.17	11.3	0
Abundance ~ Hab2 + 1 Stream size	3	89.54	12.4	0
Global	3	89.83	12.5	0
Abundance ~ Hab3 + 1 Stream size	9	90.30	13.1	0

characteristic of these changes were *E. lynceum* (present in all 14 historical samples with *N. rubrum* at a mean abundance of 37.0, present in all contemporary samples with *N. rubrum*, but a mean abundance of 9.1), and *C. venusta* (present in all 14 historical samples with *N. rubrum* at a mean abundance of 53.5, present in all contemporary samples with *N. rubrum*, but a mean abundance of 284.3). *P. vigil* also increased in abundance and is commonly found with *N. rubrum*. Historically, *P. vigil* occurred at 12 of 14 sites with *N. rubrum* at a mean abundance of 3.6. In contemporary samples, *P. vigil* was found in all samples with *N. rubrum* at a mean abundance of 60.5 (range among samples of 2–170, and 3 samples having >100). Mean abundance of *P. vigil* in contemporary samples without *N. rubrum* was just 11.8.

4. DISCUSSION

We captured *Nothonotus rubrum* at a similar proportion of contemporary samples (28%), and in similar abundance (6–7 individuals sample⁻¹) in comparison to the historical samples from 1987–1992. While current rates of occurrence and abundance are similar, the trends appear to show flat or declining abundance and continued movement up in the watershed. We chose these historical samples for direct comparison after reviewing field notes and, when possible, discussion with the researchers who conducted those early surveys. All evidence suggested these samples were from comparable sampling of fish assemblages that did not target *N. rubrum* (i.e. no bias towards riffle habitat). There are many other historical records of *N. rubrum* that do not appear to be from comparable sampling efforts (or proper documentation is lacking), complicating assessment of long-term trends in abundance. However, even with differences in sampling approaches, there are some striking

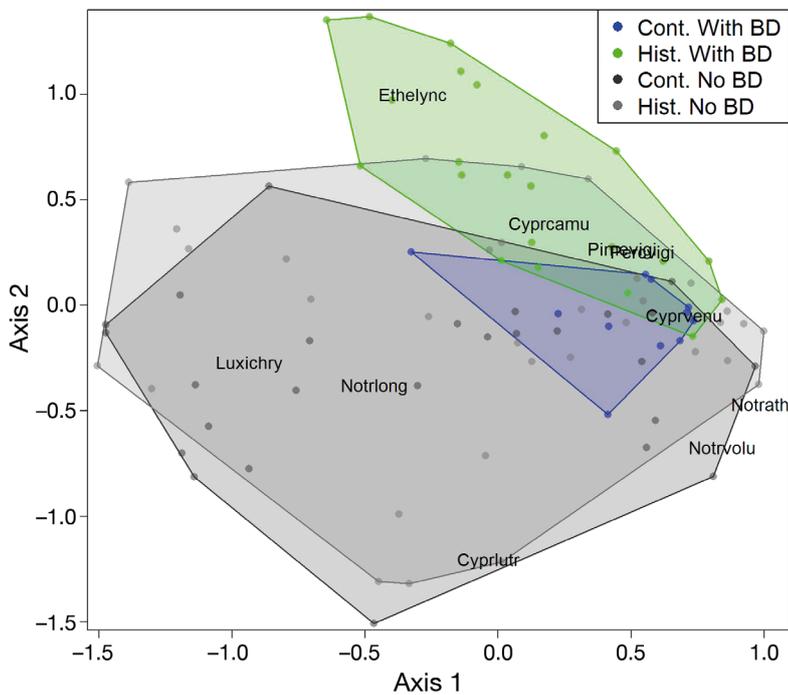


Fig. 4. Nonmetric multidimensional scaling analysis ($K = 2$, Bray-Curtis similarity) of historical and contemporary relative abundances. Minimum convex polygons surround samples parsed into 4 groups: contemporary (Cont.) and historical (Hist.) samples with and without Bayou darter (BD). Weighted average scores for the 10 most abundant species are plotted (Cyprcamu: *Cyprinella camura*; Cyprlutr: *C. lutrensis*; Cyprvenu: *C. venusta*; Ethelync: *Etheostoma lynceum*; Luxichry: *Luxilus chrosocephalus*; Notrath: *Notropis atherinoides*; Notrlong: *N. longirostris*; Notrvolu: *N. volucellus*; Percvigi: *Percina vigil*; Pimvigi: *Pimephales vigilax*)

changes in where *N. rubrum* occurs in high abundance. The largest number of vouchered *N. rubrum* specimens is found in the Tulane University collection, with 1050 individuals from 56 lots. The majority of these collections (including 7 lots with >50 individuals, 2 lots >100) were taken before 1980 from the White Oak Creek confluence downstream of Carlisle. During this same period, there were fewer than 70 individuals vouchered at sites above the White Oak Creek Confluence (Site BP11 in Fig. 1). In contrast, *N. rubrum* samples in the 1980s and 1990s focused further upstream with nearly 600 individuals vouchered from upper Bayou Pierre, the Turkey Creek confluence, and Foster Creek. During that same period, there were just 29 individuals captured from the White Oak Creek confluence and below. In our sampling, we captured 10 individuals from the White Oak Creek confluence and below, and 55 from sites higher in the watershed. Some of our most productive sites (Bayou Pierre at Cline Road, sites at the confluence of White Oak Creek and Little Tallahalla Creek) were sites higher in the watershed with lower historical abundance.

Much of the early research was aimed at describing the species, and its ecology and life history in order to properly manage it. Those objectives require larger sample sizes, and efforts to document abundance were somewhat secondary. Thus, researchers at that time were targeting areas with the highest local abundance. The areas where *N. rubrum* appear to be in highest abundance shifted upstream from 1960–1970 to 1980–1990. It seems unlikely that there are any areas with abundances as high as observed in the 1960s or 1970s. Given our observed and estimated abundances, even if sampling targeted riffle habitat at the highest abundance sites, it seems inconceivable that one could capture >100 individuals at a site today. More troubling, our estimate does not distinguish among age-classes; rather it was quantified using counts of both juveniles and adults at a site. Knight & Ross (1994) reported densities of 2.5 to 3.4 individuals m^{-2} , presumably in ideal riffle habitat. Today, these densities from the 1980–1990 period seem like a best-case scenario and certainly not typical. The long-term trends for this species are troubling, as the distribution has moved up the watershed, while abundance seems to be declining. Continued push of this

species into headwaters would likely result in smaller and more isolated populations, complicating conservation efforts. It should be noted that our assessment here is based on limited temporal sampling (2019–2020) and could be biased from population stochasticity. While we do not feel this is the case, given that observed size distributions (our Fig. 2) were similar to those previously published (Slack et al. 2004), more frequent sampling of these populations is warranted. Our findings suggest that *N. rubrum* was generally sampled from reaches typified by stable active channels. The magnitude and variability in elevation change within stream reaches where we sampled 80% (52 individuals, 8 sites) of *N. rubrum* individuals was reduced (0.53 ± 0.09) in relation to all other sampled localities (0.63 ± 0.21). Following Schumm et al. (1984), these sites occurred in geomorphic zones that were historically classified as either stage II or III (Ross et al. 2001). Contemporary habitat data suggests that *N. rubrum* occupied sites that were characterized by moderately sloping banks, defined berms with vegetation, stable point bars, and

consolidated riffle habitats typified by cobble and gravel substrates. Given the qualitative approach used in Ross et al. (2001), e.g. visual assessment of aerial photographs, to classify geomorphic zones, it is difficult to ascertain whether geomorphic variability at these localities has resulted in substantial habitat change at the reach scale over the last 26 yr. A more quantitative approach similar to the method used in the present study (i.e. standardized cross-sections to assess geomorphic variation) should be used in future studies to assess the degree of habitat change at sites typified by Bayou darter presence.

The shifting *N. rubrum* distribution is consistent with geomorphological changes in the Bayou Pierre watershed. Ross et al. (2001) documented erosional waves rapidly moving up through the watershed. These erosional waves resulted in the loss of riffle habitat, due primarily to downstream transport of finer sediments, and channel modifications. At the same time, there was creation of some new riffle habitat above knickpoints, leading to the hypothesis that *N. rubrum* populations may move with erosional waves. The system has been quite dynamic, with knickpoints moving upstream at rates close to 750 m yr⁻¹. However, conserving *N. rubrum* by having populations 'ride' these waves up the watershed is not sustainable, as there is only so far to go. *N. rubrum* are likely responding to substrate changes, but they are adapted to large creek and small river habitat in the middle/lower portions of the watershed. The high-abundance habitats where they were found historically have cumulative watershed areas of ~1500 km² (near White Oak Creek Confluence), compared to most sites where we sampled >5 individuals that have a cumulative watershed area <500 km². Such inferences are supported by our occupancy modeling results, which make it clear that the microhabitat preferences of this darter are most commonly found in large streams (Fig. 3). While these smaller creeks may contain the most suitable substrate, there are a variety of other differences in those habitats for which *N. rubrum* may not be adapted, putting populations at risk.

Current and historical assemblages were generally quite similar, with a few notable exceptions. First, historical and current assemblages at sites without *N. rubrum* overlapped broadly, indicating little change. The subset of sites that contained *N. rubrum* show more change with less overlap between historical and current samples (Fig. 4). Most of the sites with *N. rubrum* are in the middle and upper portions of the watershed where the most active erosion is occurring. Thus, it appears there may be more fish assemblage changes at sites that are undergoing more recent

physical change. Assemblage changes in darters include a reduction in the numbers of *Etheostoma lynceum*, which are often found in shallower habitat with larger substrate, and increases in *Percina vigil* and *Crystallaria asprella*. Both *P. vigil* and *C. asprella* are more abundant in large swift streams with sand, gravel, or hard packed clay substrate (Ross 2000, Boschung & Mayden 2004). In cyprinids, there were fewer red shiner *Cyprinella lutrensis*, and more *Cyprinella venusta* and *Notropis volucellus* in contemporary samples. In the historical data, *C. lutrensis* was often numerically dominant at fewer sites (in the historical data, it was second most abundant while only occurring in 45% of samples). The contemporary samples only contained 1 site dominated by *C. lutrensis*, James Creek (JC1), which is the lowest tributary in the system and <10 km from Mississippi River.

Current management recommendations for *N. rubrum* include action to reduce ongoing geomorphic change in the system. It is not entirely clear how successful any such efforts have been, and a thorough analysis of how knickpoints continue to move through the system is needed. Increased frequency and resolution of remote sensing data, in combination with historical data and analyses (Ross et al. 2001), should provide a clearer picture of how this system continues to change physically and biologically. There are occasional reports of *N. rubrum* seen downstream, which may be a result of the fairly mobile life history (Slack et al. 2004, 2010). As noted above, it has been over 30 yr since Bayou darters were sampled in large numbers at and below the confluence with White Oak Creek. Given the overall patterns in abundance, additional and more frequent sampling would be valuable in assessing whether lower numbers observed in 2019 are part of a continuing trend or an anomaly. The large abundances seen in lower portions of the basin in the 1960s and 1970s sampling needs to be better understood. A review of pertinent field notes, and study of the demographic patterns in those samples (e.g. size distributions to infer age), would be beneficial in putting those numbers in context. Our contemporary data represents a single snapshot that may not fully represent the status of these populations. Regular surveys are needed (and planned) to assess the longer-term stability of these populations.

Acknowledgements. Funding was provided by the US Fish and Wildlife Service. We thank S. Ross, T. Slack, and M. Wagner for assistance and insights regarding vouchered collections, and historical field notes and efforts. We thank M. Aiken, S. Barrett, A. Coomes, M. Dunning, A. Grieshober, and R. Spiers for assistance with field collections.

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