

## ORIGINAL ARTICLE



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# Spatiotemporal assessment of Sickie Darter (*Percina williamsi* Page and Near, 2007) distribution in the upper Tennessee River Basin

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## Abstract

The Sickie Darter *Percina williamsi* (Page and Near, 2007) is a species of fish endemic to the upper Tennessee River basin in eastern Tennessee, southwestern Virginia, and western North Carolina. Because of its narrow range and presumed decline in occupied sites over the last half century, it is being proposed for federal listing under the Endangered Species Act. We analyzed the current distribution of the Sickie Darter and temporal trends in its distribution in relation to temporal trends in environmental and habitat covariates for each of the historically occupied sub-basins (upper Clinch, Emory, upper French Broad, Little, Little Pigeon, Middle Fork Holston, North Fork Holston, Powell, South Fork Holston, and Watauga) with multiple linear regression modelling. A total of 154 Sickie Darters were observed at 15 sites throughout the upper Tennessee River Basin. Sickie Darters were observed in the Little River, Emory River, and Middle Fork Holston River sub-basins. A total of 133 unique historical occurrences were used for the spatiotemporal analyses. Sickie Darters have declined in 8 out of 10 historically occupied sub-basins. Our best model for the whole distribution scale (Mallow's  $C_p = -0.87$ ; Adjusted  $R^2 = .92$ ) suggests that habitat fragmentation due to damming has had adverse effects on Sickie Darter populations across its distribution. Models were very similar for the sub-basin specific models as well. The results from this study highlight the drivers of decline in Sickie Darter distribution and outline the future research needs for this species that should be used to inform future conservation decisions regarding this species.

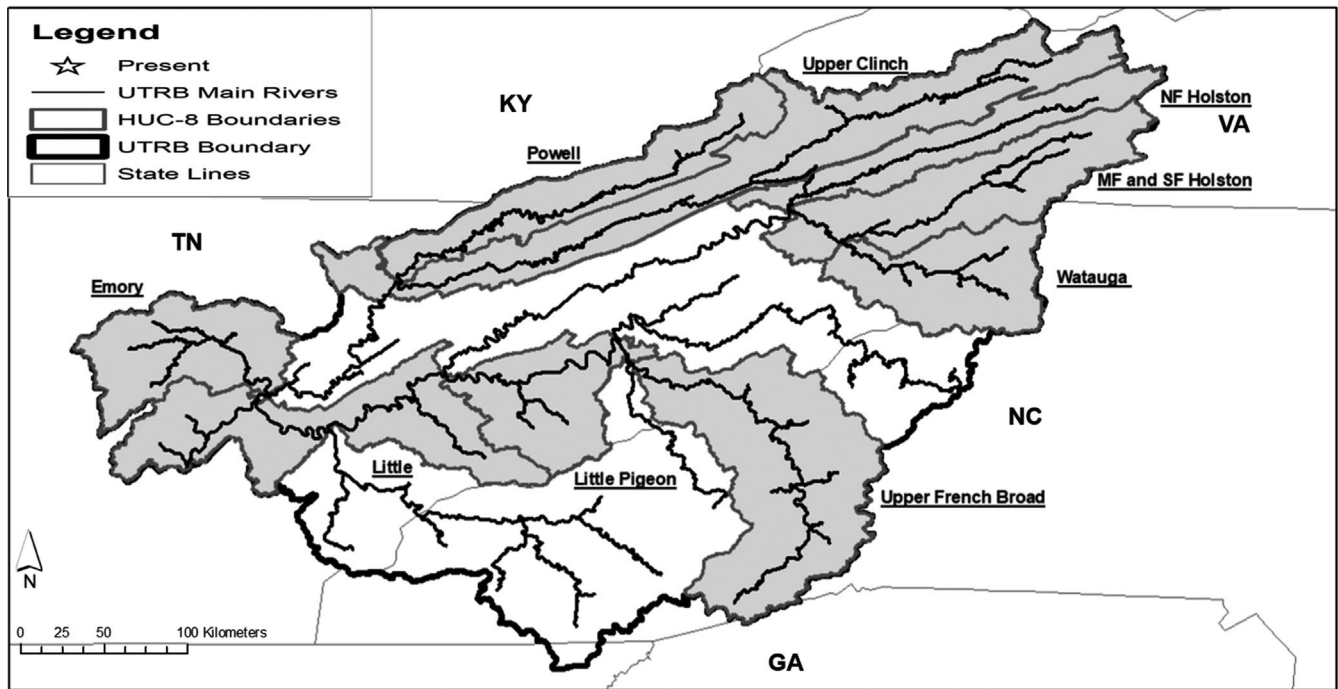
## KEYWORDS

conservation, fisheries, modelling, rivers

## 1 | INTRODUCTION

The Sickie Darter *Percina williamsi* (Page & Near, 2007) is a species endemic to the upper Tennessee River basin (UTRB) of North Carolina, Tennessee, and Virginia (Jett, 2010). It was once thought to be widespread throughout the UTRB, but now it may only occur in the upper Clinch River and North Fork Holston River sub-basins in Tennessee and Virginia, Middle Fork Holston River sub-basin in Virginia, and

the Emory River and Little River sub-basins in Tennessee (Figure 1; Page & Near, 2007). It is considered extirpated from its historic localities in North Carolina. This species can be considered rare following the classifications of Rabinowitz (classification D; 1981) because it inhabits specific habitat types (sparsely available habitat) within a range of other available environmental characteristics. Unlike most darters (Family Percidae) that are benthic, this species is benthipelagic and has a fusiform body, where it can be found swimming in



**FIGURE 1** The historically occupied HUC-8 sub-basins (shaded) by the Sickle Darter in the upper Tennessee River Basin

the water column and benthic areas of low-gradient medium-sized creeks and small rivers. Anecdotal observations suggest that within these systems the species occurs almost entirely in pool habitats adjacent to flow  $>10$  cm/s, and it is commonly found in or near woody debris piles or aquatic vegetation over a mix of cobble, gravel, sand, and silt substrates (Page & Near, 2007).

The spatiotemporal distribution of the species has been understudied, but it is presumed to have declined across much of its historical range (Page & Near, 2007; USFWS, 2011). However, causes of decline are currently unknown, but are speculated to be habitat degradation and fragmentation due to damming across the UTRB (USFWS, 2011). This uncertainty brings into question the species' conservation status on state and federal levels (TWRA, 2015; VDWR, 2015; USFWS, 2011). The current conservation status of the Sickle Darter is a species of greatest conservation concern (GCN) and threatened in Tennessee and Virginia, extirpated in North Carolina, vulnerable by the International Union for Conservation of Nature (IUCN), threatened by the American Fisheries Society (AFS), and it is currently being proposed to be listed as threatened by the U.S. Fish and Wildlife Service (USFWS) under the Endangered Species Act (Angermeier & Pinder, 2015; Burns et al., 2012; Jelks et al., 2008; NatureServe, 2013; TWRA, 2015; Tracy et al., 2020; United States, 1973; VDWR, 2015; USFWS, 2011). State listings are due to the species' endemism and habitat specialization in Tennessee and Virginia (TWRA, 2015; VDWR, 2015). While the spatiotemporal trends of Sickle Darter distribution are widely unknown, more information is available on spatiotemporal changes in the UTRB (Hampson et al., 2000; USFWS, 2014).

The UTRB has undergone immense physicochemical and hydrological changes in the last ~150 years (Hampson et al., 2000;

USFWS, 2014). With the creation of Tennessee Valley Authority (TVA) in 1933, many streams and rivers of the drainage were dammed for hydroelectric power (Etnier & Starnes, 1993; Hampson et al., 2000; Jenkins & Burkhead, 1994). With 50 dams having been constructed in the UTRB drainage (not including mill dams; Hampson et al., 2000), aquatic habitats for aquatic fauna have become fragmented. Many of these dams have caused system restarts in flow and temperature regime, as predicted by the serial discontinuity concept of human-altered riverine ecosystems (Ward & Stanford, 1983). Serial discontinuity is a problem for all fish because each species requires a specific flow and temperature regime (Poff et al., 1997). There has been a vast increase in industrial/commercial land use in this drainage in the past ~150 years, such as coal mining, silviculture, agriculture, and urbanization (Hampson et al., 2000). Decades of land cover change has impaired water quality, aquatic habitat suitability, and ecosystem function in the UTRB (Diamond et al., 2002; Hampson et al., 2000). Cumulatively, these landscape-level changes have led to the decline and imperilment of UTRB aquatic fauna (Elkins et al., 2016; USFWS, 2014). The UTRB boasts one of the highest aquatic faunal diversities of all river systems in the North America (Elkins et al., 2016; Hampson et al., 2000). It is historically home to over 175 fish species, with 14 of these species being endemic to the drainage. There are 60 mussel species, with 5 of those being endemic (USFWS, 2014), 9 threatened and endangered fish species (USFWS listing; Environmental Conservation Online System, Washington D.C., <https://ecos.fws.gov/ecp/>), and 25 threatened and endangered mussel species in the UTRB (Burns et al., 2012; Etnier & Starnes, 1993; Jenkins & Burkhead, 1994; TWRA, 2015; USFWS, 2014; VDGIF, 2015). Range contraction and population declines of mussels and fish in the last 50 years have

provided the impetus for their imperilment (Burns et al., 2012; Etnier & Starnes, 1993; Hampson et al., 2000; Jenkins & Burkhead, 1994; USFWS, 2014). Causes for their decline include habitat fragmentation from dams, poor water quality from non-point and point source effluents, and the introduction of invasive species. (Burns et al., 2012; Elkins et al., 2016; Etnier & Starnes, 1993; Hampson et al., 2000; Jenkins & Burkhead, 1994; USFWS, 2014).

A spatiotemporal assessment of Sickle Darter distribution is needed to understand how the distribution of this species has changed within its historical range in the UTRB and to ascertain likely causes of this species' decline. Furthermore, more information is needed at the sub-basin spatial scale to understand why the Sickle Darter no longer occurs in some sub-basins within the UTRB (Little Pigeon River sub-basin, for example) but persists in others. Potentially, the damming of aquatic systems has resulted in fragmented populations and prevented the dispersal of this species, which in turn may have contributed to its decline. Deteriorating water quality and habitat degradation in the UTRB have quite possibly added to the decline of this species. The goal of our study was to assess the changes in distribution of this species and set the goal of understanding the spatiotemporal relationships of Sickle Darter distribution and environmental/habitat covariates. We achieved this goal by setting the following objectives: (i) determine the current distribution of the Sickle Darter, (ii) assess the temporal changes in the distribution of the Sickle Darter on the whole-basin scale (UTRB) and the sub-basin scale, and (iii) explore the factors influencing changes in the distribution of the Sickle Darter across both spatial scales. The data presented in this study will aid our understanding of why the Sickle Darter has experienced changes in its distribution across multiple scales and help inform where this species needs conservation measures to help preserve it for the future.

## 2 | METHODS

### 2.1 | Study area

The UTRB originates as a spring-fed system in the southern portion of the Appalachian Mountains (Figure 1). With a drainage area of 5.5-million hectares, it flows through four different Level-III ecoregions: the Blue Ridge Mountains, the Ridge and Valley, the Southwestern Appalachians, and the Central Appalachians (Hampson et al., 2000; Omernik, 1987). It consists of 6 major hydrologic units: Watts Barr Lake, the Little Tennessee River, the Hiwassee River, the Clinch River, the Holston River, and the French Broad River (Hampson et al., 2000).

### 2.2 | Site selection

Sickle Darter sample sites were selected from a pool of sites where they had been previously observed and at sites where they have not been sampled prior to this study. A site consisted of a 100 to 500-m

reach that included pool and riffle-run macrohabitats. Contemporary sites for this study were sampled in the upper Clinch River, Emory River, French Broad River, Little Pigeon River, Little River, Middle Fork Holston River, North Fork Holston River, Powell River, South Fork Holston River, and Watauga River sub-basins.

### 2.3 | Sickle Darter surveys

Sickle Darters were sampled by the authors during late spring to fall months during 2017–2019 using multiple gears that are standard for sampling fishes in wadeable warmwater-streams (Bonar et al., 2009; Weaver et al., 2014). The gears selected for observing Sickle Darters were backpack electrofishing with dip nets and/or seines, seine hauls, and snorkeling. Multiple gears were employed to increase the probability of detecting Sickle Darters. At a site, run-areas were sampled with backpack electrofishing into seine nets or with dip nets, using a Smith-Root® backpack electrofishing unit. We deployed a 10 × 1.5-m minnow seine, with 6-mm nylon mesh, and pools were sampled with seine hauls, using a 15 × 1.5-m minnow seine, with 6-mm nylon mesh. Backpack electrofishing was conducted using AC settings and shocking took place within 10–40 Hz, which is standard for percid fishes (Bonar et al., 2009). On some occasions, a single-pass technique was used while sampling with a backpack electrofisher and a dip netter (Meador et al., 2003). Snorkel surveys were done with two or more snorkelers and covered the entire reach of a site (Davis et al., 2011; Weaver et al., 2014). All habitats (e.g. riffles, runs, and pools) of a site that were visible were snorkeled. All fish captured or observed while sampling were identified to the species level. Fish captured by seining and electrofishing were identified and released immediately after capture. A subsample of Sickle Darters ( $n = 18$ ) were sacrificed in an overdose of MS-222, fixed in 10% buffered formalin, and later preserved in 70% ethanol for other analyses under approved scientific collection permits from the States of Tennessee and Virginia.

### 2.4 | Historical occurrences

Historical occurrence data were gathered from a variety of sources. To ensure we included every possible occurrence record for this species, we performed a search for Longhead Darter (*P. macrocephala* Cope, 1867) historical occurrence as well since the Sickle Darter was “recently” split from that species (Page & Near, 2007). We concluded that if a historical occurrence record for the Longhead Darter occurred in the range of the Sickle Darter, then it was an occurrence record for the Sickle Darter. Historical occurrence records were obtained from the Global Biodiversity Information Network (GBIF, 2020), Freshwater Information Network (FIN; TNACI, 2019), FishNet2. (2020), FishMap (2020), Tennessee Wildlife Resources Agency (TWRA) fish sampling data base (personal communication with TWRA Region 4 Fisheries Coordinator Bart Carter), Virginia Department of Wildlife Resources (VDWR) fish sampling data base

(personal communication with VDWR Region 3 Aquatic Biologist Mike Pinder) and with and Conservation Fisheries Inc. (CFI) snorkel-monitoring database (personal communication with Senior Conservation Biologist Crystal Ruble). Every acquired occurrence record was cross-referenced with repeating occurrence points in multiple databases. Data associated with each occurrence record generally consisted of date, sub-basin, gear type, geographic coordinates, and geographic locality. Gear type used to sample Sickle Darters in each of these databases varied. For example, TWRA sampling data used multiple methods (seining, backpack electrofishing with seining, backpack electrofishing with dip netters, etc.) and targeted the whole community, while VDWR used backpack electrofishing with dip netters targeted to target game species, and CFI sampling was by snorkel only. Museum data mostly consisted of seine haul collections made by ichthyologists. Because of this disparity, we could not make any population abundance estimates, but occurrence analyses (i.e. presence-absence) are suitable for these data.

## 2.5 | Environmental and habitat covariates

A large set of environmental and habitat covariates was considered for our analyses. We selected available covariate data that covered the same period for known Sickle Darter occurrences (1880–present). The covariates used were total human population (as a surrogate for anthropogenic disturbance), number of dams (hydropower and low-head, as a surrogate for stream connectedness), median annual discharge ( $\text{m}^3/\text{sec}$ ), median spawning season discharge ( $\text{m}^3/\text{sec}$  during February to April), median total annual precipitation (cm), median total spawning season precipitation (cm), median annual air temperature ( $^{\circ}\text{C}$ ), and median spawning season air temperature ( $^{\circ}\text{C}$ ). We gathered human population data from the U.S. Census Bureau (2018) for counties that occurred within each sub-basin. To standardize the data, we did not differentiate the proportion of a county's population that occurred in a sub-basin. Data for dams were gathered from

the National Inventory of Dams (NID) database (USACE, 2020). We only counted dams that occurred on the main stem or major tributaries in each sub-basin, and we included dams that had been removed. Associated data included construction date, type of dam, and geographical location. We sorted the NID data into three different groups: hydropower, low-head, and total (hydropower + low-head). Discharge covariate data were gathered from U.S. Geological Survey (USGS) gauges in each sub-basin. We selected the USGS gauge in each sub-basin that offered the most complete data coverage for our period (1880–2020; Table 1). We collected median annual discharge for each year in each sub-basin and median spawning season discharge for each year in each sub-basin. Median annual total precipitation and median annual air temperature data were gathered from the proximal National Oceanic Atmospheric Administration (NOAA) primary or secondary climatological data site in each sub-basin (NOAA, 2020; Table 1). Precipitation and air temperature data were also collected for each year in each sub-basin and median total spawning season precipitation and median annual spawning season air temperature for each year in each sub-basin. Air temperature was used because water temperature data was only patchily available for our temporal period and sub-basins. Harvey et al. (2011), provides justification for our use of air temperature, by highlighting the importance of air temperature on water temperature and other water quality parameters.

## 2.6 | Data organization

Sickle Darter occurrences were organized spatially by sub-basin and temporally by decade (Emory River and 1990–1999 for example). Consequently, we had 15 data points of Sickle Darter occurrence for each of the ten sub-basins. Upper French Broad River and Powell River sub-basins were removed from analyses because they lacked sufficient sampling data. Sickle Darter occurrences were transformed into an estimation of distance of stream occupied (km) for sub-basins

**TABLE 1** The USGS gauges (median annual discharge and median spawning season discharge) and the NOAA Climatic Data site (median total annual precipitation, median spawning precipitation, median annual air temperature, median spawning season air temperature) used to collect respective environmental variables in this study

Sub-Basin	USGS Gauge	NOAA Climactic Sites
Little	USGS 03498500 Little River near Maryville, TN	Knoxville Airport, TN GHCND:USW00013891
Emory	USGS 03540500 Emory River at Oakdale, TN	Crossville Memorial Airport, TN GHCND:USW00003847
Little Pigeon	USGS 03470000 Little Pigeon River at Sevierville, TN	Gatlinburg, TN GHCND:USC00403420
Upper Clinch	USGS 03527000 Clinch River at Speers Ferry, VA;	Kingsport, TN GHCND:USC00404858
NF Holston	USGS 03488000 NF Holston River near Saltville, VA	Kingsport, TN GHCND:USC00404858
MF Holston	03475000 MF Holston River near Meadowview, VA	Kingsport, TN GHCND:USC00404858
SF Holston	USGS 03473000 SF Holston River near Damascus, VA	Kingsport, TN GHCND:USC00404858
Watauga	USGS 03485500 Doe River at Elizabethton, TN	Elizabethton, TN GHCND:USC00402806
Upper French Broad	USGS 03451500 French Broad River at Asheville, NC	Asheville, NC GHCND:USW00013872
Powell	USGS 03532000 Powell River near Arthur, TN	Kingsport, TN GHCND:USC00404864

by decade. We estimated these values by considering the most upstream and downstream occurrence records, while also factoring in barriers, such as dams or natural barriers. Once our upstream and downstream thresholds were estimated, we measured the distance (km) from the most downstream (potential) occurrence-threshold, to the most upstream occurrence-threshold. Stream measurements were done in ArcMap (v.10.7; ESRI, 2020) using the measure tool. To discern changes in distribution for Sickle Darters across decades in a sub-basin, we explored fish community sampling studies that were devoid of Sickle Darter occurrences. For sub-basins that did not have sufficient temporal fish community data, we considered the occurrence of Sickle Darters in these sub-basins to be constant. For our whole-basin estimates, we summed the values of distance of stream occupied across all sub-basins.

Environmental and habitat covariate data were organized in a similar manner to Sickle Darter occurrence data. For each environmental and habitat covariate, we estimated the median and range for each sub-basin during each decade. For the whole basin by decade estimate, we summed the county population and number of dams by year. For the discharge covariates we used two-types of data: (i) discharge covariates from a high impacted sub-basin with many dams (multiple hydropower and mill dams) and (ii) from a low impacted sub-basin. We used estimates for our discharge covariates for a low-impacted sub-basin from the Emory River, and we used South Fork Holston River estimates of discharge covariates for a high-impacted sub-basin. This provided us with a good representation of discharge covariates throughout the whole basin. For ambient temperature and precipitation estimates, we estimated median annual, spawning season air temperature, median total annual precipitation, and median total spawning season precipitation for each sub-basin. For our whole basin estimates, we used the median of all sub-basins for median air temperature, median air spawning season temperature, median total annual precipitation, and median total spawning season precipitation.

## 2.7 | Data analyses

Our spatiotemporal data were analyzed in multiple ways. Each individual covariate was assessed for temporal trends. We used simple linear regressions to assess the relationship of time on each covariate. These regressions were done for each covariate at the whole basin and sub-basin scales. If the relationship was significant, it was inferred that there have been temporal changes in the covariate. We performed a similar analysis of our distance of stream occupied estimated for each sub-basin and at the whole distribution level. It was inferred that if there was a significant relationship, then there has been a change (positive or negative) in the distance of stream occupied for the Sickle Darter in a sub-basin.

Temporal distribution of Sickle Darters was analyzed by creating time-series maps in ArcMap to observe temporal changes in distribution. We mapped occurrences and absences from the contemporary survey (2016–2019) for this species. For our temporal

observations, we generated 3 different maps of distribution for the whole-basin scale. Each of the three maps consisted of different time periods: pre-damming (prior to 1960), post damming (post 1960), and modern (2000–present). The year cutoffs for these three periods were chosen to capture occurrences in the UTRB associated with varying levels of stream connectivity. Our high connectivity period included years before damming was completed by TVA (i.e. prior to 1960). The next period was selected to capture occurrences of Sickle Darters in response to fragmented habitats due to damming by TVA (1960–2000) when damming ceased. The last period was selected to capture the modern occurrences of Sickle Darters in the UTRB (2000–present). To avoid redundancy, we did not generate sub-basin specific maps since the distribution data were already displayed in the whole-basin maps. We used simple linear regressions to assess the relationship of time on distance of stream occupied at each spatial level (basin and sub-basin). We only performed simple linear regressions in each sub-basin using the decades that also included a corresponding data point for the environmental covariates. For example, distance of stream occupied was available for the Middle Fork Holston sub-basin from 1880–2010, but covariate data was only available for that sub-basin from 1920–2010; so simple linear regression was used with distance of stream occupied from 1920–2010.

We modeled the distance of stream occupied by Sickle Darters on the various temporal environmental and habitat covariates. We did this by creating best-subsets multiple linear regression models following Zar (1999). We chose best-subsets regression modelling because the data were structured in a quantitative manner. That is, response and predictor variables were on the quantitative integer scale. Mallow's  $C_p$  and Adjusted  $R^2$  were used to select models with the best fit at each spatial scale (whole basin and sub-basin). Models with lower Mallow's  $C_p$  values and higher adjusted  $R^2$  values were retained for interpretation (thus considered the best performing). Using these two evaluation statistics, we were able to select the most parsimonious models (i.e. lowest risk of overparameterization). We further interpreted our selected models at each spatial scale by assessing model fit of the best model using Analysis of Variance. Further, we used corrected Akaike information criterion ( $AIC_c$ ) to select the number of models to interpret at each spatial scale. Corrected Akaike information criterion was used to account for the small samples size used in our analyses. At each spatial scale, the best 5 models with a  $\Delta AIC_c \geq 5$  were retained for interpretation (Akaike, 1973; Burnham & Anderson, 2004; Liao et al., 2018). These analyses were done separately at the whole basin scale and sub-basin scale. Only sub-basin models were performed when a significant relationship was found between distance of stream occupied and time. We used 11 environmental covariates as predictors in the models. Each covariate was checked for normal distribution (at each spatial scale) using a Shapiro-Wilk test and multicollinearity test, and spatial correlation effects were tested among each covariate using a Pearson's correlation coefficient. If a covariate was strongly correlated with another covariate ( $r > 0.65$  or  $r < -0.65$ ), then the more ecologically relevant covariate was retained for use in the analyses.



The data used for each sub-basin model varied due to the availability and completeness of temporal environmental and habitat covariate data in each sub-basin. Due to a lack of available occurrence data (1 occurrence record) in the upper French Broad River sub-basin and Powell River sub-basin, we did not perform sub-basin specific models for these two sub-basins, but we included them in the whole basin model. All analyses were completed in the software RStudio (2020). An alpha level of 0.05 was used for significance testing in all analyses.

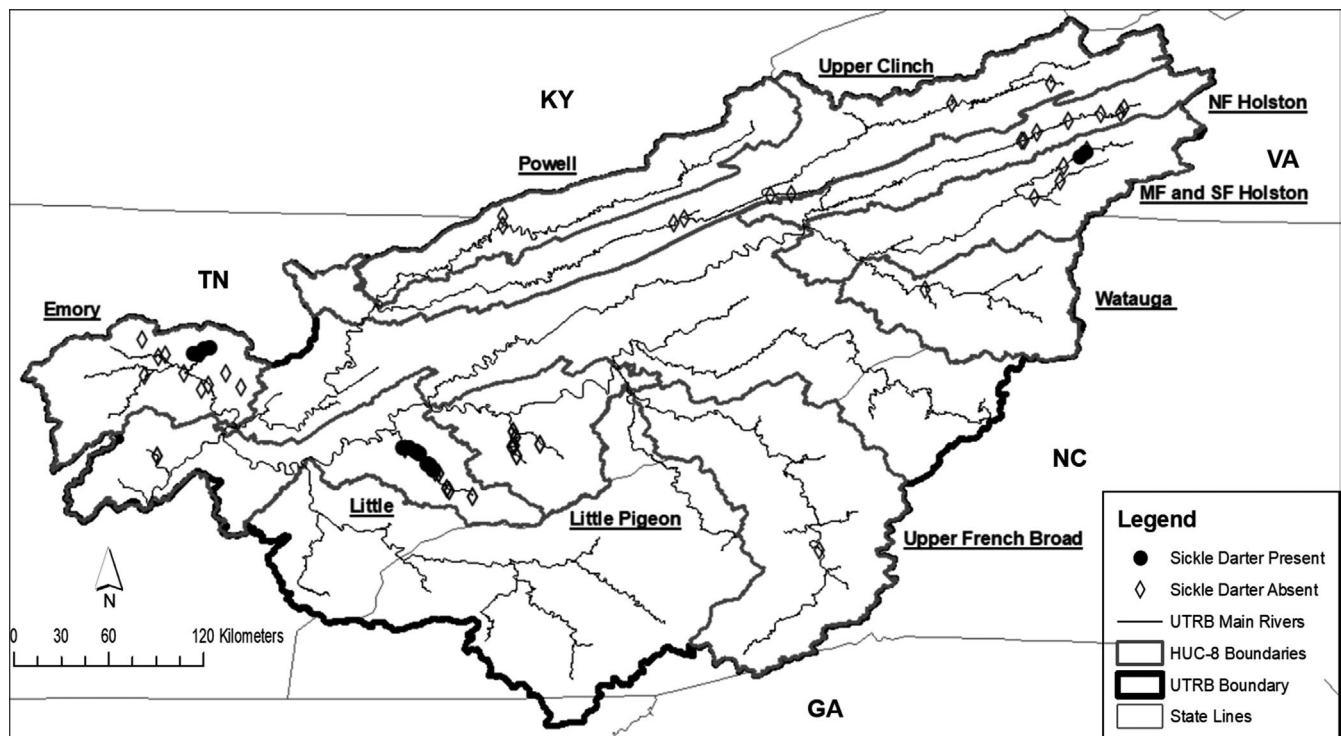
### 3 | RESULTS

From our contemporary survey, a total of 154 Sickie Darters were observed at 15 out of 58 sites throughout the UTRB (Figure 2). Sickie Darters were observed in the Emory River (5 sites), Little River (8 sites), and Middle Fork Holston River (2 sites) sub-basins. More Sickie Darters were observed in the Emory River (83) and Little River (66) sub-basins than the Middle Fork Holston River (5) sub-basin.

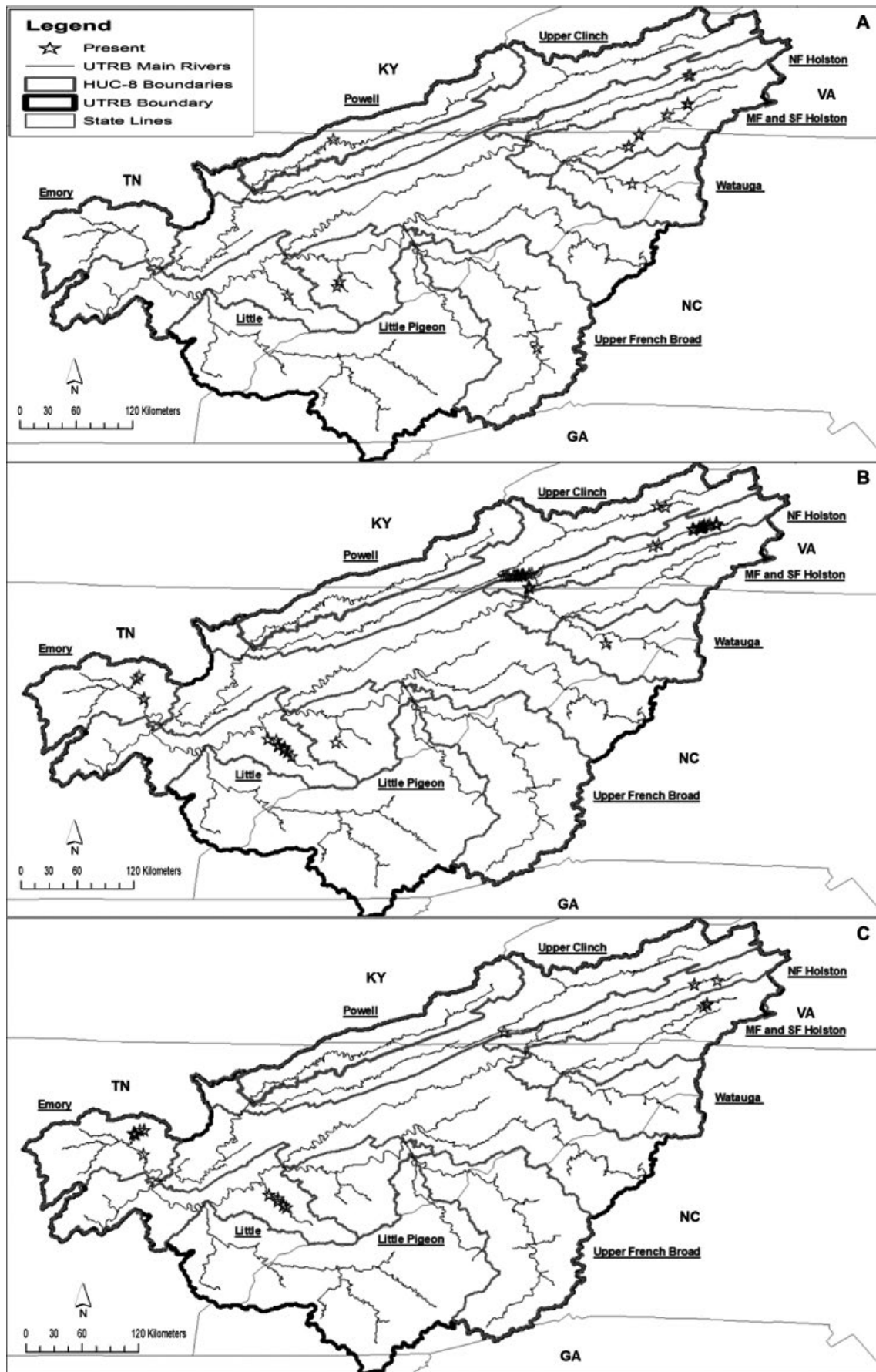
A total of 133 unique occurrences of Sickie Darters were compiled from a search in historic occurrence-record databases. Sickie Darter distribution appears to have declined throughout its range (Figure 3). Sickie Darter distribution seems to contract after the post-damming period (post-1960), and even further into the modern period (2000-present). Distance of stream occupied by Sickie Darters varied by sub-basin (Table 2). In some sub-basins we estimated that distance of stream reach occupied was 0 m, suggesting extirpation from a sub-basin.

The distance of stream occupied by Sickie Darters varied spatially across sub-basins. There was a significant negative relationship of distance of stream occupied over time in the Little Pigeon River ( $p$ -value =  $<.03$ ,  $R^2 = .49$ ), upper Clinch River ( $p$ -value =  $<.01$ ,  $R^2 = .70$ ), North Fork Holston River ( $p$ -value =  $<.01$ ,  $R^2 = .70$ ), South Fork Holston River ( $p$ -value =  $.03$ ,  $R^2 = .49$ ), Watauga River ( $p$ -value =  $<.01$ ,  $R^2 = .61$ ; Table 3). There was also a significant negative relationship of distance of stream occupied and time for the whole distribution of the Sickie Darter ( $p$ -value =  $<.01$ ,  $R^2 = .94$ ). There was no significant relationship of distance of stream occupied and time in the Little River ( $p$ -value =  $0.12$ ,  $R^2 = 1.00$ ), Emory River ( $p$ -value =  $0.12$ ,  $R^2 = 1.00$ ), and Middle Fork Holston River ( $p$ -value =  $0.12$ ,  $R^2 = 1.00$ ; Table 3). Consequently, Little River, Emory River, and Middle Fork Holston sub-basin multiple regressions models were not attempted since there was no significant temporal change in distance of stream occupied.

The environmental covariates varied temporally and by sub-basin. Because there was some correlation among our covariates, only total dams were used, and total hydropower dams and total low-head dams were removed from consideration in our multiple regression models. There was a significant increase in dams within the Emory, South Fork Holston, and Watauga sub-basins ( $p$ -value =  $<.01$ ,  $R^2 = .76$ ;  $p$ -value =  $<.01$ ,  $R^2 = .64$ ;  $p$ -value =  $<.01$ ,  $R^2 = .63$ ; Table 3), as well at the whole basin level ( $p$ -value =  $<.01$ ,  $R^2 = .91$ ; Figure 4). There was a significant increase in low-head and hydropower dams in the Emory Basin ( $p$ -value =  $<.01$ ,  $R^2 = .76$ ;  $p$ -value =  $<.01$ ,  $R^2 = 0.63$ ), and at the whole basin level ( $p$ -value =  $<.01$ ,  $R^2 = .82$ ;  $p$ -value =  $<.01$ ,  $R^2 = .92$ ). There was a significant increase



**FIGURE 2** The sites sampled for Sickie Darters during the current survey (2016). Sites with an open diamond signify Sickie Darter absence, and sites with a solid black circle signify Sickie Darters presence



**FIGURE 3** The distribution of the Sickle Darter through our three temporal periods: pre-damming (pre-1960, a), post-damming (post-1960–1999, b), and modern (2000–present, c)

**TABLE 2** The stream distance occupied by Sickle Darters for each sub-basin and the whole basin (1880–2010)

Stream distance occupied by decade (km)														
Sub-basin	1880	1890	1900	1910	1920	1930	1940	1950	1960	1970	1980	1990	2000	2010
Middle Fork Holston	57.5	29.8	29.8	18.2	18.2	18.2	18.2	18.2	18.2	18.2	18.2	18.2	18.2	18.2
South Fork Holston	62.3	62.3	62.3	62.3	62.3	62.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
North Fork Holston	151.4	151.4	151.4	145.0	145.0	145.0	145.0	30.9	30.9	30.9	30.9	21.3	21.3	21.3
Watauga	41.5	41.5	41.5	38.2	38.2	38.2	6.2	6.2	6.2	6.2	6.2	6.2	0.0	0.0
Powell	6.0	6.0	6.0	6.0	6.0	6.0	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Upper Clinch	37.6	37.6	37.6	37.6	37.6	37.6	37.6	37.6	37.6	37.6	30.0	30.0	7.7	7.7
Upper French Broad	35.0	35.0	35.0	35.0	35.0	35.0	35.0	35.0	35.0	17.0	17.0	0.0	0.0	0.0
Little	57.3	57.3	57.3	38.6	38.6	38.6	38.6	38.6	38.6	38.6	38.6	38.6	38.6	38.6
Little Pigeon	32.4	32.4	32.4	32.4	16.7	16.7	16.7	16.7	16.7	16.7	16.7	16.7	0.0	0.0
Emory	40.4	40.4	40.4	40.4	40.4	40.4	40.4	40.4	40.4	40.4	40.4	40.4	40.4	40.4
Whole Basin	521.4	493.7	493.7	453.7	438.0	438.0	343.7	223.6	223.6	205.6	198.0	171.4	126.2	126.2

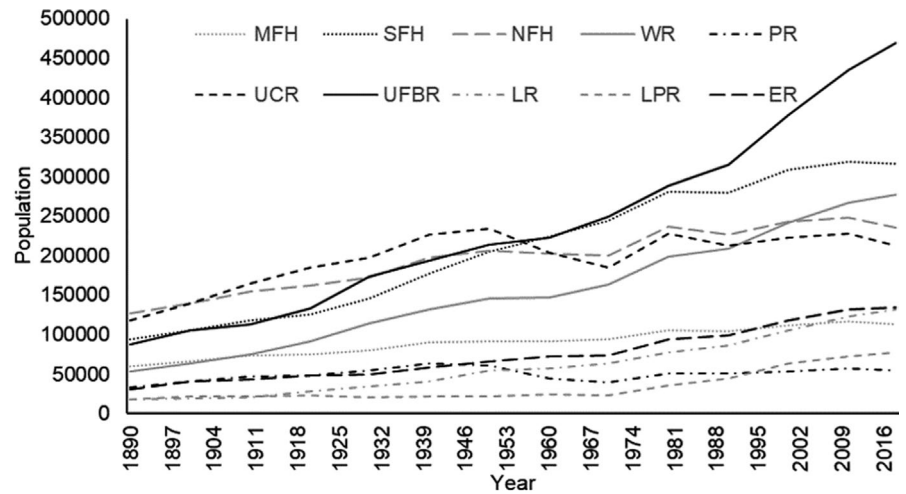
**TABLE 3** The results from simple linear regression modelling that assessed the temporal relation for each of the environmental covariates by sub-basin and whole basin

<i>p</i> -value, <i>R</i> <sup>2</sup>										
Sub-basin	Spawning season		total precipitation	Total spawning season precipitation	Air temperature	Spawning season air temperature	Dams (Low-head)	Dams (Hydropower)	Dams (Total)	Human population
	Discharge	discharge								
Little	0.46, 0.07	<b>0.04, 0.47</b>	0.13, 0.26	0.99, 0.01	0.62, 0.03	0.64, 0.03	NA	NA	NA	<0.01, 0.96
Emory	0.78, 0.01	0.36, 0.10	<b>0.02, 0.52</b>	0.31, 0.13	0.53, 0.05	0.52, 0.05	<0.01, 0.76	<0.01, 0.73	<0.01, 0.76	<0.01, 0.96
Little Pigeon	0.92, 0.01	0.08, 0.33	0.10, 0.30	0.75, 0.02	0.73, 0.02	0.36, 0.11	NA	NA	NA	<0.01, 0.75
Upper Clinch	0.26, 0.18	0.44, 0.09	0.43, 0.09	0.67, 0.03	0.62, 0.04	0.47, 0.08	NA	NA	NA	0.53, 0.06
NF Holston	0.70, 0.02	0.64, 0.03	""	""	""	""	NA	NA	NA	<0.01, 0.91
MF Holston	<b>0.05, 0.40</b>	<b>0.05, 0.41</b>	""	""	""	""	—	NA	0.23, 0.18	<0.01, 0.96
SF Holston	0.72, 0.02	<b>0.03, 0.43</b>	""	""	""	""	NA	—	<b>0.01, 0.64</b>	<0.01, 0.98
Watauga	0.18, 0.22	0.13, 0.26	0.54, 0.05	0.44, 0.08	0.31, 0.13	0.33, 0.12	NA	—	<b>0.01, 0.64</b>	<0.01, 0.97
Whole Basin	0.76, 0.01	0.38, 0.07	< <b>0.01, 0.69</b>	0.12, 0.21	0.92, 0.01	0.58, 0.03	< <b>0.01, 0.82</b>	<0.01, 0.92	<0.01, 0.91	<0.01, 0.98

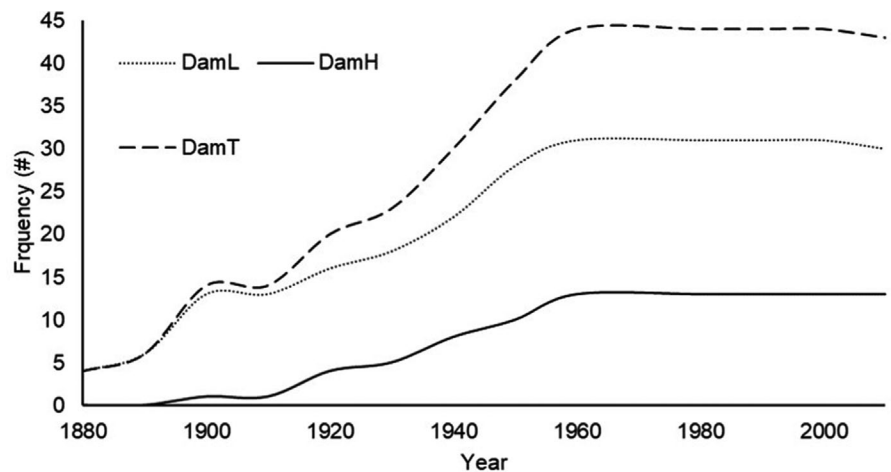
Note: Bold font indicates a significant *p*-value (<0.05) for the respective basin and environmental variable. "" signifies redundancy of values, since precipitation and temperature variable data for the upper Clinch, NF Holston, MF Holston, and SF Holston were gathered from the same NOAA climatic data site. NA signifies no available value for the respective basin and variable due to the variable being constant over the temporal period examined. - signifies no data for that respective variable in a basin.



**FIGURE 4** Temporal variation of human population across the Sickle Darter's range by sub-basin



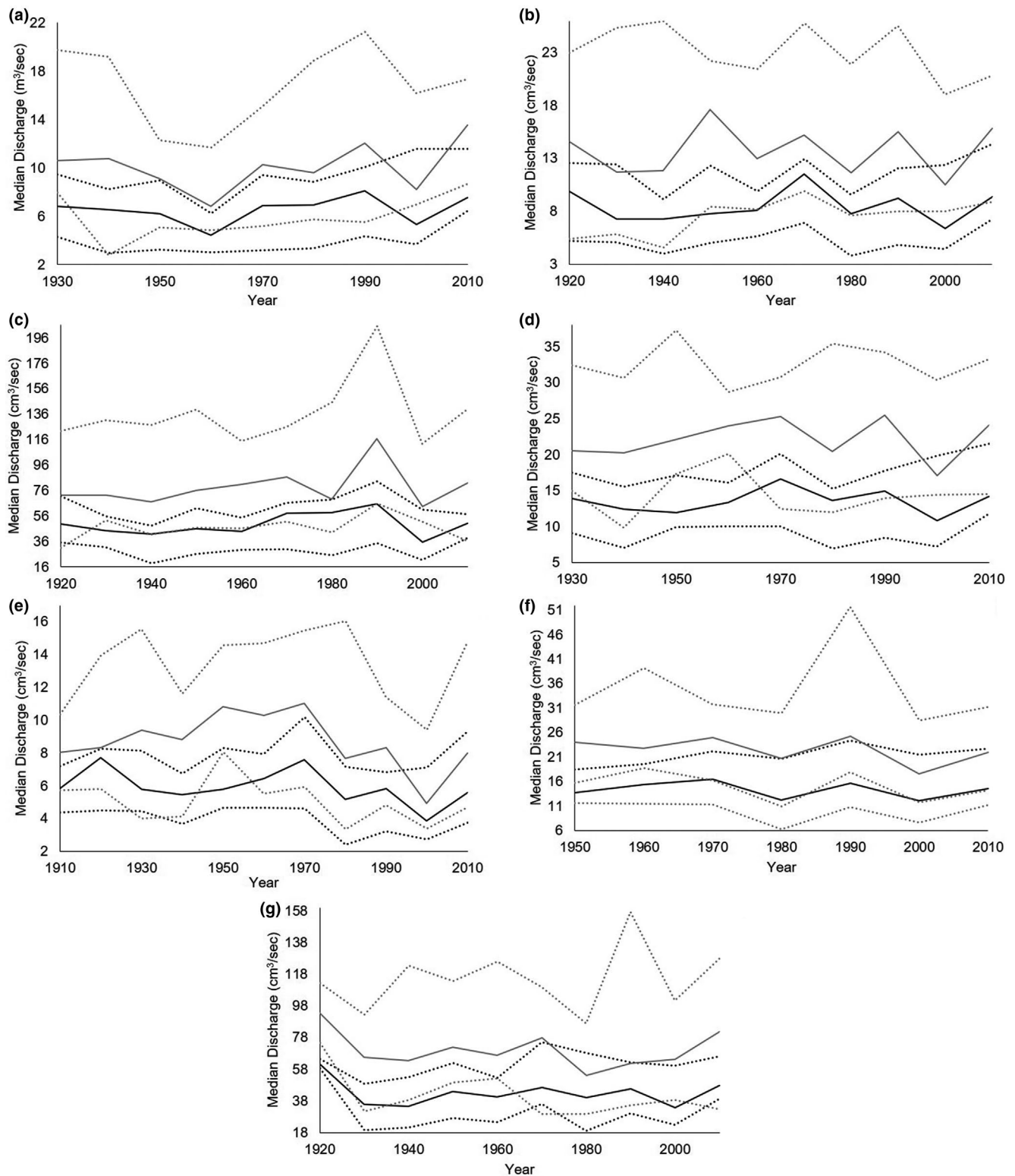
**FIGURE 5** Temporal variation in the number of total dams (DamsT), hydropower dams (DamsH), and low-head dams (DamsL) across the historic range of the Sickle Darter



in human population density for every sub-basin and at the whole basin level, except for the upper Clinch River sub-basin (Table 3; Figure 5). There was a significant increase in median annual spawning season discharge in the Little, Middle Fork Holston, and South Fork Holston sub-basins ( $p$ -value =  $<.04$ ,  $R^2 = .47$ ;  $p$ -value =  $<.05$ ,  $R^2 = .41$ ;  $p$ -value =  $<.03$ ,  $R^2 = .43$ ; Figure 6). There was a significant increase in median annual discharge in the Middle Fork Holston sub-basin ( $p$ -value =  $<.05$ ,  $R^2 = .40$ ). There was also a significant increase in median annual total precipitation for the Emory sub-basin and at the whole basin level ( $p$ -value =  $<.02$ ,  $R^2 = .52$ ;  $p$ -value =  $<.01$ ,  $R^2 = .69$ ; Figure 7). There were no significant relationships for median annual temperature or median spawning season temperature (Figure 8). For every model-set, hydropower dams, low-head dams, and median total annual precipitation were removed from consideration for our models due to strong correlation ( $>0.65$ ) with our other environmental covariates.

The relationships between distance of stream-occupied and the environmental covariates varied at each spatial scale and at each sub-basin. At the whole basin scale, the 5 best model sub-sets included the covariates total dams, air temperature, spawning season air temperature, and discharge (Table 4). At the Little Pigeon River sub-basin scale, the 5 best model sub-sets included human population,

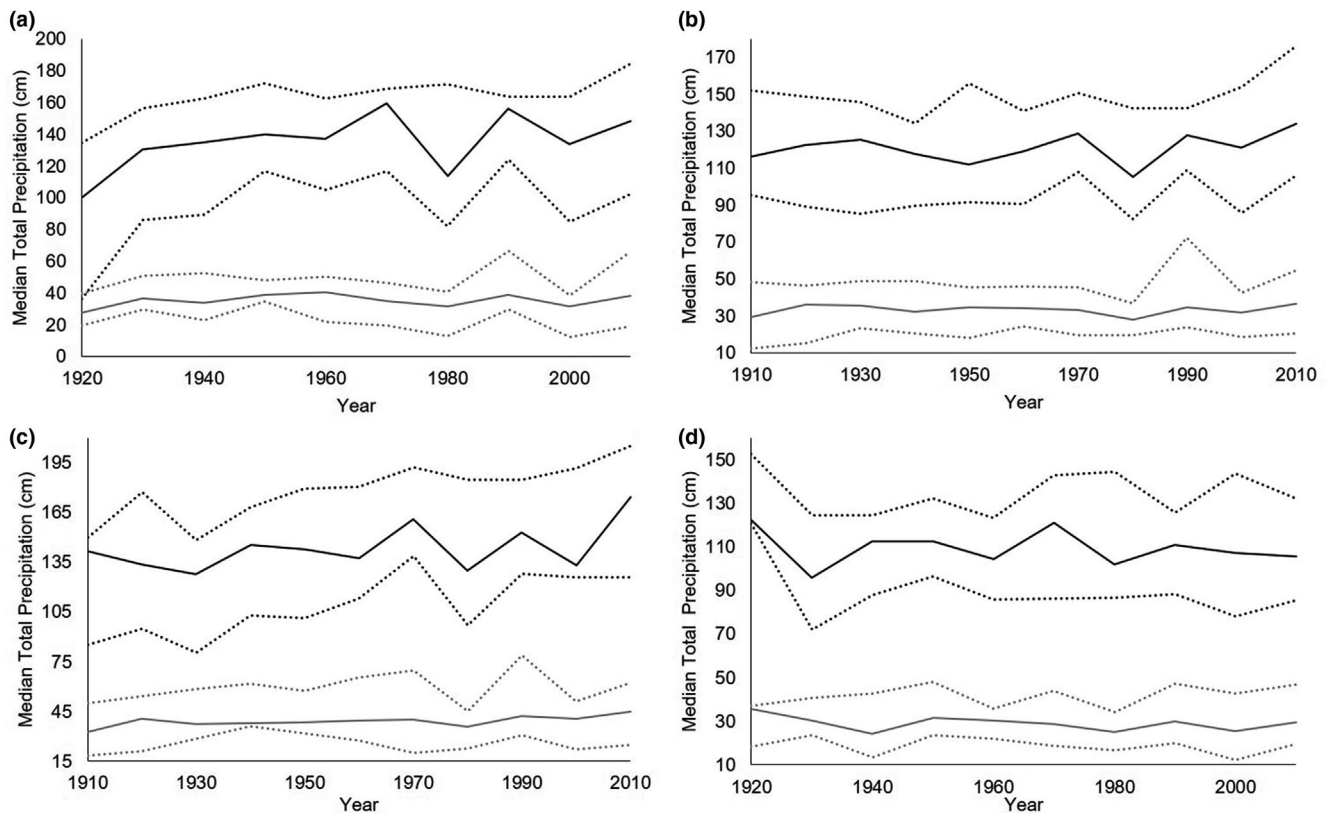
discharge, spawning season discharge, air temperature, and spawning season precipitation (Table 4). At the North Fork Holston River sub-basin scale, the 5 best model sub-sets included human population, discharge, air temperature, and spawning season precipitation (Table 4). At the South Fork Holston River sub-basin scale, the 4 best model sub-sets included total dams, precipitation, discharge, and air temperature, (Table 4). Only 4 model sub-sets were considered best in the South Fork Holston River sub-basin because only 4 models met the best sub-sets criteria. At the upper Clinch River sub-basin scale, the 5 best model sub-sets included human population, total dams, discharge, and air temperature (Table 2). At the Watauga River sub-basin scale, the 5 best model sub-sets included total dams, spawning season precipitation, air temperature, and spawning season discharge (Table 4). There was no significant decline in distance in stream occupied in the Emory River sub-basin, Little River sub-basin, and Middle Fork Holston River sub-basin, so no best sub-sets models were run for these sub-basins. The top model from each scale and response variable was retained for interpretation because they met assumptions regarding least-squared regression analyses (Table 5). At the whole basin scale, the number of total dams was negatively associated with distance of stream occupied and was statistically significant ( $t = -6.38$ ;  $p$ -value =  $<.01$ ). In the South Fork



**FIGURE 6** The median (range) annual discharge (black line) and median spawning season discharge (grey line) or the sub-basins included in analyses; Middle Fork Holston (a), North Fork Holston (b), Clinch (c), South Fork Holston (d), Watauga (e), Little (f), Emory (g). \*Black dotted lines are the range for median annual discharge, and gray dotted lines are the range for median spawning season discharge

Holston sub-basin, the total number of dams had a slightly positive association with distance of stream occupied, and this association was significant ( $t = 0.01$ ;  $p$ -value =  $<.01$ ). In the Watauga River

sub-basin, the number of total dams was significantly and negatively associated with distance of stream occupied ( $t = -5.44$ ;  $p$ -value =  $<.01$ ). Further interpretation was not conducted for the top



**FIGURE 7** The median (range) total precipitation (black line) and median total spawning season precipitation (grey line) from the respective NOAA climatological data sites used in analyses; Gatlinburg (a), Maryville (b), Crossville (c), and Kingsport (d). \*Black dotted lines are the range for median total precipitation, and grey dotted lines are the range for median total spawning season precipitation

model in the Little Pigeon River sub-basin, North Fork Holston sub-basin, and upper Clinch River sub-basin because the top model from those sub-basins did not contain variables with a variance inflation factor (VIF) < 4. (Table 5).

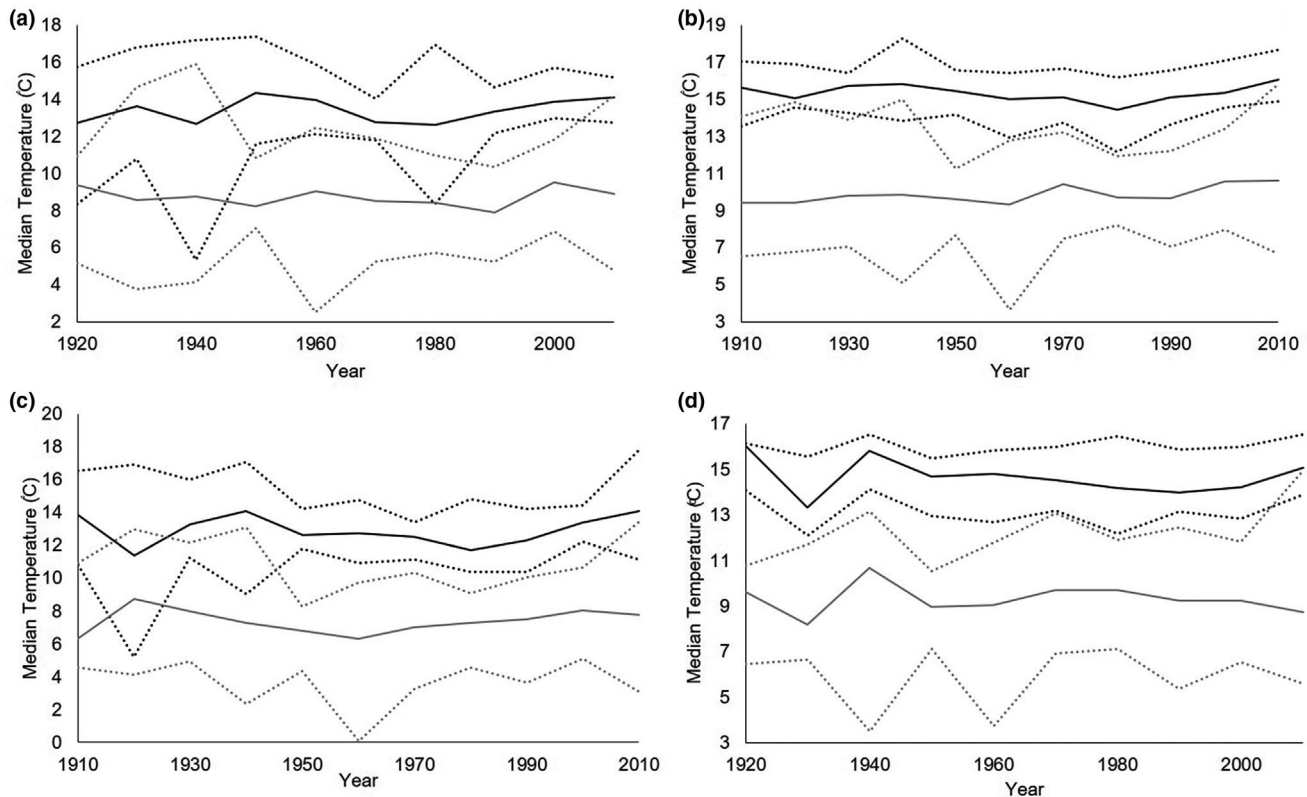
The relative accuracy of the sub-basin models was 8 times greater (Root MSE = .01 and 4.95 for both) than the whole basin model (Root MSE = 31.9). Standardized  $B_j$  coefficients environmental covariates suggested that, with the exception of the Little Pigeon River, North Fork Holston, upper Clinch sub-basins best models, total dams, tended to have a stronger influence than other environmental covariates such as discharge and air temperature (Table 5).

## 4 | DISCUSSION

Our study is the first attempt to discern the current status and distribution of the rare Sickle Darter. Anthropogenic, climatic, and hydrologic influences on Sickle Darter occurrence at large spatial and temporal scales had not been assessed prior to this study (Jett, 2010; Page & Near, 2007). The occurrence of Sickle Darters in the UTRB, particularly in certain sub-basins, has declined since it was first documented. However, Sickle Darter occurrence have remained steady in three of the sub-basins where they have historically been observed: the Little River, Emory River, and Middle Fork Holston River sub-basins. We were unable to detect any Sickle Darters in the upper

Clinch River sub-basin or in the North Fork Holston sub-basin, where they have been recently observed (Etnier & Starnes, 1993; Page & Near, 2007). Some populations of Sickle Darters may occur at such low abundance that they appear undetectable. Welsh et al. (1996), Rosenberg et al. (1995), Bayley and Peterson (2001) have highlighted how species at low-abundance levels are harder to detect, no matter the gear/effort/method used to observe them, which supports why we employed two different methods for detecting this species (snorkel surveys and standardized back-pack electrofishing with a seine). This also highlights the cryptic nature of the Sickle Darter, since it has been observed scarcely from a historical perspective (Etnier & Starnes, 1993; Page & Near, 2007). It is also quite possible that Sickle Darters occupy dynamically available patches, but when these patches are disconnected by press disturbances associated with dams and their impoundments (Townsend, 1989; Ward, 1998), then populations within these impacted patches become extirpated. Future research should consider how elimination of habitat patches (i.e. sub-basins within the UTRB that are dammed) prevents dispersal and recruitment. Likewise, research should be conducted to understand if or how the removal of barriers such as dams may increase populations throughout the UTRB.

The likely causes of Sickle Darter decline are variable depending upon scale. However, Sickle Darter decline can be generally associated with habitat fragmentation and habitat destruction due to damming across multiple spatial scales (whole basin and sub-basin).



**FIGURE 8** The median (range) annual temperature (black line) and median spawning season temperature (grey line) from the respective NOAA climatological data sites used in analyses; Gatlinburg (a), Maryville (b), Crossville (c), and Kingsport (d). \*Black dotted lines are the range for median annual temperature, and grey dotted lines are the range for median spawning season temperature

Habitat fragmentation has been highlighted as one of the key factors influencing a species' conservation status in fishes (Allan, 2004; Nilsson & Berggren, 2000; USFWS, 2014; Wilcove et al., 1998). While it is plausible that other factors may have influenced the temporal distribution of the Sickle Darter, some of these other environmental factors may have more of an impact at smaller spatial-scales than what was explored in this study, such as the stream reach or stream segment scale. Other variables not assessed in this study that may also have a negative impact on the temporal distribution of the Sickle Darter, such as water quality variables (water temperature °C), and many other microhabitat factors, both of which, are hard to quantify from a temporal perspective, because data for microhabitat are not widely and completely available for the UTRB. With regard to other species that have experienced declines of a similar nature, habitat fragmentation and destruction have been the primary stressors (USFWS, 2014). For example, the Snail Darter (*P. tanasi*; Etnier, 1975), is a species endemic to the UTRB that also declined due to the 20th century "damming boom" in the basin (Etnier, 1975; Starnes, 1977). The Yellowcheek Darter (*Nothonotus moorei* Raney & Suttkus, 1964) is another species that declined in its distribution due to damming of the Little Red River in Arkansas (Wine et al., 2008). Future conservation measures of the Sickle Darter should consider removal of small, low-head dams in the sub-basins within then UTRB. Low-head dam removal would have positive impacts on all aquatic species, by reconnecting fragmented habitats for multiple species.

The results from this study highlight the need for further research on this imperiled species. For example, information is needed on if and how microhabitat utilization varies by occupied sub-basin. Jett (2010) estimated the microhabitat preference of Sickle Darters in the Little River, but this pattern may be different in other occupied sub-basins. Understanding the availability of preferred microhabitat and combined with knowing the broad-scale ecological constraints identified in our study will aid in the further understanding of why this species has declined. Ecological niche-modelling should be conducted to estimate the probability of suitable habitat available to the Sickle Darter. Very little information is also available on the diet of the Sickle Darter (see Page, 1978), and the only available information on Sickle Darters comes from a few individuals collected in the Little River sub-basin. Further assessment of its diet and how it varies spatially may provide further evidence into this species' decline. As previously mentioned, the dispersal ability of Sickle Darters needs to be assessed to determine if this species is capable of repopulating other sub-basins that may have suitable microhabitat. It is unknown if this species moves out of certain patches within a sub-basin during disturbance events, like floods or droughts. (Hill & Grossman, 1987; Roberts & Angermeier, 2007). Page (1978) suggests that this species makes short movements to shallow gravel riffles from runs and shallow pools for spawning and moves to the bottom of deep pools during the winter months (December-February). Dispersal ability of Sickle Darters to other more distant riffle-pool areas is currently



**TABLE 4** Results of best subsets multiple linear regression modeling as a variable selection procedure for distance of stream occupied by the Sickle Darter in the upper Tennessee River basin at two spatial scales (whole basin and sub-basin)

Variables included in Model	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	Mallows' C(p)	Adj. R <sup>2</sup>	Number of model parameters
<b>Whole Basin</b>					
DamsT	7.43	0.00	2.44	0.93	1
DamsT, Temp	7.63	0.19	7.95	0.87	2
DamsT, Discharge, Temp	8.98	1.55	2.27	0.95	3
DamsT, SpawnTemp	9.68	2.24	7.55	0.88	2
DamsT, Precip, Temp	10.41	2.98	4.1	0.93	3
<b>Little Pigeon Sub-basin</b>					
Pop	10.24	0.00	43.23	0.80	1
Discharge, Pop	11.53	1.29	25.64	0.86	2
SpawnDischarge, Pop	11.63	1.39	26.69	0.86	2
Pop, Temp	12.63	2.39	39.32	0.80	2
Pop, SpawnPrecip	12.94	2.70	44.25	0.78	2
<b>North Fork Holston Sub-basin</b>					
Pop	8.84	0.00	14.55	0.59	1
Pop, Temp	9.22	0.38	6.19	0.77	2
SpawnPrecip, Temp, Pop	10.26	1.42	3.86	0.84	3
Temp	10.54	1.70	26.26	0.36	1
SpawnPrecip, Pop	10.78	1.94	11.49	0.65	2
<b>South Fork Holston Sub-basin</b>					
DamsT	6.69	0.00	4.14	0.99	1
DamsT, Precip	9.36	2.67	5.00	0.99	2
DamsT, Discharge, Temp	9.89	3.21	6.14	0.98	2
DamsT, Discharge, Temp	13.91	7.22	8.14	0.98	3
<b>Upper Clinch Sub-basin</b>					
Pop	4.29	0.00	-0.85	0.09	1
DamsT	4.73	0.44	0.07	-0.07	1
Discharge, Pop	4.74	0.45	0.08	-0.08	1
Temp	4.89	0.60	0.35	-0.12	1
Discharge, Pop	6.56	2.27	1.04	-0.02	2
<b>Watauga Sub-basin</b>					
DamsT	6.39	0.00	4.30	0.85	1
DamsT, SpawnPrecip	7.33	0.94	1.87	0.90	2
DamsT, Temp	8.27	1.87	3.80	0.87	2
DamsT, SpawnDischarge	8.86	2.47	5.22	0.84	2
DamsT, SpawnPrecip, Temp	8.97	2.58	2.25	0.92	3

Note: The top 5 models are shown that achieved the lowest AIC<sub>C</sub>, lowest Mallows' Cp statistic, and highest adjusted R<sup>2</sup>. Variables retained for interpretation had variance inflation factors (VIF) < 4.0. Assumptions of regression analysis were met by the top model. Variable definition: DamsT (Total number of Dams), Discharge (median discharge), Precipitation (total precipitation), Pop (total human population number), SpawnDischarge (median discharge during spawning season), SpawnPrecip (total spawning season precipitation), SpawnTemp (median spawning season air temperature), and Temp (median air temperature).

Distance of stream occupied: scale	Variable	t-value	p-value	Stand. Bi.	VIF
Whole Basin					
Root MSE = 31.9	Intercept	3.99	.02	0.00	0.00
	DamsT	-6.38	<.01	-1.14	3.81
South Fork Holston Sub-basin					
Root MSE = 0.01	Intercept	0.01	<.01	0.00	0.00
	DamsT	0.01	<.01	0.01	1.1
Watauga Sub-basin					
Root MSE = 4.95	Intercept	1.23	.29	0.00	0.00
	DamsT	-5.44	<.01	-0.92	2.16

Note: Results shown are for the best model from Table 4. Root MSE, root mean square error, Stand. Bi. = standardized beta coefficient, VIF, variance inflation factor. The ± sign for t-value indicates the direction of the association between the environmental covariate and distance of stream occupied. Further interpretation was not done for the top model in the Little Pigeon River sub-basin, North Fork Holston sub-basin, and upper Clinch River sub-basin because the top model from those sub-basins did not contain variables with a VIF (<4). Variable definition: DamsT (total number of dams).

unknown. Holcomb et al. (2020) determined the habitat-abundance relationships of the Harlequin Darter (*Etheostoma histrio* D. S. Jordan & C. H. Gilbert, 1887) in Florida and outlined an exceptional method for assessing a species' status by using mark-recapture, snorkel surveys, and side-scan sonar to estimate the abundance of this cryptic species and its available habitat.

Analyzing temporal changes in a species' distribution and/or status is a challenging task because data are lacking or most often incomplete. However, previous studies have attempted to assess temporal changes in darter species status, abundance, and distribution. Wine et al. (2008) assessed temporal changes in the abundance of the Yellowcheek Darter (*Nothonotus moorei* Raney & Suttkus, 1964) in the Little Red River basin of Arkansas, where they compared site-densities over a 25-year period. Their estimates of site-density for the Yellowcheek Darter were highly variable due to variation in sampling effort towards this species over the temporal scale explored (Wine et al., 2008). We experienced similar results in variability of sampling effort when compiling occurrence data for the Sickle Darter, as this species was mainly observed as part of community fish sampling, with no targeted sampling efforts. One study, Sterling et al. (2013) assessed the changes in distribution of the Yazoo Darter (*E. raneyi* Suttkus & Bart, 1994) in Mississippi, but used sites occupied rather than distance of stream occupied, and they were able to observe changes in Yazoo Darter occurrence. However, unlike the Sickle Darter, more sampling effort has been employed for the Yazoo Darter. Sterling et al. (2013) suggested that with even more sampling effort more and/or new occurrence localities are likely to be discovered for the Yazoo Darter, this would most likely be true for the Sickle Darter as well. Other studies have attempted to capture spatiotemporal variation fish community composition, but many of these studies are done on various temporal scales and do not focus on single species assessments (Calloway et al., 2017; Parks et al., 2014). From a global perspective, most spatiotemporal assessments of freshwater fish distributions have focused on community

**TABLE 5** Analysis of variance results for best subsets MLR for distance of stream occupied by the Sickle Darter across 2 spatial scales (whole basin and sub-basin)

composition over shorter temporal periods (Garcia et al., 2001; Sylvie et al., 1999). Thus, spatiotemporal assessments of rare freshwater fish species are relatively new to the management of fishes. This study provides an outline for a novel way for assessing temporal changes in the range-wide distribution of a rare and imperiled stream fish species.

In summary, we conclude that the Sickle Darter has declined on a temporal scale. However, there are still many questions that need to be answered to determine what conservation measures need to be taken to preserve this species. Previous studies on this species have not addressed the causes of decline for the Sickle Darter, except for anecdotally alluding to habitat fragmentation from dams and water quality degradation (Angermeier & Pinder, 2015; Page & Near, 2007). This study highlights the multi-scale causes of Sickle Darter decline based off best subsets regression modeling. Our models found that Sickle Darters have declined due to habitat fragmentation caused by damming at the whole basin and sub-basin scales. These results should inform what habitat/environmental problems (i.e. habitat fragmentation) should be addressed for potentially reintroducing this species into previously occupied sub-basins, such as the Little Pigeon River. USFWS (2014) addressed the conservation needs and developed a conservation strategy for imperiled aquatic species in the UTRB, this strategy should also be considered when determining future conservation efforts for this species. This species is in need of conservation efforts to ensure the preservation of this species, and the results of this study provide the foundation for some of those conservation decisions to be made.

Recent changes in river operations of the UTRB may provide some opportunities to conserve the aquatic diversity within this basin. In the mid-1990s river operations were changed and started to mimic normal flow regimes experienced by many species in decline (Scott et al., 1996). These changes in river operations provided minimum flows and improved water quality, mainly dissolved oxygen in fragmented areas of the UTRB (Scott et al., 1996)

There may be reason to believe that better river operations and subsequent improvements to water quality in the UTRB could lead to the recovery of populations of species in decline. One species, the Lake Sturgeon (*Acipenser fulvescens* Rafinesque, 1817), once extirpated from the UTRB, has benefited from these changes in river operations (Amacker & Alford, 2017; Collier et al., 2001). Since 2000, Lake Sturgeon have been reintroduced in the UTRB annually, where populations have become established and should be approaching ages of sexual maturity in the next 5–10 years (Amacker & Alford, 2017, Dave Matthews, Tennessee Valley Authority, pers. comm.). Another species, the Snail Darter, has benefitted from changes in river operations and improved water quality (Williams & Plater, 2019). The Snail Darter has experience population increases and was recently petitioned for delisting from the Endangered Species Act (Williams & Plater, 2019). The changes in river operations may have already had a positive impact on the Sickle Darter, because one individual Sickle Darter was captured in the Sequatchie River sub-basin in 2016 (Jon Michael Mollish, Tennessee Valley Authority, personal communication). However, it is unknown if a self-sustaining population has been established there. The recovery of the Lake Sturgeon and the Snail Darter provide hope for reconnecting fragmented populations of declining species like the Sickle Darter.

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## CONFLICT OF INTEREST

This study and results offer no conflict of interest with any other studies.

## DATA AVAILABILITY STATEMENT

Data will be made available per request from the authors.

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