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A Multiscale Investigation of Habitat Use and Within-river Distribution of Sympatric Sand Darter Species

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Abstract

The western sand darter Ammocrypta clara, and eastern sand darter Ammocrypta pellucida, are sand-dwelling fishes of conservation concern. Past research has emphasized the importance of studying individual populations of conservation concern, while recent research has revealed the importance of incorporating landscape scale processes that structure habitat mosaics and local populations. We examined habitat use and distributions of western and eastern sand darters in the lower Elk River of West Virginia. At the sandbar habitat use scale, western sand darters were detected in sandbars with greater area, higher proportions of coarse grain sand and faster bottom current velocity, while the eastern sand darter used a wider range of sandbar habitats. The landscape scale analysis revealed that contributing drainage area was an important predictor for both species, while sinuosity, which presumably represents valley type, also contributed to the western sand darter’s habitat suitability. Sandbar quality (area, grain size, and velocity) and fluvial geomorphic variables (drainage area and valley type) are likely key driving factors structuring sand darter distributions in the Elk River. This multiscale study of within-river species distribution and habitat use is unique, given that only a few sympatric populations are known of western and eastern sand darters.

Keywords: Ammocrypta, GIS, habitat, maximum entropy, sand, species distribution models

Introduction

Western sand darters Ammocrypta clara (Jordan and Meek 1885) and eastern sand darters A. pellucida (Putnam 1863) are slender, benthic, sand-dwelling fishes in the family Percidae (Williams 1975). These two species are the only sympatric species of the genus Ammocrypta (Near et al. 2000), and are currently sympatric within the Ohio River drainage (Cincotta and Welsh 2010). Over the years, the number of rivers within the Ohio River drainage where both species occur has declined, possibly owing to adverse anthropogenic practices, which degrade and often fragment instream habitat (Kuehne and Barbour 1983). As a result, western and eastern sand darters have a threatened or imperiled status in the majority of the states where each species occur (Warren et al. 2000, Grandmaison et al. 2004, Driver and Adams 2013). Despite these far-reaching declines, the life history and ecology of these species have been relatively poorly studied...
of the western sand darter are poorly understood (Driver and Adams 2013), especially from areas where it is sympatric with the eastern sand darter.

In West Virginia, both species are sympatric and syntopic within the lower 36 river km (rkm) of the Elk River. This appears to be the known upstream-most extent of western sand darter’s range, while the eastern sand darter occurs up to 135 rkm from the mouth (Cincotta and Welsh 2010). The western sand darter was recently discovered in the Elk River, which extends the species’ known range to the Eastern Highlands region of North America (Cincotta and Welsh 2010). The restricted range of the western sand darter compared to that of the eastern sand darter is of conservation concern, since the Elk River is the only known location in West Virginia where the western sand darter persists and represents the southeastern extent for both species (Cincotta and Welsh 2010).

Areas of quality habitat are a fundamental component of a fish’s ability to survive, grow, and reproduce (e.g., Rice 2005, Fisher et al. 2012). Aquatic ecosystems are often subdivided into various classes depending on scale and the species of interest (e.g., ecosystems, streams and rivers, macrohabitats, mesohabitats, and microhabitats). Darters are benthic fishes that reside in rivers and lakes (Kuehne and Barbour 1983). Many species like the western and eastern sand darters coexist, but are segregated by differences in microhabitat use (Fisher and Pearson 1987). Substrate composition, depth, and flow velocity are recognized as primary factors influencing the microhabitat use of darters (Chipps et al. 1994, Welsh and Perry 1998, Welsh et al. 2013). However, because of the sand darter’s burying behavior, individual microhabitat use can be difficult to identify, limiting field observations of sand darter habitat use to the sandbar scale.

The availability of fish habitat within a river is influenced by water quality, energy source, substrate, channel morphology, flow regimes, and thermal regimes, which are all determined by the various landscape scale factors in the watershed. Watershed characteristics that influence these variables include surficial geology, soil type, bedrock type and depth, watershed topography, land cover, and climate (Wiley et al. 1997, Wang et al. 2003).

Understanding the effect of landscape scale variables in structuring fish habitat and thus, a species distribution, is essential for fishes of conservation concern. Frequently, the conservation of rare freshwater stream fish is limited by a deficiency of spatial distribution data and information regarding the association between environmental variables and distribution patterns (Olden et al. 2002, Gibson et al. 2004). Predictive species distribution models (SDMs) can aid in filling these knowledge gaps by linking environmental variables to areas that are suitable for a species’ survival (Guisan and Zimmermann 2000). Determining sandbar preference and landscape scale variables that influence habitat availability are critical for the conservation and management of both species.

**Objectives**

The purpose of this study was to (1) examine sandbar habitat use for the western and eastern sand darters; (2) model the probability of suitable habitat for both species in the Elk River; and (3) explore how environmental variables and landscape scale features vary in importance for each species.
Methods

Study area

The Elk River is a tributary of the Kanawha River, a part of the Ohio River drainage, and the greater Mississippi River watershed. The Elk River follows a western course, stretching approximately 290 rkm through central West Virginia from northwestern Pocahontas County to the capital city of Charleston, where the Elk River joins the Kanawha River. Throughout its course, the Elk River has an elevation change of approximately 900 m and roughly drains 4,000 km$^2$ of the Appalachian Plateau (Stauffer et al. 1995). The study area for this project is the lower 190 rkm located below the Sutton Dam, which impounds a 6 km$^2$ reservoir. Further downstream, away from the tailwaters of the dam, the river has a low gradient with long deep pools separated by short shoals (Welsh et al. 2013).

Fish collections

Collections of western and eastern sand darters occurred at 63 sites in the lower 190 rkm of the Elk River between June and October 2015 and 2016 (Fig. 1). This section of the river was selected because prior surveys of the upper Elk River did not yield either species of sand darter. The lower 190 rkm below the Sutton Dam was divided into 7 sections, with 3 reaches that were 2 rkm in length per reach, with the target of sampling 3 to 5 sites (i.e., sandbars) per reach. This sampling design was an attempt to evenly distribute the sampling locations throughout the study area; however, this was challenging due to issues of river access across private property. All presence locations were taken using a handheld Garmin Oregon 550 global positioning system (GPS) unit using the waypoint averaging feature. A straight 1.5 x 3 m seine with 3 mm mesh was used at each site to comprehensively sample a sandbar. This included upstream and downstream parallel seine hauls and perpendicular hauls pulled into shore (O’Brien and Facey 2008, Driver and Adams 2013). Sampling events were intermittent because sampling was restricted to periods of low flow (< 400 cfs), decent water clarity in order to identify sandbars, and wadeable areas of the river (< 1.5 m). Sampled sandbars were generally free of large woody debris and contained at least 90% sand. The number of seine hauls per site was dependent upon the shape and area of a sandbar. All western and eastern sand darters captured were placed in a holding bucket between hauls, identified to species, counted, and released post-seining.
Figure 1. Western and eastern sand darter sampling locations in the lower 190 rkm of the Elk River, WV shaded by elevation.

Sandbar habitat use sampling

At each of the 63 sites, habitat data were recorded at two spatial scales, including the stream site and the individual sandbar. At a given site, focal current velocity (m/s; bottom velocity), average current velocity (m/s; 60% of the depth), and depth (m) were measured at five evenly spaced points across the river channel. Substrate composition was evaluated using four parallel transects perpendicular to the river flow at 1 m intervals, noting the substrate type at each point (silt <0.06 mm, sand 0.0-2 mm, small gravel 2-16 mm, large gravel 16-64 mm, cobble 64-250 mm, and boulder >250) (Wentworth 1922, Kondolf and Li 1992, Kaufmann et al. 1999). River width (m) was recorded at each of the four substrate transects using a handheld Bushnell Scout DX100 laser range finder. At the sandbar, bottom current velocity, average current velocity, and depth were measured at three evenly spaced points. A 200 ml sand sample was collected from the upper 6 cm of river substrate at the center of a seine haul where sand darters were detected (Facey and O’Brien 2004). We were unable to gather substrate samples from all locations. Sand samples were later dried, sifted using a Gilson 20.3 cm (8 in) sieve Shaker (115V/60Hz) with U.S. Standard sieve screens, and weighed (0.1 g) to estimate the percent contribution of each sand grain size category (silt >0.10 mm, fine sand 0.125-0.25 mm, medium sand 0.25-0.5 mm, coarse sand 0.5-1.0 mm, very coarse sand 1.0-2.0 mm, and granule gravel 2.0-4.0 mm; Wentworth 1922, Facey and O’Brien 2004).

Sandbar habitat use analysis

Principal components analysis (PCA) was used to compare sandbar habitat variables between sand darter species.
PCA is a heuristic procedure of unconstrained ordination and is able to elicit trends from multivariate data in reduced space (e.g., Borcard et al. 2011, Gibbs et al. 2014). This approach is based on eigenvectors, which account for the greatest variation explained in the data. Eigenvalues greater than one were retained for the analysis (Kwak and Peterson 2007). Sandbar average current velocity and bottom current velocity were collinear \((r = 0.92)\), therefore sandbar average current velocity was removed from further analysis. Data transformation included logit transformation of substrate proportions, square root transformation of depth, bottom current velocity, and natural log transformation of sandbar area. The PCA incorporated eight habitat variables: sandbar depth, sandbar bottom current velocity, sandbar area, % fine sand, % medium sand, % coarse sand, % very coarse sand, and % granule gravel. Habitat variables with factor loadings \(\geq 0.40\) were used to elucidate the PCA plot (Kwak and Peterson 2007). The PCA was conducted using R version 3.2.3 statistical software (R Development Core Team 2015). The mean, standard error, and range were calculated for all of the habitat variables for each species. These measurements were then used to examine relationships between habitat variables, species occurrence, and aid in the interpretation of the PCA results.

**Landscape scale analysis**

Fishes that are rare or threatened often have restricted distributions, are habitat specialists and have a limited number of known occurrence locations, restricting the use of species distribution models to solely modeling presence locations (Hernandez et al. 2006). Because of their small size, cryptic coloration, and burying behavior, sand darters that are present at a site are often difficult to detect. Consequently, absence data can be misleading – resulting in the misidentification of important variables influencing spatial distribution. Maximum Entropy Modeling (MaxEnt) is one of the few species distribution models designed specifically for presence-only data (Phillips et al. 2006), and is effective with small sample sizes (Hernandez et al. 2006, Elith et al. 2011). MaxEnt is a machine learning and data driven approach that links georeferenced presence locations with site-level or landscape-level features to generate a probability of occurrence (Phillips et al. 2006). This output can also be used as a proxy for the relative suitability of habitat in a given region or a species given niche (Warren and Seifert 2011). Multiple studies have employed this method to examine the probably of occurrence of rare stream fishes that are of conservation concern or have limited distributional information (Endries 2011, Labay et al. 2011, Williams et al. 2012, Liang et al. 2013, Albanese et al. 2014).

The models were built using MaxEnt version 3.3.3k (Schapire 2016) with program defaults. The western and eastern sand darter presence locations were used as training and test points for the models. To test the models for accuracy a subset of the training data (25%) was randomly selected and withheld. Model performance was assessed using receiver operating characteristic (ROC) curves, a high ROC value \((\geq 0.80)\) for the test data indicates good model fit or that there is a high likelihood that the model properly predicts areas of occurrences (high sensitivity) and minimizes the chance of a false positive (high specificity) (Phillips 2011). The logistic output was selected to generate the probability of suitable habitat for each stream reach. The importance of individual environmental variables was examined by assessing the percent contribution to the gain in model fit, response curves, and a jackknife procedure executed in MaxEnt. The jackknife procedure calculates how the gain in the model fit fluctuates as individual environmental variables are included or withheld and the response curves demonstrate how the logistic prediction changes as an environmental variable is varied, keeping all other environmental variables at their average value (Phillips 2011). MaxEnt is sensitive to selection biases from sampling locations. An attempt was made to
account for this by sampling a wide range of sandbars throughout the lower river; however, the lowest reaches of the Elk River below Mink Shoals were not sampled. Because of MaxEnt’s sensitivity to site selection biases, MaxEnt has a tendency to overfit models for species that have a patchy distribution or small range; potentially influencing our model results.

Environmental variables

The explanatory environmental variables used for the sand darter habitat suitability models were derived using ArcGIS version 10.4, which included stream derived and regional land cover factors (Table 1). The environmental variable layers were all extracted to include 14-digit Hydrologic Unit Code (HUC) catchments that intersected the main channel of the Elk River, and were used as proxies for individual river segments (Liang et al. 2013). The catchment scale as a proxy for stream reach was appropriate for the data because it elucidated broad patterns across the landscape that a smaller scale may have overlooked. Environmental variables included contributing drainage area (km$^2$), river gradient (m), sinuosity (ratio of deviation from a path), island area (m$^2$), geologic classes and land cover classes (Table 1).

Contributing drainage area and gradient were derived using digital elevation models (DEM) at a 10 x 10 m cell size. The DEM was further processed using a “stream burning” technique, to ensure proper overland flow and true instream elevation values (e.g., Saunders 1999, Callow et al. 2007). The burned DEM was used to generate the contributing drainage area and gradient layers. Sinuosity was estimated by measuring the center line of the Elk River compared to the straight line distance for each river segment in a catchment. The percentage of land cover and geologic classes per catchment were calculated within ArcGIS using tabulate area. The catchment data for each environmental variable were joined with the 14 digit HUC catchment boundary layer. The environmental variable layers were further processed to generate environmental variable raster grids with a 30 m cell size. The raster grids were then converted to ASCII files, which is the required file type for MaxEnt. The outputs from MaxEnt in ASCII format were later imported back into ArcGIS, converted to raster grids, and plotted for visual interpretation.

Results

Fish survey

Western and eastern sand darters were detected in dissimilar proportions throughout the lower Elk River. Of the 63 sites sampled only western sand darters were detected at two sites, only eastern sand darters were detected at 41 sites, both species overlapped at six sites, and neither species was detected at 14 sites (Fig. 1). Western sand darters were detected predominantly near the town of Clendenin (36 rkm), and at two sites further downstream near Blue Creek (19 rkm). In contrast, eastern sand darters were detected from Mink Shoals (7.8 rkm) upstream to Frametown (135 rkm) (Fig. 1). Due to high flows and deeper channel depth, sampling did not occur below Mink Shoals. Previous surveys of the lower Elk River detected western sand darters near Big Chimney and Mink Shoals (Cincotta and Welsh 2010, Fig. 1). Because of the sand darter’s elusive nature, it is possible that western and eastern sand darters were present at a site and not detected. The greatest abundances of western sand darters were detected at two locations near Clendenin (n=12 and n=8). The greatest abundances of eastern sand darters were located near Porter Creek (n=99), Strange Creek (n=77), and Big Chimney (n=50). The number of sites where western sand darters were detected was low (sites = 8) compared to the eastern sand darter (sites = 47).
Table 1. Environmental layers used to generate the species distribution models.

All layers had a UTM NAD83 Zone 17 projection.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Scale</th>
<th>Source</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Stream derived</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drainage area</td>
<td>1:24,000</td>
<td>USGS National Elevation Dataset</td>
<td>Cumulative maximum drainage area in km$^2$ per catchment. Derived from 10 m Digital Elevation Models (DEMs).</td>
</tr>
<tr>
<td>Gradient</td>
<td>1:24,000</td>
<td>USGS National Elevation Dataset</td>
<td>Slope of a stream segment in m (rise/run). Derived from 10 m DEMs.</td>
</tr>
<tr>
<td>Sinuosity</td>
<td>1:24,000</td>
<td>Natural Resource Analysis Center, West Virginia University, High-resolution National Hydrography Dataset</td>
<td>A measure of deviation from a path between two points (centerline stream distance/straight line distance).</td>
</tr>
<tr>
<td>Island area</td>
<td>1:4,800</td>
<td>WV GIS Technical Center Statewide Addressing and Mapping Project (streams SAMB)</td>
<td>Area of islands in each catchment in m$^2$.</td>
</tr>
<tr>
<td><strong>Land cover classes</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Developed</td>
<td>1:40,000</td>
<td>USGS Multi-resolution Land Characteristics Consortium, National Land Cover Database 2011</td>
<td>Consists of a range of developed intensities that include constructed materials, impervious surfaces, and densely populated area. Class types 21-24 and 31.</td>
</tr>
<tr>
<td><strong>Geologic classes</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Shale</td>
<td>1:250,000</td>
<td>WV Geological &amp; Economic Survey</td>
<td>Clastic sedimentary rocks composed of mud, clay, silt and other minerals like quartz and calcite.</td>
</tr>
<tr>
<td>% Sandstone</td>
<td>1:250,000</td>
<td>WV Geological &amp; Economic Survey</td>
<td>Clastic sedimentary rocks composed of manily sand-sized minerals that are primarily quartz and/or feldspar.</td>
</tr>
</tbody>
</table>
**Sandbar habitat use**

The occupancy of a sandbar by either sand darter species varied depending upon the attributes of the sandbar. Western and eastern sand darters were detected in longitudinal sandbars downstream from a riffle with rippled sand and at sandbars located on the downstream end of an island. Additional sand bars where eastern sand darters were exclusively detected included meander point bars, longitudinal bars downstream from a meander, shallow embayments, main channel pool sections, and at sandbars where a tributary joins the main channel. Western sand darters were associated with sandbars that had a higher average current velocity (mean = 0.20 m/s, SE = 0.03 m/s), compared to those that were occupied by eastern sand darters (mean = 0.10 m/s, SE = 0.02 m/s). The sandbars where western sand darters were detected were on average larger than the sandbars where eastern sand darters were detected (Table 2). Generally, western sand darters were detected at sites with higher proportions of sand and smaller substrates compared to the eastern sand darter only sites (Table 2). Sandbars where western sand darters were detected were comprised of higher proportions of coarse sand, while eastern sand darter sandbars contained higher proportions of fine and medium sand (Table 3).

Table 2. Means, standard errors (SE) and ranges of western and eastern sand darter habitat use variables for 63 sites in the Elk River, WV. Western sand darters were detected at eight sites, eastern sand darters were detected at 47 sites, and neither species were detected at 14 sites. A total of six sites contained both species. Bottom current velocity (FCV) and average current velocity (ACV) for the site and sandbar.

<table>
<thead>
<tr>
<th></th>
<th>Western Sand Darter</th>
<th>Eastern Sand Darter</th>
<th>None</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site depth (m)</td>
<td>0.41 (0.04)</td>
<td>0.62 (0.03)</td>
<td>0.59 (0.07)</td>
</tr>
<tr>
<td>Site FCV (m/s)</td>
<td>0.12 (0.04)</td>
<td>0.10 (0.02)</td>
<td>0.15 (0.02)</td>
</tr>
<tr>
<td>Site ACV (m/s)</td>
<td>0.28 (0.03)</td>
<td>0.24 (0.02)</td>
<td>0.35 (0.05)</td>
</tr>
<tr>
<td>Sandbar FCV (m/s)</td>
<td>0.09 (0.02)</td>
<td>0.05 (0.01)</td>
<td>0.08 (0.02)</td>
</tr>
<tr>
<td>Sandbar ACV (m/s)</td>
<td>0.20 (0.03)</td>
<td>0.10 (0.01)</td>
<td>0.16 (0.04)</td>
</tr>
<tr>
<td>Sandbar depth (m)</td>
<td>0.31 (0.02)</td>
<td>0.34 (0.02)</td>
<td>0.38 (0.05)</td>
</tr>
<tr>
<td>Sandbar area (m²)</td>
<td>263.44 (89.27)</td>
<td>130.81 (19.93)</td>
<td>46.77 (8.93)</td>
</tr>
<tr>
<td>River width (m)</td>
<td>59.61 (3.34)</td>
<td>52.94 (2.65)</td>
<td>45.95 (3.76)</td>
</tr>
<tr>
<td>% Silt</td>
<td>6.43 (3.12)</td>
<td>1.76 (0.52)</td>
<td>0.10 (0.10)</td>
</tr>
<tr>
<td>% Sand</td>
<td>34.50 (4.37)</td>
<td>29.70 (2.05)</td>
<td>24.45 (3.29)</td>
</tr>
<tr>
<td>% Small gravel</td>
<td>13.81 (2.12)</td>
<td>11.45 (1.06)</td>
<td>11.65 (1.86)</td>
</tr>
<tr>
<td>% Large gravel</td>
<td>26.38 (3.72)</td>
<td>23.39 (1.56)</td>
<td>21.17 (1.48)</td>
</tr>
<tr>
<td>% Cobble</td>
<td>10.53 (2.83)</td>
<td>24.33 (1.83)</td>
<td>30.23 (2.68)</td>
</tr>
<tr>
<td>% Boulder</td>
<td>2.13 (0.79)</td>
<td>6.10 (0.94)</td>
<td>11.90 (2.58)</td>
</tr>
</tbody>
</table>

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Table 3. Mean values for percent composition of sandbar grain size, standard error (SE) and ranges. Sand samples for the western sand darter were collected at six sites, and 36 sites for the eastern sand darter.

<table>
<thead>
<tr>
<th></th>
<th>Western sand darter</th>
<th></th>
<th>Eastern sand darter</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
<td>Range</td>
<td>Mean</td>
</tr>
<tr>
<td>% Silt</td>
<td>0.39</td>
<td>0.15</td>
<td>0.00–0.94</td>
<td>1.27</td>
</tr>
<tr>
<td>% Fine sand</td>
<td>0.94</td>
<td>0.21</td>
<td>0.32–1.42</td>
<td>6.36</td>
</tr>
<tr>
<td>% Medium sand</td>
<td>40.81</td>
<td>3.91</td>
<td>28.37–51.46</td>
<td>67.65</td>
</tr>
<tr>
<td>% Coarse sand</td>
<td>54.48</td>
<td>3.58</td>
<td>46.28–66.67</td>
<td>22.19</td>
</tr>
<tr>
<td>% Very coarse sand</td>
<td>2.88</td>
<td>0.69</td>
<td>1.42–6.08</td>
<td>2.15</td>
</tr>
<tr>
<td>% Granule gravel</td>
<td>0.51</td>
<td>0.22</td>
<td>0.00–1.42</td>
<td>0.40</td>
</tr>
</tbody>
</table>

The PCA plot likewise demonstrated differences among habitat use between species (Fig. 2). The first three principal components (PCs) contained eigenvalues greater than one, which accounted for 67% of the variation in the data (Table 4). A total of 54% of the variation was explained by the first (39%) and by the second (15%) principal components used for the PC plot (Table 4, Fig. 2). Principal component 1 factor loadings ≥ 0.40 include %fine sand (0.84), %medium sand (0.64), %coarse sand (-0.92), %very coarse sand (-0.82), and %granule gravel (-0.68) (Table 3). Values that loaded highly on PC2 include sand bar depth (0.52), and sandbar area (-0.76). Habitat use between the two sand darter species differed along both PC axes. Based on the factor loadings, the PC1 axis represents a depositional gradient from larger substrate to smaller substrate, while the PC2 axis represents sandbar area and sandbar depth. Based on the factor loadings, western sand darters most often occurred in areas with a higher percentage of coarse grained sand, faster bottom current velocity and larger sandbars, while eastern sand darters were more of a generalist, occurring in a wide variety of sandbars throughout the lower Elk River (Fig. 2).

Table 4. The principal components (PC) with eigenvalues ≥ 1.0, the percent variance explained by each PC, and a list of variables examined by principal components analysis (PCA) with their corresponding factor loading. Bolded factor loadings (≥ 0.40) were used to interpret the axes of PC1 and PC2.

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvalues</td>
<td>3.49</td>
<td>1.32</td>
<td>1.2</td>
</tr>
<tr>
<td>% Variance explained</td>
<td>39</td>
<td>15</td>
<td>13</td>
</tr>
<tr>
<td>Variables</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sandbar depth (m)</td>
<td>0.28</td>
<td></td>
<td>0.52</td>
</tr>
<tr>
<td>Sandbar area (m²)</td>
<td>-0.11</td>
<td>-0.76</td>
<td>0.17</td>
</tr>
<tr>
<td>Sandbar average FCV (m/s)</td>
<td>-0.40</td>
<td>-0.34</td>
<td>0.24</td>
</tr>
<tr>
<td>%Fine sand</td>
<td>0.64</td>
<td>0.27</td>
<td>0.47</td>
</tr>
<tr>
<td>%Medium sand</td>
<td>0.84</td>
<td>-0.22</td>
<td>-0.11</td>
</tr>
<tr>
<td>%Coarse sand</td>
<td>-0.92</td>
<td>0.07</td>
<td>-0.10</td>
</tr>
<tr>
<td>%Very coarse sand</td>
<td>-0.82</td>
<td>0.32</td>
<td>0.14</td>
</tr>
<tr>
<td>%Granule gravel</td>
<td>-0.68</td>
<td>0.19</td>
<td>0.32</td>
</tr>
</tbody>
</table>
Landscape scale

The MaxEnt species distribution models displayed a medium probability of suitable habitat within the currently occupied reaches; with higher probabilities downstream and lower probabilities further upstream (Fig. 3). The highly suitable areas for the western and eastern sand darter reflect known historical locations (Welsh and Perry 1998, Cincotta and Welsh 2010), but the western sand darter sample size was near the minimum level for using MaxEnt (Hernandez et al. 2006). The highest probabilities of suitable habitat in the study area were 0.76 for the western sand darter and 0.77 for the eastern sand darter. The probability of suitable habitat for the western sand darter increased downstream of 40 rkm and decreased upstream of 46 rkm (Fig. 3). The probability of suitable habitat for the eastern sand darter began to increase downstream of 80 rkm, and decreased upstream of 123 rkm (Fig. 3).
The areas where the probability of suitable habitat for both species was highest ranged from 7 to 36 rkm (Fig. 3). The size of the catchments varied, with a mean area of 6.69 km$^2$ (SD = 6.05) and mean river length of 2.43 km (SD = 3.07), which may have influenced the model results.

![Figure 3. Probability of suitable habitat for the western sand darter (WSD) and eastern sand darter (ESD) by 14 digit HUC catchments in the lower Elk River.](image)

Performance within the models and on the test data was high for both species. The receiver operating characteristic (ROC) curve for the test data for the western sand darter model was 0.888, while the ROC curve for the eastern sand darter was 0.884. The western sand darter model had 6 training points and 2 test points. The eastern sand darter model used 34 presence locations for the training data and 11 for testing. The high AUC value for the western sand darter model is related to the small sample size and the species’ narrow range (Phillips 2011). The ROC curves for both models are well above the random prediction line indicating the models are better than random.
Contributing drainage area had the largest percent contribution to model gain for each species (Table 5). Percent contribution to model gain for the western sand darter included contributing drainage area (79.3%), sinuosity (18.8%), island area (1.7%), and percent developed (0.2%). Compared to the eastern sand darter model, which included contributing drainage area (80.9%), percent developed (11.0%), island area (5.7%), and percent shale (1.0%). Contributing drainage area, sinuosity, percent developed, and island area comprised at least 90% of the contribution to model gain for both species. Jackknife tests produced similar results for each species, with contributing drainage area and percent developed providing the largest gain when included separately in the model (Fig. 4). The equal test sensitivity and specificity results indicate significant presence thresholds with logistic values greater than 0.508 for the western sand darter ($p < 0.01$) and 0.453 for the eastern sand darter ($p < 0.01$). Overall, a wider range of suitable habitat is available for the eastern sand darter compared to the western sand darter.

Table 5. The estimates of the relative percent contribution of the environmental variables to the MaxEnt models created for the western and eastern sand darters.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Western Sand Darter</th>
<th>Eastern Sand Darter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Drainage area (km²)</td>
<td>79.3</td>
<td>80.9</td>
</tr>
<tr>
<td>Gradient (m)</td>
<td>0.0</td>
<td>0.1</td>
</tr>
<tr>
<td>Island area (m²)</td>
<td>1.7</td>
<td>5.7</td>
</tr>
<tr>
<td>Sinuosity</td>
<td>18.8</td>
<td>0.2</td>
</tr>
<tr>
<td>%Sandstone</td>
<td>0.0</td>
<td>0.9</td>
</tr>
<tr>
<td>%Shale</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>%Developed</td>
<td>0.2</td>
<td>11.0</td>
</tr>
<tr>
<td>%Forested</td>
<td>0.0</td>
<td>0.2</td>
</tr>
</tbody>
</table>
Dissimilarities between the variables were further examined by assessing response curves for the variables with the highest contribution to model gain. The response curves for contributing drainage area showed a low probability (< 50%) of suitable habitat below approximately 2,650 km$^2$ for both species (Fig. 5). Sinuosity impacted model gain inversely for each species, the probability of presence drastically declined with values > 1.0 for the western sand darter, whereas the eastern sand darter probability of presence increased with higher values (Fig. 5). When percent developed was included individually for the western sand darter model the response curve did not vary. In contrast, when percent developed was included individually for the eastern sand darter model, the probability of presence initially increased with low values and then declined with higher values (Fig. 5). The probability of presence increased with island area for both species (Fig. 5). Overall, western sand darters were restricted to the lower reaches, while the probability of suitable habitat is higher further upstream for the eastern sand darter. The main landscape scale factors that appear to impact range differences for both species are contributing drainage area, sinuosity and island area.
Figure 5. The response curves demonstrate how the logistic prediction changes as the environmental variables are varied, keeping all other environmental variables at their average value. Drainage area is in thousands (i.e., 1.0 = 1,000) and island area is one hundred thousand (i.e., 1.0 = 100,000).
Conclusion
This research represents the first inquiry into western and eastern sand darter habitat use at multiple scales in a region where they are sympatric as well as syntopic. Sand darters are commonly considered rare and elusive, which has resulted in a scarcity of information regarding habitat and ranges (Kuehne and Barbour 1983). The assessment of multiple scales for habitat use is essential to understanding the persistence of threatened species (e.g., Labbe and Fausch 2000). The sandbar habitat use assessment provided more detailed insight on specific sandbar characteristics, while the landscape scale approach allowed us to investigate habitat suitability, despite limited western sand darter locations and the restriction of presence only data. The sand darter focused survey of the lower Elk River found that western sand darters continue to be restricted to the lower 36 rkm, whereas the eastern sand darters’ distribution extends another 100 rkm upstream. However, a caveat of this study is that detection probabilities were not estimated for either species. Western sand darters were detected at larger more contiguous sandbars with moderate flow and at sites with high proportions of coarse grained sand. In contrast, eastern sand darters were not limited to faster velocities and were detected in a wide variety of sandbars. Geology and land cover types minimally impacted the habitat suitability models, while physical characteristics of the river contributed to the greatest proportions of model gains.

Eastern sand darters were occasionally detected in areas that initially seemed suboptimal on account of low flow and fine sediment, whereas western sand darters were typically detected in large sandbars with moderate flow. Results from a substrate selection laboratory study of the western and eastern sand darter reported significant differences amongst sand grain size preferences between species (Thompson et al. 2017). The authors reported that western sand darters selected for a narrower range of coarser grains (0.25-1.0 mm), compared to the more generalist eastern sand darter (0.125-1.0 mm). These finding were mirrored with data from the field, with the western sand darter occurring in sandbars with higher proportions of coarse grained sand, compared to the sandbars that were occupied by eastern sand darters. Additionally, our field results were similar to past eastern sand darter habitat use studies, with the species preferring sandbars with high proportions of medium to fine sand (Daniels 1993, Facey and O’Brien 2004, Tesslar et al. 2012, Dextrase et al. 2014). Thus, the sorting of sand gain sizes may vary depending on the type and location of a sandbar, which could influence differences in habitat suitability between the two species.

The landscape scale western and eastern sand darter models reflected known range differences between the two sand darter species in the lower Elk River, and further supports the idea that individual sandbars vary throughout the river’s course. Physical features throughout a river system change in a continuum, structuring aquatic habitat (e.g., Vannote et al. 1980, Jackson et al. 2001). Thus, physical factors like contributing drainage area and gradient are known to heavily influence stream fish distribution models (Endries 2011, Liang et al. 2013, Albanese et al. 2014). Habitat suitability for each species increased with higher contributing drainage area values and decreased with higher river gradient values, while the relationship between species to sinuosity was inversely related.

Given that western sand darters are restricted to the lower Elk River; it is important to consider how contributing drainage area may influence the creation of sandy depositional areas. As contributing drainage area increases downstream, the river’s discharge and cumulative sediment supply increases concurrently with a decrease in...
erosional energy, allowing for greater deposition in the lower reaches of the river (e.g., Charlton 2007). Sediment is deposited during a number of circumstances, which include a reduction in flow discharge, a decrease in river gradient, an increase in river width, an increase in boundary resistance, flow separation (large difference in velocity between fast moving flow and slowly recirculating flow), and obstruction to flow (e.g., Charlton 2007). These deposits create various types of sandbars (smaller depositional features) within a river’s channel, which are commonly located on the inside of meander bends (point bars), downstream of islands, along the edges of channels (shallow embayments & longitudinal bars), main channel pool sections, and where tributaries join the main channel. Eastern sand darters were detected in all the sandbars mentioned above, whereas western sand darters were solely collected from sandbars with rippled sand downstream of a riffle or from sandbars located on the downstream end of an island.

The relationships among sinuosity, sand darter presence, and habitat suitability are likely important toward understanding sand darter distributions. Sinuosity is a measure of the ratio between channel length and straight-line valley length. Rivers typically adjust their channel pattern (i.e., sinuosity) to compensate for changes in external variables such as changes in gradient, sediment supply, and/or local geology (e.g., Leopold and Wolman 1957, Schumm 1993). The change in sinuosity that occurs along the lower 36 rkm of the Elk River corresponds with a significant change in valley type. At the head of the lower 36 rkm (near Clendenin, WV; Fig. 3), the valley widens and large terraces become present. Terraces typically form when a river’s channel incises into the valley floor, which is in turn driven by changes in a river’s baselevel, the lowest elevation to which a river can flow (e.g., Schumm 1993). During the North American ice-age, many of the ancestral rivers of the Ohio River drainage flowed northward into ponded ice-marginal lakes (e.g., Wayne 1952). This ponding possibly forced a region-wide baselevel rise and subsequence aggradation of sediment. When the ice-sheet retreated the river’s baselevel was lowered, which caused incision of the modern channel into legacy sediment that may be present in the terraces (J.S. Kite personal communication, November 9, 2016). Thus, sinuosity as a variable is slightly misleading because in the case of the lower Elk River, sinuosity is collinear with valley type. The higher proportions of coarse grained sediment in the lower 36 rkm, could be supplied from these larger terraces, but further research is necessary concerning soils and geomorphology of the area to better understand valley type differences in the Elk River and how this relates to sand darter distributions.

Furthermore, the presence of the Sutton Dam in the Elk River likely alters seasonal flow and temperature regimes, the frequency and magnitude of channel discharge, and sediment scour and depositional patterns (Baxter 1977, Power et al. 1996). Discharge patterns are known to influence cohort success via the maintenance of sandy depositional habitats and increased nutrient inputs from flood-pulse events (Gutreuter et al. 1999, Lin and Caramaschi 2005). High mean annual discharge and sand-dominated habitat provided the greatest first year growth for eastern sand darters in Ontario (Drake et al. 2008). The strong positive relationship of age-0 growth and high mean annual discharge was related to the flood-pulse concept, where frequent high discharge events decrease the amount of siltation, and increase nutrient inputs to nearshore areas (Junk et al. 1989). The Elk River experiences seasonal flooding; however, the dam alters the duration of those events, reducing sediment below the dam, eroding channel banks, and altering variation in seasonal discharge (Poff and Hart 2002). The effect of sediment reductions downstream may be less pronounced in the lower reaches of the Elk River by additional sediment added to the
system from contributing tributaries (Ligon et al. 1995). This highlights the importance of natural flow regimes and the need to enhance our understanding of how impoundments effect the geomorphic processes that drive the creation of physical habitats in rivers.

Conservation and management of freshwater fishes must consider multiple scales (Lewis et al., 1996, Labbe and Fausch 2000). With the combination of small-scale sandbar habitat use data and a large-scale landscape analysis we provided some insight into the factors that influence the sand darters’ range dissimilarities in the Elk River. Results from this study show that sediment sorting varies as a function of the sandbar’s position in the river and that landscape scale processes (e.g., valley type) play a role in structuring sand darter instream habitat. These results support the explanation of within-river sand darter distribution differences in the Elk River. Biotic factors like competition or predation may play a role in structuring the sand darter community; however, for the purpose of this project we were limited to examining habitat use factors. Because these species do bury in the sand, individuals can be difficult to detect, especially in deep water or areas with a large proportion of debris. Sampling for this study was restricted to wadeable areas of the river and did not include deeper pool sections that may contain either species. Future monitoring efforts in the Elk River and other rivers that contain both species are needed to improve the applicability of our sandbar habitat use results and the sand darter habitat suitability models. A study by Naiman and Latterell (2005) focused on improving the conservation and management of fishes by emphasizing the importance of viewing fish habitat as more than just water. Incorporating ArcGIS to create layers for our habitat suitability models allowed us to explore broader landscape scale patterns that would have been difficult to observe with using only in-stream habitat use data. Information gained from studying the western and eastern sand darters within-river distribution and habitat use may be applied to future monitoring efforts, as well as conservation and management decisions in the Elk River watershed.

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References


