Habitat and fish assemblage associations and current status of northern leatherside chub *Lepidomeda copei* in western Wyoming

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Due to the cumulative effects of overexploitation, habitat degradation, and interactions with introduced species, numerous western native fishes are currently imperiled (Jelks et al. 2008). Effective conservation efforts for these fishes require knowledge of distributional patterns, information on basic biology, an understanding of community and autecology, and an assessment of potential limiting factors for the species (or assemblage) of interest (Minckley and Deacon 1991). Though addressing these information gaps has improved the
success of management actions for native sport fishes (e.g., salmonids of the genera *Oncorhynchus* and *Salvelinus*; Dunham et al. 2008), conservation of native nongame fish has been hampered by a limited understanding of their life histories and a general perception of these fishes as being undesirable (Cooke et al. 2005). Conservation and restoration of native fishes and ecosystems for long-term persistence can benefit from addressing these issues (Brouder and Scheurer 2007).

Northern leatherside chub *Lepidomeda copei* (hereafter northern leatherside) is a small cyprinid native to the Bear River Basin in Idaho, Utah, and Wyoming and the Snake River Basin of Idaho, Nevada, and Wyoming (see UDWR 2009 for historical distribution information). Although the species was originally described to include populations of leatherside chub from southern Utah, recent molecular, morphological, and ecological evidence supports designation of northern leatherside and southern leatherside chub *Lepidomeda aliciae* as separate species (Johnson et al. 2004). Across the range of both species, leatherside chub have declined in distribution relative to historical records, have apparently been extirpated from numerous locations across their range, and are highly fragmented in areas of persistence (Wilson and Belk 2001, Belk and Johnson 2007). Jelks et al. (2008) included both species on their list of imperiled freshwater fishes of North America and reported northern leatherside as endangered, while others have listed northern leatherside as critically imperiled (NatureServe 2011). In Wyoming, northern leatherside is classified as a species of greatest conservation need (WGFD 2010).

Historically, the distribution of northern leatherside in Wyoming was described only coarsely, and recent studies have documented numerous previously unknown occurrences (Baxter and Stone 1995, Sigler and Sigler 1996, Zafft et al. 2009). Currently, some native populations within Wyoming are thought to be located in the Bear River Basin and a small portion of the Upper Snake River Basin, and recent genetic and geologic evidence suggest that 2 small northern leatherside populations in the Upper Green River Basin are also native (Blakney et al. 2014). The habitat and biotic associations of northern leatherside (Wesner and Belk 2012) appear to be similar to those of southern leatherside (Belk and Johnson 2007). Southern leatherside is usually restricted to lotic habitats below 2200 m in elevation, is strongly associated with pools and other low-velocity areas (Wilson and Belk 2001), and is thought to have broad tolerance for extreme environmental conditions (Belk and Johnson 2007). At the reach scale, southern leatherside is negatively associated with brown trout *Salmo trutta* (Wilson and Belk 2001). In the presence of brown trout, southern leatherside tends to occupy side-channel refuge habitats, when they are available (Walser et al. 1999, Olsen and Belk 2005). Loss of natural channel forms due to habitat manipulation (e.g., channelization and dam/diversion construction) and degradation (e.g., riparian habitat impairment due to overgrazing) has been identified as potentially contributing to decreased productivity and fragmentation of northern leatherside populations (WGFD 2010).

Conservation actions for northern leatherside have recently been coordinated among multiple state, federal, and nongovernmental agencies (UDWR 2009). The conservation agreement and recovery plan for northern leatherside coordinated the conservation efforts of several state and federal agencies and targeted areas of management action, including habitat protection and enhancement, restoration of natural hydrologic conditions, and control of nonnative species. The plan also addressed efforts to restore northern leatherside (via translocations) in areas where it has been extirpated (e.g., UDWR 2010). To inform management decisions relative to the conservation agreement, and to improve understanding of the basic ecology of northern leatherside and other native fishes in Wyoming, our study contained 3 objectives. First, we looked to document the current (i.e., 2010–2011) distribution of northern leatherside in the Bear and Upper Snake River Basins of Wyoming. We then examined habitat associations of stream fishes in the Bear River Basin with multivariate analyses, and finally we evaluated biotic and abiotic factors specifically associated with the distribution of northern leatherside (i.e., 2011). Distribution and abundance information for northern leatherside in Wyoming can be coupled with other data to identify and prioritize areas of conservation interest (Williams
et al. 2011), identify potential source populations for translocation (Schultz and Cavalli 2012), and identify habitat protection and restoration actions (UDWR 2009, 2010). Furthermore, an analysis of factors associated with the distribution of native fishes across multiple spatial scales might allow managers to identify factors critical for the persistence of multiple species and the scale at which management actions may be effective (e.g., Quist et al. 2005).

**METHODS**

**Distribution Surveys**

We sampled stream reaches throughout the known and probable distribution of northern leatherside (2010–2011) to document the current distribution within its native waters in Wyoming, excluding the Green River Basin. Prior to the work of Blakney et al. (2014), northern leatherside from the Green River Basin were generally believed to be introduced (Zafft et al. 2009), so we did not target these areas during our sampling. Effort was initially prioritized in areas where northern leatherside historically occurred (Zafft et al. 2009; Fig. 1a). After we completed thorough inventories in areas of past occurrences, our additional sampling efforts targeted areas that historically had not been sampled.

We performed extensive sampling in the Upper Snake River and Bear River drainages, but sampling approaches differed in these 2 drainages. In the Upper Snake River Basin, most of the habitats where northern leatherside
were historically collected were lateral floodplain habitats of the Snake River—frequently side channels, beaver pond complexes, and isolated backwaters—and were usually associated with some type of cover (i.e., woody structure or aquatic vegetation; Zafft et al. 2009). The Snake River itself is a large nonwadeable river (mean width 50–100 m), and it was impractical to sample small-bodied fishes from it (Curry et al. 2009). Therefore, multiple-person crews opportunistically sampled these habitats using backpack electrofishing in >10-km river segments to delineate northern leatherside distribution where these small habitat patches occurred. We started in the 2 locations where northern leatherside were previously collected and then moved upstream and downstream to assess distribution in similar habitats. In contrast, most of the Bear River drainage contained wadeable streams and small stock ponds within the stream network. Therefore, we used a systematic approach where upstream sampling along stream networks ceased when fish assemblages were dominated by coldwater species, because northern leatherside were thought to occur primarily downstream of habitats dominated by trout and sculpin (Wilson and Belk 2001). We sought to allocate sample points evenly throughout the study area by selecting sites broadly, starting in proximity to previous collection/sampling locations. As sampling progressed through both field seasons, we added supplemental locations to increase overall sample sizes and improve the spatial resolution of sampling. Although our sampling did not focus on habitats in the Green River Basin, we did note collections by other Wyoming Game and Fish personnel in 2010–2011 in the description of northern leatherside distribution.

In the Bear River drainage, we typically quantified fish assemblages in 200-m sample reaches (following Barbour et al. 1999). Although we didn’t specifically quantify capture probability, this sampling approach should allow an accurate assessment of presence/absence of fish within the reach (Patton et al. 2000, Rabeni et al. 2009). In some instances, stream access and other logistical constraints resulted in shorter reaches. For example, if a stream reach was positioned between a road crossing and a property boundary, we adjusted the reach length to accommodate these limitations. Generally, block nets were placed at the upstream and downstream end of sample reaches; natural barriers (e.g., diversion or beaver Castor canadensis dams) were occasionally used as upstream or downstream barriers. We primarily used single-pass backpack electrofishing to assess assemblage composition and species richness within sample reaches by moving in an upstream direction with an electrofisher. Output (100–350 V, 20–80 Hz) was adjusted to a level that allowed capture of individual fish with dip nets. Larger stream systems (i.e., mean width > 6 m) were sampled with longer reaches (i.e., 400 m) using a raft-mounted electrofishing unit (Curry et al. 2009). If conditions precluded effective use of electrofishing gear (e.g., high turbidity, extremely high or low conductivity, equipment malfunction), bag seining was used to characterize fish assemblages in study reaches.

In addition to standardized reaches, lentic and lotic habitats (e.g., stock ponds and reaches consisting of mainly isolated pools) that appeared to be suitable for fish were opportunistically sampled with electrofishing gear or seines to supplement distributional information. Northern leatherside is known to occur in these habitats and may persist longer than other species in these extreme environments (Belk and Johnson 2007). Although we attempted to sample all habitats encountered, permission from landowners and accessibility determined which could be included.

All fish captured were identified to species and counted following completion of each pass. The exception was sculpins (i.e., mottled sculpin Cottus baikdii and Paiute sculpin C. beldingii) which are difficult to differentiate in the field and were therefore not separated to species. The first 30 northern leatherside and salmonids were measured (total length), and the length range for other fishes (e.g., redside shiner Richardsonius balteatus) was noted by measuring the longest and shortest individuals of each species captured.

Habitat Associations of Stream Fishes

To evaluate habitat features related to the distribution of fishes in the Bear River Basin, we quantified stream habitat variables within wadeable sample reaches during field sampling in 2011 (see Schultz and Cavalli 2012 for details). At each sample reach, we placed
11 evenly spaced transects (1 each at the upstream and downstream ends with 9 in between) across the stream channel. At each transect we measured wetted stream width. Water depth and dominant substrate (following Platts et al. 1983) were measured at 5 evenly spaced points across each transect. At each transect, the amounts of aquatic and overhanging vegetation, woody structure coverage, and bank undercutting were visually estimated within 5 m upstream and downstream of the transect. Categories were the following: 0 = absent, 1 = sparse (0%–25%), 2 = medium (26%–50%), 3 = heavy (51%–75%), and 4 = very heavy (76%–100%). To delineate individual channel units and describe substrate conditions, we measured thalweg depth and substrate at 100 evenly spaced points longitudinally along each sample reach. Elevation at the midpoint of each sample reach was obtained from a handheld Global Positioning System (GPS) unit. Some of these habitat features vary seasonally (e.g., vegetation), so it is important to note that our inferences were limited to the factors that were present on the day of sampling.

Analyses

Habitat data summaries.—For each sample reach, we summarized habitat variables for species-habitat association analyses. Reach-scale habitat metrics included maximum and mean depth, mean substrate size, mean wetted stream width, mean wetted width-to-depth ratio, aquatic vegetation, bank undercutting, overhanging vegetation, and woody structure. Mean substrate size was calculated as the mean particle size of the dominant substrate in each quadrat in each sample reach. Northern leatherside is positively associated with increased pool habitat and depth variability (Wesner and Belk 2012, Dauwalter et al. 2014), so we computed 2 additional metrics from our longitudinal depth profile: percent pool habitat and thalweg depth coefficient of variation (CV). We defined pool habitat as where the thalweg profile had a residual depth measurement greater than one-tenth the mean channel width. We defined residual depth as the difference in depth between each thalweg profile depth measurement and the shallowest depth measurement along the profile (Lisle 1987). The number of all points defined as pool habitat was divided by the total number of thalweg depth measurements to calculate the percent pool metric. Thalweg depth CV was a metric of depth variability in each reach.

Multivariate analysis of fish assemblages.—We used canonical correspondence analysis (CCA, vegan package in R version 2.3-4: Oksanen et al. 2016) to analyze the effect of multiple habitat factors on the catch rates of different fishes. This technique is a direct gradient analysis that uses empirically derived species and environmental data to create multivariate gradients, which maximize dispersion among species and among environmental (habitat) variables in ordination space and which identify important variables in community composition (ter Braak 1995, ter Braak and Verdonschot 1995). Ordination biplots were constructed to help visualize dispersion of species along eigenvectors weighted by environmental variables (ter Braak and Verdonschot 1995). Fish assemblage, sample reach, and habitat variables were included in the CCA, and initial variable screening and data processing were used to maximize interpretability of analyses. For environmental variables, we included multiple reach-scale habitat variables and one segment-scale variable (i.e., elevation). From these potential variables, Pearson correlations were used to identify redundancy among variables. For any pair of redundant variables \( r > 0.60 \), we chose one as an explanatory variable based on which was more biologically encompassing; the corresponding factor was eliminated from further analyses. For example, maximum depth and mean depth were correlated \( r = 0.86 \), so maximum depth was omitted in further analyses because mean depth encompassed multiple measurements. To better approximate normality, the mean reach scores for overhanging vegetation data were logarithmically transformed \( \log_{10} + 1 \); Shapiro–Wilk tests indicated that the transformed data better approximated normality. Similar screening procedures were used with species data for inclusion in the CCA. Because we only completed one electrofishing pass at most sample reaches, we standardized the fish-species matrix for the CCA to the density of fish (fish per \( m^2 \) stream area sampled) of each species captured in the first pass of each sampling reach. Single-pass and multiple-pass catch-per-unit effort were strongly correlated in most areas,
and single pass samples provide a reliable approximation of both density and species diversity (Jones and Stockwell 1995, Bertrand et al. 2006, Reid et al. 2009). To reduce the confounding influence of rare species, species were only included in the CCA if present in >5% of all the sample reaches.

Initially, all candidate variables were included in the CCA, but variables were removed from the analysis post hoc if they did not explain variation along major axes in an easily interpretable way (ter Braak and Verdonschot 1995). In addition to our initial variable screening, we eliminated variables with variance inflation factors (VIFs) >20 from the CCA (ter Braak and Verdonschot 1995). The final CCA from this iterative process was used for interpretation of species-habitat associations.

**NORTHERN LEATHERSIDE HABITAT AND BIOTIC ASSOCIATIONS.**—To examine factors related to the distribution of northern leatherside in Wyoming, we used logistic regression to model occurrence as a function of reach-scale habitat variables and fish assemblage variables (Meyer et al. 2010, Schultz et al. 2015). We used habitat and biotic factors that the CCA identified as associated with northern leatherside to develop a set of predictive variables to explain the distribution of northern leatherside. To identify explanatory variables from these candidates, we used a stepwise backward-elimination procedure to remove variables with little explanatory power (R version 2.3-4; R Core Development Team 2011). At each step, we used Akaike’s information criterion (AIC) to evaluate the relative support for each model. We followed the recommendations of Arnold (2010) and computed 85% confidence intervals for parameter estimates. If 85% confidence intervals included zero, parameters were interpreted to be uninformative. We assessed logistic regression model performance based on a receiver operating characteristic (ROC) curve, where ROC values 0.5–0.7 indicated low, 0.7–0.9 indicated medium, and 0.9–1.0 indicated high model accuracy (Manel et al. 2001).

To assess factors potentially related to northern leatherside abundance, we used simple Pearson correlations to identify relationships between northern leatherside abundance (density) and each measured environmental variable in reaches where they occurred (n = 35). We examined habitat factors associated with density, and species that tended to co-occur with northern leatherside.

Prior to implementing statistical models, we performed additional variable screening. Of the 108 sample reaches where we measured habitat in 2011, we omitted 14 fishless reaches from multivariate analyses and species distribution modeling. These reaches were all very small (<1 m mean width) and may have been fishless and ephemeral naturally or due to water diversion impacts. Similarly, northern leatherside were not collected in any of the 26 sample reaches in the Thomas Fork drainage. We assumed that northern leatherside was not available in the potential species pool within this drainage, so these reaches were also omitted from habitat association analyses. After this screening process, our total sample size for multivariate and species distributional models was 68 reaches.

**RESULTS**

**Northern Leatherside Distribution**

We collected northern leatherside from several portions of the Bear River and Upper Snake River Basins in western Wyoming (Fig. 1b); the limited sampling in the Green River Basin also yielded northern leatherside from 2 locations (details in Schultz and Cavalli 2012). We captured northern leatherside from a variety of habitats across all areas sampled, but we did not collect it from standing waters larger than 1 ha. Northern leatherside occurred in densities ranging from 0.0015 to 0.197 fish m⁻². Numerous length classes were represented in most populations, and length ranged from 25 to 137 mm. The highest densities of northern leatherside were collected in Sulphur Creek (up to 0.197 fish m⁻²) and Dry Fork (up to 0.114 fish m⁻²). Extensive sampling (26 sample reaches) in the Thomas Fork drainage failed to detect northern leatherside.

Northern leatherside was found in relatively small patches within this broad distribution in the Twin Creek, Upper Bear River, and Smiths Fork drainages. Populations in each of these drainages were located over 30 river kilometers from populations in adjacent drainages. Some populations appeared to be relatively isolated within drainages. For
Table 1. Weighted correlation matrix of stream habitat variables and species values for stream fish assemblages in the Bear River Basin, southwestern Wyoming, 2011. Eigenvalues equal the dispersion of species scores on the axis and indicate the importance of the habitat. Habitat factors in bold are strongly associated with the corresponding canonical axes. For interpretive purposes, species values that load strongly on a given axis are associated with habitat factors that also load strongly on that axis. For example, Bonneville cutthroat trout loaded strongly on axis 1 and were positively associated with depth coefficient of variation and overhanging vegetation and negatively associated with mean stream width and depth.

<table>
<thead>
<tr>
<th>Variable</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat factors</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Depth coefficient of variation</td>
<td>0.66</td>
<td>0.43</td>
<td>0.24</td>
</tr>
<tr>
<td>Mean stream width</td>
<td>−0.73</td>
<td>0.20</td>
<td>−0.24</td>
</tr>
<tr>
<td>Mean depth</td>
<td>−0.81</td>
<td>0.33</td>
<td>−0.17</td>
</tr>
<tr>
<td>% Pool habitat</td>
<td>0.43</td>
<td>0.46</td>
<td>0.08</td>
</tr>
<tr>
<td>Aquatic vegetation</td>
<td>−0.42</td>
<td>−0.36</td>
<td>0.67</td>
</tr>
<tr>
<td>Woody structure</td>
<td>0.33</td>
<td>−0.31</td>
<td>0.16</td>
</tr>
<tr>
<td>Overhanging vegetation</td>
<td>0.49</td>
<td>−0.34</td>
<td>−0.22</td>
</tr>
<tr>
<td>Species</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brown trout Salmo trutta</td>
<td>−0.13</td>
<td>−2.26</td>
<td>−0.32</td>
</tr>
<tr>
<td>Brook trout Salvelinus fontinalis</td>
<td>−1.06</td>
<td>−1.04</td>
<td>0.02</td>
</tr>
<tr>
<td>Bonneville cutthroat Oncorhynchus clarkii utah</td>
<td>1.13</td>
<td>−0.54</td>
<td>−0.87</td>
</tr>
<tr>
<td>Northern leatherside chub Lepidomeda copei</td>
<td>0.58</td>
<td>0.26</td>
<td>0.33</td>
</tr>
<tr>
<td>Sculpins Cottus spp.</td>
<td>−0.09</td>
<td>−0.19</td>
<td>0.15</td>
</tr>
<tr>
<td>Mountain sucker Catostomus platyrhynchos</td>
<td>0.61</td>
<td>0.21</td>
<td>−0.02</td>
</tr>
<tr>
<td>Speckled dace Rhinichthys osculus</td>
<td>0.10</td>
<td>0.09</td>
<td>−0.15</td>
</tr>
<tr>
<td>Longnose dace Rhinichthys cataractae</td>
<td>−0.67</td>
<td>−0.32</td>
<td>0.32</td>
</tr>
<tr>
<td>Redside shiner Richardsonius balteatus</td>
<td>−0.36</td>
<td>0.20</td>
<td>0.04</td>
</tr>
<tr>
<td>Mountain whitefish Prosopium williamsoni</td>
<td>−1.58</td>
<td>1.34</td>
<td>−2.24</td>
</tr>
<tr>
<td>Fathead minnow Pimephales promelas</td>
<td>−1.50</td>
<td>0.29</td>
<td>−0.53</td>
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<tr>
<td>Utah sucker Catostomus ardens</td>
<td>−0.95</td>
<td>0.73</td>
<td>−0.81</td>
</tr>
<tr>
<td>Eigenvalue (% variation explained)</td>
<td>0.192 (39.5)</td>
<td>0.163 (33.4)</td>
<td>0.074 (15.3)</td>
</tr>
</tbody>
</table>

example, northern leatherside populations in Muddy Creek and Dry Fork (both in the Smiths Fork drainage) were separated by more than 20 river kilometers. The majority of northern leatherside populations were in the Bear River Basin. In addition to sampling in the Snake River and its tributaries downstream of Jackson Lake Dam, we also collected northern leatherside from portions of Pacific Creek and Triangle X Creek (a new location for the species).

Habitat and Biotic Associations

Fish assemblage and stream habitat sampling in 2011 represented typical habitats of foothills streams in the Bear River Basin of southwestern Wyoming. Mean stream width ranged from 0.5 to 14.7 m and elevation ranged from 1971 to 2507 m. As is typical in Mountain West streams, fish assemblages transitioned from cyprinid-catostomid assemblages in downstream reaches to coldwater trout-sculpin assemblages in higher gradient and colder reaches. Of the 108 reaches we sampled, northern leatherside was collected at 35 (frequency of occurrence 32%). In these collections, speckled dace Rhinichthys osculus was the most frequently occurring species (56%), followed by sculpins (52%), Bonneville cutthroat trout Oncorhynchus clarkii utah (51%), and mountain sucker Catostomus platyrhynchos (46%).

Multivariate Analysis of Fish Assemblages.—Variable screening resulted in the retention of 7 explanatory variables in our final CCA: thalweg depth coefficient of variation, mean depth, mean stream width, percent pool habitat, amount of aquatic vegetation, presence of woody structure, and amount of overhanging vegetation. Variables included in the final CCA were not redundant; no retained variables had VIFs >5. The first 2 canonical axes of our CCA explained 39.5% and 33.4% of variation in species abundance among sample reaches, respectively (Table 1). The first axis was correlated with the depth coefficient of variation, mean depth, and mean stream width (Fig. 2). The second axis was correlated with percent pool habitat and amount of aquatic vegetation. The third CCA
axis was correlated with aquatic vegetation, but only explained 15.3% of variation in assemblage structure. Within the CCA, thalweg depth coefficient of variation, mean depth, and stream width showed the strongest gradients, while aquatic vegetation, percent pool habitat, and woody structure had relatively weak gradients.

Centroids of species distributions elucidated habitat associations of stream fishes in southwestern Wyoming. The centroids of sculpins and speckled dace were positioned close to the origin, indicating no strong association with any habitat factor. Bonneville cutthroat trout was associated with overhanging vegetation and shallower/narrower stream channels. Mountain sucker and northern leatherside were both associated with increased thalweg depth coefficient of variation and percent pool habitat. Other species were less common and displayed variable habitat associations (Fig. 2).

**NORTHERN LEATHERSIDE HABITAT AND BIOTIC ASSOCIATIONS.—** Using the backward-elimination procedure, we selected a model containing 3 predictor variables associated with the occurrence of northern leatherside: mean substrate size, thalweg depth coefficient of variation, and mean depth (Table 2). However, confidence intervals (85%) for mean substrate size included zero, suggesting this parameter was uninformative. Northern leatherside tended to occur at sites with greater mean depth, higher depth variability, and finer substrates (Table 2). The ROC value for the

**Table 2.** Parameter estimates ($b_i$), standard error, and 85% confidence intervals for a logistic regression model that predicts occurrence of northern leatherside chub in the Bear River Basin of southwestern Wyoming, 2011. Thalweg depth CV is the coefficient of variation for depths measured longitudinally along stream reaches.

<table>
<thead>
<tr>
<th>Variable</th>
<th>$b_i$</th>
<th>SE</th>
<th>85% Confidence limits</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-7.18</td>
<td>2.006</td>
<td>-10.31, 0.012</td>
</tr>
<tr>
<td>Mean substrate size (mm)</td>
<td>-0.01</td>
<td>0.0038</td>
<td>-0.016, 0.99</td>
</tr>
<tr>
<td>Thalweg depth CV</td>
<td>11.38</td>
<td>3.220</td>
<td>7.04, 16.38</td>
</tr>
<tr>
<td>Mean depth (cm)</td>
<td>0.127</td>
<td>0.0367</td>
<td>0.08, 1.20</td>
</tr>
</tbody>
</table>

Fig. 2. Canonical correspondence analysis ordination of the distribution of fishes in the Bear River Basin, southwestern Wyoming. Habitat variables are represented as vectors, and species are represented by 3-letter species codes: BNT = brown trout, BKT = brook trout, BRC = Bear River (Bonneville) cutthroat, LND = longnose dace, MSC = sculpins, SPD = speckled dace, FHM = fathead minnow, RSS = redside shiner, MTS = mountain sucker, LSC = northern leatherside chub, UTS = Utah sucker, MWF = mountain whitefish. Habitat vectors project toward higher values for each variable. Species centroids can be interpreted relative to these vectors. Centroids parallel with habitat vectors indicate strong relationships with that habitat factor; centroids perpendicular to habitat vectors are unrelated to those habitat factors. Longer habitat vectors indicate more influence in explaining variation in assemblage structure relative to shorter vectors. For example, Utah sucker and mountain whitefish are positively associated with deeper/wider reaches with less overhanging vegetation but are neutrally associated with aquatic vegetation and pool habitat.
selected model was 0.84, suggesting acceptable model performance.

At reaches where northern leatherside occurred, its abundance was related to depth variability ($r = 0.415$) and elevation ($r = 0.229$). Northern leatherside abundance also showed a positive association with abundance of 3 native nongame fishes: mountain sucker ($r = 0.34$), redside shiner ($r = 0.38$), and speckled dace ($r = 0.38$; Table 3).

**DISCUSSION**

This study documented the distribution and habitat associations of northern leatherside and other stream fishes in southwestern Wyoming. Although the coarse distribution of northern leatherside in this study differed little from Zafft et al. (2009), our work provides a finer-scale delineation of the species’ distribution and provides measures of relative abundance in the state. The size of the distribution did not appear to have diminished from that of the previously known distribution, and we documented additional populations (Fig. 1). This information is directly applicable to conservation and management efforts directed towards northern leatherside in Wyoming (Schultz and Cavalli 2012). Furthermore, our habitat analyses can address information gaps and inform management efforts across the range of northern leatherside. These habitat analyses are also applicable to management of co-occurring nongame fishes across the expanse of the Intermountain West, species for which little information exists.

Northern Leatherside Distribution

Northern leatherside was widely distributed across western Wyoming. Most individuals were concentrated in small areas within this broad distribution (see Schultz and Cavalli 2012 for details). The distribution of northern leatherside in Wyoming represents more than half of the known rangewide distribution of the species (USFWS 2011), which presents unique conservation challenges and opportunities for Wyoming.

The current distribution of northern leatherside in Wyoming relative to its ostensible historical distribution (Zafft et al. 2009) appears to be relatively intact when compared to other imperiled fishes of the Intermountain West. In contrast, native bluehead sucker *Catostomus discobolus*, flannelmouth sucker *C. latipinnis*, and roundtail chub *Gila robusta* occur in less than half of their historical range (Bezzerides and Bestgen 2002), and Colorado River cutthroat trout *Oncorhynchus clarkii pleuriticus* occupies approximately 14% of its historical range (Hirsch et al. 2006). Northern leatherside does not appear to have been extirpated from any of its confirmed historical distribution in Wyoming (Zafft et al. 2009). Because of the species’ intact distribution, we can infer that Wyoming populations of northern leatherside (1) are likely fairly resilient, (2) represent core populations of the species, or (3) are exposed to minimal threats in Wyoming. For these reasons, Wyoming populations of northern leatherside could play a critical role in conservation of the species across its range. In addition to providing fish for translocations and reintroductions, management work in Wyoming may provide valuable information that is broadly applicable (e.g., UDWR 2010). For instance, translocations within Wyoming might be used to develop predictive tools for assessing suitable reintroduction sites in other areas. Wyoming

<table>
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<th>Habitat features</th>
<th>Aq_veg</th>
<th>CVdepth</th>
<th>Mean depth</th>
<th>Overhang</th>
<th>%Pool</th>
<th>Width</th>
<th>Wood</th>
<th>Elev</th>
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<td></td>
<td>0.12</td>
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<td>−0.05</td>
<td>0.11</td>
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<th>Fish assemblage variables</th>
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populations may also be studied to examine the life history of the species (e.g., growth rates, movement, swimming performance, response to habitat perturbation/restoration) to supplement existing studies on some of these questions (Billman et al. 2008a, 2008b).

The broadly spread but locally abundant distribution of northern leatherside is characteristic of imperiled fishes (Haak et al. 2010). Connectivity of these population patches might present issues for the long-term persistence of northern leatherside. Hilderbrand and Kershner (2000) found that inland cutthroat trout required at least 8 km of stream for high-density population persistence, and more for lower-density populations. As a small-bodied fish, northern leatherside likely requires less stream distance than larger salmonids (Pyron 1999). Because most populations contained multiple size (and presumably age) classes, northern leatherside in these patches currently appear to have all necessary habitat elements to complete their life history. Over evolutionary time, however, isolation and lack of connectivity between adjacent populations might present long-term genetic diversity or population viability issues due to stochastic demographic processes (e.g., Perkin et al. 2015). Furthermore, seasonal use patterns (Schultz 2014) suggest that northern leatherside may be more mobile than originally thought. Maintaining and restoring connectivity between population patches will increase the likelihood of viability of northern leatherside in Wyoming, with concomitant benefits to other associated native fishes.

Habitat Associations

Multivariate and logistic modeling showed congruent results, allowing strong inferences about important habitat components for northern leatherside and other native fishes of southwestern Wyoming. Northern leatherside occurred in a variety of habitats, but showed a strong association with highly variable stream depths and several other native nongame fishes (Schultz and Cavalli 2012). These findings can help prioritize conservation areas for northern leatherside, as well as help identify suitable areas for translocation (UDWR 2009, 2010).

Our multivariate analyses identified habitat components structuring fish assemblages in the Bear River Basin of Wyoming that were very similar to those described in other assessments. Sculpins and speckled dace were positioned near the origin of our ordination biplot. Because these small-bodied fishes are riffle dwellers (Baxter and Stone 1995), suitable habitat is likely available in small patches within most 200-m reaches. Redside shiner was associated with deeper and wider stream reaches, possibly because it is more productive in warmer habitats (Reeves et al. 1987). Bonneville cutthroat trout was associated with narrow, shallower stream reaches with wood cover, similar to results from other studies (e.g., White and Rahel 2008). However, the habitat associations for Bonneville cutthroat are likely not truly reflective of its preferences across the Bear River Basin because only a narrow portion of the entire habitat it uses was sampled. Utah sucker Catostomus ardens and mountain whitefish Prosopium williamsoni were associated with larger stream reaches, as would be expected of these larger-bodied insectivores (Moyle and Herbold 1987).

Northern leatherside responded to habitat conditions in small streams in patterns generally similar to those observed for southern leatherside. Occurrence of northern leatherside was explained by depth variability, mean depth, and (weakly) by substrate variability. Southern leatherside is typically found in low-velocity habitats with fine substrate (Walser et al. 1999). It is vulnerable to habitat changes induced by channelization because the loss of lateral habitats forces it to occupy microhabitats containing predators (Olsen and Belk 2005, Belk and Johnson 2007). Although northern leatherside was occasionally collected from riffle habitats, its occurrence was associated with increased mean depth—habitats that contain slower water velocities. In larger, complex streams, northern leatherside used off-channel habitats more frequently. Similar to the Upper Snake River populations from this study, southern leatherside in Diamond Fork Creek, Utah, was found nearly exclusively in lateral habitats (Walser et al. 1999).

Northern leatherside showed habitat associations similar to those of mountain sucker and other native fishes. These species were generally associated with higher depth variability and pool habitat, and were found in relatively narrower stream reaches. In Utah, mountain sucker has been suggested as a
suitable indicator of leatherside chub occurrence (M. Grover, Utah Division of Wildlife Resources, personal communication), and recent evidence suggests that both species respond similarly to introduced salmonids (Wilson and Belk 2001, Schultz and Bertrand 2012, Schultz et al. 2015). Similarly, Quist et al. (2004) found that northern leatherside occurred with catostomids in warmer low-elevation stream segments with abundant deep-pool habitat in the Salt River drainage of Idaho and Wyoming. Northern leatherside has also been linked with higher fish species diversity in other portions of the Great Basin (Wesner and Belk 2012). Though it is uncertain whether this is driven by habitat conditions or factors related to the associated fish assemblage, these studies suggest that conservation measures directed at any of these fishes should be mutually beneficial to the entire native nongame assemblage.

In reaches where it occurred, abundance of northern leatherside varied as a function of depth variability and elevation; higher elevation and more variable depths supported higher abundances. Our study contrasts with the findings of Wilson and Belk (2001), who were unable to detect any reach-scale factors related to abundance of southern leatherside but did find an elevational limit to its distribution. They attributed the lack of strong relationships to the broad range of environmental conditions that southern leatherside evolved in and suggested that the elevational pattern observed was reflective of longitudinal thermal patterns of stream systems. In our study, reaches in the Upper Bear River drainage were at higher elevations than most other reaches sampled and also exhibited some of the highest population densities we observed. Because our upstream sampling ceased when assemblages transitioned to trout without northern leatherside presence, an elevation gradient likely does constrain northern leatherside distribution, but we were unable to detect it. We also hypothesized that northern leatherside would be associated with naturally functioning stream channels, which create a diversity of habitats for multiple life history stages (Wesner and Belk 2012, Dauwalter et al. 2014). The positive relationship between depth variability and northern leatherside abundance supported this hypothesis. Higher habitat diversity within a stream reach was also supportive of greater species diversity, as has been shown elsewhere (Schlosser 1982).

Our results indicate that the distribution and abundance of northern leatherside were related to habitat conditions in the Bear River Basin, and that other native fishes also shared these associations. In these small foothills streams, watershed processes that maintain and enhance natural channel form (Rosgen 1994) can be promoted to enhance habitats for these native fishes. Management actions to achieve these conditions include maintaining water quantity and quality in stream channels for natural hydrologic function, protecting and restoring native riparian vegetation, and improving grazing management (Kauffman et al. 1997). Riparian grazing exclosures, a common management tool in western Wyoming, effectively remedy historically degraded stream conditions (Ranganath et al. 2009, Batchelor et al. 2015). Focused grazing management is another tool available to rangeland managers to meet objectives of riparian habitat recovery without construction of grazing exclosures (Swanson et al. 2015). Work on northern leatherside in the Goose Creek Basin, Idaho, also suggests that restoration of beavers can also be an important natural source of habitat complexity in stream ecosystems (Dauwalter et al. 2014). While many of these actions are currently being implemented, this study provides additional support for these ongoing activities.

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