

ARTICLE

Identifying Translocation Sites for a Climate Relict Population of Finescale Dace

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Abstract

Translocation is a management strategy that seeks to address threats to fish and wildlife populations by establishing new populations in ecologically suitable areas. Populations of Finescale Dace *Chrosomus neogaeus* in the Great Plains may benefit from translocation, as they exhibit a climate relict natural history that has led to a disjunct distribution and minimal dispersal opportunities. We assessed the translocation suitability of sites for Finescale Dace in the Belle Fourche River basin, Wyoming–South Dakota, using a ranking approach for output from multiple analyses. We used multivariate analysis to evaluate dissimilarity in fish occurrence and habitat between sites with and without Finescale Dace in contemporary surveys (2018–2019; $n = 68$). We further evaluated the capacity for sites to support Finescale Dace under base case and future climate change scenarios using the predicted probability of occurrence (P) from species distribution models (SDMs) fitted with basinwide fish occurrence data from surveys conducted in 2008–2019 ($n = 124$) and spatially continuous environmental variables, including forecasted stream temperature scenarios. Sites with Finescale Dace tended to occur close to standing waterbodies, contained emergent vegetation cover, and did not exhibit large overlap in species-space with either native or nonnative species. Predicted P of Finescale Dace exhibited nonlinear relationships with mean August stream temperature, channel slope, and base flow index. The amount of suitable habitat (i.e., high predicted P) declined with forecasted stream warming scenarios in the SDMs. This study highlights the utility of using field observations, historical data, and forecasted climate change scenarios to assess translocation site suitability and inform management of at-risk native fish populations, and the results may be transferable to other populations with limited data or restricted distributions.

In the Great Plains region of North America, disturbance pressures (e.g., climate change and the spread of nonnative species) can interact with regional threats (e.g., stream fragmentation) to reduce fish community diversity and increase the risk of extirpation for threatened populations (Dodds et al. 2004; Matthews and Marsh-Matthews 2007; Brook et al. 2008). To assess the

viability of imperiled fish populations, managers evaluate ecologically limiting factors that operate at multiple spatial scales (Labbe and Fausch 2000; Falke et al. 2012; Perkin et al. 2017). Fish populations exhibiting highly disjunct distributions may be particularly challenged due to limited dispersal opportunities. In these situations, intervention by managers may be needed to ensure

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Received June 23, 2021; accepted December 5, 2021

long-term population persistence (Hulme 2005; Olden et al. 2011).

Managed translocation is a conservation tool that involves the intentional release of animals to establish, reintroduce, or augment an existing population (Griffith et al. 1989). Across various taxa and locations, this strategy has demonstrated mixed success (Fischer and Lindenmayer 2000; Harig and Fausch 2002). Cochran-Biederman et al. (2014) identified factors associated with the success or failure of translocations, including (1) an inadequate understanding of the initial cause of population decline; (2) species-specific habitat associations; and (3) variables related to stocking history, such as source population genetic diversity and the duration of stocking events. Translocations are increasingly being used as a conservation strategy for native fishes, with goals that include boosting population size, increasing dispersal ability, and maintaining genetic diversity (Minckley 1995; Groce et al. 2012; Schumann et al. 2017). Important considerations for native fish translocations include the species composition of the recipient waterbody, the probability that nonnative species will expand into candidate translocation sites, and ethical issues raised with potential establishment of new populations outside of a known historical range (Olden et al. 2011; Galloway et al. 2016). When successful, translocations may safeguard pools of biodiversity by increasing the number of extant populations of rare species, thus reducing their risk of regional or global extirpation.

Select fish species occur in the Great Plains region as climate relicts, which are remnants of more widely distributed populations that have been isolated by climate-driven changes in the environment and thus habitat suitability (Woolbright et al. 2014). The long-term demography of isolated relict populations can lead to decreased abundance and increased sensitivity to environmental stochasticity (e.g., floods and drought; Lande 1993). Additional characteristics that threaten climate relicts include potentially depressed genetic diversity and limited dispersal ability (Hampe et al. 2005). These fishes may be particularly vulnerable to biological invasions due to their ecological naivete in regard to competitive or predatory interactions with invasive species (IUCN 1987). Populations of Finescale Dace *Chrosomus neogaeus* in the Great Plains are emblematic of a climate relict natural history: they exhibit disjunct distributional patterns that likely reduce or eliminate between-population connectivity.

Finescale Dace exhibit a wide distribution in North America, including Canada and northern portions of the USA within upper regions of the Mississippi, Missouri, and St. Lawrence River drainages. Climate relict populations occur at the southwestern extent of their rangewide distribution in the Great Plains in Wyoming, South Dakota, and Nebraska, where the Finescale Dace is listed either as a species of greatest conservation need or as endangered under

state law due to decreased prevalence, potential habitat loss, and risk of regional extirpation (Schneider et al. 2011; SDGFP 2014; WGF 2017). In the Great Plains, Finescale Dace have been associated with groundwater-influenced habitats characterized by cool thermal regimes. Climate warming and associated regional drying have driven natural contraction and fragmentation of suitable habitat for Finescale Dace in the Great Plains, which helps to explain the spatially disjunct status of populations on the periphery of the species' range (Stasiak and Cunningham 2006). Management efforts focused on maintaining Finescale Dace populations in this region included managed translocations dating to the late 1970s in tributary drainages of the Belle Fourche River in the Wyoming Black Hills (Bradshaw 2015). Periodic surveys for Finescale Dace documented the persistence of several translocated populations during the 1990s (Supplementary Figure 1), suggesting the potential viability of establishing new conservation populations of Finescale Dace in the Belle Fourche River basin.

Habitat characteristics that have been associated with Finescale Dace occurrence include low stream channel gradients, clear water, abundant cover, and cool temperature regimes (Stasiak 1987; Booher and Walters 2021). Finescale Dace have been shown to use a variety of habitat types, including headwater streams, lakes, man-made reservoirs, and irrigation ditches. Previous work has demonstrated associations between Finescale Dace presence and beaver pond complexes, where excavation and flooding create perennial water, deepen the water column, and facilitate establishment of algal, vegetative, and invertebrate communities (Schlosser and Kallemeyn 2000; Ray et al. 2004). Multiple studies have shown that Finescale Dace and associated native cyprinids are highly sensitive to predation by introduced littoral predators, including multiple species of sunfish (family Centrarchidae) and Northern Pike *Esox lucius* (Findlay et al. 2000; MacRae and Jackson 2001; Jackson 2002).

The goal of our research was to identify and evaluate potential translocation sites for Finescale Dace in the Belle Fourche River basin, Wyoming–South Dakota. Our objectives were to (1) assess the contemporary distribution of Finescale Dace in the study area, (2) characterize Finescale Dace habitat and fish community associations by using multivariate analysis (MVA), (3) assess potential suitability of stream reaches for Finescale Dace under base case and forecasted climate change scenarios by using species distribution models (SDMs), and (4) rank the relative suitability of candidate translocation sites for Finescale Dace by using output from modeling in objectives 2 and 3. We expected highly ranked candidate translocation sites in our study to reflect established habitat associations of Finescale Dace (e.g., low stream gradient, cool water temperature, and abundant cover). We also expected that the proportion of suitable stream reaches would decrease

under climate change. Our approach to evaluate translocation sites incorporated limited prior knowledge of the ecology of Finescale Dace and historical and contemporary fish survey data and forecasted climate change scenarios to inform species–environment relationships. This provides an adaptable framework for fisheries managers to incorporate climate change scenarios into management plans for threatened fish populations with restricted distributions.

METHODS

Study area.—Our study was conducted in the Belle Fourche River basin within the Black Hills of northeastern Wyoming and western South Dakota (watershed area = 3,711 km²). The Black Hills represent a topographic anomaly in the Great Plains region—a forested highland surrounded by mixed grasslands at lower elevations (Raventon 1994). Elevations in our study area ranged from 943 to 2,024 m. The Madison and Minnelusa formations provide groundwater-fed base flow to numerous streams and several small lakes in the region (Naus et al. 2001).

Site selection.—Specific stream reaches and waterbodies with a history of Finescale Dace occurrence or prior sampling effort targeting this species were nonrandomly selected for sampling efforts. We also developed a list of potential streams from which to draw additional random survey sites based on subjective criteria that included historical Finescale Dace occurrence, past translocation activity, potential suitability inferred from topography and imagery, and translocation potential based on professional opinion (Supplementary Figure 1 available in the online version of this article). Spatial coordinates of stocking locations were not available for all identified translocation drainages; for locations without coordinates available, we approximated translocation areas by using available documentation from fisheries managers within the Belle Fourche River basin. We filtered spatial data representing 16 streams to segments classified as perennial (Black Hills National Forest, unpublished data) and divided them into potential sampling reaches by splitting flowlines in the U.S. Geological Survey's National Hydrography Dataset (NHD) into 150-m-long segments (USGS 2021). Reaches from filtered stream segments were then randomly sampled to produce a list of additional candidate sites within the study area. We sampled five additional nonrandom sites in Sundance Creek to further refine the distribution of Finescale Dace in this drainage. We sampled one to eight locations within each of 16 streams for a total of 68 sites (Supplementary Table 1 available in the online version of this article). Although our site selection was nonrandom and may inhibit inference beyond our study system, the targeted nature of a subset of our sites was essential for updating the distribution and status of Finescale Dace in the Belle Fourche River basin.

Fish surveys and community data.—Our fish survey data set for the Belle Fourche River basin integrated (1)

basinwide historical surveys conducted from 2008 to 2015 by natural resource agencies in Wyoming and South Dakota and (2) contemporary surveys that we conducted in 2018–2019 with the aim of updating the distribution of Finescale Dace within the study area (Table 1; Booher and Walters 2021). Fish collection methods for basinwide historical surveys were varied and included seining, single-pass electrofishing, and passive gears (e.g., minnow traps). Sampling methods during the 2018–2019 surveys included active sampling with single-pass backpack electrofishing (Smith-Root Model LR-24) in streams and passive sampling with standardized gear sets in standing waters. Gears used included minnow traps (Gee's galvanized-steel minnow traps with 2.5-cm openings and 3.2-mm mesh) and mini hoop nets (Promar TR-503 collapsible bait traps with 12.7-cm openings and 18-mm mesh) in both stream (lotic) sites and standing-water (lentic) sites, such as small lakes and ponds. Our sampling units for fish and habitat consisted of either 150-m stream reaches or stand-alone waterbodies. At standing-water sites, traps were placed at equidistant intervals along the perimeter of lakes and ponds, and the number of traps deployed was stratified by waterbody size. In stream reaches that better approximated the geomorphic conditions of standing-water sites (e.g., minimal stream velocity and extensive areas of standing water), we deployed 14 traps that were evenly spaced across 10-m sections of each 150-m stream reach. Collected fish were identified to species, counted, and released into their waterbody of origin.

Basinwide environmental data.—We compiled a data set of spatially continuous environmental covariates for stream segments (with a stream segment defined as a contiguous section of stream between upstream and downstream tributaries) to assess the suitability of stream reaches for Finescale Dace. For each stream segment encompassing a study site, we obtained predicted mean August stream temperature (°C) from the NorWeST data set (Chandler et al. 2016) to incorporate forecasted stream temperature data and facilitate prediction across our river network. We calculated the percentage of open water and wetlands (%) within catchments (i.e., the portion of the landscape draining directly to the stream segment, excluding upstream contributions) using the 2011 National Land Cover Database (Homer et al. 2015), and we extracted upstream drainage area (km²) as an estimate of stream size, stream channel slope, and base flow index values (i.e., an estimate of the proportion of streamflow comprised of groundwater) from the NHDPlus version of the NHD (USGS 2021). We retrieved a metric of catchment disturbance, the index of catchment integrity, from the U.S. Environmental Protection Agency's StreamCat data set (Hill et al. 2016; Thornbrugh et al. 2018). The index of catchment integrity ranges from 0 to 1, with higher values representing areas with better ecological function, and

TABLE 1. Habitat variables used in multivariate analyses (MVAs) with 2018–2019 survey data and species distribution models (SDMs) fitted with integrated survey data from the period 2008–2019 for sites in the Belle Fourche River basin, Wyoming–South Dakota.

Variable	Description	Mean (SD)	Range	Analysis
Base flow index (%)	Proportion of groundwater comprising streamflow	71.47 (6.02)	54.00–82.00	SDM
Distance from a standing waterbody (m)	Linear stream distance from standing water	5,498.13 (8,997.28)	0.00–36,325.61	MVA
Emergent vegetation cover (%)	Proportion of cover classified as emergent cover	6.00 (7.48)	0.00–30.86	MVA
Index of catchment integrity (%)	Metric of catchment disturbance integrating six watershed functions: hydrologic regulation, regulation of water chemistry, sediment regulation, hydrologic connectivity, temperature regulation, and habitat provision	0.89 (0.07)	0.55–0.96	SDM
Open water and wetlands (%)		8.52 (16.80)	0.00–87.37	SDM
Stream size (km ²)	Upstream drainage area of stream reach	767.00 (2,176.99)	0.81–8,402.82	SDM
Stream slope (%)	Channel gradient; stream reach length divided by the change in elevation from upstream to downstream endpoints of a reach	0.02 (0.02)	<0.01–0.11	SDM
Stream temperature (°C)	Mean August stream temperature from 1993 to 2003	14.81 (3.92)	8.05–22.82	SDM
Turbidity (NTU)	Optical water clarity	5.58 (6.62)	0.09–31.2	MVA

characterizes disturbance from land use in terms of six watershed functions: hydrologic regulation, regulation of water chemistry, sediment regulation, hydrologic connectivity, temperature regulation, and habitat provision. We could not retrieve GIS-derived environmental data for three sites where Finescale Dace were not detected, thus yielding a total of 47 unoccupied sites for inclusion in the translocation analysis.

Habitat metrics for the 2018–2019 surveys.— We characterized several habitat metrics with potential biological relevance for Finescale Dace at 2018–2019 survey locations (Table 1). At stream sites, we measured turbidity (NTU) with an Oakton WD-35635-00 meter at three equidistant locations (25, 75, and 125 m). We established transects within each reach at equidistant stations with 20-m spacing ($n = 7$), and we estimated percent instream cover and substrate size at one to five evenly spaced, 33- \times -33-cm quadrats along each transect (Schultz et al. 2012). We visually estimated the proportion of each quadrat area occupied by the following cover type classes: emergent vegetation, submerged vegetation, wood and woody debris, and boulder cover (Fisher et al. 2012). Substrate size at the center of each quadrat was classified into major substrate and sediment classes (Platts et al. 1983). Habitat at standing waterbodies was assessed similarly to the habitat at stream sites, with the following exceptions: cover and substrate size were taken at evenly spaced trap locations along the perimeter of each site, and turbidity

measurements were taken at three equidistant locations along the perimeter of the standing waterbody. We estimated the linear stream distance from a standing waterbody (m) for each site by using imagery from the ArcGIS Image Server (DigitalGlobe; <https://www.digitalglobe.com/resources>) and NHD flowlines.

Multivariate analysis.— We assessed dissimilarity in habitat and fish communities among the 2018–2019 study sites by using nonmetric multidimensional scaling (NMDS; Kenkel and Orlóci 1986) following Hickerson and Walters (2019) with the vegan package (Oksanen et al. 2019) in R (R Core Team 2019). Fish community data ordination was performed using the Jaccard dissimilarity index (Cha 2007) with binary species occurrence data. Given the potential viability of fishless sites for managed translocations, we applied a zero-adjustment to our distance measures by coding a “dummy species” to the original presence/absence species occurrence matrix for empty and populated sites (Clarke et al. 2006). An NMDS ordination for habitat variables with continuous distributions was conducted by using a Jaccard dissimilarity index. Stress values were calculated to assess model convergence, and Shepard plots were used to assess the fit (R^2) of the observed versus transformed distances of each NMDS model. We calculated the median NMDS scores of Finescale Dace-occupied sites for both fish community and habitat ordinations to characterize their position in ordination space. We then characterized site dissimilarity

from Finescale Dace-occupied sites by calculating the distance between unoccupied sites and the median Finescale Dace location in ordination space.

Species distribution model.—We evaluated the potential of stream reaches to support Finescale Dace populations by using predictive SDMs. Briefly, we used zero-inflated random forest classification models, a type of classification and regression tree, with the R package *randomForest* to predict the stream reach-specific probability of Finescale Dace occurrence (Liaw and Wiener 2003; Evans and Cushman 2009). We used these values as our SDM-derived metric of habitat suitability for Finescale Dace in the Belle Fourche River basin. Models were fitted with Finescale Dace occurrence as the response variable and unstandardized basin-scale predictors with potential biological relevance, including mean annual streamflow (m^3/s), water temperature ($^{\circ}\text{C}$), stream slope (%), and base flow index (%). We used unstandardized predictor variables to maintain the interpretability of species–environment relationships in model output. We used the predicted probability of occurrence (P) from this model as the suitability score for a given stream reach. Variable selection was performed using the model improvement ratio, a calculation of variable importance representing the mean decrease in out-of-bag error for a given predictor variable, which minimizes the number of retained predictors and the model mean square error while maximizing the percentage of variation explained (Murphy et al. 2010). Spatial predictions of P for Finescale Dace in the Belle Fourche River basin were made using a customized NHD flowline set with continuous values of selected predictor variables as new data. We assessed model accuracy by measuring the percentage of sites correctly classified (PCC), evaluated predictive performance with area under the receiver operating characteristic curve (AUC) measures (Manel et al. 2001), and evaluated cross-classification error using Cohen's kappa statistic (κ ; Cohen 1968). Model significance ($\alpha = 0.05$) was assessed by using a randomization test with 999 permutations (Murphy et al. 2010). We used the Gini index to assess the relative importance of each predictor variable, where a higher value of the mean decrease in Gini score translates to a more important variable in the classification model (Breiman et al. 1984). We used partial dependence plots to visualize the marginal effect of predictor variables on the predicted P for Finescale Dace (Cutler et al. 2007).

In addition to the SDMs described above that were used to evaluate effects of future climate scenario analyses and fitted with basinwide environmental data and integrated historical fish surveys from the period 2008–2019, we also fitted random forest classification models to just the contemporary fish survey data (i.e., 2018–2019) and corresponding field-collected habitat data. These data were used in the MVA to assess dissimilarity between sites with and

without Finescale Dace. The goal of this additional model was to better understand the shape of species–environment relationships between Finescale Dace and habitat covariates suggested in the MVAs. Finescale Dace occurrence was the response variable, and emergent vegetation cover (%), distance from standing water (m), mean substrate classification, and turbidity (NTU) were predictor variables in the model. The same evaluation metrics for the SDM were applied to the final random forest model for 2018–2019 habitat data to assess accuracy and performance.

Climate change effects on Finescale Dace habitat.—To assess climate change effects on the distribution of Finescale Dace and the suitability of candidate translocation sites, we used a base case stream temperature scenario representing the mean August water temperature ($^{\circ}\text{C}$) from 1993 to 2003 in our SDM. We then fitted the base case model with predicted stream temperature scenarios representing global climate model projections of August air temperature for (1) 2040 and (2) 2080 as well as (3) a 3.0°C increase in stream temperature ($+3.0^{\circ}\text{C}$ scenario). Global climate model projections were based on an ensemble of Intergovernmental Panel on Climate Change climate models for the northwestern USA (Hamlet et al. 2013; Chandler et al. 2016). Stream temperature projections for 2040 and 2080 were based on the A1B greenhouse emissions trajectory (hereafter, "A1B 2040" and "A1B 2080"), where economic growth and global population peak around 2050 and energy sources represent a balance between fossil-intensive and non-fossil-fuel energy sources (IPCC 2007). We used stream temperature deltas that were adjusted for differential stream sensitivity, wherein the coldest streams are less sensitive to warming than the warmest streams (Isaak et al. 2015). To examine potential changes in the amount of suitable Finescale Dace habitat attributable to climate change, we summed the total stream length (km) in our study basin with a predicted P of 0.75 or higher (Guinotte and Davies 2014; Noviello et al. 2021) for each forecasted stream temperature scenario.

Site suitability rankings.—Candidate translocation sites at which we did not detect Finescale Dace ($n = 47$) were ranked based on (1) the predicted P in the SDM and (2) measures of distance to sites occupied by Finescale Dace in the NMDS analyses of fish community and habitat. We then summed the rank values for each site from each of the three analyses to achieve a final ranked score representing relative site suitability (i.e., $\text{rank}_{\text{final}} = \text{rank}_{\text{SDM}} + \text{rank}_{\text{fish}} + \text{rank}_{\text{habitat}}$). Predicted P for the base case scenario and for the mean of the three climate change scenarios (A1B 2040, A1B 2080, and $+3.0^{\circ}\text{C}$) were used to create two rankings: a base case summed rank and a climate change summed rank, respectively. To evaluate potential redundancy among analyses, we calculated Spearman's rank correlation coefficients (r_s) among site

ranks of SDM-derived predicted *P*, NMDS habitat, and NMDS fish (Hickerson and Walters 2019). All analyses and data compilation were performed in R (R Core Team 2019).

RESULTS

Finescale Dace Distribution in the Belle Fourche River Basin

Finescale Dace were present at 10.5% (13 of 124) of locations assessed in the basinwide fish survey data set from the years 2008–2019. Our contemporary surveys in 2018 and 2019 documented Finescale Dace at 26.5% (18 of 68) sites, including Blacktail Creek, Cox Lake, Cub Creek, Medicine Lake, Medicine Flat Creek, Middle Fork Hay Creek, Middle Redwater Creek, Mud Lake,

Spottedtail Reservoir, and Sundance Creek (Figure 1). We documented persistence at five locations with a history of managed translocation in Wyoming: Blacktail Creek, Cub Creek, Middle Fork Hay Creek, Lame Jones Creek, and Spottedtail Reservoir (Supplementary Figure 1).

Habitat and Fish Community Associations

In the MVA, our fish community NMDS ordination converged on a solution after 20 iterations (stress = 0.15) and transformed distances were well preserved against the observed distance matrix (linear fit: $R^2 = 0.90$; nonmetric fit: $R^2 = 0.98$). The first NMDS axis (NMDS1) separated sites largely by species origin, with nonnative species clustered at lower values and native species clustered at higher values (Figure 2). The second axis (NMDS2) portrayed a gradient from warmwater species at lower values to coldwater species at higher values. Convex hulls drawn around

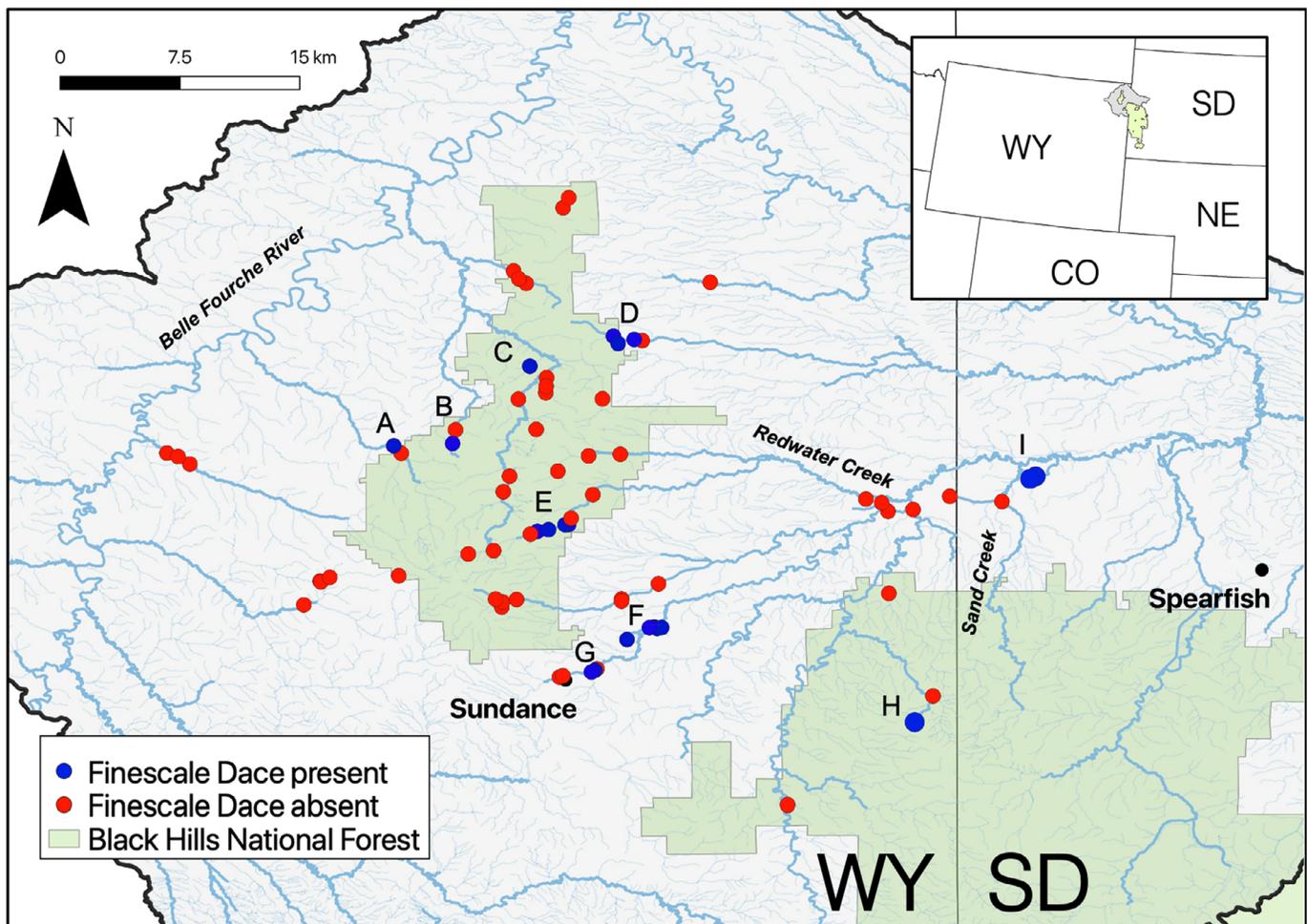


FIGURE 1. Distribution of Finescale Dace in the Belle Fourche River basin, Wyoming–South Dakota, from surveys conducted during 2018–2019. Drainages where we detected Finescale Dace are represented by letters A–I (A = Blacktail Creek; B = Lame Jones Creek; C = Cub Creek; D = Middle Fork Hay Creek; E = Middle Redwater Creek; F = Medicine Lake/Medicine Flat Creek; G = Sundance Creek; H = Spottedtail Reservoir; I = Cox and Mud lakes).

Finescale Dace-occupied and unoccupied sites demonstrated little overlap in species-space between these site groupings. Species that co-occurred with Finescale Dace included Brook Trout, Bluegill, Fathead Minnow, Longnose Dace, Rainbow Trout, and White Sucker.

The habitat NMDS ordination converged on a solution after 20 iterations (stress=0.12), and transformed distances were well preserved against the observed distance matrix (linear fit: $R^2=0.93$; nonmetric fit: $R^2=0.99$). The first axis (NMDS1) exhibited a gradient in sites based on emergent vegetation cover (%), with more cover at higher values and less cover at lower values (Figure 2). The second axis (NMDS2) portrayed gradients in the distance from standing water (m) and mean substrate classification; sites at or near standing water and with smaller substrates had higher values, and sites at a greater distance from standing water and with larger substrates had lower values. Sites with Finescale Dace present had higher values for both NMDS1 and NMDS2, suggesting an association with high emergent vegetation cover (%), standing water, and smaller substrate size.

These results aligned with output from random forest models; the association of Finescale Dace presence to predictor variables, listed in order of importance (mean decrease in Gini score shown in parentheses), was positive for the amount of emergent vegetation cover (11.19), nonlinear for linear stream distance from a standing waterbody (6.21), and negative for mean substrate size-

class (5.12) and exhibited little variance in response to turbidity (4.66; Figure 3). Classification accuracy measures indicated moderate predictive performance (PCC = 78.87; AUC = 0.72; $\kappa=0.45$), and the model provided a good fit to the data based on the randomization test ($P=0.001$). Visual inspection of partial dependence plots indicated that even low amounts of emergent vegetation cover greatly increased the predicted P for Finescale Dace.

Species Distribution Model and Forecasted Stream Warming

The variable selection process for the SDM retained three predictor variables and had out-of-bag error prediction rates ranging from 0.20 to 0.25 among three ensemble models. User's accuracy, indicating how often the predicted class will occur in the data, was 81.5% for absences and 66.7% for presence points. The final model was a good fit to the data based on the randomization test ($P=0.001$). Mean August stream temperature ($^{\circ}\text{C}$) was the most important variable, with a mean decrease in Gini score of 6.9, followed by stream channel slope (5.61) and base flow index (4.64). The relationships between the predictors and Finescale Dace occurrence were nonlinear; the maximum predicted P for Finescale Dace occurred at a mean August stream temperature of 13–14 $^{\circ}\text{C}$, a mean slope value of around 0.04%, and a mean base flow index value of 65% (Figure 3). Classification accuracy measures

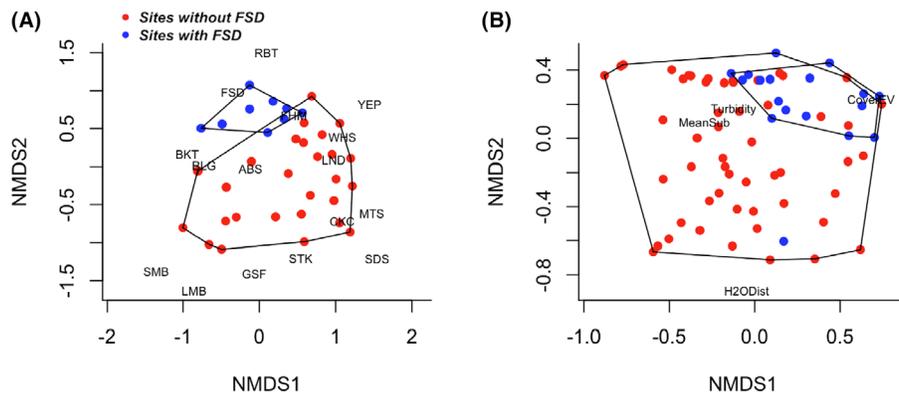


FIGURE 2. (A) Nonmetric multidimensional scaling (NMDS) ordination of fish occurrence data from 2018–2019 surveys in the Belle Fourche River basin ($n=68$). Convex hulls delineating sites where we detected Finescale Dace (FSD) and sites where we did not detect FSD indicated little overlap in the fish community between these groups of sites. The position of species codes indicates community-based distances between sites based on a Jaccard dissimilarity index (species codes: ABS = absent/no fish detected; BKT = Brook Trout *Salvelinus fontinalis*; BLG = Bluegill *Lepomis macrochirus*; CKC = Creek Chub *Semotilus atromaculatus*; FHM = Fathead Minnow *Pimephales promelas*; GSF = Green Sunfish *Lepomis cyanellus*; LMB = Largemouth Bass *Micropterus salmoides*; LND = Longnose Dace *Rhinichthys cataractae*; MTS = Mountain Sucker *Catostomus platyrhynchus*; RBT = Rainbow Trout *Oncorhynchus mykiss*; SDS = Sand Shiner *Notropis stramineus*; SMB = Smallmouth Bass *M. dolomieu*; STK = Brook Stickleback *Culaea inconstans*; WHS = White Sucker *Catostomus commersonii*; YEP = Yellow Perch *Perca flavescens*). (B) The NMDS ordination of habitat metrics measured during 2018–2019 surveys in the Belle Fourche River basin ($n=68$) is presented (habitat codes: MeanSub = mean substrate size-class; CoverEV = emergent vegetation cover; H2ODist = distance from a standing waterbody). The position of habitat codes indicates habitat-based distances between sites based on a Jaccard dissimilarity index. Convex hulls delineating sites where we did or did not detect FSD indicated that FSD occupied a subset of habitats represented along ordination axes.

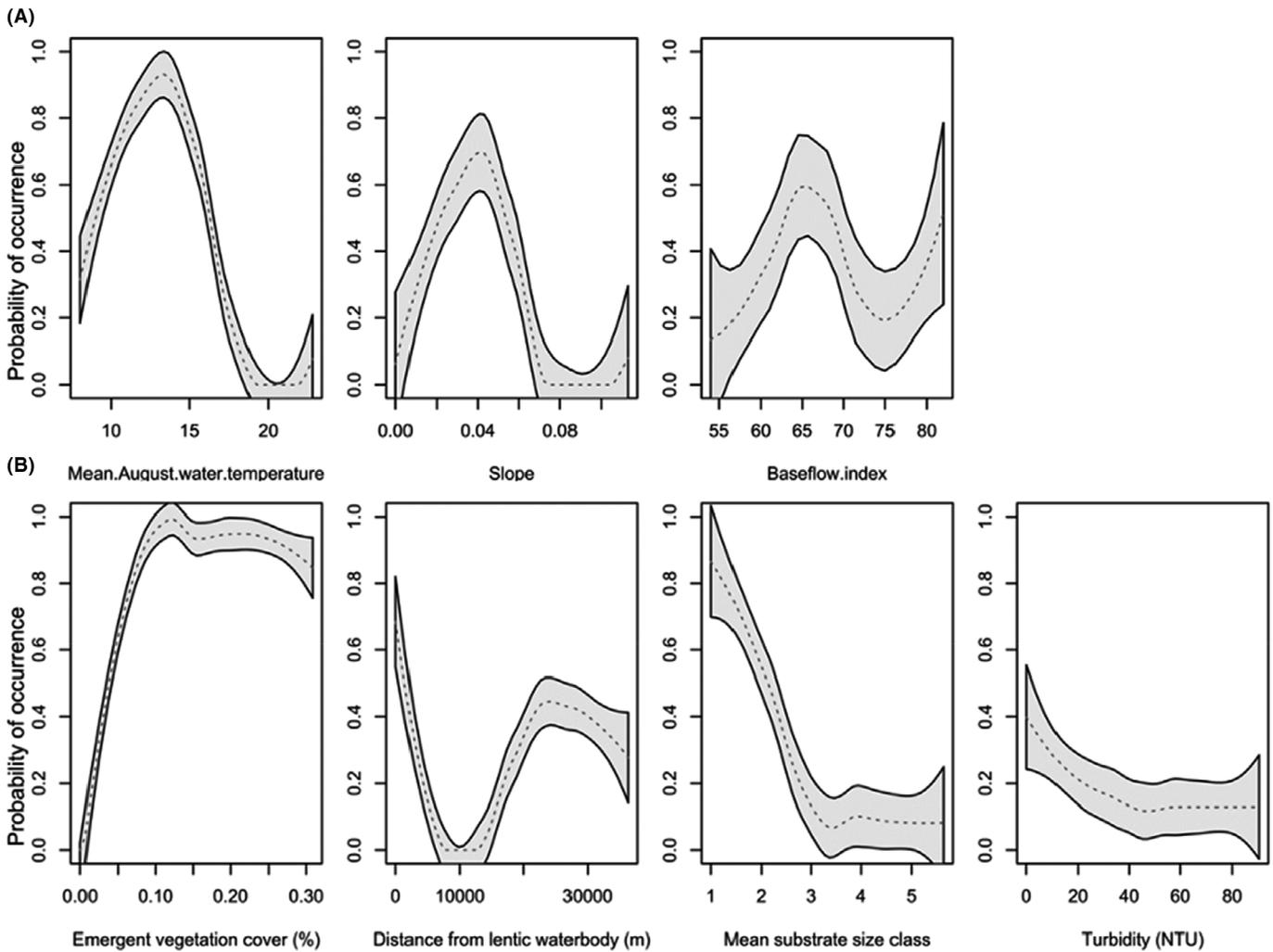


FIGURE 3. (A) Predicted probability of occurrence of Finescale Dace as a function of mean August stream temperature for 1993–2003 ($^{\circ}\text{C}$), stream channel slope (%), and base flow index (%) in partial dependency plots from the random forest model fitted with basinwide occurrence data from the period 2008–2019 in the Belle Fourche River basin. (B) Probability of occurrence of Finescale Dace is presented as a function of emergent vegetation cover (%), mean substrate size-class, distance from a standing waterbody (m), and turbidity (NTU) in partial dependency plots from the random forest model fitted with site-level habitat data collected during 2018–2019 in the Belle Fourche River basin. Plots in both panels are fitted with a LOESS (locally estimated scatterplot smoothing) curve.

indicated moderately good predictive performance ($\text{PCC} = 76.92$; $\text{AUC} = 0.73$; $\kappa = 0.47$).

The amount of suitable habitat for Finescale Dace, measured in stream length (km), with a predicted P of at least 0.75, was 133 km under the base case scenario, representing mean August stream temperatures from 1993 to 2003. The effect of forecasted stream temperature on the predicted P for Finescale Dace in stream reaches was variable, but under all examined scenarios the frequency of stream reaches with a predicted P of at least 0.75 decreased (Figure 4; Supplementary Table 2). Relative to the base case scenario, the climate change scenarios AB1 2040 and AB1 2080 yielded losses of 60 and 86 km of suitable habitat, respectively. The most extreme climate

change scenario, a future increase in stream temperature of 3.0°C , resulted in a loss of 127 km of suitable habitat in comparison with the base case scenario. Relative to the base case stream temperature scenario, the mean climate change predicted P was lower or equivalent for most of the candidate translocation sites (Figure 5; Supplementary Table 2; paired Wilcoxon's signed rank test: $P < 0.00001$). There was no clear spatial clustering of sites relative to predicted P sensitivity to climate change (Figure 6).

Site Suitability Ranks

Summed ranks from each analysis yielded suitability scores for 47 sites where Finescale Dace were not detected in 2018–2019. Sites in the top 25% of all summed rank

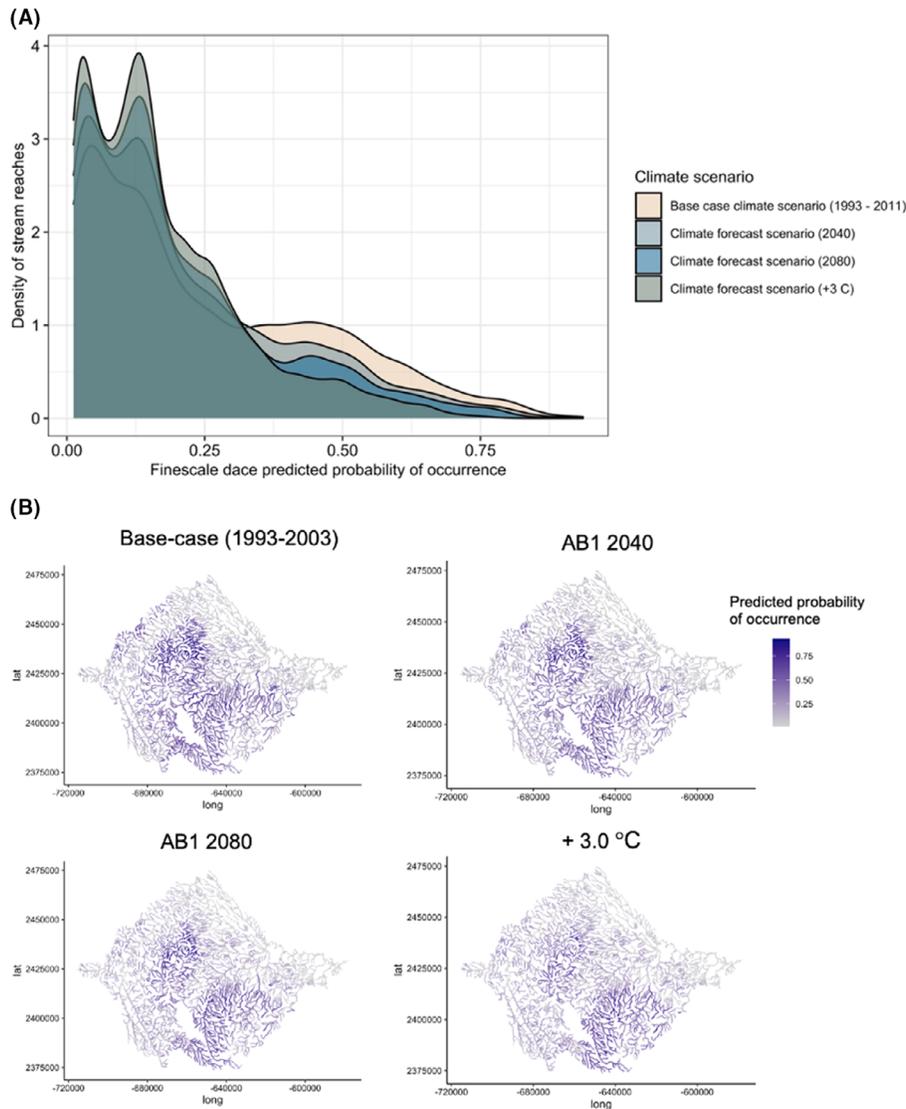


FIGURE 4. (A) Density plot depicting the frequency of occurrence of stream reaches at a given predicted probability of occurrence (P) of Finescale Dace under stream temperature scenarios representing mean August water temperature ($^{\circ}\text{C}$) for a base case scenario from 1993 to 2003, global climate model projections based on an ensemble of Intergovernmental Panel on Climate Change climate models for the northwestern USA (AB1) for 2040 (AB1 2040) and 2080 (AB1 2080) and a 3.0°C increase ($+3.0^{\circ}\text{C}$) in stream temperature. Increased warming under climate change scenarios decreased the predicted frequency of occurrence of stream reaches with a predicted P of at least 0.50. (B) Maps depict the predicted P of Finescale Dace in the Belle Fourche River basin for the base case (1993–2003), AB1 2040, AB1 2080, and $+3.0^{\circ}\text{C}$ stream temperature scenarios from the species distribution model (random forest classification) fitted with fish occurrence data from the period 2008–2019. Lines shaded in darker blue indicate a higher predicted P , while lighter areas indicate a lower predicted P .

scores within or near drainages that were historically occupied by Finescale Dace or in close proximity to existing populations included Blacktail, Lane Jones, Middle Redwater, Rocky Ford, and Sundance creeks (Figure 6; Table 2). Sites in the top 25% of predicted P without a documented history of Finescale Dace occurrence or stocking were located in the Beaver and Beaverdam Creek drainages. The top-two ranked sites were consistent between the base case and climate change scenarios, but some sites showed substantial shifts and dropped out of

the top 25% completely (e.g., Sundance Creek [sndnck_03] declined in rank from 7 to 21), while others moved up to the top 25% (e.g., Whitelaw Creek [whlck_03] ascended in rank from 13 to 4; Table 2; Supplementary Table 3).

Spearman's rank correlations between the habitat NMDS and SDM predicted P indicated low negative and positive correlations (predicted $P_{base\ case}$: $r_s = 0.08$; predicted $P_{climate\ change}$: $r_s = -0.12$; Supplementary Table 4). Correlations between fish NMDS ranks and the three

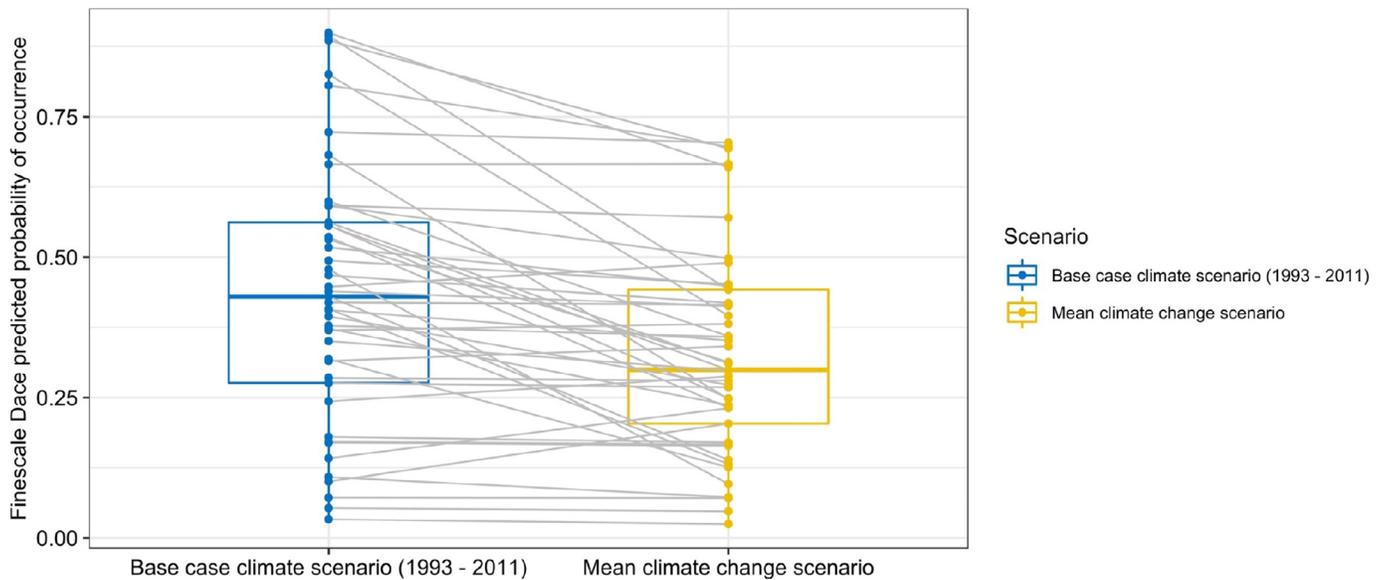


FIGURE 5. Paired plot of the predicted probability of occurrence (P) for Finescale Dace at unoccupied sites surveyed in 2018–2019 for the (1) base case (1993–2003) stream temperature scenario and (2) mean climate change scenario, averaging the predicted P from the ABI 2040, ABI 2080, and +3.0°C stream temperature scenarios (defined in Figure 4). The predicted P for Finescale Dace was lower under the mean climate change scenario for most candidate translocation sites (paired Wilcoxon's signed rank test: $P < 0.00001$). Notably, several locations exhibited relative stability in their suitability for Finescale Dace under the mean climate change scenario.

habitat-related ranks were minimal (predicted $P_{base\ case}$: $r_s = -0.04$; predicted $P_{climate\ change}$: $r_s = -0.04$; habitat NMDS: $r_s = -0.04$). The correlation between the base case and climate change predicted P was positive ($r_s = 0.76$; Supplementary Table 4).

DISCUSSION

The conservation of imperiled freshwater fishes in the face of climate change will necessitate flexible and proactive efforts, such as managed translocations. We used new and historical occurrence data for a climate relict population of Finescale Dace in the Black Hills of Wyoming and South Dakota to elucidate species–environment relationships, with the explicit aim of informing targeted management actions for this species at the southern edge of its North American range. We documented the persistence of translocated Finescale Dace populations at 38% (5/13) of surveyed locations in our study area—a notable finding given the largely unsuccessful nature of fish translocations in other systems (Hendrickson and Brooks 1991). These results provide evidence of both success and failure, which can guide future translocation considerations for Finescale Dace in the study area. Although our study drew heavily from historical fish records, our field observations during 2018–2019 were critical for establishing an updated baseline of Finescale Dace distribution in the Wyoming Black Hills. Our use of SDMs improves on other translocation studies, which did not develop spatially explicit predictions

of habitat suitability in their study areas (Harig and Fausch 2002; Hickerson and Walters 2019). In addition, the inclusion of future stream warming scenarios provides insight into which sites will be more sensitive to climate change. Collectively, patterns from this study demonstrated the relatively narrow habitat breadth and low degree of species co-occurrence with Finescale Dace in the study area, highlighting the abiotic and biotic dimensions of rarity (i.e., range size, habitat breadth, and patterns in species co-occurrence; Rabinowitz 1981).

Our approach using a predictive model to examine environmental correlates to Finescale Dace occurrence provides a means for managers to assess habitat suitability in areas where little or no previous data collection has occurred. For example, unsampled streams with a predicted P of at least 0.75, including Akers Canyon, Alum, South Fork Hay, and Slaybaugh creeks, could be targets for additional sampling efforts aimed at further characterizing the biotic and abiotic suitability of other candidate translocation sites in the study area (Young et al. 2019). Furthermore, the nonlinear relationships exhibited by mean August water temperature (°C) and stream channel slope (%) variables in the SDM indicate that these environmental traits could have a strong filtering effect on Finescale Dace occurrence within the Belle Fourche River basin. The importance of temperature is suggested by the sharp decrease in predicted P at sites with mean August stream temperatures above 16°C (Figure 3) and by the decline in predicted P for most sites under projected

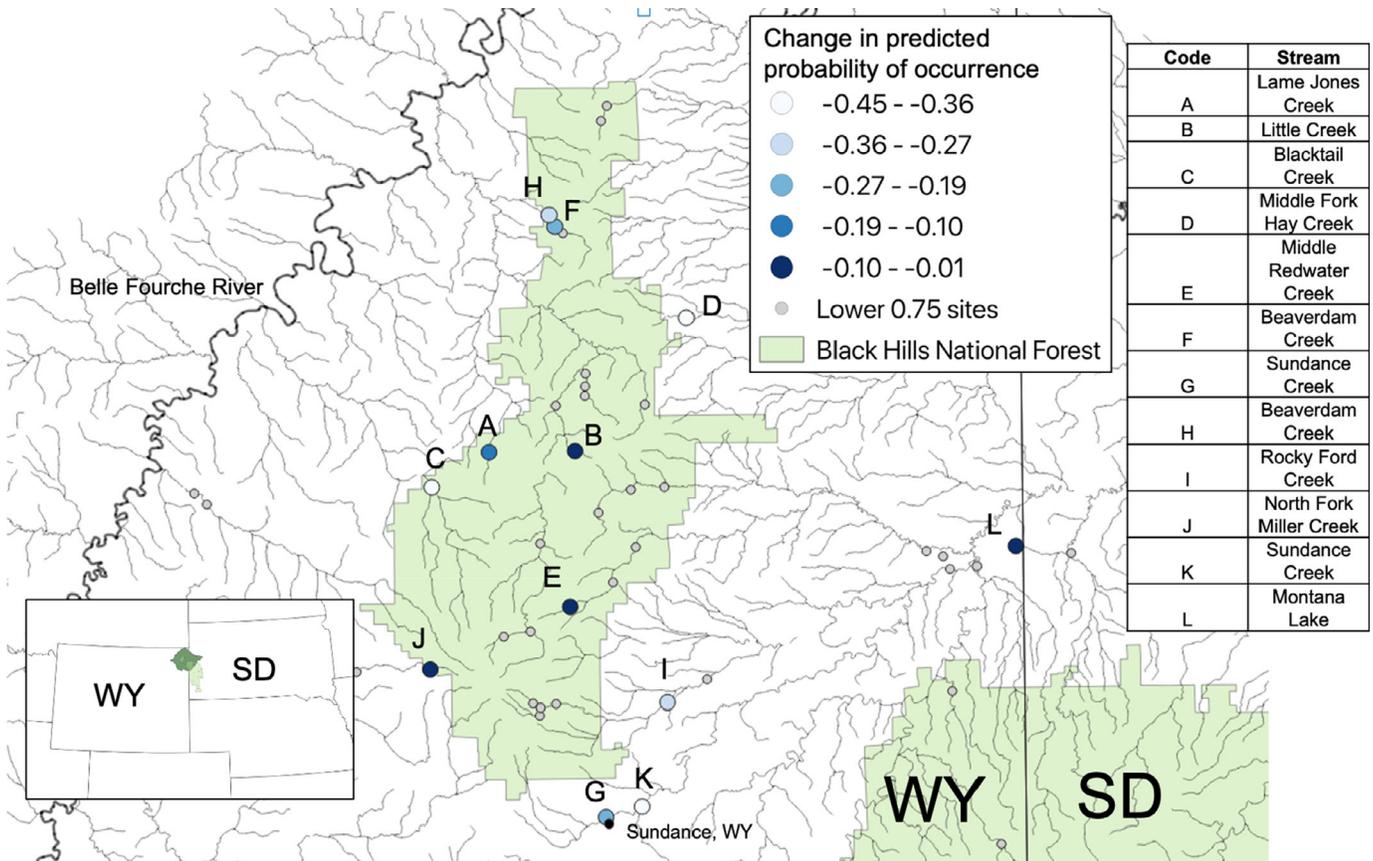


FIGURE 6. Potential translocation sites in Belle Fourche River basin drainages without detections of Finescale Dace. Darker points represent sites that have lower-magnitude delta values for the change in predicted probability of occurrence between base case and mean climate change stream temperature scenarios and thus are potentially less sensitive to future stream warming. Sites in the top 25% of ranks from our analysis are labeled with letters, while sites in the lower 75% of rankings are included without labels.

warming scenarios. While this finding aligns with the Finescale Dace’s geographic range as a northern species, limited physiological data suggest that Finescale Dace can withstand highly variable thermal conditions, with an upper lethal temperature of around 30°C (Brett 1944). Thus, the importance of water temperature for Finescale Dace likely depends on other important environmental factors (e.g., hydrology and biotic interactions).

Our sampling strategy in 2018–2019 emphasized delineating the distribution of Finescale Dace across the Belle Fourche River basin but did not account for imperfect detection (MacKenzie et al. 2002). However, the fish sampling methods used for our surveys during 2018–2019 (e.g., standardized passive gear sets in standing waters and backpack electrofishing in streams) were also used in a repeat-visit sampling design at the Niobrara River in 2018. In that sampling, naïve detection probabilities were 0.73 (SE = 0.19) during an early sampling period in June and July and 0.94 (SE = 0.06) during a late sampling period in September, with seasonal variation likely related to flow (Booher 2020). Our experience in the Niobrara River

basin suggests that our methods likely produced at least moderate detection of Finescale Dace in the Belle Fourche River basin but may represent a conservative estimate of Finescale Dace occurrence, especially during the early season when flows are higher.

Clustering of Finescale Dace sites in the habitat NMDS ordination indicated correlates to Finescale Dace occurrence in our study area, with potential implications for site-specific factors leading to successful translocations of this species. The relatively high incidence of lakes, reservoirs, and relict beaver ponds at or near sites with Finescale Dace was exhibited in the negative relationship to the measured distance from a standing waterbody (m). These waterbodies may provide fish with refugia related to seasonal and interannual hydroclimatic variability. While not directly measured, we observed that springs fed several waterbodies where Finescale Dace were present, including Lame Jones Creek, Medicine Lake, Cox Lake, and Mud Lake. Although anecdotal, these observations suggest that groundwater plays an important role in maintaining suitable conditions by providing perennial

TABLE 2. Study sites representing the top 25% for ranked suitability for the base case (1993–2003) stream temperature scenario, calculated as the sum of ranks from multivariate distance measures of (1) fish community and (2) habitat between sites with and without Finescale Dace and (3) predicted probability of occurrence (P) extracted from the species distribution model (SDM) used to evaluate P for Finescale Dace in stream reaches across the Belle Fourche River basin (NMDS = nonmetric multidimensional scaling; site identification codes [IDs] are defined in Supplementary Table 1). Predicted P and summed ranks of translocation suitability from the mean climate change scenario (derived from the three examined future stream temperature scenarios; see Methods) are provided for comparison to base case values. The ΔP represents the change in predicted P between the base case and mean climate change stream temperature scenarios. Final ranks are shown in parentheses after the base case and climate change summed ranks.

Site ID	Distance		Distance		SDM		SDM		SDM		ΔP
	fish NMDS	Fish rank	habitat NMDS	Habitat rank	base case	base rank	base case	base rank	climate change	climate rank	
lamjock_02	0.88	6	0.34	9	0.81	5	20 (1)	0.70	2	17 (1)	-0.11
litleck_06	0.95	9	0.37	11	0.59	10	30 (2)	0.57	6	26 (2)	-0.02
blktlck_01	0.95	8	0.52	19	0.83	4	31 (3)	0.40	14	41 (6)	-0.43
mfhayck_01	1.68	33	0.12	1	0.89	2	36 (4)	0.44	10	44 (7)	-0.45
mredwtc_11	0.95	9	0.29	6	0.44	21	36 (5)	0.41	13	28 (3)	-0.03
bvrdmck_27	1.18	19	0.32	8	0.56	12	39 (6)	0.31	21	48 (10)	-0.25
sndnck_03	1.19	20	0.45	15	0.68	7	42 (7)	0.25	29	64 (21)	-0.43
bvrdmck_01	1.42	26	0.19	4	0.56	13	43 (8)	0.25	28	58 (16)	-0.31
rkyfdck_21	0.95	8	0.44	14	0.41	24	46 (9)	0.13	38	60 (17)	-0.28
nfmilck_05	0.95	9	0.41	13	0.41	25	47 (10)	0.35	18	40 (5)	-0.05
sndnck_02	0.97	17	0.48	18	0.56	14	49 (11)	0.30	22	57 (15)	-0.26
montlak_01	0.95	8	0.14	3	0.17	38	49 (12)	0.16	36	47 (9)	-0.01

surface water and buffering against changes in air temperature (Snyder et al. 2015). One highly ranked translocation site, Montana Lake, is notable as a site that formerly harbored Finescale Dace (Evermann and Cox 1896). The mechanism driving extirpation of Finescale Dace in Montana Lake is unknown, although the lake reportedly dried up in the 2000s (B. Bradshaw, Wyoming Game and Fish Department [WGFD], personal communication). The potential desiccation of habitat that formerly supported Finescale Dace suggests that (1) a better understanding of hydrologic variability in this system is critical when identifying sites with the capacity to support long-term persistence of native fishes and (2) dewatering could have been a causal factor for failed translocations at other sites.

Patterns in fish species co-occurrence and habitat associations between sites with and without Finescale Dace demonstrated realized niche spaces that are consistent with this species' classification as a climate relict species in the Great Plains. The low degree of overlap between these two site groupings suggests that Finescale Dace are not a common member of the global fish fauna within our study area. The relatively small distance between Finescale Dace and fishless sites in the NMDS ordination (ABS in Figure 2) provides an indication that when other critical habitat parameters are met, fishless waters may be a viable option for consideration as translocation sites. For example, the highly ranked Middle Redwater Creek site is a fishless site

upstream of a current Finescale Dace stronghold. The positions of fishes in species-space in our NMDS ordination were consistent with the findings of Jackson (2002), who demonstrated negative associations between small-bodied native cyprinids and introduced centrarchid species in Ontario lakes. Additional studies from north temperate ecosystems provide strong evidence that where introduced, species like Largemouth and Smallmouth bass can profoundly alter the composition and structure of native fish assemblages (He and Kitchell 1990; Findlay et al. 2000). The apparent clustering of Finescale Dace in our NMDS ordination with coolwater and coldwater species, such as Brook and Rainbow trout, could indicate similar thermal preferences and potential overlap in habitat affinities among these fishes in our study area.

The complementary models addressing abiotic and biotic drivers of the Finescale Dace's distribution provide a more comprehensive and robust evaluation of potential translocation sites. The lack of correlation between the ranks derived from the habitat NMDS and SDM indicate that these measures of site suitability were not redundant in the analysis and may identify environmental correlates to Finescale Dace that operate at different spatial scales. Similarly, the rank derived from the fish community NMDS exhibited little correlation to the habitat NMDS or SDM ranks, indicating that site-level biotic suitability for Finescale Dace may be highly context dependent. The use of multiple methods can provide managers with the

means to independently assess ecological patterns stemming from abiotic or biotic processes, which may promote or threaten the persistence of a target species.

The analytical approaches also differ in their strengths and weaknesses. The MVAs require extensive field sampling that may be expensive to carry out in a rigorous manner across broad spatial scales. They do, however, provide insights into factors (e.g., emergent vegetation cover, turbidity, and nonnative predator presence) that have clear mechanistic relevance for Finescale Dace (Stasiak 1972; Booher and Walters 2021). Collection of these data could be implemented by managers with a rapid habitat or fish protocol similar to the field methods used in this study. Alternatively, the SDMs require less fieldwork but present tradeoffs in effort required toward data acquisition and management. Historical data often require aggregation across state, federal, and tribal entities, and for data-poor species the availability of such data will be limited. In addition, the mechanistic linkages for some variables may be less clear. However, the results can be extrapolated across space and time, thus increasing predictive power and allowing the incorporation of climate change scenarios.

One advantage to our approach is that it considers future climate conditions, as managers are becoming increasingly aware of the need to incorporate climate change into management decisions (Ficke et al. 2007). Another potentially useful analysis could incorporate fish occurrence data at broader spatial scales into translocation ranking criteria to evaluate the risk of invasion by nonnative fishes. Patterns in fish communities at a larger scale may be particularly important when considering future changes to fish assemblages, as invasive fishes have been shown to colonize and persist under highly variable environmental conditions (Jarić et al. 2014; McCallum et al. 2014).

The trend toward an increased emphasis on management to conserve native fishes throughout the USA will likely increase the call for translocations as a way to mitigate the widespread loss of fish biodiversity (Dudgeon et al. 2006). Translocation evaluations focusing on well-studied species, such as Cutthroat Trout *Oncorhynchus clarkii*, can leverage known habitat requirements of their study species (Wagner et al. 2001; Peterson et al. 2004; Roberts et al. 2013). For less-studied native nongame fishes, our study represents a flexible modeling framework with utility for applied fisheries conservation. We incorporated the limited a priori knowledge of Finescale Dace in our study system with contemporary and historical surveys to develop indices of site suitability. We also considered future stream warming scenarios to assess site suitability into the future, which is especially important for climate relict species (e.g., Finescale Dace) whose occurrence is strongly related to temperature. Our results

suggested potential translocation sites that included a mix of historical localities and new drainages, providing managers with flexibility to implement our results based on considerations of habitat conditions and fish community composition. This approach may be transferable to efforts to conserve other wild animal populations in data-limited systems and will be an increasingly important tool for conserving biological diversity from regional to global scales.

ACKNOWLEDGMENTS

We thank the private landowners of Crook County, Wyoming, and Lawrence County, South Dakota, for providing site access. We are also grateful to seasonal technicians Andrew Kaneb and Taren Giberti for assistance in the field. Bill Bradshaw and Gordon Edwards (WGFD), Chelsey Pasbrig and Greg Simpson (South Dakota Department of Game, Fish, and Parks [SDGFP]), and Steven Hirtzel (U.S. Forest Service) provided data, assistance in the field, or advice in project planning. Historic fish survey data were provided by WGFD, the South Dakota Natural Heritage Database, and SDGFP. This project was funded by WGFD through U.S. Fish and Wildlife Service State Wildlife Grant 1003586. Field data (2018–2019) were collected under Chapter 33 Permit 1177 from WGFD, under Scientific Collector's Permit 41 and an Endangered Species Permit from SDGFP, and in accordance with Protocol 20180625AW00316-01 approved by the Institutional Animal Care and Use Committee at the University of Wyoming. We thank Bryan Maitland and two anonymous reviewers for suggestions that improved the manuscript during peer review. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. There is no conflict of interest declared in this article.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.