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Fish Assemblage Structure in Black Hills, South Dakota Streams

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ABSTRACT Understanding factors structuring fish assemblages in a particular area is valuable to both sport fishery management and native species conservation. Fish assemblages in the Black Hills are unique to South Dakota because they contain economically valuable introduced salmonids as well as native species of conservation need. Our objective was to examine the relationship between fish assemblages and geomorphic and reach-scale habitat features across multiple stream reaches in the Black Hills. Canonical correspondence analysis, a direct gradient ordination analysis, indicated that factors operating at multiple spatial scales interacted to structure fish assemblages. There also was indication of segregation between native species and introduced salmonids. Fish assemblages were primarily structured by variables related to longitudinal stream gradients, followed by reach-scale habitat factors and biotic interactions. Habitat associations of fishes from this study provide insight into their ecology and can aid effective fisheries management in the Black Hills.

KEY WORDS Black Hills, canonical correspondence analysis, environmental gradients, fish assemblage structure, South Dakota

Understanding factors involved in the distribution and abundance of organisms across the landscape is a fundamental challenge in community ecology. Factors structuring fish assemblages are of interest in stream ecology (Matthews 1998). Biotic and abiotic filters interact across broad hierarchical spatial and temporal scales to structure species composition within a given stream reach (Tonn 1990). Human interactions (e.g., habitat perturbations, species introductions) may greatly influence fish assemblages and circumvent natural structuring forces (Ross 1991, Jones et al. 1999, Rahel 2000, Lau et al. 2006). For these reasons, an understanding of the response of fish populations and fish assemblages to environmental variation or disturbance is of interest to fishery managers (Lyons 1996). By examining the factors that structure a fish assemblage, fishery managers can characterize diagnostic landscape- and reach-scale biotic and abiotic features influential to fish assemblages (Lyons 1996) and identify factors that management actions can effectively target (Quist et al. 2005).

Historically, the Black Hills of South Dakota contained a relatively depauperate native fish fauna consisting of mountain sucker (*Catostomus platyrhynchus*) and longnose dace (*Rhinichthys cataractae*) throughout the area. Scattered populations of white sucker (*C. commersoni*), creek chub (*Semotilus atromaculatus*), and fathead minnow (*Pimephales promelas*) are considered to be native to the lower portions of drainages (Dodge 1876, Bailey and Allum 1962, Koth 2007). Other species (e.g., lake chub [*Couesius plumbeus*], finescale dace [*Phoxinus neogaeus*], and longnose sucker [*C. catostomus*]) were present in isolated populations but many appear to have been extirpated (Isaak et al. 2003). The introduction of three species of salmonids (e.g., brook trout [*Salvelinus fontinalis*], brown trout [*Salmo trutta*], and rainbow trout [*Oncorhynchus mykiss*]) increased total species richness and these fishes now constitute the majority of fish biomass in

many stream reaches where their natural reproduction occurs. Our objective was to examine the relationship between fish assemblages and geomorphic and reach-scale habitat features in the Black Hills of South Dakota. Using multivariate analyses, we evaluated how individual fish species respond to environmental gradients and interpret ecological patterns. Furthermore, understanding factors that structure fish assemblages can be used to evaluate sport fish potential of stream reaches or areas of conservation interest for native fishes in the Black Hills.

Study Area

The Black Hills are a ponderosa pine (*Pinus ponderosa*) forested dome shaped uplift surrounded by mid- and short-grass prairie and represent an island of suitable habitat for montane and forest-dwelling species, both aquatic and terrestrial. Streams in the Black Hills originate near the center of this uplift and increase in width and discharge from groundwater seepage as they flow radially outwards to the surrounding plains. Forest management practices in the Black Hills have increased tree cover across much of the Black Hills relative to historic levels (Brown and Sieg 1999). Increased canopy cover has likely resulted in decreased stream baseflow due to evapotranspiration and, in combination, increased allocthanous carbon input and reduced autocthanous stream production. Similarly, local geology and land use can have a substantial effect on stream hydrology and fish distribution in the Black Hills, especially in dry years. Streams passing through sedimentary formations that encircle the Black Hills uplift lose much or all of their surface discharge as they flow north and east towards the plains across this Loss Zone (Williamson and Carter 2001). Mining activities (Rahn et al. 1996) and stream habitat degradation from livestock grazing (Modde et al. 1986) have altered fish assemblages in some

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streams. Of the native fishes in the Black Hills, the South Dakota Department of Game, Fish and Parks lists mountain sucker, longnose sucker, finescale dace, and lake chub as species of greatest conservation need (SDGFP 2006).

METHODS

Fish and habitat sampling

To evaluate how geomorphic and local habitat factors influence the distribution of fishes, we sampled fish and physical habitat in May–August 2008–2010, during baseflow conditions. Sampling reaches were located across the Black Hills to capture the variation in stream networks throughout the study area (Fig. 1; Schultz 2011). We placed block nets at the upstream end of each 100-m sample reach, and single-pass electrofished sample reaches in an upstream direction with one or two backpack electrofishers (Halltech HT-2000, Guelph, ON, Canada; Smith Root LR-24, Vancouver, WA, USA; Engineering Technical Services ABP-3-300, University of Wisconsin, Madison, WI, USA); we sampled streams with mean width exceeding 6 m with 2 electrofishers. We adjusted output at each sample reach to a level that allowed fish to be captured; captured fishes were identified to species and counted. Fish density (fish · m⁻²) was calculated as the number of individuals of each species captured divided by the total area of each sampling reach. Although stocking of non-native trout is a common fishery management action in the Black Hills, it is concentrated in reservoir and high angler-use areas. Our sampling did not closely overlap these areas and hatchery produced trout, which have degraded fin condition relative to naturally reproduced trout, were considered separately from other trout.

In each sample reach we quantified physical stream habitat (Table 1). We quantified stream habitat along transects that were measured at the midpoint of each electrofished sample reach, and 25 m upstream and downstream from the midpoint. Along each transect, we measured water depth (cm), dominant substrata (after Platts et al. 1983), velocity (m/s; Marsh McBirney Flo-Mate, Hach Company, Loveland, CO, USA), percent terrestrial and emergent vegetation coverage, and periphyton coverage within each of five evenly-spaced 33 cm × 33 cm quadrats. We visually estimated periphyton coverage as the percent of substrate within each quadrat containing algal filaments or an adnate algal turf. At the middle transect of the sample reach, we estimated primary productivity from substrata and stream water placed into a transparent resealable bag (see Gelwick and Matthews 1992 for detailed methodology). We measured canopy cover with a convex densitometer and computed discharge for each reach using the velocity-area method. We estimated the geomorphic variables channel slope, Strahler stream order (see Strahler and Strahler 1979 for explanation of ordering system), and elevation from GIS data layers that were developed by the

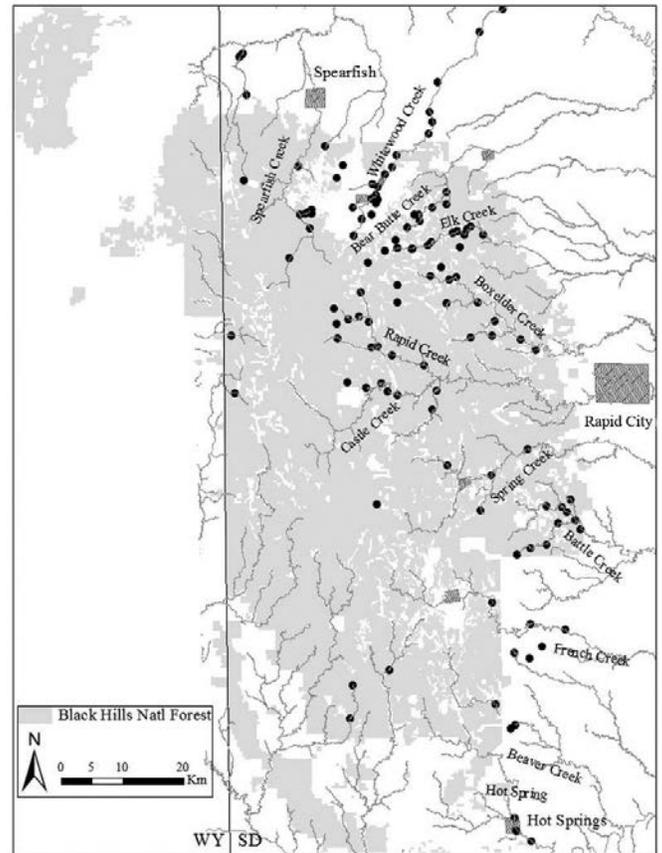


Figure 1. Locations sampled 2008–2010 in the Black Hills of South Dakota to assess species-habitat associations of native and introduced fishes.

Black Hills National Forest from 1:24000 scale topographic maps (Dauwalter and Rahel 2008). These geomorphic attributes were computed for stream segments 1–10 km in length, usually located between tributary confluences. Protocols for research involving vertebrate animals were approved by the SDSU Institutional Animal Care and Use Committee under permit 09-054A.

Multivariate Fish Assemblage Analysis

We used canonical correspondence analysis (CCA) to analyze the multivariate response of fish assemblage structure to multiple habitat factors across the Black Hills. This technique is a direct gradient analysis that uses empirically-derived species and environmental data to create multivariate gradients that maximize dispersion among species and environmental variables in ordination space and identify important variables in community composition (ter Braak 1995, ter Braak and Verdonschot 1995). We constructed ordination biplots to help visualize dispersion of species along eigenvectors weighted by environmental variables.

We included eight reach-scale and three geomorphic habi-

Table 1. Segment-scale and reach-scale habitat variables (unit) included in multivariate analyses of fish assemblage patterns in the Black Hills of South Dakota, 2008–2010.

Variable	Description
Geomorphic	
Ord	Strahler order
Elev	elevation (m)
Slope	gradient, channel slope (m/km)
Sample reach habitat	
Dep	depth, mean (cm)
Sub	substrate, mean particle size (mm)
SubVeg	in-channel submergent vegetation (mean %)
Terr	in-channel terrestrial vegetation (mean %)
Peri	periphyton coverage (%), mean ($\log_{10} + 0.001$) transformed
Can	canopy cover (%)
Prod	primary productivity (g O ₂ /L/hour) (Gelwick and Matthews 1992)
Disch	discharge (m ³ /s)

tat variables in the CCA (Table 1). For any pair of redundant variables ($r > 0.60$), we retained the variable to which fish density was more responsive (e.g., more biologically meaningful based on knowledge of the system) in further analyses, and the other explanatory variable was eliminated. For example, mean and maximum depth and velocity and discharge were strongly correlated ($r = 0.88$ and $r = 0.78$, respectively), but mean depth was a more logical predictor of fish density across the Black Hills based on experience sampling in the region. Thus, maximum depth and velocity were omitted from further analyses. We standardized the fish species matrix for the CCA to the density of fish of each species captured in each sample reach. To minimize the influence of rare species in the analysis, species were only considered in the CCA if they were present in more than five sample reaches (>5% of total sample reaches). To eliminate heteroscedasticity, we \log_{10} transformed periphyton data.

Initially, all candidate variables were included in the CCA. In addition to our initial variable screening, we used variance inflation factors (VIFs) to assess independence of variables included in the analysis within the CCA. Variance inflation factors greater than 20 indicate correlation among variables (ter Braak and Verdonschot 1995); variables with VIFs exceeding 20 were eliminated from the CCA. Other 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). The final CCA from this iterative process was used for interpretation of species-habitat associations. To infer habitat associations of individual species, our ordination biplot contained species and environmental scores.

RESULTS

We sampled fish assemblages and stream habitat in 103 stream reaches that represented variability of streams throughout the Black Hills of South Dakota from 2008–2010 (Fig. 1). Sample reaches were distributed widely across the study area, Strahler stream order ranged from 2 to 5 and elevation ranged from 862 to 1,916 m above sea level. Mean wetted width ranged from 0.9 to 10.6 m ($\bar{x} = 4.1$ m, SE = 0.24), and mean depth ranged from 6.9 cm to 60.8 cm ($\bar{x} = 25.4$ cm, SE = 1.06). Stream substrate was generally cobble and rubble, but slack water portions of channels accumulated finer sediments and organic debris. Naturally reproduced (wild) salmonids represented >90% of total fish abundance in 34% (35/103) of the stream reaches we sampled. Three general assemblage types repeated across stream orders in our analysis of fish relative frequency: brook trout zone, native zone, and brown trout transitional zone. In general, brook trout dominated the fish assemblage in cold, narrow headwater streams, and as water temperature, stream width and stream order increased, peak abundance transitioned from brook trout to mountain sucker and longnose dace, followed by brown trout, and finally white sucker and shorthead redhorse (*Moxostoma macrolepidotum*) as streams flowed out of the highlands and onto the prairie (Fig. 2). Further, introduced salmonids (primarily wild brown trout) were more abundant in the northern Black Hills (e.g., Crow, Spearfish, and Lower Rapid Creek watersheds), whereas eurythermal generalists (e.g., creek chub and longnose dace) were more abundant in the southern Black Hills (e.g., Spring, Battle, French, and Beaver Creek watersheds). Within the northern Black Hills, Elk, Bear Butte, and Whitewood creeks contained mostly native fish assemblages.

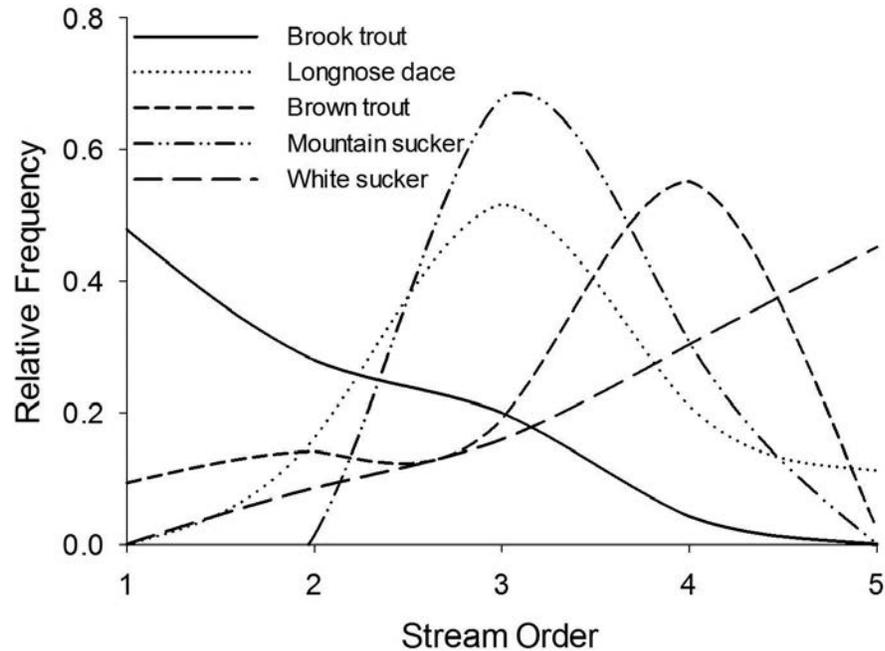


Figure 2. Relative frequency of five fish species along longitudinal gradients in the Black Hills of South Dakota during 2008–2010. Relative frequency is the percentage of total catch for each stream order sampled.

Species-habitat relationships

Ten species were included in the final CCA (Table 2); other species were excluded for rarity, including all trout of hatchery origin. Variable screening resulted in the retention of eight explanatory variables in the final CCA: mean depth, discharge, primary productivity, periphyton, submergent vegetation, stream order, elevation, and gradient. Variables included in the final CCA were not redundant ($r < 0.60$); no retained variables had VIFs > 5 . In the CCA, the first two axes explained 54.5% and 16.9%, respectively, of the variation in species abundance among sample reaches. Stream order, channel slope, periphyton, and elevation were stronger gradients than the other variables analyzed. The first CCA axis was explained by variation in order, elevation, and depth. Higher order, deeper reaches with greater discharge were located on the right side of CCA axis 1, while higher elevation reaches were located on the left. The second CCA axis was explained by periphyton, and channel slope (Table 2, Fig. 3). Reaches with high periphyton standing stocks were located near the bottom of CCA axis 2, whereas reaches with steeper gradient were located near the top.

Species centroids elucidated habitat associations of species across the Black Hills (Fig. 3). Brook trout were positioned furthest left on CCA axis 1, and were associated with higher gradient and elevation reaches. In contrast, rainbow trout, creek chub, fathead minnow, white sucker, and green sunfish (*Lepomis cyanellus*) were associated with higher discharge and depth. Mountain sucker was neutrally associated with CCA axis 1 but was positively associated with higher

periphyton. Longnose dace, the most frequently occurring native species, was located near the origin indicating no strong association with any habitat factor.

DISCUSSION

Stream fish assemblages in the Black Hills of South Dakota were structured by multiple interacting spatial scales. Biotic interactions also appear to be important; other work in the Black Hills suggest that native species and non-native trout have non-overlapping distributions (Schultz and Bertrand 2012). Concordant with fish assemblage patterns in other parts of the Rocky Mountains (e.g., Rahel and Hubert 1991), our multivariate analyses indicated that assemblages were primarily structured by variables associated with stream size (e.g., depth, order, elevation), followed by reach-scale habitat and biotic conditions. Microhabitat features (e.g., substrate, in-channel vegetation) did not strongly structure fish assemblages. Although habitat and biotic conditions in the Black Hills have been altered by human activities over the last two centuries (Modde et al. 1986), our analyses suggest fish assemblages still are influenced by habitat conditions. These habitat associations provide insight into the ecology of Black Hills fishes and might aid in effective fisheries management for the Black Hills.

Longitudinal stream gradients have long been recognized as influential in stream ecology (Vannote et al. 1980), particularly in forested stream systems. Increasing stream order influences a suite of physical habitat variables (e.g., habitat volume, stream temperature, allocthanous carbon sources;

Table 2. Weighted correlation matrix of stream habitat variables and species values with canonical ordination axes for Black Hills region of South Dakota, 2008–2010. Eigenvalues equal the dispersion of species scores on the axis and indicate the importance of the axis. Variable descriptions are provided in Table 1. Species are identified as native (N) or introduced (I).

Variable	Canonical axis		
	1	2	3
Habitat factors			
Dep	0.70	-0.17	-0.09
Peri	0.08	0.72	0.18
Disch	0.54	-0.44	-0.34
SubVeg	0.36	0.40	-0.32
Prod	0.19	-0.55	0.20
Ord	0.85	-0.22	-0.29
Slope	-0.50	0.34	-0.39
Elev	-0.80	0.05	-0.16
Species			
Mountain sucker <i>Catostomus platyrhynchus</i> (N)	-0.03	0.47	0.18
Longnose dace <i>Rhinichthys cataractae</i> (N)	-0.03	0.00	0.24
Brown trout <i>Salmo trutta</i> (I)	-0.05	-0.12	-0.38
Brook trout <i>Salvelinus fontinalis</i> (I)	-0.71	0.20	-0.01
Rainbow trout <i>Oncorhynchus mykiss</i> (I)	0.75	-0.72	-0.47
White sucker <i>Catostomus commersoni</i> (N)	0.58	0.12	-0.02
Creek chub <i>Semotilus atromaculatus</i> (N)	1.13	0.65	-0.25
Fathead minnow <i>Pimephales promelas</i> (N)	0.37	0.12	0.07
Green sunfish <i>Lepomis cyanellus</i> (I)	1.71	-0.21	0.74
Rock bass <i>Ambloplites rupestris</i> (I)	0.54	0.63	0.75
Eigenvalue (% variation explained)	0.280 (54.4)	0.087 (16.9)	0.064 (12.5)

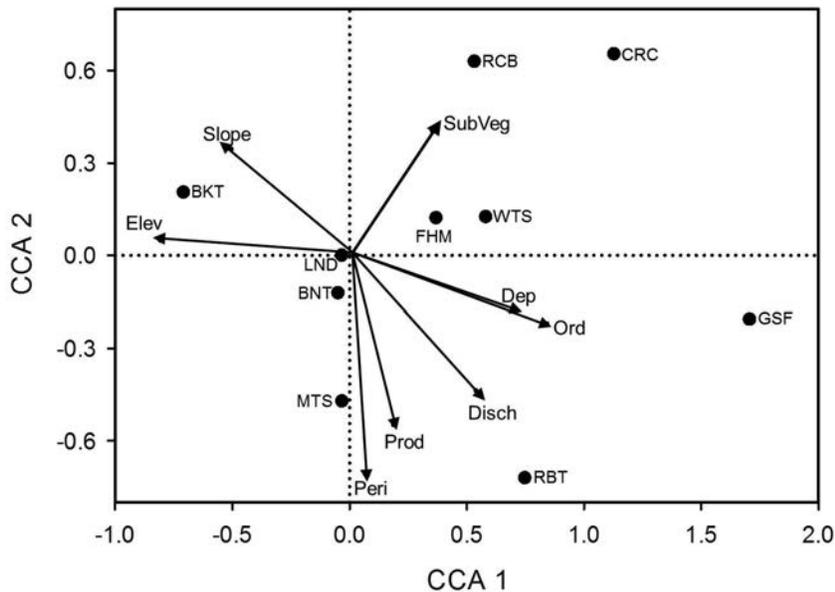


Figure 3. Individual species-habitat factor ordination from canonical correspondence analysis (CCA) ordination of fish assemblages in the Black Hills, South Dakota sampled 2008–2010. The ordination biplot illustrates the influence of three habitat variables on the distribution of 10 fish species in the Black Hills. Stream habitat variables are represented by vectors and species are represented by their abbreviations. Species codes: BKT – brook trout *Salvelinus fontinalis*, BNT – brown trout *Salmo trutta*, CCB – creek chub *Semotilus atromaculatus*, FHM – fathead minnow *Pimephales promelas*, LND – longnose dace *Rhinichthys cataractae*, MTS – mountain sucker *Catostomus platyrhynchus*, RBT – rainbow trout *Oncorhynchus mykiss*, RKB – rock bass *Ambloplites rupestris*, WTS – white sucker *C. commersoni*.

Matthews 1998), which are highly influential at structuring fish assemblages (Gorman and Karr 1978, Schlosser 1991). In the Black Hills, brook trout characterize cold, headwater systems (Modde et al. 1986) and other fishes tend to be added to the assemblage downstream (*sensu* Rahel and Hubert 1991). Previous work in the Black Hills indicated that interacting coarse-scale geomorphic factors were influential to the distribution of a native fish, mountain sucker (Dauwalter and Rahel 2008). The thermal tolerance of fishes in the Black Hills also support these observed longitudinal changes (Schultz and Bertrand 2011).

While coarse-scale variables appear to be the primary factor structuring fish assemblages in the Black Hills, reach-scale habitat and biotic interactions were also important. Periphyton coverage is a food resource for some native fishes in the Black Hills and is strongly related to their distributions (Schultz 2011). Because our analyses were focused at the reach scale, microhabitat factors (e.g., substrate, submergent vegetation) did not strongly structure fish assemblages, but they are probably important at finer spatial scales (e.g., Wilson and Belk 2001). Distributions of native and introduced fishes appeared to be non-overlapping across many sample reaches, particularly in altered habitats (e.g., tailwater reaches of Rapid and Castle creeks). Fisheries managers should consider these ecological patterns to balance native fish conservation and sport fishery management.

MANAGEMENT IMPLICATIONS

Our study is directly applicable to fish management efforts in the Black Hills. By providing habitat associations of individual species and assemblages, management actions can be prioritized to achieve desired outcomes. For example, because brook trout dominate assemblages in headwater stream reaches, management for quality brook trout sport fisheries would be most effective in these areas, and brown trout sport fisheries could be better developed in stream segments further downstream. Similarly, in systems where natural habitat conditions have been highly altered (e.g., by reservoir creation), conservation actions for native fishes would likely be ineffective, and sport fisheries would take priority. For example, tailwater stream reaches below reservoirs in Rapid and Castle creeks are well suited for producing quality salmonid fisheries. These areas might continue to be managed as sport fisheries with no negative effects on native fishes.

Other areas (e.g., Elk and Bear Butte creeks) provide marginal habitats for self-sustaining salmonid populations that are acceptable to anglers, but have been historically stocked to maintain fisheries. These streams are critical conservation areas for native fishes. Maintaining habitat conditions and fish assemblages in these areas will contribute to long-term persistence of native species. Streams in the southern Black Hills (e.g., portions of Battle, French, and Spring creeks) are good candidates for active re-introduction of extirpated

native fishes (e.g., mountain sucker; Schultz and Bertrand 2012). Thermal conditions of these streams are not suitable for long-term persistence of salmonids, but are favorable to native fishes. Furthermore, the conflict between angler desires and native fish management is likely to be reduced because these systems have historically not provided quality sport fisheries outside of heavily stocked areas in the lower portions of the drainages. Using the balanced approach outlined here, fishery management in the Black Hills can successfully achieve both quality sport fisheries and conservation of native fish assemblages.

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