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ZOOGEOGRAPHIC PATTERNS AND FAUNAL CHANGE OF SOUTH DAKOTA FISHES

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ABSTRACT.—We summarized historic and recent fish distributions in South Dakota and analyzed fish faunal similarity at 2 spatial scales (geomorphic province and river drainage) for both historic (native) and recent (post-1990) faunas. We quantified zoogeographic patterns between geomorphic provinces and among neighboring river drainages for historic and recent faunas. We also quantified faunal change (species losses and additions) between provinces and among drainages. Ninety-seven fishes were native to South Dakota, but 111 fishes were present in recent collections because 8 native species were missing, and 22 nonnatives were present. There was high β diversity among historic and recent river drainage fish faunas, but there was between 22% and 56% faunal change between periods. Recent faunas were homogenized compared to historic faunas at both provincial and river drainage spatial scales. Patterns of nonnative species establishment were geographically distinct from patterns of native species loss. Most nonnative species additions were in cold-water or human-made habitats of the Great Plains. Most native species declines stemmed from warm water streams of the Central Lowlands and Missouri River valley. Conservation of rare and declining native species and containment of nonnatives are both necessary to preserve historical patterns of fish biodiversity in South Dakota.

Key words: South Dakota, freshwater fish biodiversity, faunal similarity, taxonomic homogenization, introduced species, Great Plains, Central Lowlands, riverine archipelago.

There is increasing concern for freshwater fish conservation in North America (Pister 1999, Abell 2002, McKinney 2002). Forty North American fish taxa are extinct (Miller et al. 1989). Extinction rates have increased throughout the 20th century (Wilcove et al. 1992) and are expected to increase further (Ricciardi and Rasmussen 1999).

A biogeographic perspective is important for a comprehensive conservation plan for North American freshwater fishes (Sheldon 1988). For example, river drainage location, area, isolation, and fragmentation influence fish species diversity, composition, and faunal similarity (Sheldon 1988, Oberdorff et al. 1997, Hoagstrom and Berry 2006). Sheldon (1988) demonstrated that neighboring river drainages constitute "riverine archipelagos" with isolated fish faunas among river drainage "islands." Human activities have reduced isolation and increased habitat similarity among North American river drainages which, as predicted by Sheldon (1988), is homogenizing faunas of the riverine archipelago he studied (Scott and Helfman 2001, Walters et al. 2003, Carlson and Daniels 2004).

Taxonomic homogenization results from the disappearance of native species with localized distributions and the concurrent range expansions of invasive species (McKinney and Lockwood 1999, Olden et al. 2004). In North America, taxonomic homogenization has been documented among freshwater fish faunas of eastern Texas (Hubbs et al. 1997), California (Marchetti et al. 2001), New York (Carlson and Daniels 2004), and British Columbia (Taylor 2004). It is considered a major threat to biodiversity (Olden and Poff 2003, Olden et al. 2004).

Fish distributions in South Dakota have received a modest amount of study, and zoogeographic patterns of fish distributions in South Dakota have never been documented. Further, the impacts of faunal change on zoogeographic patterns have never been assessed. Here we present a revised list of distributions

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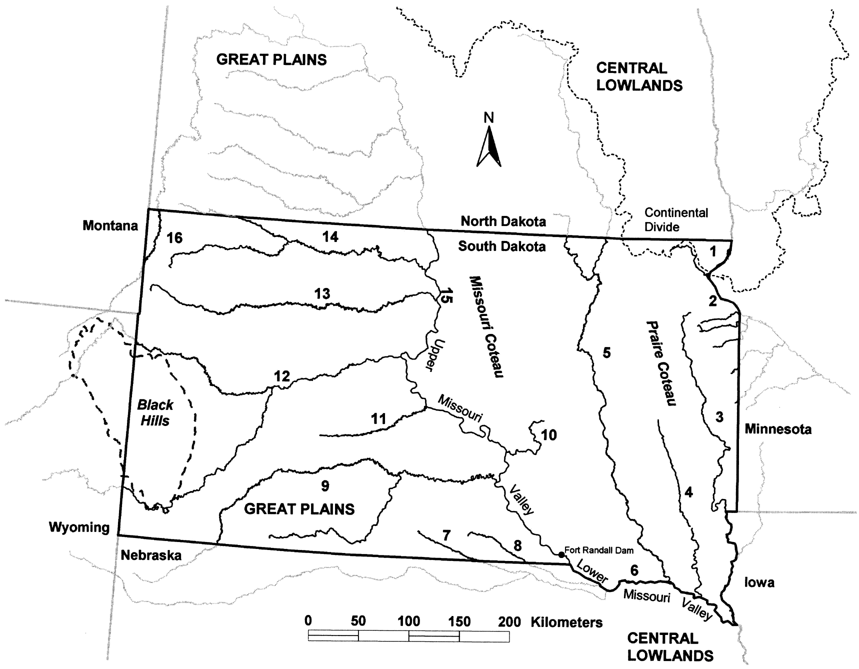

Fig. 1. Map of South Dakota and adjacent areas showing the 14 river drainages, 2 sections of the Missouri River Valley, 2 geomorphic provinces, and important geographical features. The Bois de Sioux River drainage (1) is part of the Hudson Bay drainage. All other drainages belong to the Mississippi River drainage. The upper Minnesota River drainage (2) is part of the upper Mississippi River drainage. All other river drainages—Big Sioux River (3), Vermillion River (4), James River (5), lower Missouri River valley (6), Niobrara River (7), Ponca Creek (8), White River (9), Crow Creek (10), Bad River (11), Cheyenne River (12), Moreau River (13), Grand River (14), upper Missouri River valley (15), and Little Missouri River (16)—belong to the Missouri River drainage. The Central Lowlands geomorphic province extends east from the western edge of the James River drainage. The remainder of the state is within the Great Plains geomorphic province.

of South Dakota fish by river drainage, along with an analysis of zoogeographic patterns and faunal change within the state. Our objectives are (1) to update and expand the distributional summary of South Dakota fishes (sensu Bailey and Allum 1962), (2) to quantify zoogeographic patterns, and (3) to measure change between historic and recent fish faunas and assess the effects of change on patterns of biodiversity.

STUDY AREA

South Dakota is a large state with a small human population (De Blij 2005). Part or all of 14 major river drainages are present therein (Fig. 1). In addition, the mainstem Missouri River, which is fed by many small streams, flows from north to south through central South Dakota and along the southeastern state boundary. We refer to the mainstem Missouri River and its small direst tributaries collectively as the Missouri River valley.

The most noteworthy river drainage boundary in South Dakota is the continental divide between the Hudson Bay and Gulf of Mexico drainages. This divide crosses the northeast corner of the state. The majority of South Dakota (>99%) is within the Mississippi River drainage. The Bois de Sioux River drains the portion of South Dakota that lies within the Hudson Bay drainage. South Dakota waters that flow to the Gulf of Mexico are all within the Mississippi River drainage.

Another noteworthy river drainage boundary divides the Mississippi River drainage of South Dakota into 2 subdrainages: the Minnesota River and Missouri River drainages. This divide crosses northeastern South Dakota. Approximately 97% of South Dakota lies within the Missouri River drainage and includes all or portions of 12 major tributary drainages along with the Missouri River valley. Less than 3% of South Dakota lies within the Minnesota River drainage. This region is drained by the Upper Minnesota River.

South Dakota includes portions of 2 geomorphic provinces, the Central Lowlands and Great Plains (Thornbury 1965, Hogan 1995, Holliday et al. 2002). The Missouri Coteau forms the western edge of the Central Lowlands. Geomorphic provinces are defined based on geology and topography. The Central Lowlands is lower in elevation than the Great Plains. Rocks of the Central Lowlands are mainly 223 million years old or older (Paleozoic) while rocks of the Great Plains are mainly younger than 223 million years (Mesozoic and Cenozoic). The Central Lowlands in South Dakota was entirely glaciated and the present topography has low relief and is characterized by abundant lakes, wetlands, and low-gradient streams of glacial origin. The Big Sioux, Vermillion, and James rivers are the major drainages of the Central Lowlands in South Dakota. In contrast, the Great Plains was glaciated only near the boundary between provinces. The Great Plains landscape has high topographic relief, which reflects the dominance of uplift and erosion in the province. The Grand, Moreau, Cheyenne, Bad, and White rivers are the major drainages of the Great Plains in South Dakota.

Humans have modified the waters of South Dakota through construction of reservoirs and drainage of wetlands. Wetland drainage was most common in the Big Sioux, Vermillion, and James River drainages (Central Lowlands) because the glaciated landscape and low relief naturally created an abundance of lakes and marshes (Johnson and Higgins 1997). In 1990, wetland loss from South Dakota was 35% (Dahl 1990).

Stream impoundments are widespread in South Dakota. Four mainstem reservoirs were constructed on the Missouri River in South Dakota for the purposes of flood damage reduction, water supply and irrigation, navigation, hydropower, fish and wildlife benefit, and recreation (CMRES 2002). Irrigation supply reservoirs were constructed in western Missouri River tributary drainages (Hembree et al. 1964, Sando et al. 2001) because the climate was more arid (many crops required irrigation in this region) and because relatively high relief provided suitable reservoir sites. A great many small impoundments were constructed in western South Dakota for livestock (Rieger 2004). These alter surface runoff (Culler 1961). Rivers of eastern South Dakota have many low-head dams (Sinning 1968, Owen et al. 1981) that may modify flows and create barriers to fish dispersal.

METHODS

Fish Species of South Dakota

We used literature to determine fish species presence in 14 river drainages and 2 sections of the Missouri River valley in South Dakota (Fig. 1). We divided the Missouri River valley into 2 sections, with Fort Randall Dam as the boundary. Questionable records were verified, when possible, from voucher specimens. However, there is presently no major repository for South Dakota fish specimens, so opportunities to examine vouchers were limited. We used an approach similar to one described in detail by Carlson and Daniels (2004) to determine acceptability of questionable records that could not be verified from specimens, and we noted questionable reports and controversial decisions (Hoagstrom 2006). We also reported species known from outside the borders of South Dakota for river drainages that extended into other states so that researchers would be alerted to their potential presence in South Dakota, but these species were not used in subsequent analyses.

NATIVE SPECIES.—Native fish species were presumably present within a given river drainage when humans of European descent first settled in South Dakota, roughly in 1850. Presumably, species distributions were not influenced by human impacts to aquatic habitats or by human transport of fishes prior to this date. For our analysis, we refer to “historic faunas” as composed of only native species. The designation of species as native or nonnative is difficult because humans of European descent altered aquatic habitats and introduced nonnative fishes prior to the earliest fish surveys (Bailey and Allum 1962). In addition, early surveys provided such limited fish distribution data that modern day researchers still frequently discover new native fish populations (Morey and Berry 2004, Springman and Banks 2005). Hence, it is difficult to determine the native ranges of species. Our designations primarily follow the interpretations of previous ichthyologists as summarized in Rostlund (1952), Bailey and Allum (1962), Lee et al. (1980), and Page and Burr (1991). Exceptional cases in which we did not follow these authors are noted in Table 1.

NONNATIVE SPECIES.—We classified nonnative fish species as either out-of-state nonnatives that were introduced wherever present in South Dakota or in-state nonnatives that were native to some river drainages of the state but introduced to others, thus expanding their historic distributions. In-state nonnatives are likely to be more successful invaders than out-of-state nonnatives because they were native to waters with relatively similar environmental conditions and fish assemblages (Brown and Moyle 1997, Gido et al. 2004).

RECENT SPECIES.—Recent fish species were those collected since 1990, whether native or introduced. We chose post-1990 collections as "recent" because fish sampling in South Dakota was extensive after this year and included major surveys of all river drainages except the Bois de Sioux River, Crow Creek, and the Little Missouri River. Along with literature records (Table 1), the recent statewide distribution of some fishes was determined from data provided by the South Dakota Department of Game, Fish and Parks (SDGFP 2004a, 2004b, 2004c). Recent data are the only data available for the Ponca Creek drainage, which was not sampled prior to 1990.

Zoogeographic Patterns

FAUNAL SIMILARITY.—We investigated fish faunal similarity among all South Dakota river drainages using a hierarchical, agglomerative, polythetic cluster analysis (Legendre and Legendre 1998) performed with PC-ORD 4.25 software. We used Sørensen's index (Sørensen 1948) as our distance measure because it gives double weight to double presences, which are theoretically the most meaningful indicators of faunal similarity (Legendre and Legendre 1998, McCune and Mefford 1999). We used flexible clustering with $\beta = -0.25$ as our linkage method (Legendre and Legendre 1998, McCune and Grace 2002). We scaled the cluster dendrogram with Wishart's objective function, which measures information loss for each step in a hierarchical cluster based on the amount of total variation that is present in each cluster (Wishart 1969, McCune and Grace 2002). We selected the number of clusters, with the goal of maximizing the amount of information conserved while also delimiting interpretable river drainage groups (sensu McCune et al. 2000). We analyzed faunal similarity with cluster analysis for historic and native river drainage faunas to determine whether zoogeographic patterns were consistent between periods.

FAUNAL DISPARITY.—Faunal disparity (β diversity) is the amount of total diversity that is unique to various subregions of a given area (Whittaker 1975)—in this case, geomorphic provinces or river drainages within South Dakota. We determined faunal disparity between geomorphic provinces (comparisons between provinces did not include the Missouri River valley), among neighboring river drainages of the riverine archipelago of South Dakota, and between sections of the Missouri River valley. There are 2 types of neighboring drainages: (1) those with neighboring river mouths and (2) those with neighboring headwaters (Sheldon 1988), all of which we analyzed. We summarized faunal disparity in 2 ways. First, we determined faunal turnover (number of unshared species; Allan 1975, Russell 1998). Second, we calculated faunal resemblance using Preston's index z (Preston 1962, Sheldon 1988), which is calculated as

$$z = -3.32 * \log[0.6x + 0.4y],$$

where x equals the fraction of combined fauna that is present in larger fauna and y equals the fraction of combined fauna that is present in smaller fauna. The index varies from 0 (identical faunas) to 1 (unique faunas). Values >0.27 represent isolated faunas and values <0.27 suggest that faunas are subsets of larger faunas (Preston 1962, Sheldon 1988). Faunal disparity analyses were performed separately for historic and recent faunas to determine whether patterns were similar between periods.

Faunal Change

We documented the level of fish faunal change between the historic and recent faunas of South Dakota at statewide, geomorphic province, and river drainage scales by calculating faunal turnover (percent unshared species; Rahel 2002, Taylor 2004) between periods. Unshared species were of 2 types: (1) native species absent from recent collections (species

TABLE 1. Fish species presence in South Dakota river drainages. N = native species; 1 = out of state nonnative; 2 = in state nonnative; * = present in the drainage in adjoining states but never reported from South Dakota; bold = species absent from post-1990 collections. Fish names follow Nelson et al. (2004) except we recognize subspecies.

	Central Lowlands						Great Plains									
FAMILIES, species, and subspecies	Bois de Sioux River[a]	Upper Minnesota River[b]	Big Sioux River[c]	Vermillion River[d]	James River[e]	Missouri Valley (lower)[f]	Niobrara River[g]	Ponca Creek[h]	White River[i]	Crow Creek[j]	Bad River[k]	Cheyenne River[l]	Moreau River[m]	Grand River[n]	Missouri Valley (upper)[o]	Little Missouri River[p]
PETROMYZONTIDAE lampreys																
Ichthyomyzon unicuspis silver lamprey				**n**		**n**				n						
ACIPENSERIDAE sturgeons																
Ascipenser fulvescens lake sturgeon						n										
Scaphirhynchus albus pallid sturgeon						n									**n**	
Scaphirhynchus platorynchus shovelnose sturgeon			n	n	n	n	*[q]								n	
POLYODONTIDAE paddlefishes																
Polyodon spathula paddlefish			**n**	n	n	n									n	
LEPISOSTEIDAE gars																
Lepisosteus osseus longnose gar	*[q]	**n**	**n**	n	n	n	*[q]			n						
Lepisosteus platostomus shortnose gar		n	n	n	n	n	*[q]								n	
AMIIDAE bowfins																
Amia calva bowfin		**n**														
HIODONTIDAE mooneyes																
Hiodon alosoides goldeye			n	n	n	n	*[q]		n	n	n	n	n	n	n	n
Hiodon tergisus mooneye			**n**													
ANGUILLIDAE freshwater eels																
Anguilla rostrata American eel		**n**	**n**	**n**	n	n									**n**	
CLUPEIDAE herrings																
Alosa chrysochloris skipjack herring		**n**				2[r]									**2**	
Alosa pseudoharengus alewife						**1**										
Dorosoma cepedianum gizzard shad			n	n	n	n			**n**			2		2	n	
CYPRINIDAE carps and minnows																
Campostoma anomalum pullum central stoneroller	*[q]	n	n	n	n	n	n		n	n						
Carassius auratus goldfish			1			1	1		1			1			**1**	
Couesius plumbeus lake chub							*[q]		*[q]	n		n				**n**
Ctenopharyngodon idella grass carp			1		1	1										
Cyprinella lutrensis lutrensis red shiner			n	n	n	n	n	n	n	n	n	n			n	

TABLE 1. Continued.

FAMILIES, species, and subspecies	Central Lowlands									Great Plains						
	Bois de Sioux River[a]	Upper Minnesota River[b]	Big Sioux River[c]	Vermillion River[d]	James River[e]	Missouri Valley (lower)[f]	Niobrara River[g]	Ponca Creek[h]	White River[i]	Crow Creek[j]	Bad River[k]	Cheyenne River[l]	Moreau River[m]	Grand River[n]	Missouri Valley (upper)[o]	Little Missouri River[p]
Cyprinella spiloptera spotfin shiner		*q		1		1										
Cyprinus carpio common carp	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Hybognathus argyritis western silvery minnow			**n**	**n**	*q	n	n	*q	n	n	**n**	n	n	n	n	n
Hybognathus hankinsoni brassy minnow	**n**	n	n	n	n	n	n	n	n	n		n	n	n	n	**n**
Hybognathus placitus plains minnow						**n**	**n**		n		n	n	n	n	n	n
Hypophthalmichthys molitrix silver carp			1	1	1	1										
Hypophthalmichthys nobilis bighead carp			1		1	1										
Luxilus cornutus common shiner	**n**	n	n	n	n	n	n		*q			*q			n	*q
Macrhybopsis gelida sturgeon chub						n			n			n		**n**	**n**	**n**
Macrhybopsis meeki sicklefin chub						n									**n**	
Macrhybopsis hyostoma shoal chub						n										
Macrhybopsis storeriana silver chub	*q		n			n	n									
Margariscus margarita nachtriebi pearl dace							n		n						n	
Nocomis biguttatus hornyhead chub	**n**	n	**n**		*q							*q				
Notemigonus crysoleucas golden shiner	*q	n	**n**	n	**n**	n	n		n		n	n	n	n	n	n
Notropis atherinoides emerald shiner	n	n	n	n	n	n	n		n		n	n	n	n	n	*q
Notropis blennius river shiner				**n**		n	*q		*q						**2**	
Notropis dorsalis bigmouth shiner	**n**	n	n	n	n	n	n	n	n						n	
Notropis heterodon blackchin shiner	*q	**n**														
Notropis heterolepis blacknose shiner	**n**	n	n		**n**	**n**	n		**n**						**n**	
Notropis hudsonius spottail shiner	*q	n	n		n	n						2		2	2	
Notropis percobromus carmine shiner	*q	n	**n**													
Notropis shumardi silverband shiner				**n**		**n**									**n**	
Notropis stramineus missuriensis plains sand shiner						n	n	n	n	n	n	n	n	n	n	n
Notropis stramineus stramineus eastern sand shiner	*q	n	n	n	n											
Notropis topeka Topeka shiner			n	n	n	*q									**2**	
Notropis volucellus mimic shiner	*q					1										
Phenacobius mirabilis Suckermouth minnow			**n**			n	*q			n					n	
Phoxinus eos northern redbelly dace		n	n				n		n	n				n	n	*q

TABLE 1. Continued.

FAMILIES, species, and subspecies	Central Lowlands						Great Plains									
	Bois de Sioux River[a]	Upper Minnesota River[b]	Big Sioux River[c]	Vermillion River[d]	James River[e]	Missouri Valley (lower)[f]	Niobrara River[g]	Ponca Creek[h]	White River[i]	Crow Creek[j]	Bad River[k]	Cheyenne River[l]	Moreau River[m]	Grand River[n]	Missouri Valley (upper)[o]	Little Missouri River[p]
Phoxinus erythrogaster southern redbelly dace			n													
Phoxinus neogaeus finescale dace	*q						n		n			n				
Pimephales notatus bluntnose minnow	**n**	n	n		n	n								**2**	2	
Pimephales promelas fathead minnow	**n**	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n
Platygobio gracilis flathead chub			**n**	**n**		n	n		n		n	n	n	n	n	n
Rhinichthys cataractae cataractae longnose dace	**n**						n	n	n		**n**	n	n	n	**n**	n
Rhinichthys obtusus western blacknose dace	*q	n	n	n	n	**n**	n		**n**	n					**2**	
Scardinus erythrophthalmus rudd			1									1				
Semotilus atromaculatus creek chub	**n**	n	n	n	n	n	n	n	n	n		n	n	n	n	*q
CATOSTOMIDAE suckers																
Carpiodes carpio carpio northern river carpsucker			n	n	n	n	n		n	n	n	n	n	n	n	n
Carpiodes cyprinus hinei central quillback carpsucker	n	n	n	**n**	n	n										
Carpiodes velifer highfin carpsucker		*q	**n**			n										
Catostomus catostomus longnose sucker							*q		*q			n				
Catostomus commersonii white sucker	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n
Catostomus platyrhynchus mountain sucker							*qs		*q			n				
Cycleptus elongatus blue sucker			n	n	n	n									n	
Hypentelium nigricans northern hog sucker		**n**	**n**													
Ictiobus bubalus smallmouth buffalo			n	n	n	n	*q								n	*q
Ictiobus cyprinellus bigmouth buffalo	n	n	n	n	n	n	*q								n	
Ictiobus niger black buffalo			**n**		**n**	**n**										
Moxostoma erythrurum golden redhorse	n	n	*q		**n**	n										
Moxostoma macrolepidotum shorthead redhorse	n	n	n	n	n	n	n		n	n	n	n	n	n	n	n
ICTALURIDAE North American catfishes																
Ameiurus melas black bullhead	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	**n**
Ameiurus natalis yellow bullhead	2	n	n		n	**n**	*q					2				
Ameiurus nebulosus brown bullhead	n	n			*q											
Ictalurus furcatus blue catfish			n		**n**	**n**									n	
Ictalurus punctatus channel catfish	n	n	n	n	n	n	n		n		n	n	n	n	n	n

TABLE 1. Continued.

FAMILIES, species, and subspecies	Central Lowlands						Great Plains									
	Bois de Sioux River[a]	Upper Minnesota River[b]	Big Sioux River[c]	Vermillion River[d]	James River[e]	Missouri Valley (lower)[f]	Niobrara River[g]	Ponca Creek[h]	White River[i]	Crow Creek[j]	Bad River[k]	Cheyenne River[l]	Moreau River[m]	Grand River[n]	Missouri Valley (upper)[o]	Little Missouri River[p]
Noturus flavus stonecat		**n**	n	n	n	n	n		n			n	n	n	n	n
Noturus gyrinus tadpole madtom	*q	n	n	n	n	**n**										
Pylodictis olivaris flathead catfish			n	n	n	n			**n**						n	
ESOCIDAE pikes																
Esox americanus vermiculatus grass pickerel						n	*q		*q							
Esox lucius northern pike	n	n	n	2	n	2	2	2	2	2	2	2	2	2	2	2
Esox masquinongy muskellunge			1		1	1									1	
UMBRIDAE mudminnows																
Umbra limi central mudminnow		n	n													
OSMERIDAE smelts																
Osmerus mordax rainbow smelt						1						1			1	
SALMONIDAE trouts and salmons																
Coregonus artedi cisco			1												1	
Coregonus clupeaformis lake whitefish															1	
Oncorhynchus clarkii bouvieri Yellowstone cutthroat trout						**1**						1			1	
Oncorhynchus kisutch Coho salmon															**1**	
Oncorhynchus mykiss rainbow trout		**1**	1	1	1	1			1			1	1	1	1	
Oncorhynchus nerka kokanee (sockeye) salmon						**1**						1				
Oncorhynchus tschawytscha chinook salmon															1	
Prosopium gemmifer Bonneville cisco															**1**	
Salmo trutta brown trout		1	*t		1				**1**			1	1	1	1	
Salvelinus fontinalis brook trout		**1**							**1**			1				
Salvelinus namaycush lake trout												1			1	
PERCOPSIDAE trout-perches																
Percopsis omiscomaycus trout-perch	*q	**n**	n													
GADIDAE cods																
Lota lota maculosa burbot				**n**		n	*q					**n**			n	*q
FUNDULIDAE topminnows																
Fundulus diaphanus menona western banded killifish	*r	n	n												2	

TABLE 1. Continued.

FAMILIES, species, and subspecies	Central Lowlands						Great Plains									
	Bois de Sioux River[a]	Upper Minnesota River[b]	Big Sioux River[c]	Vermillion River[d]	James River[e]	Missouri Valley (lower)[f]	Niobrara River[g]	Ponca Creek[h]	White River[i]	Crow Creek[j]	Bad River[k]	Cheyenne River[l]	Moreau River[m]	Grand River[n]	Missouri Valley (upper)[o]	Little Missouri River[p]
Fundulus kansae northern plains killifish							*q					n[u]				
Fundulus sciadicus plains topminnow			n	**n**	n	**n**	n		n			n				
GASTEROSTEIDAE sticklebacks																
Culaea inconstans brook stickleback	**n**	n	n	n	n	n	*r		n	n		n	n	*q	**n**	*q
COTTIDAE sculpins																
Cottus bairdii mottled sculpin															1	
MORONIDAE temperate basses																
Morone chrysops white bass	2	n	n	**2**	2	2						2	2	2	2	
Morone saxatilis striped bass						1										
CENTRARCHIDAE sunfishes																
Ambloplites rupestris rock bass	*q	n	n		**2**	2						2				
Lepomis cyanellus green sunfish	*t	n	n	n	n	n	n	n	n	n	2	2	2	2	2	2
Lepomis gibbosus pumpkinseed	*q	n	n		**2**	**2**			2		**2**			**2**		
Lepomis humilis orangespotted sunfish	**2**	n	n	n	n	n				n	n	n		n	n	
Lepomis macrochirus macrochirus bluegill	2	n	n	2	2	n	2	2	2		2	2	2	2	2	
Lepomis microlophus redear sunfish			1													
Micropterus dolomieu smallmouth bass	*t	**n**	2	2	2	2					2	2	2	2	2	
Micropterus salmoides salmoides largemouth bass	2	n	n	2	2	2	2	2	2		2	2	2	2	2	**2**
Pomoxis annularis white crappie	2	**n**	n	2	2	2			2			2			2	
Pomoxis nigromaculatus black crappie	2	n	n	2	2	2	2	2	2		2	2	2	2	2	
PERCIDAE perches																
Etheostoma caeruleum rainbow darter		*q														
Etheostoma exile Iowa darter	**n**	n	n	n	n	**n**	n		n	n		n	n	n	n	**n**
Etheostoma flabellare lineolatum striped fantail darter		*q														
Etheostoma microperca least darter	*q															
Etheostoma nigrum johnny darter	n	n	n	n	n	n	n	n					2	2	2	
Etheostoma zonale banded darter		*q														
Perca flavescens yellow perch	n	n	n	n	n	n	2	2	2	2	2	2	2	2	2	2
Percina caprodes logperch			n													

TABLE 1. Continued.

FAMILIES, species, and subspecies	Central Lowlands						Great Plains									
	Bois de Sioux River[a]	Upper Minnesota River[b]	Big Sioux River[c]	Vermillion River[d]	James River[e]	Missouri Valley (lower)[f]	Niobrara River[g]	Ponca Creek[h]	White River[i]	Crow Creek[j]	Bad River[k]	Cheyenne River[l]	Moreau River[m]	Grand River[n]	Missouri Valley (upper)[o]	Little Missouri River[p]
Percina maculata blackside darter	*[q]	n	n		*[q]											
Percina phoxocephala slenderhead darter		**n**														
Sander canadensis sauger			n	n	n	n	*[q]		n		n	n	n	n	n	n
Sander vitreus vitreus walleye	n	n	n	n	n	n	*[q]		n[v]	n	n[v]	n[v]	n[v]	n[v]	n	*[t]
SCIANIDAE drums and croakers																
Aplodinotus grunniens freshwater drum	n	n	n	n	n	n	*[q]					n			n	*[q]

[a]Bois de Sioux River drainage refers to the portion of the Red River of the North drainage upstream from where the Otter Tail River and Bois de Sioux River join (including the Otter Tail River drainage). Anderson (personal communication) reported recent surveys.

[b]Upper Minnesota River drainage refers to the portion of the Minnesota River drainage upstream from the Lac qui Parle River confluence (including the Lac qui Parle River). Dieterman and Berry (1994), Pope and Willis (1994), USGS (2002, 2004), and Anderson (personal communication) reported recent surveys.

[c]Dieterman and Berry (1998), Kirby (2001), Milewski (2001), Blausey (2001), and USGS (2001, 2002, 2003, 2004) reported recent surveys from the Big Sioux River drainage.

[d]Schmulbach and Braaten (1993), Braaten and Berry (1997), Blausey (2001), and USGS (2002, 2003, 2004) reported recent surveys from the Vermillion River drainage.

[e]Berry et al. (1993), Blausey (2001), USGS (2001, 2002, 2003), and Shearer and Berry (2003) reported recent surveys from the James River drainage.

[f]The lower Missouri River Valley refers to the Missouri River from Fort Randall Dam downstream to the South Dakota–Iowa border and includes all tributary streams except those reported separately in this table. Johnson et al. (1992), Wickstrom (1999, 2004), USGS (2001, 2002), Berry and Young (2004), Shuman et al. (2005), and Kral (personal communication) reported recent surveys from the lower Missouri River Valley.

[g]Cunningham et al. (1995), USGS (2002, 2003), and Harland and Berry (2004) reported recent surveys from the Niobrara River drainage.

[h]The Ponca Creek river drainage was not sampled prior to 1990. USGS (2001, 2003) reported recent surveys from the Ponca Creek river drainage.

[i]Cunningham et al. (1995), USFWS (1997), Fryda (2001), USGS (2001, 2002, 2003, 2004), and Harland (2003) reported recent surveys from the White River drainage.

[j]We are unaware of recent surveys from the Crow Creek drainage. The USGS (2001) made 1 visit to the Crow Creek drainage but no fish were collected.

[k]Milewski (2001), USGS (2002), and Harland (2003) report recent surveys from the Bad River drainage.

[l]Meester (1994, 1999), SDGFP (1993), Cunningham et al. (1995), Hampton and Berry (1997), Doorenbos (1998), Erickson (1998), Erickson et al. (2001), USGS (2001, 2002, 2003, 2004), and Duehr (2004) reported recent surveys from the Cheyenne River drainage.

[m]Loomis et al. (1999), USGS (2001, 2002, 2004), and Duehr (2004) reported recent surveys from the Moreau River drainage.

[n]USGS (2001, 2002, 2003, 2004), Morey and Berry (2004) and Erickson (personal communication) reported recent surveys from the Grand River drainage.

[o]The upper Missouri River Valley refers to the Missouri River from the South Dakota–North Dakota border downstream to Fort Randall Dam and includes all portions of mainstem reservoirs and all tributary streams except those reported separately in this table. Johnson et al. (1992, 1995, 1998, 1999), Riis and Johnson (1995), Stone (1995), Stone and Sorensen (1999), Smith and Brown (2002), USGS (2002, 2003, 2004), Lott et al. (2003, 2004), and Sorensen (2004) reported recent surveys from the upper Missouri River Valley.

[p]Erickson (personal communication) reported recent surveys from the Little Missouri River drainage.

[q]Species or subspecies native to specific river drainages but only known outside the borders of South Dakota and thus representing potential former or future inhabitants.

[r]Cross and Huggins (1975) concluded that *A. chrysochloris* invaded the Missouri River following human modifications that altered river conditions.

[s]Bailey and Allum (1962) believed the *C. platyrhynchus* specimen reported from the Niobrara River Drainage in Nebraska was mislabeled. Recent geological and ichthyological studies suggest *C. platyrhynchus* was more widespread in prehistoric times (Cross et al. 1986). Stream captures and interdrainage connections (Swinehart et al. 1985, Mayden 1987) could have given the species access to the Niobrara Drainage from the Platte, Cheyenne, or White drainages.

[t]Species or subspecies introduced to the drainage outside the borders of South Dakota making the future presence in the state a possibility.

[u]Miller (1955) considered *F. kansae* to be introduced to the Cheyenne River downstream from Angostura Dam due to their absence from 2 collections prior to their discovery (Bailey and Allum 1962). Other species that were absent from the same 2 collections include *Hybognathus argyritis, Notropis stramineus missuriensis, Pimephales promelas, Semotilus atromaculatus,* and *Carpiodes carpio carpio* (Evermann and Cox 1896), all of which are considered native (Bailey and Allum 1962). *Fundulus kansae* populations are highly variable over time and patchy in distribution (Fausch and Bestgen 1997) so it is possible the 2 early surveys missed the species although it was present elsewhere in the drainage. Prehistoric stream captures between the Cheyenne and Platte drainages (Swinehart et al. 1985) may have allowed *F. kansae* to naturally populate the Cheyenne River drainage. In the absence of more objective evidence of human introduction, we thus consider *F. kansae* native to the Cheyenne River drainage.

[v]*Sander vitreus vitreus* is introduced to Wyoming (Simon 1946, Baxter and Simon 1970, Baxter and Stone 1995) and Montana (Brown 1971, Holton and Johnson 2003). Thus, Nebraska, South Dakota, North Dakota, and possibly Kansas constitute the southwestern edge of the historic range (Johnson 1942, Bailey and Allum 1962, Cross 1967, Cross and Collins 1995). The western extent of the native range in these states is difficult to determine because *S. vitreus vitreus* was stocked widely prior to extensive fish surveys. However, many early stocking attempts were unsuccessful and the success of *S. vitreus vitreus* introductions to the Great Plains and Rocky Mountains largely followed the construction of reservoirs (Simon 1946, Bailey and Allum 1962, Cross and Collins 1995), so collections from streams prior to reservoir construction are probably the best available evidence of the historic range. We report *S. vitreus vitreus* as native to all major drainages of South Dakota except the Little Missouri Drainage, which follows Rostlund (1952) and Bailey and Allum (1962) among others, but the limited extent of pre-reservoir surveys in the western tributaries of the Missouri River in South Dakota (White, Bad, Cheyenne, Moreau, and Grand rivers) leaves open the possibility that *S. vitreus vitreus* did not inhabit them prior to plantings of the species in newly formed reservoirs.

losses) and (2) nonnative species present in recent collections (species additions). Comparisons between provinces did not include the Missouri River valley.

We assessed changes in statewide faunal similarity by comparing similarity patterns between historic and recent faunas at the geomorphic province and river drainage scales. Increasing similarity indicates taxonomic homogenization and decreasing similarity indicates taxonomic differentiation. We used Jaccard's index (Jaccard 1912) to assess changes in faunal similarity. It is the traditional measure for studies of faunal change and thus facilitates comparisons with former studies (Rahel 2000, Marchetti et al. 2001, Taylor 2004, Olden et al. 2004). However, we also conducted analyses using Sørensen's index because it is superior to Jaccard's index (Legendre and Legendre 1998, McCune and Mefford 1999) and thus may provide a more sensitive measure of changing faunal similarity. Both Jaccard's and Sørensen's indexes may be expressed as percentages, and they vary from 0% to 100%, with 100% indicating identical faunas. We conducted comparisons between all river drainage pairs for historic and recent faunas and summarized the frequency distribution of similarity values among historic and recent river drainage faunas. We used a 2-tailed *t* test (Sokal and Rohlf 1995) to compare the means of all pairwise comparisons from historic and recent faunas. We also summarized changes in similarity between native and recent river drainage faunas to determine whether the sum of all changes increased or decreased faunal similarity. We compared the mean of all similarity changes to 0 using a 1-sample *t* test (Sokal and Rohlf 1995).

We compared historic fish ranges (number of drainages occupied) to recent fish ranges to investigate how different species groups affected patterns of faunal change. We separated recent fishes into 3 groups: natives with stable or declining ranges (recent natives), natives with expanding ranges (in-state nonnatives), and out-of-state nonnatives—and determined the skewness of frequency distributions for each group. Frequency distributions that are strongly right-skewed contribute to taxonomic differentiation, while nonskewed distributions contribute to taxonomic homogenization (McKinney 2004).

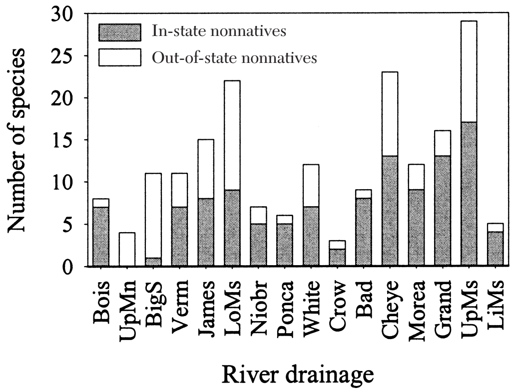

Fig. 2. Nonnative fish species richness by river drainage. Nonnatives are divided into 2 groups: out-of-state nonnatives (introduced wherever present) and in-state nonnatives (native to some river drainages). River drainage abbreviations follow Table 2.

Results

Fish Species of South Dakota

NATIVE SPECIES.—Based on our findings, 97 fish species and subspecies (henceforth referred to collectively as "species") were native to South Dakota (Table 1). An additional 4 species were known from adjacent waters of the Bois de Sioux River or Upper Minnesota River drainages, but these 4 species were not considered in subsequent analyses. Only 1 species, sand shiner *Notropis stramineus,* was represented by multiple subspecies. Native species richness was 83 in the Central Lowlands and 47 in the Great Plains (excluding the Missouri River valley). Forty-five species were only native to the Central Lowlands and 9 were only native to the Great Plains. Native species richness varied by river drainage from 64 in the lower Missouri River valley to 11 in the Ponca Creek drainage.

NONNATIVE SPECIES.—According to our records, 25 fish species were introduced to South Dakota. Three of these (alewife *Alosa pseudoharengus*, Coho salmon *Oncorhynchus kisutch,* and Bonneville cisco *Prosopium gemmifer*) failed, so 22 nonnative species were present in recent collections. Introductions of many species failed in certain tributary drainages, but were successful in others (Table 1). Failed introductions were not included in subsequent analyses. There were also 22 in-state nonnatives that had expanded distributions within the state. In-state nonnatives were present in all river drainages except the upper Minnesota River and composed the majority of nonnatives in most drainages (Fig. 2). Out-of-state nonnatives were most prevalent in the upper Minnesota, Big Sioux, lower Missouri, Cheyenne, and upper Missouri river drainages.

RECENT SPECIES.—Based on our findings, the recent fish fauna of South Dakota included 111 fish species—89 natives and 22 nonnatives. Recent species richness was 79 in the Central Lowlands and 64 in the Great Plains (this analysis did not include the Missouri River valley). Thirty-two species were present only in the Central Lowlands and 17 were present only in the Great Plains. Recent species richness varied from 72 in the lower Missouri River valley to 17 in the Ponca Creek drainage (Table 1).

Zoogeographic Patterns

FAUNAL SIMILARITY.—Zoogeographic patterns of faunal similarity were distinct and persistent. Cluster analyses of historic and recent fish faunas indicated that there were 3 major river drainage groups in South Dakota based on faunal similarity at a level where 40% of the information was remaining (Fig. 3). Historic river drainage groups were (1) Bois de Sioux River and Ponca Creek (drainages with only headwater reaches extending into the state), (2) major Great Plains river drainages, and (3) Central Lowlands river drainages and both sections of the Missouri River valley. Recent river drainage groups were (1) the Bois de Sioux River, (2) Central Lowlands river drainages and both sections of the Missouri River valley, and (3) major Great Plains river drainages, including Ponca Creek.

FAUNAL DISPARITY.—There was substantial faunal disparity (β diversity) between geomorphic provinces and neighboring river drainages for both historic and recent faunas. There was 59% faunal turnover (unshared species) between historic Central Lowlands and Great Plains faunas (the Missouri River valley was excluded from this analysis), due primarily to species restricted to the Central Lowlands, which represented 49% of the historic fauna. Similarly, there was 51% faunal turnover between recent faunas of the Central Lowlands and Great Plains, but only 33% of the recent species were restricted to the Central Lowlands. These results indicated an increase in the proportion of unique intraprovincial species

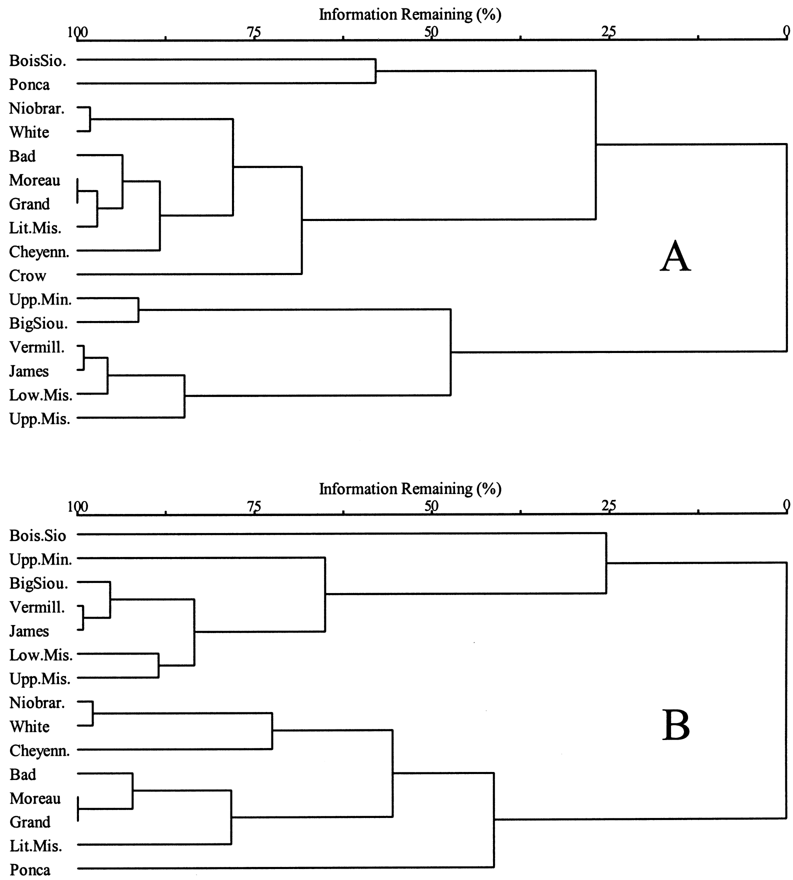

Fig. 3. Dendrogram depicting results of a hierarchical, agglomerative, polythetic cluster analysis based on Sørensen's coefficient of faunal similarity among historic (A) and recent (B) river drainage fish faunas. The dendrogram is scaled with Wishart's objective function that measures information loss for each step in a hierarchical cluster. We differentiated clusters for which 40% of the information remained.

that were restricted to the Great Plains. Historic faunal resemblance between provinces (Preston's z) was 0.42, and recent resemblance was 0.39, indicating that provincial faunas were distinct from each other in both periods.

There was substantial faunal disparity between neighboring river drainages (Fig. 4). There was 14%–72% faunal turnover (unshared species) between drainages of historic and recent faunas. Resemblance values (Preston's z) indicated that most neighboring faunas were distinct from each other, but a few river drainage pairs had resemblance values <0.27, which suggested they were subsets of larger regional faunas. Historic and recent species richness patterns were similar among neighboring river drainages. Faunal turnover (unshared species) between the upper and lower Missouri River valleys was 35% among historic faunas and 42% among recent faunas. Faunal resemblance (Preston's z) was 0.25 for historic faunas and 0.32 for recent faunas.

Faunal Change

SOUTH DAKOTA FAUNA.—Historic and recent fish faunas of South Dakota were substantially different. There was a net increase of 14 species between historic and recent fish faunas because 22 nonnatives were successfully established in the state, but 8 natives were missing (Table 1). This accounted for 25% faunal turnover (unshared species) between historic and recent faunas.

PROVINCIAL FAUNAS.—Patterns of fish faunal change differed between geomorphic provinces. In both cases, there was substantial

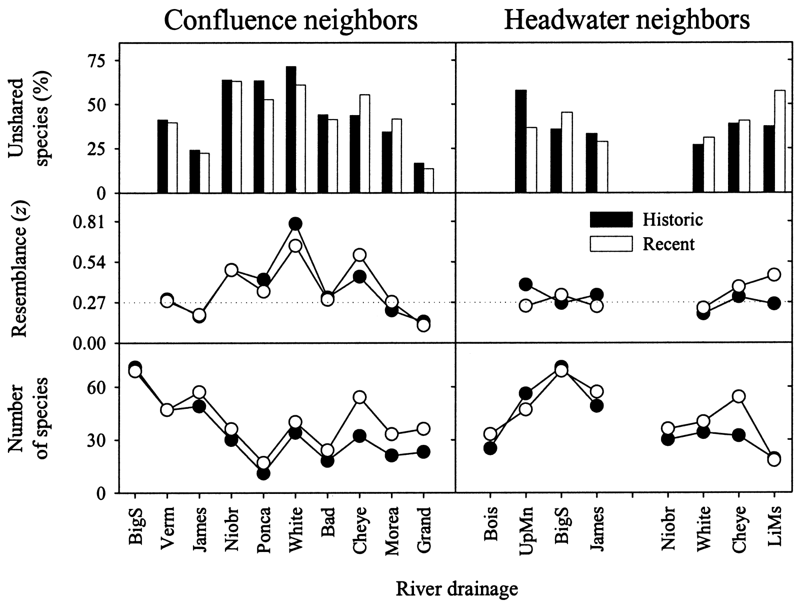

Fig. 4. Plot showing 3 measures that quantify faunal disparity (β diversity) between river drainages of the "riverine archipelago" of South Dakota for historic and recent fish faunas. The 3 measures are percent unshared species (top graphs), faunal resemblance (Preston's z; middle graphs) and species richness (bottom graphs). Comparisons between drainages with adjacent river mouths along the Missouri River are shown on the left. Comparisons between drainages with adjacent headwaters are shown on the right. River drainage abbreviations follow Table 2.

faunal turnover (unshared species), with 29% turnover between historic and recent faunas of the Central Lowlands and 39% turnover between historic and recent faunas of the Great Plains. Change in the Central Lowlands led to a net loss of 4 species because 16 natives were missing from recent collections and only 12 nonnatives were present. In contrast, change in the Great Plains resulted in a net increase of 17 species because, although 5 native species were missing from recent collections, 22 nonnatives were present. Faunal similarity values were 41% between historic provincial faunas and 49% between recent provincial faunas based on Jaccard's index (8% increase), and 58% between historic provincial faunas and 66% between recent provincial faunas based on Sørensen's index (8% increase).

RIVER DRAINAGE FAUNAS.—Historic fish faunas were substantially different from recent fish faunas in all river drainages. Fifty native species were missing from 1 or more historically occupied drainages (Table 1). In contrast, the river drainage distributions of 17 native species (in-state nonnatives) increased. Skipjack herring, *Alosa chrysochloris,* and smallmouth bass, *Micropterus dolomieu,* fit within both categories because they were missing from their native river drainages but introduced into others. Faunal turnover (unshared species) by river drainage ranged from 22% in the Niobrara River drainage to 56% in the Bois de Sioux River drainage (Fig. 5).

Overall, there was higher similarity among recent faunas than among historic faunas (Fig. 6), but the frequency distributions of faunal similarity values were statistically similar. Historic faunal similarity based on Jaccard's index ranged from 12% between Ponca Creek and the Big Sioux River drainages to 83% between the Moreau River and Grand River drainages. Recent faunal similarity based on Jaccard's index ranged from 8% between the Little Missouri River and Bois de Sioux River drainages to 89% between the Grand River and Moreau River drainages. Mean Jaccard's similarity between all river drainage pairs was similar between historic ($\bar{x}$ = 40%, s = 17.3%) and recent ($\bar{x}$ = 42%, s = 13.9%) faunas (t = 1.1, df = 208, P = 0.27; Table 2). Similarly, historic faunal similarity based on Sørensen's index ranged from 22% between Ponca Creek and the Big Sioux River drainages to 91% between the Moreau River and Grand River drainages.

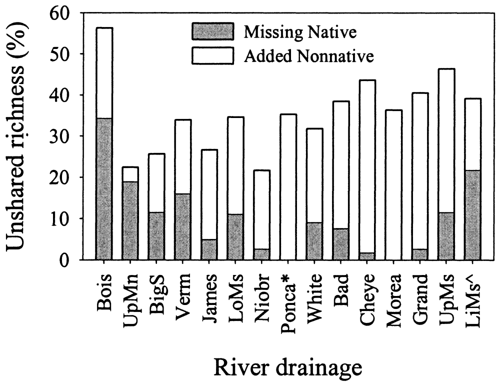

Fig. 5. Percent of total species richness by river drainages that was unshared between historic and recent fish faunas. Percentages are subdivided into 2 components: native species missing from recent surveys and nonnative species present in recent surveys. *Ponca Creek river drainage was not surveyed prior to 1990, so recent collections represent historic and recent faunas.

Recent faunal similarity based on Sørensen's index ranged from 15% between the Little Missouri River and Bois de Sioux River drainages to 94% between the Grand River and Moreau River drainages. Mean Sørensen's index similarity between all river drainage pairs was also similar between historic ($\bar{x}$ = 55%, s = 17.3%) and recent ($\bar{x}$ = 58%, s = 13.8%) faunas (t = 1.5, df = 208, P = 0.13; Table 3).

Overall, the magnitude of change in river drainage similarity among all pairs was positive (Fig. 7) and statistically >0, indicating taxonomic homogenization. The mean magnitude of change in similarity based on Jaccard's index was 2.4% (s = 9.3%; t = 2.6, df = 104, P = 0.01). The mean magnitude of change in similarity based on Sørensen's index was 3.3% (s = 10.0%; t = 3.4, df = 104, P < 0.01).

Frequency distributions of out-of-state nonnatives were highly right-skewed (Fig. 8), indicating that, as a group, out-of-state nonnative species contributed to taxonomic differentiation. In contrast, frequency distributions of in-state nonnatives were slightly left skewed, indicating that, as a group, in-state nonnative species contributed to taxonomic homogenization. The frequency distributions of native species with stable or declining ranges were similarly skewed to those of historic native species, suggesting that, as a group, stable and declining native species did not contribute to taxonomic homogenization or differentiation.

DISCUSSION

Zoogeographic Patterns

Fish faunal similarity among river drainages indicated distinct zoogeographic patterns between geomorphic provinces and along the riverine archipelago of South Dakota. The division between Great Plains and Central Lowlands faunas was consistent with findings elsewhere (Stevenson et al. 1974, Hawkes et al. 1986). Essentially, the Great Plains fauna represents a subset of the Central Lowlands fauna (Cross et al. 1986). Relatively harsh aquatic habitats of the Great Plains are dominated by relatively hardy generalist species, presumably because more specialized or less tolerant species cannot survive (Matthews and Hill 1980, Matthews 1987, Bramblett and Fausch 1991).

Values of faunal resemblance among neighboring river drainages were comparable to those reported by Sheldon (1988) in southeastern North America, suggesting that the river drainages of South Dakota constitute a riverine archipelago. Lowest resemblance (highest values) corresponded to the transition between Central Lowlands and Great Plains faunas (between the James and Niobrara river drainages), which supported the distinction between geomorphic provinces. There was also low resemblance from south to north within the Great Plains (Niobrara to Cheyenne river drainage), which supported the findings of Hoagstrom and Berry (2006) who documented dramatic faunal change from south to north among tributaries of the western Missouri River drainage.

Faunal Change

SPECIES LOSSES.—Species losses were a major factor in historical fish community change. Land-use changes in South Dakota were likely important in the decline of native fishes. Siltation and pollution associated with row-crop agriculture and urbanization have affected streams of the Big Sioux (Sinning 1968, Dieterman and Berry 1998, Milewski et al. 2001), Vermillion (Schmulbach and Braaten 1993), and James (Owen et al. 1981) river drainages, which suffered relatively high native species losses. Many of the species lost from these drainages are sensitive to habitat degradation and have declined elsewhere due to land-use change (e.g., Smith 1971, Karr et al.

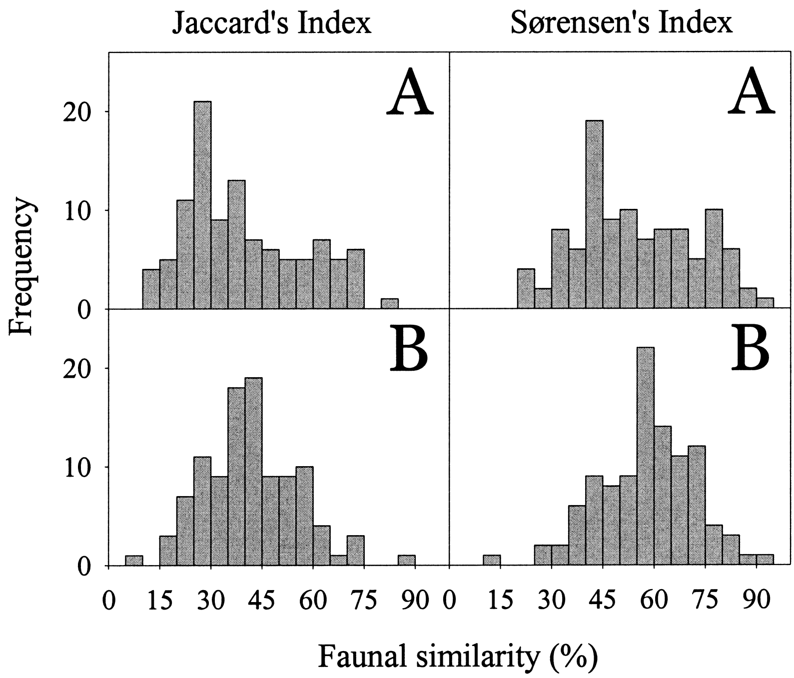

Fig. 6. Frequency of Jaccard's faunal similarity values (left graphs) and Sørensen's faunal similarity values (right graphs) for comparisons of South Dakota river drainages between historic (A) and recent (B) fish faunas.

1985, Wang et al. 1997, Haslouer et al. 2005). High species losses were also documented for big river fishes of the mainstem Missouri River, which has been impacted by impoundment (Hesse et al. 1989, Galat et al. 2005). Future species losses may continue to change fish distributions in South Dakota, particularly for species that have already declined. Because of their restricted distributions, species restricted to only 1 river drainage face a relatively high risk of extinction (Moyle and Williams 1990).

Species losses were fewer among river drainages of the Great Plains compared to the Central Lowlands, perhaps because Great Plains fishes have high tolerance for climatic fluctuation and habitat instability, and because human impacts are similar to natural disturbances of the region (Bramblett and Fausch 1991). However, some Great Plains fishes (western silvery minnow *Hybognathus argyritis*, plains minnow *Hybognathus placitus*, sturgeon chub *Macrhybopsis gelida*, and flathead chub *Platygobio gracilis*) have declined from the Great Plains of South Dakota and are declining in other states (e.g., Hesse et al. 1993, Patton et al. 1998, Haslouer et al. 2005). Historically, the mainstem Missouri River could have served as a dispersal corridor between river drainages and as a refuge during drought. Dams and reservoirs have created barriers and eliminated fluvial habitats on the mainstem Missouri River. They also have fragmented the Cheyenne River and Grand River drainages.

River fragmentation increases extinction risk for isolated fish populations (Sheldon 1987). Indeed, the combination of local drought and habitat fragmentation could explain the loss of sturgeon chub from the Little Missouri River drainage (Kelsch 1994). It is also possible that more sensitive species were historically present in the Great Plains of South Dakota, but disappeared rapidly due to human impacts. Cross and Moss (1987) documented the rapid loss of sensitive species from the Great Plains of Kansas, where historical collections were more extensive.

SPECIES ADDITIONS.—The fish fauna of South Dakota was enriched by a surplus of successfully introduced species compared to lost native species, in contrast to the majority of U.S. states (McKinney 2002). Some studies

TABLE 2. Jaccard's faunal similarity coefficients for historic (lower diagonal) and recent (upper diagonal) fish faunas among 16 river drainages of South Dakota: Bois = Bois de Sioux, UpMn = Upper Minnesota, BigS = Big Sioux, Verm = Vermillion, LoMs = Lower Missouri River Valley, Niobr = Niobrara, Cheye = Cheyenne, Morea = Moreau, UpMs = Upper Missouri River Valley, LiMs = Little Missouri.

	Bois	UpMn	BigS	Verm	James	LoMs	Niobr	Ponca	White	Bad	Cheye	Morea	Grand	UpMs	LiMs
Bois		42.0	28.2	32.0	33.9	25.0	21.7	25.8	24.0	39.4	28.8	33.3	34.9	29.2	8.1
UpMn	37.5		57.3	47.6	53.6	40.2	36.1	26.9	36.9	30.4	37.3	43.1	44.1	44.2	15.5
BigS	25.7	61.5		59.2	72.6	54.3	35.5	21.1	39.7	27.4	41.4	35.5	38.2	56.0	16.0
Verm	27.8	37.8	57.3		74.1	50.0	41.8	32.6	47.4	41.7	42.0	47.2	48.1	49.3	24.0
James	35.2	47.2	64.9	75.0		60.5	35.8	25.4	40.6	32.8	44.2	42.2	45.3	58.7	19.0
LoMs	26.5	38.4	60.7	68.2	71.6		37.2	21.6	41.3	31.1	42.7	39.0	39.7	55.2	21.3
Niobr	33.3	28.8	32.9	40.0	35.0	38.2		50.0	68.2	41.5	41.9	54.5	52.2	41.2	40.5
Ponca	32.0	13.8	12.3	18.4	17.0	15.4	36.7		39.0	41.4	26.8	41.7	39.5	25.4	29.6
White	30.2	27.1	36.4	47.3	41.7	44.1	73.0	28.6		52.4	59.3	68.2	61.7	47.8	45.0
Bad	21.2	14.1	20.3	30.0	23.2	26.2	41.2	26.1	48.6		44.4	61.1	62.2	38.7	55.6
Cheye	25.6	20.8	27.2	41.1	31.7	37.1	47.6	22.9	61.0	56.3		57.1	60.7	52.6	33.3
Morea	34.4	20.6	24.3	36.0	28.6	30.8	50.0	28.0	61.8	69.6	65.6		89.2	50.0	52.9
Grand	28.6	21.9	25.3	34.6	27.6	31.8	51.4	25.9	62.9	70.8	66.7	83.3		55.6	50.0
UpMs	26.9	26.9	43.8	59.6	55.7	61.2	45.1	19.6	59.2	40.9	52.0	47.7	52.3		27.0
LiMs	20.6	13.8	18.4	26.9	20.7	25.8	44.1	25.0	51.4	60.9	59.4	73.9	75.0	40.0	

TABLE 3. Sørensen's faunal similarity coefficients for historic (lower diagonal) and recent (upper diagonal) fish faunas among 16 river drainages of South Dakota: Bois = Bois de Sioux, UpMn = Upper Minnesota, BigS = Big Sioux, Verm = Vermillion, LoMs = Lower Missouri River Valley, Niobr = Niobrara, Cheye = Cheyenne, Morea = Moreau, UpMs = Upper Missouri River Valley, LiMs = Little Missouri.

	Bois	UpMn	BigS	Verm	James	LoMs	Niobr	Ponca	White	Bad	Cheye	Morea	Grand	UpMs	LiMs
Bois		59.2	44.0	48.5	50.6	40.0	35.7	41.0	38.7	56.5	56.5	50.0	51.7	45.2	15.0
UpMn	54.5		72.9	64.5	69.8	57.4	53.0	42.4	53.9	46.6	54.4	60.2	61.2	61.3	26.9
BigS	40.9	76.2		74.3	84.1	70.4	52.4	34.9	56.9	43.0	58.5	52.4	55.2	71.8	27.6
Verm	43.5	54.9	72.9		85.1	66.7	59.0	49.2	64.3	58.8	59.2	64.1	65.0	66.0	38.7
James	52.1	64.2	78.7	85.7		75.4	52.7	40.5	57.7	49.4	61.3	59.3	62.4	73.9	32.0
LoMs	41.9	55.5	75.6	81.1	83.5		54.2	35.6	58.4	47.4	59.8	56.1	56.9	71.1	35.2
Niobr	50.0	44.7	49.5	57.1	51.9	55.3		66.7	81.1	58.6	59.1	70.6	68.6	58.3	57.7
Ponca	48.5	24.2	22.0	31.0	29.0	26.7	53.7		56.1	58.5	42.3	58.8	56.6	40.5	45.7
White	46.4	42.7	53.3	64.2	58.8	61.2	84.4	44.4		68.8	74.5	81.1	76.3	64.7	62.1
Bad	35.0	24.7	33.7	46.2	37.7	41.5	58.3	41.4	65.4		61.5	75.9	76.7	55.8	71.4
Cheye	40.7	34.5	42.7	58.2	48.2	54.2	64.5	37.2	75.8	72.0		72.7	75.6	69.0	50.0
Morea	51.2	34.2	39.1	52.9	44.4	47.1	66.7	43.8	76.4	82.1	79.2		94.3	66.7	69.2
Grand	44.4	35.9	40.4	51.4	43.2	48.3	67.9	41.2	77.2	82.9	80.0	90.9		71.4	66.7
UpMs	42.4	42.4	60.9	74.7	71.6	75.9	62.2	32.7	74.4	58.1	68.4	64.6	68.7		42.5
LiMs	34.1	24.3	31.1	42.4	34.3	41.0	61.2	40.0	67.9	75.7	74.5	85.0	85.7	57.1	

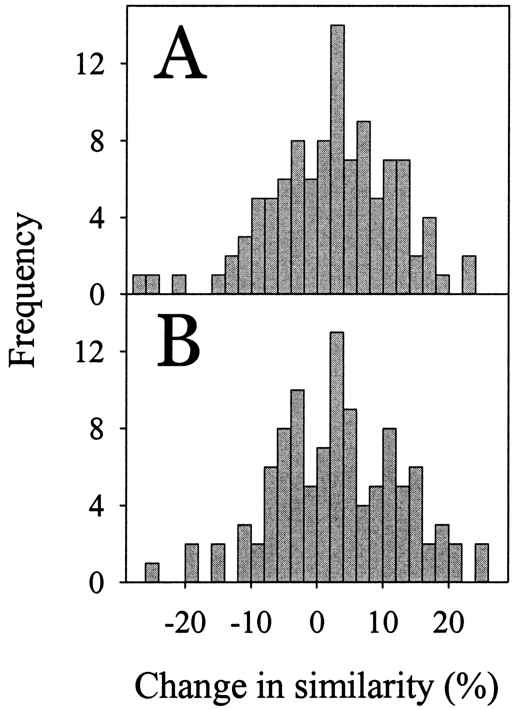

Fig. 7. Frequency of the magnitude of change in Jaccard's faunal similarity values (A) and Sørensen's faunal similarity values (B) for comparisons between historic and recent fish faunas of South Dakota river drainages.

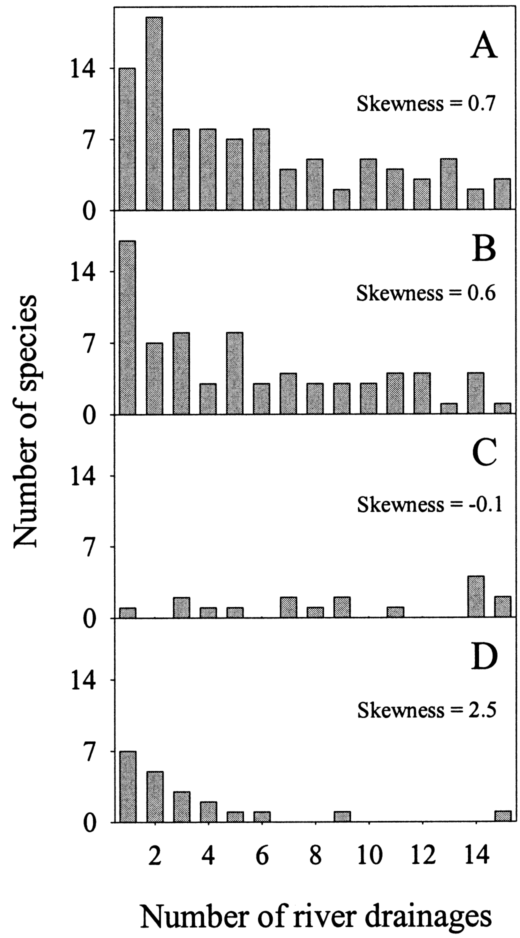

Fig. 8. Frequency distributions of fish species among river drainages for historic fishes (A), recent natives (B), in-state nonnatives (C), and out-of-state nonnatives (D).

have concluded that nonnative fishes may enrich native faunas without causing reciprocal species losses, although they note that negative impacts may yet occur (Moyle and Light 1996, Gido and Brown 1999, Irz et al. 2004). Others suggest that species richness is not an appropriate measure of ecological integrity and that faunal enrichment is a threat to global biodiversity (Marchetti et al. 2001, Taylor et al. 2001, Taylor 2004).

Increased fish species richness in South Dakota is attributable to the faunal enrichment of cold water habitats in the Great Plains and the Missouri River valley. Muskellunge *Esox masquinongy,* Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri,* rainbow trout *Oncorhynchus mykiss,* brown trout *Salmo trutta,* brook trout *Salvelinus fontinalis,* and mottled sculpin *Cottus bairdii* have been introduced either to mountain streams of the Black Hills, cool spring-fed streams throughout the state, reservoir tailwaters, or deep reservoirs. Skipjack herring, rainbow smelt *Osmerus mordax,* cisco *Coregonus artedi,* lake whitefish *Coregonus clupeaformis,* kokanee salmon *Oncorhynchus nerka,* Chinook salmon *Oncorhynchus tschawytscha,* and lake trout *Salvelinus namaycush* inhabit only human-created cold water habitats (i.e., deep reservoirs). Taxonomic enrichment of reservoir and cold water stream habitats in South Dakota is consistent with trends throughout North America (Moyle 1986). The restriction of many nonnatives to human-made habitats supports the findings of Gido et al. (2004) who found that many nonnative fishes in Kansas and Oklahoma were localized near reservoirs, possibly because they were not adapted for the harsh abiotic environment of unaltered habitats.

All 22 in-state nonnatives were native to portions of the Central Lowlands and nonnative to the Great Plains, similar to findings in Kansas and Oklahoma (Gido et al. 2004). Some of these species were more widespread during prehistoric times. For example, roughly 14,000 to 10,000 years ago, western banded killifish *Fundulus diaphanus menona,* pumpkinseed *Lepomis gibbosus,* bluegill *Lepomis macrochirus macrochirus,* largemouth bass *Micropterus salmoides salmoides,* and yellow perch *Perca flavescens* were present in the Great Plains of North Dakota and South Dakota (Clayton 1967, Cvancara et al. 1971, Ossian 1973). They eventually disappeared from the Great Plains, presumably because the climate became harsher (Newbrey and Ashworth 2004). Recently, humans have re-created suitable habitats for these fishes and provided transport, facilitating their recolonization.

TAXONOMIC HOMOGENIZATION.—The level of homogenization between the Central Lowlands and Great Plains geomorphic provinces based on Jaccard's index (8%) was comparable to that observed among U.S. states (7%; Rahel 2000) and higher than that observed among Canadian provinces (1%; Taylor 2004). This level of interprovincial homogenization was corroborated by analyses based on Sørensen's index and by opposing patterns of native species loss and nonnative species invasion between provinces. Low skewness of recent native and in-state nonnative fish species indicates that the spread of in-state nonnatives (mostly sport fishes) throughout South Dakota has been a major factor in homogenization, supporting the findings of Rahel (2000).

The level of homogenization among river drainages was less pronounced than between geomorphic provinces, in part due to relatively high variation among pairwise similarity values. Nevertheless, the overall trend was for increased faunal similarity, and Sørensen's index indicated an even higher level of homogenization than Jaccard's index. It is possible that the theoretical superiority of Sørensen's index compared to Jaccard's index (Legendre and Legendre 1998) makes it a more sensitive measure of homogenization by emphasizing shared presences between faunas. Previous studies of taxonomic homogenization of freshwater fish faunas at the river drainage scale have either not quantified faunal similarity patterns (Hubbs et al. 1997, Scott and Helfman 2001, Carlson and Daniels 2004) or have not found a clear pattern of homogenization (Marchetti et al. 2001, 2006, Taylor 2004). Thus, it is noteworthy that we found homogenization among South Dakota river drainages, even though the level of homogenization was less than it was between geomorphic provinces.

Olden and Poff (2003, 2004) concluded that homogenization is greatest when invasive species are widespread, causing either no native extinctions or differential native extinctions. Their conclusion fits with our findings in South Dakota, except that native species extinctions have not been linked to nonnative species invasions. Conceptual models of taxonomic homogenization in freshwater faunas emphasize the contribution of habitat alteration by humans and nonnative species introductions (Marchetti et al. 2001, Scott and Helfman 2001, Rahel 2002). Factors that appear to cause homogenization between geomorphic provinces in South Dakota are land-use change in the Central Lowlands (e.g., agricultural development, urbanization), which leads to native species loss, and management activities in the Great Plains (e.g., water development, sport fish introductions), which lead to nonnative species invasion. Thus, the process of taxonomic homogenization in South Dakota appeared to be spatially segregated, with species from more diverse Central Lowlands faunas declining in some cases and being spread to less diverse Great Plains faunas in other cases, similar to findings in Kansas and Oklahoma (Gido et al. 2004).

CONCLUSION

The fish fauna of South Dakota has 2 major geographical divisions that correspond to geomorphic provinces: the Central Lowlands and Great Plains. The major river drainages of the state constitute a riverine archipelago with high faunal disparity (β diversity). The Central Lowlands fauna has been diminished by the decline of sensitive fishes that were not native to the Great Plains. In contrast, other fishes that were native to certain Central Lowlands river drainages were introduced throughout the state. Native Great Plains faunas received many nonnative species introductions, but have suffered fewer native fish declines to date. The Great Plains fauna was also enriched by the introduction of cold water fishes to mountain streams of the Black Hills and to human-made reservoirs. Recent zoogeographic patterns along the riverine archipelago of South Dakota are strikingly similar to historic patterns, indicating the importance of geographic variation among river drainages. However, statewide comparisons of faunal similarity between geomorphic provinces and among river drainages indicate faunal homogenization that results from changes (declines, expansions) in the distributions of historically restricted species. Although the total richness of the South Dakota fish fauna has increased, the native fish fauna, particularly within the Central Lowlands, has declined. The pattern of native species loss is better explained by the decline of species sensitive to human impacts than by nonnative species introductions. The conservation of native fishes with restricted distributions, curtailment of interdrainage transfers in South Dakota, and containment of out-of-state nonnatives will be necessary to prevent further taxonomic homogenization.

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