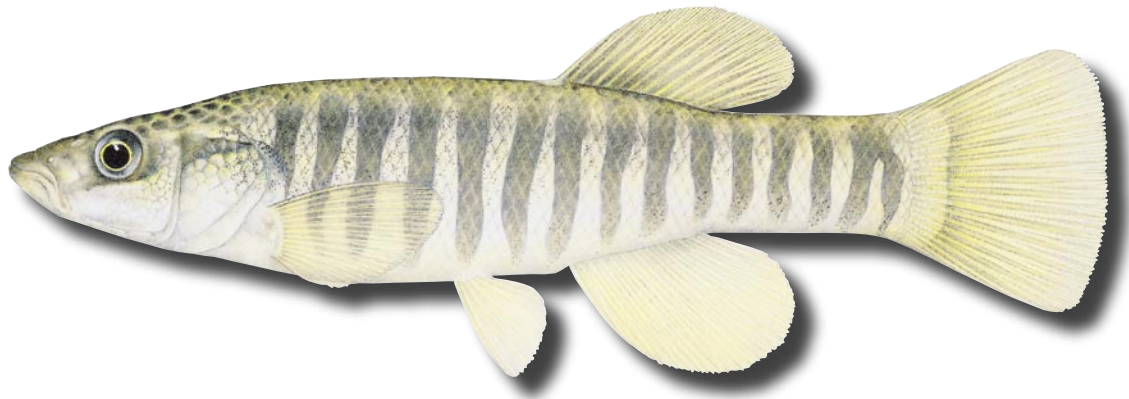


**Plains Killifish (*Fundulus zebrinus*):
A Technical Conservation Assessment**



**Prepared for the USDA Forest Service,
Rocky Mountain Region,
Species Conservation Project**

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Frank J. Rahel and Laura A. Thel
Department of Zoology and Physiology
University of Wyoming, Laramie, Wyoming 82071

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AUTHORS' BIOGRAPHIES

Frank J. Rahel is a professor in the Department of Zoology and Physiology at the University of Wyoming where he teaches courses in fisheries management, ichthyology, and conservation biology. His research interests are centered around fish ecology and the influence of anthropogenic disturbances on fish assemblages.

Laura A. Thel is a graduate research assistant in the Department of Zoology and Physiology at the University of Wyoming with research interests involving stream ecology, hydrology, and landscape ecology, especially as these are related to the management of native fishes.

COVER PHOTO CREDIT

Plains killifish (*Fundulus zebrinus*). © Joseph Tomelleri.

LIST OF ERRATA

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF PLAINS KILLIFISH

Status

The plains killifish (*Fundulus zebrinus*) is not a federally threatened, endangered, or sensitive species in the United States, nor is it considered a threatened, endangered, or sensitive species in any of the five states comprising the Rocky Mountain Region (Region 2) of the USDA Forest Service. Within the Rocky Mountain Region, the plains killifish is not present on any of the national forest districts, but it does occur on three national grasslands. Although individual populations may decline due to drought or loss of streamflow from water development activities, the species as a whole is secure at present. No major loss of native geographic range has occurred, and the species has increased its range through anthropogenic introductions in Colorado, South Dakota, Arizona, Utah, and Wyoming.

Primary Threats

Although the plains killifish is not a priority for conservation concern at present, there are factors that could potentially become threats in the future. These include water development activities that alter the natural streamflow regime, cause physical or chemical habitat degradation, as well as result in stream fragmentation. Reservoirs have dampened natural flow fluctuations and reduced sediment loads, thereby making plains streams less turbid and more confined in narrower, deeper channels. The result has been replacement of native fishes tolerant of turbid waters, including the plains killifish, by fishes characteristic of clearer waters. Another potential threat to plains killifish populations involves introduction of non-native fishes. Plains killifish are seldom found in association with larger, piscivorous fish. Historically, piscivorous gamefish were absent or rare in prairie stream drainages because of the paucity of deepwater habitat. However, construction of stock watering ponds and irrigation reservoirs has created such habitat and led to widespread stocking of these piscivorous gamefish. A non-piscivorous fish, the mosquitofish (*Gambusia affinis*), has been introduced throughout the range of the plains killifish. Through competition for common resources, there is the potential for mosquitofish to have negative effects on native small-bodied species, such as the plains killifish.

Primary Conservation Elements, Management Implications and Considerations

The plains killifish is part of an assemblage of small-bodied, warmwater fishes native to streams of the Great Plains. Conservation of plains killifish can be considered in conjunction with management of a larger group of native Great Plains fishes. The major management actions that would benefit these native fishes are preserving streamflows, maintaining stream connectivity, preventing the establishment of non-native piscivores, and avoiding introductions of non-native small-bodied fishes. Plains killifish evolved in stream systems subject to intermittency and other disturbances such as floods and winterkill. Therefore, dispersal and recolonization after local extirpation are likely important mechanisms allowing regional persistence of the species. Thus, anthropogenic features that impede fish movements, such as impoundments or highway culverts, will be detrimental to the persistence of plains killifish within a given drainage. Conversely, management actions that help to maintain streamflows, especially in larger streams/ rivers that originate on the Great Plains, would be advantageous to this species.

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INTRODUCTION

This assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2), USDA Forest Service. The plains killifish (*Fundulus zebrinus*) is the focus of an assessment because there was some level of concern for this species' viability within Region 2 (**Figure 1**) during the Regional Forester's Sensitive Species List revision process in 2001 - 2003. After full examination it was determined that the status of the plains killifish did not justify listing it as a Regional sensitive species. However, it was determined that viability may still be an issue at more localized levels within Region 2. The plains killifish is a Management Indicator Species (MIS) on the Pawnee National Grassland. As a MIS, it serves as a barometer for species viability at the forest level. Management Indicator Species have two functions: 1) to estimate the effects of planning alternatives on fish and wildlife populations (36 CFR 219.19 (a) (1)) and 2) to monitor the effects of management activities on species via changes in population trends (36 CFR 219.19 (a) (6)). This assessment will facilitate further evaluation of plains killifish leading to future decisions by the agency regarding the conservation status of this fish species.

This assessment addresses the biology of plains killifish throughout its range in Region 2. The broad nature of the assessment leads to some constraints on the specificity of information for particular locales. Furthermore, completing the assessments promptly requires establishment of some limits concerning the geographic scope of particular aspects of the assessment and further analysis of existing (but unanalyzed) field data. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

Species conservation assessments produced as part of the Species Conservation Project are designed to provide forest managers, research biologists, and the public with a thorough discussion of the biology, ecology, conservation status, and management of certain species based on available scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. The assessment does not seek to develop specific management recommendations but provides the ecological background upon which management must be based. However, it

does focus on the consequences of changes in the environment that result from management actions (i.e. management implications). Furthermore, it cites management recommendations proposed elsewhere, and when management recommendations have been implemented, the assessment examines the success of the implementation.

Scope

The plains killifish assessment examines the biology, ecology, conservation status, and management of this species with specific reference to the geographic and ecological characteristics of the USFS Rocky Mountain Region (**Figure 1**). Although some of the literature on the species may originate from field investigations outside the region, this document places that literature in the ecological and social context of the central Rockies. Similarly, this assessment is concerned with reproductive behavior, population dynamics, and other characteristics of plains killifish in the context of the current environment rather than under historical conditions. The evolutionary environment of the species is considered in conducting the synthesis, but it is placed in a current context.

In producing the assessment, we reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on plains killifish are referenced in the assessment, nor was all material considered equally reliable. The assessment emphasizes refereed literature because this is the accepted standard in science. We chose to use some non-refereed literature in the assessments, however, when information was unavailable elsewhere. Unpublished data (e.g. Natural Heritage Program records) were important in estimating the geographic distribution of the species. These data required special attention because of the diversity of persons and methods used in collection.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct critical experiments in the ecological sciences, and often observations, inference,

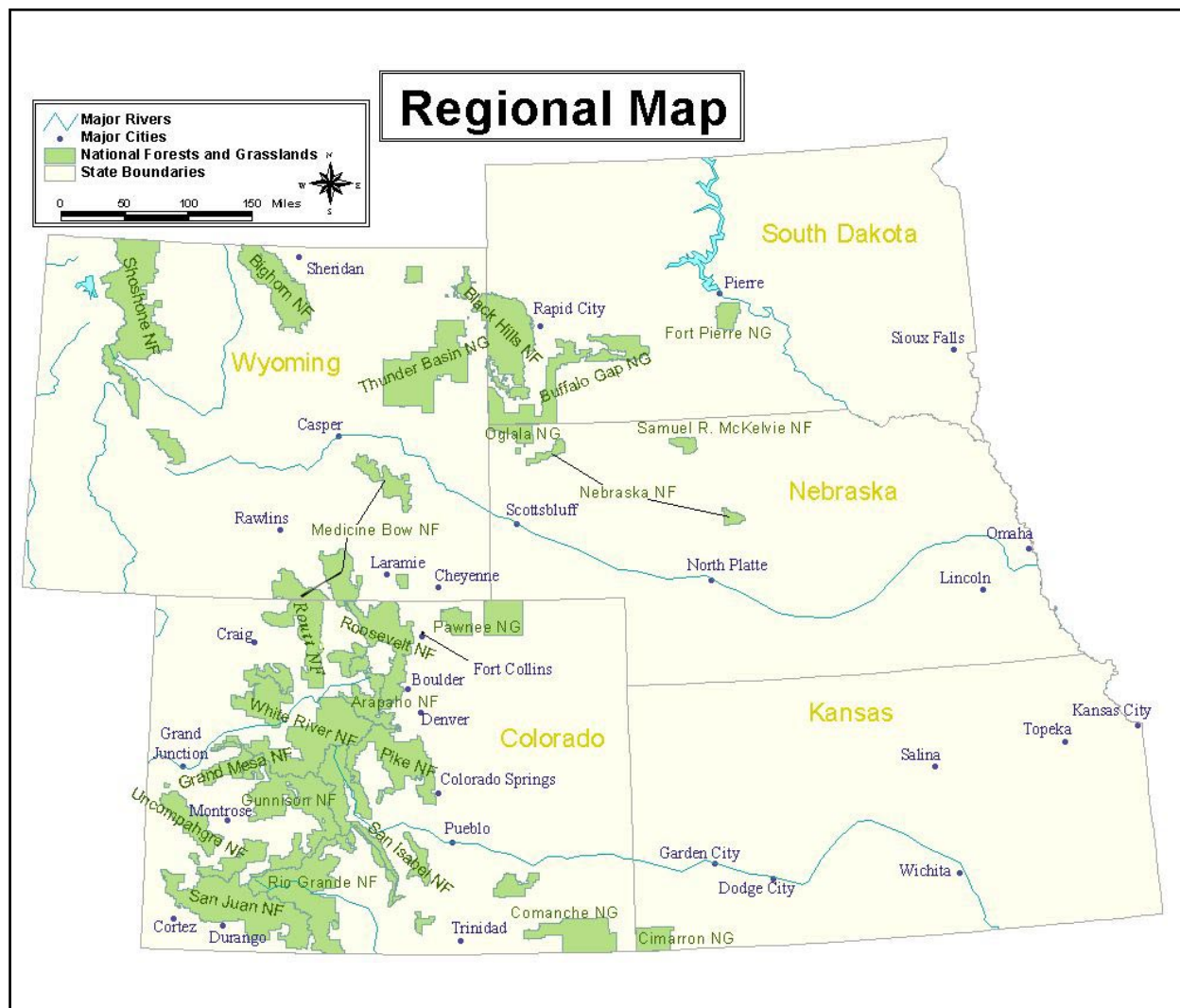


Figure 1. National forests and grasslands within the Rocky Mountain Region (Region 2) of the USDA Forest Service.

good thinking, and models must be relied on to guide the understanding of ecological relations.

In this assessment, the strength of evidence for particular ideas is noted and alternative explanations are described when appropriate. While well-executed experiments represent a strong approach to developing knowledge, alternative approaches such as modeling, critical assessment of observations, and inference are accepted as sound approaches to understanding.

Application and Interpretation Limits of this Assessment.

Information about the biology of plains killifish was collected and summarized from throughout the geographic range, which extends from Montana

to Texas. In general, life history and ecological information collected in a portion of this range should apply broadly throughout the range. However, certain life history parameters (such as growth rate, longevity, and spawning activity) could differ along environmental gradients, especially those related to length of growing season. Information about the conservation status was limited to Region 2 of the USDA Forest Service and should not be taken to imply conservation status in other portions of the species' range.

Publication of Assessment on the World Wide Web

To facilitate use of species assessments in the Species Conservation Project, they are being published on the Region 2 World Wide Web site. Placing the

documents on the web makes them available to agency biologists and the public more rapidly than publishing them as reports. More important, it facilitates revision of the assessments, which will be accomplished based on guidelines established by Region 2.

Peer Review

Assessments developed for the Species Conservation Process have been peer reviewed prior to release on the web. Peer review for this assessment was administered by the American Fisheries Society, employing at least two recognized experts for this or related taxa. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

The plains killifish is not considered a federally threatened, endangered, or sensitive species in the United States (U.S. Fish and Wildlife Service; <http://endangered.fws.gov/>). At the state level, the plains killifish is not considered a threatened, endangered, or sensitive species in any of the five states comprising Region 2 of the USDA Forest Service (**Table 1**). The Natural Heritage Rank of the Nature Conservancy is secure (S5) or apparently secure (S4) in four states and vulnerable (S3) in only one state, Kansas (**Table 1**). In Region 2, the plains killifish is not present on any of the national forest districts, but it does occur on three national grasslands where it is not considered a threatened, endangered, or sensitive species (**Table 2**). The plains killifish was not reported as present on lands managed by the Bureau of Land Management in Wyoming or Colorado (**Table 3**). We were unable to obtain information for Bureau of Land Management lands in Nebraska or South Dakota. In Kansas, the Bureau of Land Management manages only subsurface waters. The plains killifish does not appear on the list of species considered threatened, endangered, or sensitive species developed by the Bureau of Land Management in Kansas.

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies.

Given that the plains killifish is not considered a threatened, endangered, or sensitive species within Region 2, there are no regulatory mechanisms, management plans, or conservation strategies specifically aimed at this species. The species is not exploited as a gamefish. Occasionally it may be collected by anglers for use as bait, but it is not considered a prime baitfish species (Woodling 1985). Because it is considered a baitfish by the five states within Region 2, state statutes regulating the harvest of baitfish apply to the plains killifish. In Wyoming, a separate license (other than a general fishing license) is required to collect baitfish, and certain drainages are closed to baitfish collecting. However there is no limit to the number of baitfish that can be collected (Wyoming Game and Fish Department; <http://gf.state.wy.us>). In Colorado, baitfish can be collected for personal use with a general fishing license with no harvest limits. However, baitfish cannot be collected from any natural streams statewide, and in certain geographic areas baitfish may not be collected from standing water bodies (Colorado Division of Wildlife; <http://wildlife.state.co.us>). In Kansas, baitfish can be collected with a general fishing license, and the possession limit is 500 fish per person. Collecting is allowed statewide except on lands owned by the Kansas Department of Wildlife and Parks (Kansas Department of Wildlife and Parks; www.kdwp.state.ks.us). In Nebraska, a general fishing license is required to collect baitfish for personal use with the bag and possession limits both set at 100 fish (Nebraska Game and Parks Commission; <http://www.ngpc.state.ne.us>). Additionally, baitfish cannot be collected from lakes or reservoirs, and a separate license is required for commercial baitfish collection. In South Dakota, a general fishing license is required to harvest baitfish, the catch limit is twelve dozen, and there are few restrictions regarding where baitfish may be collected (South Dakota Department of Game, Fish and Parks; <http://www.state.sd.us/gfp>).

Because the plains killifish is not currently considered to be imperiled within Region 2, is not

Table 1. Occurrence and management status of plains killifish in the five states comprising Region 2 of the USDA Forest Service.

State	Occurrence	State Status	References	State Heritage Status Rank*
Colorado	Present	Not T, E, or S**	Nesler et al. (1997, 1999)	S5 = Secure
Kansas	Present	Not T, E, or S	Kansas Department of Wildlife and Parks, http://www.kdwp.state.ks.us/	S3 = Vulnerable
Nebraska	Present	Stable	Nebraska Game and Parks Commission, personal communication	S4 = Apparently Secure
South Dakota	Present	S5 = Secure	South Dakota Department of Game, Fish and Parks, http://www.sdgifp.info/Index.htm	S5 = Secure
Wyoming	Present	NSS6 = distribution expanding and habitat availability increasing	Wyoming Game and Fish Department, http://gf.state.wy.us/	S5 = Secure

*State Heritage Status Rank is the status of plains killifish populations within states based on the conservation status ranking system developed by NatureServe, The Nature Conservancy and the Natural Heritage Network, <http://www.natureserve.org/>.

**Not Threatened, Endangered, or Sensitive.

subject to exploitation as a sport fish, and has minimal value as a baitfish, it would appear that existing baitfish regulations should be adequate to protect the species from overharvest. The most likely factor to negatively impact the plains killifish in the future, along with other fishes of the Great Plains area, is loss of habitat as streams become intermittent or dry up due to water development activities. There do not appear to be any water-use or instream flow regulations that specifically address maintenance of habitat for plains killifish.

Biology and Ecology

Systematics

The plains killifish is in the class Osteichthyes; superorder Teleostei; order Cyprinodontiform; and family Fundulidae. In the new world, the genus *Fundulus* has the most species of the family with approximately 35 recognized species and three to five recognized subgenera: *Fundulus*, *Fontinus*, *Plancterus*, *Xenisma* and *Zygonectes* (Bernardi and Powers 1995).

The taxonomy of the plains killifish has been debated for over a century. Some biologists have recognized two distinct species of plains killifish, *Fundulus zebrinus* and *Fundulus kansae* (e.g., Parenti 1981), whereas others have synonymized *Fundulus zebrinus* and *Fundulus kansae* (e.g., Poss and Miller 1983), or considered them subspecies (e.g., Kreiser et al. 2001).

The following history of the systematics of plains killifish was based mainly on Kreiser (2001). Plains killifish, *Fundulus zebrinus*, were first described by Girard in 1859 as *Hydrargyra zebra* (Kreiser 2001). The genus *Hydrargyra* was synonymized with *Fundulus* by Jordan and Gilbert in 1883, and zebra, already occupied in *Fundulus*, was changed to *zebrinus* (Poss and Miller 1983). In 1895, Garman described *F. kansae* from an unspecified location in Kansas as differing from *F. zebrinus* by having a more convoluted intestine and reduced pharyngeal dentition. Garman also moved *F. zebrinus* and *F. kansae* into the subgenus *Plancterus*. In 1896, Jordan and Evermann did not refer to Garman's work, but included Kansas in the range of *F. zebrinus* (Poss and Miller 1983). In an 1898 addendum, Jordan and Evermann (1896) synonymized *F. zebrinus* and *F. kansae*.

In 1926, Hubbs considered the two to be different species and promoted *Plancterus* to generic status (Poss and Miller 1983, Kreiser et al. 2001). In 1955 Miller did not recognize *Plancterus* as a valid genus, but recognized *Fundulus zebrinus* and *F. kansae* as separate species. In his Ph.D. dissertation, Drewry (1967) described some differences in ecological behavior and male courtship sounds between the two forms but concluded that there was a single species from the ready interbreeding of the two forms in the laboratory (Poss and Miller 1983). Parenti (1981) recognized *F. zebrinus* and *F. kansae* as distinct species and used the genus *Plancterus* to separate the two species from other fundulids with less

Table 2. Occurrence and status of plains killifish in national forests and grasslands within the Rocky Mountain Region of the USDA Forest Service.

State	Management Unit	Occurrence	Information Source	ESA/USFS Status	Basis of Status
Colorado	Arapaho National Forest	Absent	Arapaho/Roosevelt National Forests and Pawnee National Grassland Supervisor's Office	Not T, E or S	Regional Forester's Sensitive Species List, USDA Forest Service, Rocky Mountain Region, 2003
Colorado	Comanche National Grassland	Uncertain*	Pike and San Isabel National Forests and Comanche and Cimarron National Grasslands Supervisor's Office	Not T, E or S	Threatened, Endangered and Sensitive Species of the Pike and San Isabel National Forests and Comanche and Cimarron National Grasslands, May 25 1994.**
Colorado	Grand Mesa National Forest	Absent	Grand Mesa, Uncompahgre, and Gunnison National Forests Supervisor's Office	Not T, E or S	Regional Forester's Sensitive Species List, USDA Forest Service, Rocky Mountain Region, 2003
Colorado	Gunnison National Forest	Absent	Grand Mesa, Uncompahgre, and Gunnison National Forests Supervisor's Office	Not T, E or S	Regional Forester's Sensitive Species List, USDA Forest Service, Rocky Mountain Region, 2003
Colorado	Pawnee National Grassland	Present	Pawnee National Grassland, 1998-1999-2000 Fish Sampling Survey; 1997 Colorado Division of Wildlife South Platte Report	Not T, E or S; MIS	Matrix of "Listed" Species in the Great Plains of North America and their Occurrence on National Grasslands***
Colorado	Pike National Forest	Absent	Pike and San Isabel National Forests and Comanche and Cimarron National Grasslands Supervisor's Office	Not T, E or S	Threatened, Endangered and Sensitive Species of the Pike and San Isabel National Forests and Comanche and Cimarron National Grasslands, May 25, 1994
Colorado	Rio Grande National Forest	Absent	Rio Grande National Forest Supervisor's Office	Not T, E or S	Regional Forester's Sensitive Species List, USDA Forest Service, Rocky Mountain Region, 2003
Colorado	Roosevelt National Forest	Absent	Arapaho/Roosevelt National Forests and Pawnee National Grassland Supervisor's Office	Not T, E or S	Regional Forester's Sensitive Species List, USDA Forest Service, Rocky Mountain Region, 2003
Colorado	Routt National Forest	Absent	Medicine Bow/Routt National Forests and Thunder Basin National Grassland Supervisor's Office	Not T, E or S	Regional Forester's Sensitive Species List, USDA Forest Service, Rocky Mountain Region, 2003
Colorado	San Isabel National Forest	Absent	Pike and San Isabel National Forests and Comanche and Cimarron National Grasslands Supervisor's Office	Not T, E or S	Threatened, Endangered and Sensitive Species of the Pike and San Isabel National Forests and Comanche and Cimarron National Grasslands, May 25, 1994.
Colorado	San Juan National Forest	Absent	San Juan National Forest Supervisor's Office	Not T, E or S	Regional Forester's Sensitive Species List, USDA Forest Service, Rocky Mountain Region, 2003
Colorado	Uncompahgre National Forest	Absent	Grand Mesa, Uncompahgre, and Gunnison National Forests Supervisor's Office	Not T, E or S	Regional Forester's Sensitive Species List, USDA Forest Service, Rocky Mountain Region, 2003
Colorado	White River National Forest	Absent	White River National Forest Supervisor's Office	Not T, E or S	Regional Forester's Sensitive Species List, USDA Forest Service, Rocky Mountain Region, 2003

Table 2 (cont.).

State	Management Unit	Occurrence	Information Source	ESA/USFS Status	Basis of Status
Kansas	Cimarron National Grassland	Present	1998 Cimarron River Fishes Survey (http://www.fs.fed.us/r2/nebraska/gpng/tes_projects/fishreport.html)	Not T, E or S	Threatened, Endangered and Sensitive Species of the Pike and San Isabel National Forests and Comanche and Cimarron National Grasslands, May 25, 1994
Nebraska	Nebraska National Forest	Absent	1998 and 1996 Nebraska Department of Environmental Quality, Fisheries surveys. Copies of fisheries surveys on USFS land acquired from Nebraska National Forest Supervisor's Office	Not T, E or S	Regional Forester's Sensitive Species List, USDA Forest Service, Rocky Mountain Region, 2003
Nebraska	Oglaala National Grassland	Absent	Nebraska Game and Parks Records and Oglaala National Grassland	Not T, E or S	Matrix of "Listed" Species in the Great Plains of North America and their Occurrence on National Grasslands
Nebraska	Samuel R. McKelvie National Forest	Absent	1998, 1996, 1995 and 1994 Nebraska Department of Environmental Quality, Fisheries surveys. Copies of fisheries surveys on USFS land acquired from Nebraska National Forest Supervisor's Office	Not T, E or S	Regional Forester's Sensitive Species List, USDA Forest Service, Rocky Mountain Region, 2003
South Dakota	Blackhills National Forest	Absent	Black Hills National Forest Supervisor's Office	Not T, E or S	Regional Forester's Sensitive Species List, USDA Forest Service, Rocky Mountain Region, 2003
South Dakota	Buffalo Gap National Grassland	Absent	Buffalo Gap National Grassland, Wall and Fall River Ranger Districts; Nebraska National Forest Supervisor's Office	Not T, E or S	Matrix of "Listed" Species in the Great Plains of North America and their Occurrence on National Grasslands
South Dakota	Fort Pierre National Grassland	Absent	Fort Pierre National Grassland, District Office; Nebraska National Forest Supervisor's Office	Not T, E or S	Matrix of "Listed" Species in the Great Plains of North America and their occurrence on National Grasslands
Wyoming	Bighorn National Forest	Absent	Bighorn National Forest Supervisor's Office	Not T, E or S	Regional Forester's Sensitive Species List, USDA Forest Service, Rocky Mountain Region, 2003 and U.S. Fish and Wildlife Service County Lists
Wyoming	Medicine Bow National Forest	Absent	Medicine Bow/Routt National Forest and Thunder Basin National Grassland Supervisor's Office	Not T, E or S	Regional Forester's Sensitive Species List, USDA Forest Service, Rocky Mountain Region, 2003 and U.S. Fish and Wildlife Service County Lists
Wyoming	Shoshone National Forest	Absent	Shoshone National Forest Supervisor's Office	Not T, E or S	Regional Forester's Sensitive Species List, USDA Forest Service, Rocky Mountain Region, 2003

Table 2 (concluded).

State	Management Unit	Occurrence	Information Source	ESA/USFS Status	Basis of Status
Wyoming	Thunder Basin National Grassland	Present	Wesche, T.A. and Johnson, L.S. 1979. Aquatic Biota and Abiota of Selected Streams on Thunder Basin National Grassland, Wyoming.****	Not T, E or S	Matrix of "Listed" Species in the Great Plains of North America and Their Occurrence on National Grasslands

*Present according to Matrix of Listed Species in the Great Plains of North American and Their Occurrence on National Grasslands. However, listing based on presence in Great Plains ecoregion without reference to specific drainages.

**Threatened, Endangered and Sensitive Species of the Pike & San Isabel National Forests and Comanche & Cimarron National Grasslands, May 25, 1994. Compiled by Nancy Ryke, Forest Wildlife Biologist, David Winters, Fish and Wildlife Program Manager; Louanne McMartin, Biological Technician; Steve Vest, Forest Botanist; Barb Masinton Forest Botanist, Version 12.19.01.

***Matrix of "Listed" Species in the Great Plains of North America and their Occurrence on National Grasslands, <http://www.fs.fed.us/r2/nebraska/gpng/matrix/fish.html>.

****Wesche, T.A. and Johnson, L.S. 1979. Aquatic Biota and Abiota of Selected Streams on Thunder Basin National Grassland, Wyoming. Annual Meeting of the Forestry Committee of the Great Plains Agricultural Council: Fort Collins, Colorado; June 18-20, 1979. Funding: U.S.D.A., Rocky Mountain Forest & Range Experiment Station, under the SEAM Program, Coop Agreement #16-733-CA.

Table 3. Occurrence and status of plains killifish on Bureau of Land Management (BLM) lands within the Rocky Mountain Region of the USDA Forest Service.

State	Management Unit	Occurrence	Information Source	BLM Status	Basis of Status
Colorado	Royal Gorge	Absent	Royal Gorge Field Office	Not T, E, or S	BLM Colorado State Director's Sensitive Species List
Colorado	Glenwood Springs	Absent	Glenwood Springs Field Office	Not T, E, or S	BLM Colorado State Director's Sensitive Species List
Colorado	La Jara	Absent	La Jara Field Office	Not T, E, or S	BLM Colorado State Director's Sensitive Species List
Colorado	Gunnison	Absent	Gunnison Field Office	Not T, E, or S	BLM Colorado State Director's Sensitive Species List
Colorado	Pagosa Springs	Absent	Pagosa Springs Field Office	Not T, E, or S	BLM Colorado State Director's Sensitive Species List
Colorado	Kremmling	Absent	Kremmling Field Office	Not T, E, or S	BLM Colorado State Director's Sensitive Species List
Colorado	San Juan	Absent	San Juan Field Office	Not T, E, or S	BLM Colorado State Director's Sensitive Species List
Wyoming	Buffalo	Absent	Buffalo Field Office	Not T, E, or S	BLM Wyoming State Director's Sensitive Species List
Wyoming	Casper	Absent	Casper Field Office	Not T, E, or S	BLM Wyoming State Director's Sensitive Species List
Wyoming	Rawlins	Absent	Rawlins Field Office	Not T, E, or S	BLM Wyoming State Director's Sensitive Species List

Information for plains killifish on BLM lands in Nebraska and South Dakota was unavailable. The BLM manages only subsurface waters in Kansas.

convoluted intestines (Kreiser 2001). The American Fisheries Society in its 1991 checklist did not accept the generic changes and retained the single species *zebrinus* in *Fundulus* (Robins et al. 1991).

Poss and Miller (1983) evaluated morphological data gathered from specimens from the entire range of the two nominal taxa *Fundulus zebrinus* and *F. kansae* and found a north-south clinal variation in several morphometric and meristic characters. Poss and Miller concluded that *F. kansae* was a junior synonym of *F. zebrinus*.

Kreiser et al. (2001) examined the geographic pattern of genetic variation in *Fundulus zebrinus*, using three allozyme loci, mitochondrial DNA restriction, fragment length polymorphisms, and sequencing of the mitochondrial cytochrome oxidase I. They found three geographic assemblages that were designated as

northern, central, and southern. Kreiser et al. (2001) found a large phylogenetic break separating the northern and central assemblages from the southern assemblage and suggested the separation supported previous attempts to recognize two species of the plains killifish, *F. zebrinus* (southern assemblage) and *F. kansae* (northern and central assemblages). However, the suggested range designations for *F. zebrinus* and *F. kansae* based on the molecular work of Kreiser et al. does not exactly coincide with ranges of *F. zebrinus* and *F. kansae* established by Miller in 1955 (Kreiser 2001). Miller described the range of *F. zebrinus* as restricted to the Brazos, Colorado, and Pecos rivers and the range of *F. kansae* to include the Red River and the drainages further north (Kreiser 2001). The molecular work of Kreiser et al. (2001) designated the range of *F. zebrinus* as drainages south of and including the Red River and *F. kansae* in drainages north of the Red River. The discrepancy in range designation is currently

unresolved. Furthermore, uncertainty regarding the collection localities for the type species (*F. zebrinus* Girard 1859 and *F. kansae* Garman 1895) further complicates the taxonomic reclassification of the two groups. For a detailed discussion of the uncertainty regarding collection localities of the type specimens see Poss and Miller (1983) and Kreiser (2001).

Species description

Topminnows (Family: Fundulidae) are a small group of species having jaws adapted for feeding at the water surface, heads covered by scales or plates, rounded tail fins, and no line of pored scales along their sides (Cross and Collins 1995).

The following description of the plains killifish is based on Woodling (1985), Baxter and Stone (1995), and Cross and Collins (1995). Plains killifish are small topminnows with stout, somewhat compressed bodies and broad, flat heads. The species has a small, terminal, upturned mouth, which opens near the top of the head, and the lower jaw extends beyond the upper jaw. The dorsal fin is posterior, and its origin is almost even with the origin of the anal fin. The caudal fin is either rounded or square. No lateral line is evident externally. The scales are moderate-sized, and the number of scales in the lateral series ranges from 53 to 65. Adult plains killifish color can be light brown, black, straw colored, or pale green fading to pale yellow, white, or silver on their stomachs. Plains killifish have dark, thin, vertical bars on their sides (the number of bars in series ranges from 12 to 28). Males have fewer, wider, and more prominent bars than females, which have narrower bars that are lighter in color. Adult plains killifish reach 9 to 10 cm (3.5 to 4 inches) in length. In breeding males, all fins except the dorsal are bright orange (Cross and Collins 1995).

Distribution and abundance

Plains killifish are native to central North America; their range extends across the Great Plains from the east slope drainages of the Rocky Mountains in the west to the gulf slope drainages in Texas (**Figure 2** adapted from Lee et al. 1980). Within this range, the species is continuously distributed where habitat is appropriate, i.e., there are no major discontinuities in the distribution (c.f. with plains topminnow (*Fundulus sciadicus*), which exists as two disjunct populations centered in Nebraska and Missouri; Lee et al. 1980). The plains killifish is present within all states comprising Region 2 of the USDA Forest Service (**Figure 3**). As regards forest and grassland management units with Region 2,

the plains killifish occurs on three national grasslands: Pawnee National Grassland in Colorado, Cimarron National Grassland in Kansas, and Thunder Basin National Grassland in Wyoming. The plains killifish does not occur on any of the national forest units within Region 2, which is consistent with the species habitat encompassing lower elevation, Great Plains streams.

Populations have been introduced in western Colorado, eastern and southern Utah, northern Arizona, northwestern New Mexico, southern Montana, central Wyoming, the Big Bend region of Texas, and western South Dakota (**Figure 3**). Although the mechanisms by which these introductions occurred are unknown, they most likely involved the release of unused baitfish. Kreiser (1999) compared the genetic variation of populations introduced to the Colorado River with genetic variation within the native range of plains killifish and determined that at least two separate introductions occurred, with the West Arkansas and Pecos rivers as source populations.

Population trends (local, regional and range wide)

At the local level, there has been no monitoring of abundance for individual populations of plains killifish that would allow population trends to be discerned.

At the regional level, three recent assessments have commented on trends in the occurrence of plains killifish populations. In Wyoming, Patton (1997) sampled fish populations at 42 stream sites that had been previously surveyed in the 1960s. The number of sites with plains killifish increased from 8 to 13, suggesting that this species was expanding its distribution within the Missouri River drainage of Wyoming. It should be noted, however, that comparisons of recent and historical survey data can be complicated by changes in sampling methodology. For example, the 1960s survey in Wyoming streams involved the use of seines to collect fish. The 1990s survey used seines but also included electrofishing, which is known to be a more effective sampling method for stream fishes. However, even when Patton et al. (1998) adjusted their data to account for the increased efficiency of the 1990s sampling, there still was evidence that the plains killifish had increased its distribution in Wyoming.

In Colorado, the plains killifish was considered to be either common or abundant and at a relatively low risk of imperilment based on a survey done from 1992 to 1994 in the South Platte River and the Arkansas River drainages (Nesler et al. 1997, Nesler et al. 1999). In part,

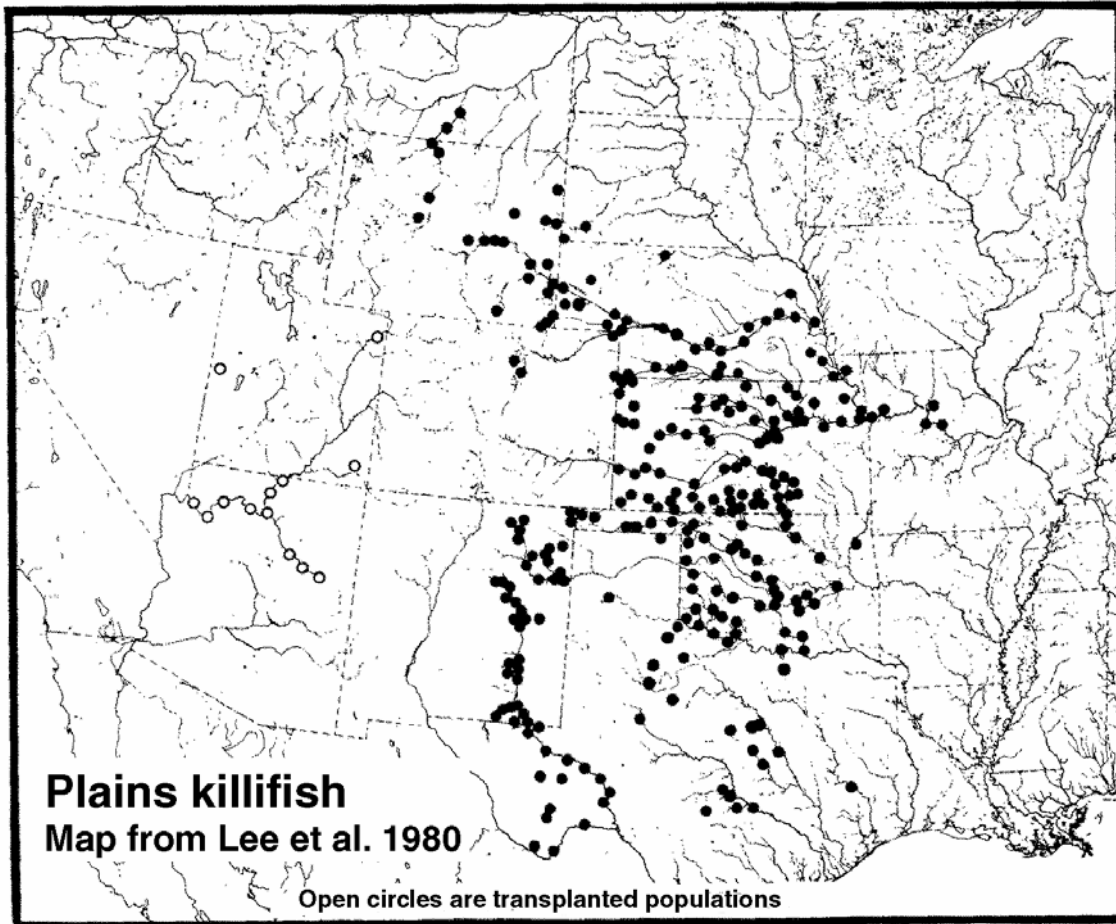


Figure 2. The distribution of plains killifish limited to the central and southern Great Plains of the United States. Subsequent to publication of the above map by Lee et al. (1980), several populations in northern Wyoming and western South Dakota were determined to have been introduced. See details in **Figure 3**.

this assessment was based on comparison with plains killifish distributions from earlier surveys done around 1980. The Platte River Basin Native Fishes Work Group (1999) compared fish species distributions pre-1980 to post-1980 and concluded that the plains killifish was not a “species of concern” for the Platte River basin in Wyoming, Colorado, or Nebraska. In Nebraska, the status of the plains killifish is considered stable (S. Schainost personal communication). Of the five states within Region 2, the plains killifish has the lowest State Heritage Status Rank in Kansas (S3 or vulnerable). Our search of the published literature and agency reports did not indicate the basis for this designation.

Outside of Region 2 of the USDA Forest Service, the plains killifish was considered to occur widely in the western half of Texas (Hubbs et al. 1991).

Activity patterns

Little is known about the activity patterns of plains killifish in the wild. To date, no broad scale movement patterns have been described. There have been no studies of dispersal or immigration/emigration movements. However, it is likely that dispersal and recolonization are important in maintaining plains killifish populations given that populations often occur in habitats subject to intermittency or stressful water quality conditions. Observations of plains killifish activity patterns, diel cycles, and behaviors are summarized below.

Plains killifish were observed to move in schools of fish of the same size class, occupying a limited segment of the stream, but highly mobile within the segment (Minckley and Klaassen 1969a). Minckley and

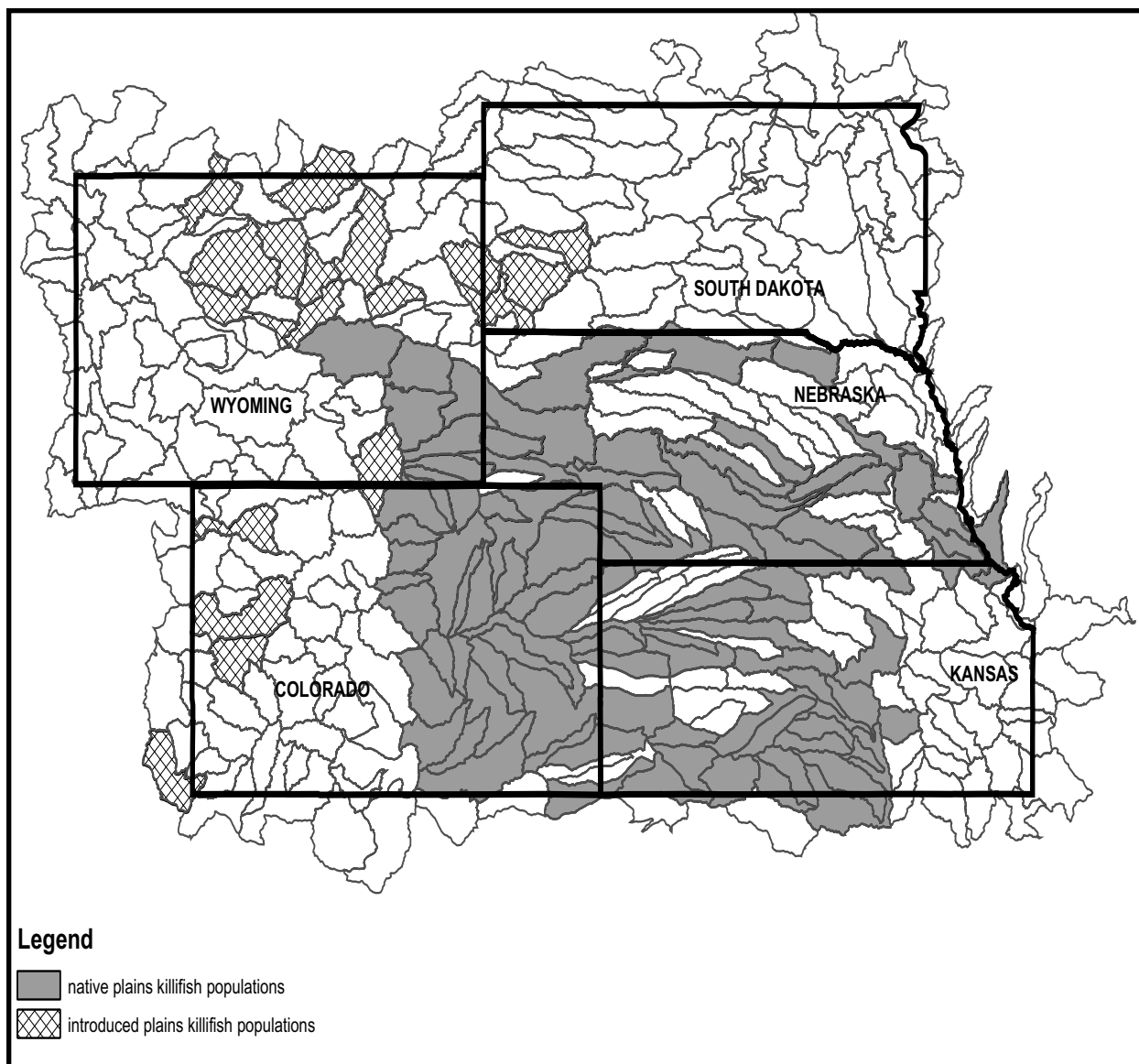


Figure 3. Distribution of plains killifish by hydrologic units (HUB 4 level) within the Rocky Mountain region (Region 2) of the USDA Forest Service. Sources of information used to produce this map are given in [Appendix B](#).

Klaassen also reported that feeding and reproductive activities took place with the schools, and when alarmed the fish responded together by either fleeing or seeking concealment.

Echelle et al. (1971a) described a diel cycle of feeding activity of plains killifish. The researchers reported that frequency of feeding increased gradually from sunrise to early afternoon, as water temperature increased, and it remained high until low light conditions inhibited accurate observations. The authors suggested that increased energetic costs at higher temperatures were reflected in increased feeding activity. The researchers also presented evidence of plains killifish

feeding activity at night although at a reduced level. The authors noted that night time feeding activity appeared to be enhanced by a full moon and suggested that because most cyprinodontids are generally sight oriented in their behavior, plains killifish may feed more actively on bright nights.

Lohr and Fausch (1996) reported that plains killifish held in experimental tanks shifted to shallower water during the day, regardless of the presence or absence of predators (green sunfish [*Lepomis cyanellus*]). Lohr and Fausch (1996) also noted the complementary distribution of plains killifish and green sunfish in the Purgatoire River, Colorado. They suggested that green

sunfish had the potential to eliminate plains killifish populations, and where sympatric populations occurred, the plains killifish were most likely maintained by dispersal from source populations.

Minckley and Klaassen (1969b) reported observing burying behavior in plains killifish in the wild (Smoky Hill River, Kansas) and in lab aquaria. In the aquaria experiments, plains killifish were observed to bury themselves when stressed, but they were also found buried after periods of no human disturbance. Minckley and Klaassen described the burying as a quick process, the fish diving headfirst into the substrate at an angle of 45 degrees or less. The fish either propelled the rest of their bodies into the sand with strong undulatory movements, or they concealed themselves further by throwing sand and allowing it to settle over them. Often only the mouth and eyes of buried fish were visible. Most of the fish concealing themselves in the gravel were large individuals over 60 mm (2.4 inches) in length. The smallest fish observed to exhibit burying behavior in the aquaria was 30 mm (1.2 inches) in length. Minckley and Klaassen suggested that fish smaller than 30 mm would not be as likely to burrow based on their observations of smaller fish being most abundant at the stream edges over flocculent materials that could be used for cover. Minckley and Klaassen proposed that this burying behavior may occur for a variety of reasons: (1) avoidance of heat and sunlight during summer; (2) avoidance of terrestrial or avian predators; (3) survival during drought conditions when daytime water levels are reduced; (4) removal of ectoparasites; (5) camouflage from prey.

Janovy et al. (1997) reported that during periods of high flow, plains killifish were collected in temporary channels flowing through pastures and bottomland woods adjacent to the river suggesting that fish moved to refuges during high flows.

Habitat

Plains killifish are most commonly associated with shallow areas in streams, but they are also found in lakes and ephemerally-connected pothole habitats. Propst (1982) found plains killifish were common to abundant in diverse stream types ranging from intermittent high plains tributaries to the main stem of the South Platte River, Colorado. Plains killifish have been found associated with a range of substrate types, exhibiting preferences for predominately clay, mud, and silt substrates in some systems (Claypool 1981, Conklin et al. 1996) and sand and gravel in others (Woodling 1985, Baxter and Stone 1995, Conklin et

al. 1996). Plains killifish have been collected in a range of water velocities but associate most commonly with lower water velocity habitats (Woodling 1985, Conklin et al. 1996). In some parts of their range, plains killifish have been associated with high alkalinity environments (Ostrand and Wilde 2001).

Plains killifish are consistently associated with shallow water throughout their native range. In Colorado, plains killifish are found in shallow, sandy bottom streams or along shallow banks and shoals in larger streams and are a major component of the fish fauna in streams where filamentous algal is present (Woodling 1985). In an analysis of habitat suitability criteria for plains killifish in the mainstem of the central Platte River in Nebraska, Conklin et al. (1996) described the preferred habitat of adult plains killifish as comparatively shallow water, ranging from 3 to 34 cm (1.2 to 13.4 inches) in depth, with most of the observations occurring at depths of 6 to 12 cm (2.4 to 4.7 inches). Cross and Collins (1995) noted that in Kansas, plains killifish were rarely found in water more than 15 cm (6.0 inches) deep. Schmeidler and Brown (1990) confirmed plains killifish preference for shallow habitats, reporting the species was most often found in habitats less than 15 cm deep throughout the Arkansas River basin in Kansas. In Wyoming, according to Baxter and Stone (1995), plains killifish are found in shallow streams with sand or gravel substrate and are the predominant species in the sandy intermittent streams near the city of Casper.

In Kansas, Cross and Collins (1995) reported that plains killifish could be abundant in either rapid current or backwater areas. Woodling (1985) described plains killifish as tolerant of some current. Conklin et al. (1996) found plains killifish used water velocities ranging from 0 to 43 cm/sec (0 to 1.3 feet/sec) and were most commonly found in areas with water velocities less than 12 cm/sec (0.4 feet/sec). Conklin et al. noted that plains killifish were associated with a wide range of substrate types, detritus to gravel, and the calculated preference curve, which predicted a highest preference for silt, was reflective of the adult plains killifish preference for shallow backwater areas of the river.

Minckley and Klaassen (1969a) reported plains killifish occurring in shallow, sandy bottomed streams with great variation in chemical and thermal features. In their study of plains killifish life history in the Smoky Hill Reservoir in Kansas, they collected the species from two sites with different habitat conditions that were separated by 29 km (18 miles) and a reservoir. One site was described as having shallow

water, little riparian vegetation, and large temperature fluctuations. The water depth rarely exceeded 15 cm as the river “meandered in a wide sand bed some distance from its main banks” and filamentous algae were abundant on the substrate most of the year. The other study site had a narrower channel with a swifter current. Shade was provided by riparian vegetation or erosion, which created undercut banks. The water in the second study site averaged 15 cm deep, and there were numerous pools.

Koster (1948) observed spawning activities in a large pool approximately 30 m long (98 feet) with an average depth of 5 to 10 cm (2 to 4 inches). The maximum pool depth was 25 cm (10 inches) at the head of the pool. The substrate was gravel with interstices filled with sand and silt, and the current was slow.

Plains killifish are well known for their tolerance of low dissolved oxygen, high temperature, and high salinity conditions. Plains killifish are reported to be tolerant of low oxygen conditions created by high levels of organic wastes that often result in fish kills in other species (Woodling 1985). Cross and Collins (1995) suggested that plains killifish survive low oxygen conditions by living near the water surface where dissolved oxygen concentrations are higher. Baxter and Stone (1995) reported that the fish assemblage of Twin Buttes Lake in Albany County, Wyoming consisted solely of plains killifish when it had high concentrations of total solids (reaching as much as 35,000 ppm) before the lake water was diluted to create a trout fishery.

Several studies have documented the tolerance of plains killifish to harsh environmental conditions. In one of the earlier studies, Griffith (1974) found that plains killifish tolerated higher salinity concentrations than other freshwater Fundulids. In lab tests, plains killifish tolerated salinities up to 89 parts per thousand, which is over twice the salinity of sea water. This supported earlier reports that plains killifish were found in waters with salinity concentrations near or above sea water. Interestingly, Griffith reported that plains killifish were difficult to maintain in low salinity tap water (salinity of 2 parts per thousand). This might have been due to low calcium concentrations (8.0 parts per million). Pickford et al. (1966) had previously noted the critical role of calcium levels in osmoregulation by plains killifish.

Ostrand and Marks (2000) observed different mortality rates among fish species of a prairie stream assemblage confined to an isolated pool in a tributary of the Brazos River in Texas. They reported that plains killifish were able tolerate the lowest dissolved

oxygen levels, 0.17 mg/L, and the highest ammonia concentration, 10.81 mg/L, in the pool whereas several species of cyprinids were observed dying. Ostrand and Marks (2000) also reported that no fish kills were observed in five other adjacent isolated pools in the same stream reach. Measurement of dissolved oxygen, pH, ammonia, maximum depth, pool volume, water temperature, conductivity, and turbidity in the six pools showed that the pool in which mortality was observed had significantly lower dissolved oxygen and higher ammonia concentrations than the others.

To explain observed temporal changes in fish assemblages in isolated stream bed pools, Ostrand and Wilde (2001) compared the maximum temperature, maximum salinity, and minimum dissolved oxygen tolerances of the plains killifish and another cyprinodontid, the Red River pupfish (*Cyprinodon rubrofluviatilis*) and three other cyprinid species. The fish used in the study were collected from tributaries of the Brazos River in May 1998. Ostrand and Wilde (2001) found that plains killifish had a significantly greater critical thermal maximum (CTM) than the Red River pupfish and the cyprinids tested. Plains killifish acclimated at 25 °C (77 °F) had a mean thermal tolerance of 40.5 °C ± 0.4 °C (105 °F ± 0.7 °F), and those acclimated at 30 °C (86 °F) had an even greater mean CTM of 42.0 °C ± 0.2 °C (108 °F ± 0.4 °F).

Red River pupfish were found to have a greater salinity tolerance than plains killifish, and both had greater salinity tolerances than the three cyprinids tested (Ostrand and Wilde 2001). The salinity tolerance measure used, LC50, was the salt concentration that resulted in 50 percent mortality of the test species over a 48-hour period. The LC50 reported by Ostrand and Wilde (2001) for plains killifish was 43 parts per thousand. The discrepancy between salinity tolerances reported by Griffith (1974; 89 parts per thousand) and Ostrand and Wilde (2001) may be accounted for by a difference in methods. Ostrand and Wilde (2001) used specific conductance as a surrogate for salinity measures and introduced fish directly into aquaria water previously adjusted to a specific conductance by addition of sodium chloride. Griffith (1974) conducted salinity tolerance trials after acclimating fish to aquaria with running dechlorinated tap water by slowly dripping seawater into aquaria over a period of days and noting the salinity at which failure (such as listlessness, loss of balance, or death) occurred. Griffith (1974) reported a rate of increase of salinity of 1 percent per day. Also, salinity in the experiments by Griffith was not due solely to sodium chloride but to the mixture of salts typical of sea water.

Ostrand and Wilde (2001) reported the mean tolerance of dissolved oxygen of plains killifish was 1.25 ± 0.09 mg/L. Compared to the three cyprinid species tested, the Red River pupfish was able to tolerate lower dissolved oxygen concentrations. However, the plains killifish tolerated lower dissolved oxygen concentrations than all of the species tested (Ostrand and Wilde 2001).

Based on their study of environmental tolerances of a prairie stream assemblage, Ostrand and Wilde (2001) concluded that differences in salinity tolerances among species coupled with differences in low dissolved oxygen concentrations and high temperature tolerance explained observed changes in assemblage structure in evaporating pools. Ostrand and Wilde (2001) reported that high temperatures and low dissolved oxygen concentrations occurred stochastically in the field and did not affect all pools similarly and that dissolved oxygen concentrations fell below tolerable limits for cyprinids in only 8 percent of the samples collected during which no fish were observed dying. Ostrand and Wilde (2001) suggested that chronic exposure to low dissolved oxygen may allow fish to acclimate, but that as salinity increased with evaporation, the lower tolerances of cyprinids for high salinity would explain the differences in observed mortality between cyprinids and cyprinodontids. The authors also reported that the high salinity tolerance of plains killifish and Red River pupfish allowed these species to persist in isolated pools in the upper Brazos River until the next flood event (Ostrand and Wilde 2001). The authors concluded that the environmental characteristics of pools, in addition to the availability of pools, affect population persistence. Because isolated pools are more likely to occur in headwater reaches of prairie streams, the different tolerances among fish species help explain differences in assemblage composition and the longitudinal zonation of fish species at larger spatial scales (Ostrand and Wilde 2001). Ostrand and Wilde (2001) found that laboratory-determined tolerances to dissolved oxygen, temperature, and salinity were consistent with the longitudinal zonation patterns in fish species composition reported by others for the Brazos and Red rivers in which plains killifish were commonly found in the upstream portions of the drainages at a wide range of salinity levels.

Food habits

Plains killifish are primarily carnivorous, feeding on the surface, in the water column, and from the bottom substrate (Minckley and Klaassen 1969a, Baxter and Stone 1995). They consume a variety of

aquatic invertebrates, especially chironomidae larvae (Minckley and Klaassen 1969a, Echelle et al. 1972, Woodling 1985).

Minckley and Klaassen (1969a) analyzed stomach contents of 155 plains killifish in March, June, August, October, and November 1967 in Smoky Hill River, Kansas. Chironomidae were the most abundant food item found in plains killifish stomachs and were present during each month sampled. Mayfly nymphs were the next most abundant food item, but usually at a lower percentage than chironomids. Mayfly larvae were present in collections for each month except November. Ostracods were identified as a minor food item most prevalent in May and June. Fish remains were present in only two stomachs of the 155 examined, and terrestrial arthropods were absent or rare.

Echelle et al. (1972) also found that Chironomidae larvae were the predominant food item of a sample of 210 plains killifish in Oklahoma. The next most abundant food items were Entomostraca and Nematoda. The Oklahoma population consumed a wide variety of animal food items including Ectoprocta, Gastropoda, Oligochaeta, Cladocera, Copepoda, Ostracoda, Hydracarina, Collembola, Zygoptera, Anisoptera, Ephemeroptera, Ceratopogonidae, Coleoptera, Corixidae, and Formicidae. As in the Smoky Hill River (Kansas) populations, fish remains and terrestrial arthropods were uncommon food items (Echelle et al. 1972).

Both studies documented the considerable occurrence of sand and other miscellaneous debris in the stomach contents of plains killifish. In the Oklahoma population, sand and miscellaneous debris (i.e. diatoms, insect eggs, plant debris, and the protozoan *Diffugia*) were a larger proportion of the stomach contents at night, which suggested to the authors that ingestion of sand and associated food items may be an important source of nutrients at night or during periods of high turbidity when sight feeding is less effective (Echelle et al. 1972). Echelle et al. (1972) also reported that the amount of filamentous green algae in the foreguts of the specimens increased with increased amount of animal food items over the daylight hours. The authors noted that certain individuals spent long periods of time pulling at and ingesting filamentous algae strands, and they suggested that ingestion of algae was intentional whether to remove animal food items from algal mats or due to the animal-like movements of the algal strands. Through a hindgut analysis of 36 plains killifish, the researchers concluded that algal material went largely undigested.

Echelle et al. (1971a) described a diel cycle of feeding activity of plains killifish. The researchers made hourly observations of feeding frequency of 10 female fish and analyzed the stomach contents of 210 fish collected over two hour intervals. Based on frequency of feeding acts and gut content data, the researchers concluded plains killifish feeding increased gradually from sunrise to early afternoon and remained high until low light precluded accurate observation. Feeding frequency and relative gut fullness also were correlated with water temperature, which increased gradually after sunrise and remained high until sunset. The authors suggested that the increased energetic cost at higher temperatures was reflected in increased feeding activity. Analysis of relative gut fullness indicated that feeding activity was relatively low at night, although a certain level of feeding activity was maintained. The authors noted that the night time feeding activity appeared to be enhanced by a full moon during one of the study days, and they suggested that because most Cyprinodontids are generally sight oriented in their behavior, plains killifish may feed more actively on bright nights.

Baxter and Stone (1995) described a feeding behavior in which plains killifish made quick sideways darting movements to stir up bottom material. Baxter and Stone also reported that after one fish stirred up a cloud of sand, several downstream fish searched the cloud, presumably for food. Baxter and Stone (1995) noted that from a distance this behavior could be mistaken for spawning activities.

Minckley and Klaassen (1969a) observed that plains killifish fed primarily from the stream bed, taking mouthfuls of sand and then expelling the sand, presumably retaining the food items. An individual would drift downstream a few seconds, orient upstream, and repeat the process taking another mouthful of sand. Minckley and Klaassen (1969a) mentioned that the use of a sideways darting movement to stir up benthic material was an infrequent feeding behavior in their study. Echelle et al (1972) described plains killifish feeding behavior as consisting primarily of “nipping and digging” on the bottom and counted an average 30 to 40 nips and digs per minute during peak feeding activity. Minckley and Klaassen (1969a) also reported that plains killifish fed on free swimming *Daphnia pulex* in an aquarium, indicating they are able to feed on food items available in open water. A study comparing the efficacy of the mosquitofish with plains killifish found no difference in mosquito control between the two species, indicating that plains killifish are also effective surface feeders (Nelson and Keenan 1992).

Breeding biology

The spawning behavior of plains killifish was described by Koster (1948) for a population in northeastern New Mexico. Other researchers have observed the behaviors described by Koster in populations in other parts of the plains killifish native range (Minckley and Klassen 1969a). The timing of spawning among plains killifish populations is correlated with water temperature and varies accordingly across their range. Water temperatures reported during observations of spawning exceed 26 °C (Koster 1948, Cross and Collins 1995). Cross and Collins (1995) describe plains killifish spawning in Kansas streams as occurring May through July, during the day, when water temperatures are above 26 °C (79 °F). Minckley and Klaassen (1969a) reported plains killifish spawning in April in Kansas, but they did not provide water temperature. Koster (1948) described plains killifish spawning in August in New Mexico (noting the higher elevation of the streams) at temperatures around 27 °C (81 °F) but not above 31 °C (88 °F). Although he had little data, based on his observations Koster (1948) suggested that spawning activities may be restricted to a short period during the day when the temperature is within a relatively narrow range.

The following is a summary of the spawning behavior as described by Koster (1948). In early morning during cool water temperatures, males were amicable, feeding in small groups. As the water temperature rose the males isolated themselves, attacking other males that approached too closely. Although no specific territory was guarded for any length of time, a certain amount of individual space was maintained. Generally, larger males would chase away smaller males, and when two similar size males confronted one another they engaged in a “deferred combat ceremonial” with no evident winner before both males departed the scene. Courtship behavior began with flight by the females when approached by a male. Whenever the female paused, the male would align himself above the female and attempt to spawn. Rival males routinely disrupted courtship by lunging at the male in the pair. When spawning, both fish turned on their sides, forming a flattened “S-shape” with head and anal region of the female pressed to the substrate and the thoracic and caudal regions elevated. The spawning pair appears to vibrate for approximately a second in the S-shape position, during which time milt and eggs are released. Koster describes both males and females as promiscuous in their breeding behavior, and both sexes were observed to continue to feed between spawning acts. The eggs are deposited in the sandy

substrate and left unattended (Woodling 1985, Cross and Collins 1995).

Plains killifish eggs and embryos are able to withstand a wide range of temperatures during development. Wilson and Hubbs (1972) found that plains killifish eggs (from south central Oklahoma) incubated at temperatures between 15 °C (59 °F) and 34.3 °C (94 °F) successfully hatched, swam normally, and used up yolk reserves. In fact, more than 50 percent of the eggs hatched at temperatures between 16.8 °C (62° F) and 33.5 °C (92 °F). The fertilized eggs gastrulated in one day at incubation temperatures over 30 °C (86 °F) but took up to eight days at temperatures less than 13 °C (55 °F). Similarly, cooler temperatures prolonged days to hatching. Hatching occurred after six days in eggs incubated above 30 °C and after up to 40 days in eggs incubated below 16° C (61 °F). Within this study, extreme temperatures during the incubation period caused egg death and larval deformities. Wilson and Hubbs (1972) proposed that because plains killifish are summer breeders in streams that reach daily maximum temperatures near their thermal tolerance limits and their eggs are deposited in shallow, slow current, thermally variable habitats, plains killifish embryo development is hastened so that hatched larvae can move to temperature refuges.

Demography

Genetic characteristics and concerns

Little research has been done on plains killifish population demographics and genetic characteristics. Furthermore, the roles of dispersal, movement, and emigration/immigration in plains killifish populations have not been described. Although the habitats of plains killifish have probably become more fragmented (Brown 1986), the potential effects of isolation on the structure or genetic characteristics of plains killifish populations are not well understood.

Plains killifish populations may become isolated by reduced habitat availability and connectivity, resulting from activities associated with surface and groundwater management (Brown 1986). Brown (1986) suggested that western Kansas populations of plains killifish were becoming increasingly isolated due to reduced habitat availability, as surface water flows decreased and groundwater tables fell. There also has been a loss of habitat connectivity as deep water impoundments replace shallow, sandy bottom stream reaches.

Brown (1986) investigated the demographic and genetic population structure of plains killifish populations from the Kansas and Arkansas river basins. Additionally, Brown (1986) sought to determine if the environmental changes that had occurred in the Kansas River basin were associated with reduced genetic heterozygosity and increased genetic differentiation of plains killifish populations in the system. Brown (1986) found greater genetic variation among plains killifish populations in the less altered Arkansas River basin than in the more impacted Kansas River basin. However, the greater heterozygosity of populations from two tributaries of the Arkansas River accounted for most of the difference. The genetic diversity among sites within rivers was important in explaining total site differentiation in the Kansas River basin, despite the lower overall genetic diversity observed in that basin. Using the measures of standard length and weight, Brown (1986) found no evidence that lower levels of heterozygosity had adversely affected fitness of plains killifish populations but noted that other researchers have reported that heterozygosity is positively correlated with fitness measures in other species. Brown (1986) suggested that other fitness measures, such as fecundity or growth rate gathered earlier in the breeding season, should be used to test for negative consequences of reduced heterozygosity.

In another study, Schmeidler and Brown (1990) tested the prediction that the environmental fluctuations associated with prairie streams should cause random changes in the demographics and genetic characteristics of plains killifish populations. The researchers found that plains killifish populations exhibited spatial and temporal variation in standard length and allele frequencies (Schmeidler and Brown 1990). The mean standard length of plains killifish populations was found to be spatially heterogeneous among sites within rivers. At a larger spatial scale, fecundity was found to be highest among plains killifish populations in the most altered rivers. However, the authors reported significant positive relationships between mean standard length of females and fecundity for the three rivers studied. Because one river had significantly lower mean standard length of mature females, the differences in fecundity among river populations could be partially explained by the differences in mean standard length of mature females among rivers (Schmeidler and Brown 1990). Schmeidler and Brown (1990) suggested that plains killifish populations in the more altered river systems were allocating more energy for reproduction, as evidenced by greater mean lengths and fecundity, than those populations in the less altered river. The

authors concluded that plains killifish are an “r-selected” species and that their population regulation includes an important density-independent component. However, because of the temporal and spatial variability in demographic measures across sites, some populations appeared to be more “r-selected” than others.

Schmeidler and Brown (1990) also found significant spatial and temporal variability in the genetic characteristics of plains killifish stocks in comparisons of populations within and among rivers. At smaller spatial scales, between sites within rivers, most spatial differences and temporal changes in genetic characteristics among populations were without a perceived pattern. At the larger spatial scale, between rivers, a qualitative comparison of genetic characteristics among populations suggested a potential relationship between the amount of habitat alteration and the degree of heterozygosity, which supports the prediction that populations in more perturbed environments are more likely to lose genetic variability (Schmeidler and Brown 1990).

Life history characteristics

Plains killifish mature as yearlings and rarely live longer than two years (Minckley and Klaassen 1969a, Cross and Collins 1995). Minckley and Klaassen (1969a) in a study of two populations in the Smoky Hill River (Kansas) found that two year classes were represented for most of the year, until young-of-year (age 0) fish appeared in early summer and became the third year class represented. Fish from the oldest age class seemed to disappear from the population in midsummer. In the Smoky Hill River populations, young-of-year were about 35 mm (1.4 inches) at the end of their first summer. The following year, Age 1 fish were around 50 mm (2.0 inches) long. The largest Age 2 specimen collected was 76 mm (3.0 inches) total length. A small number of plains killifish up to 85 mm (3.4 inches) in total length were collected. The researchers did not age the fish, but suggested that they were likely Age-class 3 fish.

Brown (1986) found the ratio of males to females was nearly equal for populations of plains killifish sampled in the Arkansas and Kansas river basins in Kansas, but sex could be determined, on average, for only 45 percent of the fish in each population. Plains killifish less than 38 mm (1.50 inches) standard length exhibited no sexual differentiation and were never observed to be gravid (Brown 1986).

A comparison of gonadal weights taken each month from February to November 1967 by Minckley and Klaassen (1969a) indicated that egg ripening occurs from February through April or May (for Smoky Hill River, Kansas populations). Mature eggs had an average diameter of 2.1 mm (0.08 inches), and this size egg was maintained throughout the spawning period from late April to July. By August, female ovaries were spent (Minckley and Klaassen 1969a). Wilson and Hubbs (1972) reported 1.6 mm (0.06 inches) as the average diameter of eggs collected from plains killifish populations in south central Oklahoma during June and July. This average egg size is smaller than that reported for the Kansas populations, but it does fall within the range reported by Minckley and Klaassen (1969a), measuring approximately 0.7 to 2.1 mm (0.027 to 0.08 inches) in diameter. This may be a result of the age class/size of fish collected in Oklahoma since Wilson and Hubbs (1972) did not report the number, lengths, or ages of the female plains killifish used to supply eggs for the development experiments.

Fecundity of females, as measured by number of mature eggs per female, increases with fish length (Minckley and Klaassen 1969a, Schmeidler and Brown 1990). Wilson and Hubbs (1972) proposed that the larger yolk volumes observed in plains killifish eggs, compared to the other summer breeding fish, may result in delayed hatching time but increased post-hatching survival. Male plains killifish exhibited a gonadal cycle in which testicular weights increased in April and peaked in May (Minckley and Klaassen 1969a).

Although the plains killifish in the Smoky Hill River became sexually mature during their second summer (Age 1), older fish (Age 2) were the major spawning group, being larger, more fecund, and more vigorous than Age 1 fish (Minckley and Klaassen 1969a). Young-of-year were first collected in mid-May 1967, which would indicate that spawning began in April; in 1968 spawning was observed in early April (Minckley and Klaassen 1969a).

Life cycle diagram and analysis of demographic matrix. A life cycle graph (**Figure 4**) was constructed for plains killifish and used as the basis for an analysis of how population demographics might influence the long-term persistence of plains killifish populations (**Appendix A**). The approach is to use a stage-based variation of a Leslie matrix to project population sizes under various scenarios of environmental and demographic stochasticity. A major reason for doing a

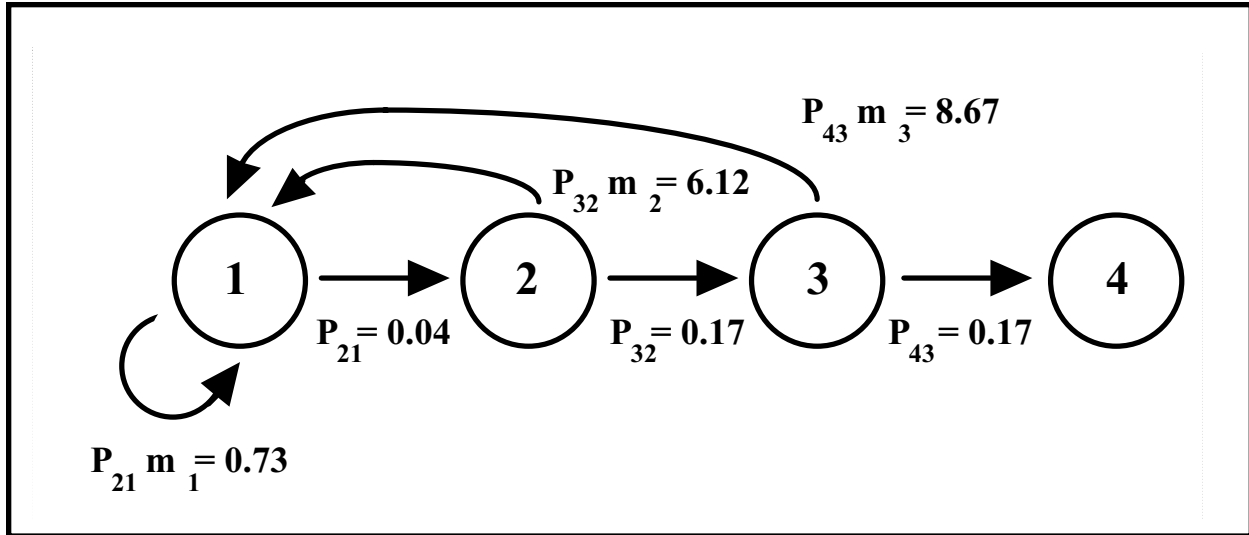


Figure 4. Life cycle graph for plains killifish, showing both the symbolic and numerical values for the vital rates. The circles (nodes) denote the four age-classes in the life cycle — first-year, through fourth-year females. Arrows (arcs) denote the vital rates — survival and fertility rates providing the transitions between age-classes. Note that fertilities involve offspring production, m_i (the number of female eggs per female), as well as the survival of the mother, P_{ij} , from the time of the census, just after breeding, through almost a year until the next breeding pulse. Self-loop on first node indicates that females can reproduce as yearlings. Note also the very low first-year survival rate (0.04) and the considerable improvement in fertility after the first year (from 0.73 to 6.12).

matrix demographic analysis is to identify which age-specific vital rates (such as the probability that a fish of a given age survives during the next year or the number of eggs produced by a female of a given age) are likely to be most influential in determining population growth rate. Population growth rate, in turn, is critical in allowing plains killifish populations to recover from low-points in abundance and thus avoid going extinct.

Input data needed for a population projection matrix model consist of age-specific survival and fecundity rates. We assembled the sparse data available in the literature on these rates for plains killifish

(**Table 4**). The model has two kinds of input terms: P_i describing survival rates, and m_i describing fertilities (**Table 4**). Fertilities are given as female offspring per female. In contrast to fisheries terminology, the convention here is ordinal numbering beginning with 1 (first, second, third, and fourth age-classes). Thus, age-class 0 in fisheries terminology corresponds to the age-class 1 in the matrix model. Each age-class describes a one-year census interval period, and the age-class that begins with an egg at the census and proceeds to the first clutch produced by a yearling is described by the self-loop $P_{21} m_1$ in **Figure 4**.

Table 4. Parameter values for the component terms (P_i and m_i) that make up the vital rates in the projection matrix for plains killifish. Parameters were estimated from data presented by Minckley and Klaassen (1969a), Brown (1986), and Schmeidler and Brown (1990).

Parameter	Numeric value	Interpretation
m_1	20.6	Number of female eggs produced by a first-year female
m_2	36	Number of female eggs produced by a second-year female
m_3	51	Number of female eggs produced by a third-year female
P_{21}	0.03547	First-year survival rate
P_a	0.17	Annual survival rate of adults

Sensitivity analysis. Sensitivity is the effect on population growth rate (λ) of an absolute change in the vital rates (a_{ij} , the arcs in the life cycle graph, **Figure 4**). Sensitivity analysis can show how important a given vital rate is to population growth rate (λ) or fitness. One can use sensitivities to assess the relative importance of survival versus reproductive transitions. Sensitivities also can be used to evaluate the effects of inaccurate estimation of vital rates, to quantify the effects of environmental perturbations, and to identify stage-specific survival or fertility rates that are most critical to increasing the population growth rate (λ) of an endangered species. The major conclusion from the sensitivity analysis is that first-year survival is overwhelmingly important to population viability (details are given in **Appendix A**). The plains killifish shows large sensitivity to changes in survival, with first-year survival alone accounting for 85 percent of the total sensitivity.

Elasticity analysis. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. For instance, a change of 0.5 in survival may be a big alteration, e.g., a change from a survival rate of 0.9 to 0.4 corresponds to a reduction in survival from 90 percent to 40 percent. On the other hand, a change of 0.5 in fertility may be a small proportional alteration, e.g., a change from an average clutch size of 100 eggs to 99.5 eggs. Elasticities are the sensitivities of the population growth rate (λ) to proportional changes in the vital rates (a_{ij}) and thus largely avoid the problem of differences in units of measurement. Details of the elasticity analysis for plains killifish are given in **Appendix A**. The population growth rate (λ) is most elastic to changes in first-year reproduction ($P_{21}m_1$ in **Figure 4**), followed by first-year survival (P_{21}) and then second-year

reproduction ($P_{32}m_2$). The sensitivities and elasticities for plains killifish do not correspond because the first and third most elastic transitions involve reproduction, in contrast to the first-year survival so heavily emphasized by the sensitivity analysis. Thus, survival and reproduction in the first year and, to a lesser extent survival and reproduction in the second year, are the data elements that warrant careful monitoring in order to refine the matrix demographic analysis.

Other demographic parameters. The stable age distribution (**Appendix A; Table A1**) describes the proportion of each age-class in a population at demographic equilibrium. For plains killifish at the time of the post-breeding annual census (just after the end of the breeding season), eggs represent 96 percent of the population, second-year individuals represent another 3.4 percent, and older fish are extremely rare (**Table A1**). Reproductive values describe the “value” of a stage as a seed for population growth relative to that of the first (in this case, egg) stage. The reproductive value of the first stage is always 1.0. For example, a female plains killifish in Age-class 2 is “worth” 7.59 eggs (**Table A2**). The peak reproductive value (8.67) occurs at the third age-class indicating these females are an important stage in the life cycle even though they represent <1 percent of the population. It is important to remember, that the third age-class in the demographic matrix analysis corresponds to Age-class 2 fish using conventional fisheries terminology.

Stochastic model. We conducted a stochastic matrix analysis for plains killifish in order to see how variation in survival and fecundity rates might influence the likelihood of extirpation of local populations. We incorporated stochasticity in several ways, by varying different combinations of vital rates or by varying the

Table 5. Parasites of plains killifish in the Platte River drainage (Janovy et al. 1997).

Parasite	Infection site	Intermediate Host	Transmission Stages
<i>Myxobolus funduli</i> (Myxozoa)	gill tissues	possibly freshwater oligochaetes	spore-bearing triactinomyxons
<i>Trichodina</i> sp. (Ciliophora)	gill surface	none	swimming telotroch stage
<i>Gyrodactylus bubacanthus</i> (Monogenea)	gill surface	viviparous	fish to fish contact and passing of juvenile worms
<i>Salsuginus thalkeni</i> (Monogenea)	gill surface	egg	free swimming larva encounters host
<i>Gyrodactylus stableri</i> (Monogenea)	body surface, fins	viviparous	fish to fish contact and passing of juvenile worms
<i>Posthodiplostomum minimum</i> (Digenea)	within eyes or body cavity	snails	free swimming cercariae penetrate fish

amount of stochastic fluctuation (Details in **Appendix A**). The stochastic matrix analysis produced two major results. First, varying first-year reproduction had a greater effect on population growth rate (λ) than did varying all the survival rates (**Table A3**). Second, the magnitude of stochastic fluctuation largely determined the negative effect on population dynamics. These results indicate that populations of plains killifish are vulnerable both to stochastic fluctuations in production of newborns (due, for example, to annual climatic change or to human disturbance) and, to a far lesser degree, to variations in survival.

Summary of major conclusions from the matrix projection models:

- ❖ First-year survival accounts for 85 percent of total “possible” sensitivity. Any absolute changes in this rate would be expected to have major effects on population dynamics.
- ❖ First-year reproduction accounts for 55 percent of the total elasticity, compared to the 20 percent (next highest value) accounted for by first-year survival. Proportional changes in first-year reproduction would be expected to have a major effect on population dynamics.
- ❖ The contrast between the conclusions from the sensitivity and elasticity analyses suggests that survival and reproduction in the first year of life are both critical to the population dynamics of plains killifish.
- ❖ Where the potential exists for survival through to the third year, reproductive values of females in that age-class will be high. Such populations may be important sources of recolonization for other sites or in periods where local conditions improve.
- ❖ Stochastic simulations echoed the elasticity analyses in emphasizing the importance of variation in first-year reproduction to population dynamics. In comparison to life histories of other vertebrates, killifish appear vulnerable to local extinction. Management should take into account the potential for considerable variability in population trajectories and the need for multiple habitat sites as a buffer against the likelihood of reasonably frequent local

population extinctions.

Ecological influences on survival and reproduction

Because they occupy shallow water habitats and remain small throughout their life, plains killifish are preyed upon by numerous fish, avian, and mammalian predators (see section on Predators). However, there is little information that would allow mortality of plains killifish to be partitioned among various causes for the various life history stages. Therefore, it is not possible to identify which source of mortality (predation, competition, parasitism, mortality from abiotic stressors) is the most limiting factor for survival in this species. Fecundity increases with female size, and thus it is related to both fish age and growth rate (see section on Life history characteristics). Factors that facilitate faster individual growth rate and/or increased overwinter survival would enhance the population growth rate for plains killifish.

Social pattern for spacing

The plains killifish is not a territorial species, and individuals do not defend home ranges or spawning areas. In fact, individuals often associate in schools of similar-sized fish (see section on Activity patterns). Therefore, territoriality does not play a role in population regulation for this species.

Patterns of dispersal of young and adults

Little is known about patterns of dispersal in plains killifish although this species is not known to make the type of long distance spawning migrations common in some species of salmonids. The species evolved in plains streams subject to intermittency and has the ability to recolonize habitats quickly after the return of normal water conditions. However, the nature of such movements has not been studied in detail. Because the species is not territorial, dispersal of young to new areas at the time of sexual maturity is not a life history characteristic. Dispersal is more likely related to population crowding and the existence of corridors that allow movement among suitable habitat patches.

Spatial characteristics of populations

Spatial characteristics of populations such as sources and sinks, or metapopulation dynamics, have not been studied in plains killifish. Brown (1986) found

no evidence of genetic isolation among plains killifish populations within major river drainages in Kansas. This would indicate that there is considerable gene flow and thus fish movement among these populations (see section Genetic characteristics and concerns). However, the extent to which these populations function as sources and sinks, or metapopulations is not known. Across their geographic range, plains killifish populations show genetic differentiation and were even considered to represent two species at one point (see section on Systematics and species description). Thus, at larger spatial scales, there is a limited exchange of individuals among major drainages.

Limiting factors

The main factors limiting population growth for specific populations or the species in general have not been identified but likely involve habitat availability. The species is generally limited to warm, shallow waters that lack piscivorous fish species, and such habitats are inherently unstable in the naturally arid Great Plains region. Consequently, stream desiccation and/or lethal water quality conditions in summer and extremely low oxygen levels in winter are likely to be important limiting factors for plains killifish populations.

Predators

Piscivorous birds such as the great blue heron (*Ardea herodias*) and the belted kingfisher (*Megaceryle alcyon*) are reported to be major non-aquatic predators of plains killifish (Minckley and Klaassen 1969a and 1969b). The burying behavior of the plains killifish described by Minckley and Klaassen (1969b) may be a response to predation threat in habitats with sandy substrates and little cover.

Plains killifish are not usually found in habitats that support many aquatic predators. In habitats of sufficient depth for piscivorous fish, largemouth bass (*Micropterus salmoides*), green sunfish, black bullhead (*Ictalurus melas*), channel catfish (*Ictalurus punctatus*), and creek chub (*Semotilus atromaculatus*) in addition to turtles have been mentioned as potential aquatic predators of plains killifish (Minckley and Klaassen 1969a). Several studies have revealed that a low level of intraspecific predation occurs in plains killifish populations (Minckley and Klaassen 1969a, Echelle et al. 1972). Egg predation is suggested as a potentially important form of intraspecific predation due to the bottom feeding habits of plains killifish (Echelle et al. 1972)

In an experimental study of green sunfish predation on plains killifish, 16 percent of plains killifish were consumed by large green sunfish in tanks over a 24-hour period (Lohr and Fausch 1996). The plains killifish use of deep water or simulated vegetative cover during daylight did not differ significantly between tanks with and without green sunfish. The authors suggested that the lack of response of plains killifish to predators might be due to the crepuscular feeding activity of green sunfish, their efficacy as ambush predators, or the insufficiency of the artificial cover that was provided (Lohr and Fausch 1996). The high predation rates on plains killifish by green sunfish is a likely explanation for the rare co-occurrence of the two species in the pools of intermittent tributaries of the Purgatoire River in southeast Colorado (Lohr and Fausch 1996).

Despite their apparent vulnerability to piscivorous fishes, plains killifish are not considered good baitfish (Baxter and Stone 1995). Although they are occasionally sold for that purpose, Woodling (1985) noted that killifish are often ignored by crappie and other game species.

Competitors

Despite the ability of plains killifish to survive low oxygen, high alkalinity, high salinity, and warm water temperatures, they are poor competitors and are not abundant where many other species of fish occur (Cross and Collins 1995). Typically, two species of topminnows are not likely to be found in the same place, or in the case of co-occurrence one species is usually much more abundant (Echelle et al. 1971b, Kodric-Brown and Mazzolini 1992). Echelle et al. (1971b) noted the similarity in the diurnal feeding patterns, diets, and microhabitats of plains killifish to those of the Red River shiner (*Cyprinodon rubrofluviatilis*), and they suggested that direct competition for food accounted for the depression of plains killifish in saline waters that supported both species.

In another example, the greater tolerance of Pecos pupfish (*Cyprinodon pecosensis*) for higher salinities than plains killifish, explained the pupfish's larger size, greater abundance, and competitive dominance in one lake where the two species co-occurred. In another less saline lake, plains killifish were larger, more abundant, and competitively dominant (Kodric-Brown and Mazzolini 1992). Similarly Echelle et al. (1971b) found the Red River pupfish depressed the abundance of plains killifish at high salinities due to the pupfish's ability to increase its abundance more quickly. Red River pupfish were found to spawn earlier in the

year and at a broader range of temperatures, and male pupfish were more aggressive in guarding their territory and disrupting spawning pairs than plains killifish. Furthermore, Red River pupfish eggs developed more rapidly, and larvae hatched at a larger size than plains killifish. Plains killifish were more abundant than Red River pupfish in less saline streams that had a more diverse fish fauna and presumably more resources and adaptive habitat segregation (Echelle et al. 1971b). In these systems the authors suggested that aggressive behavior of breeding male pupfish would contribute to a disadvantage in energetic efficiency in contrast to the less aggressive male plains killifish thus explaining the dominance of plains killifish over Red River pupfish in less saline and more diverse systems.

Although introduced populations of the mosquitofish can have negative effects on small-bodied native fishes, we found no evidence that mosquitofish have caused the decline of plains killifish populations in the Rocky Mountain region (see discussion in section Potential threats). In some cases, plains killifish populations that have been introduced outside of their historic range have been suspected of negatively affecting native fishes through competition (Hubbs and Wauer 1973, Valdez et al. 2001).

Parasites and disease

The parasite community of plains killifish populations in the South Platte River of Nebraska was described in a study of the effects of streamflow fluctuations on parasite community dynamics (Janovy and Hardin 1988, Janovy et al. 1997). Plains killifish were selected for study as hosts of the parasite community because of their abundance and wide distribution in the South Platte River system and because they were infected with seven different species or ecotypes of parasites (Janovy and Harding 1988, Janovy et al. 1997). The seven types of parasites infecting the South Platte River plains killifish, their infection site, life cycle, intermediate hosts, and transmission stages are summarized in **Table 5**. One of these parasites, *Salsuginus thalkeni*, was described as an extreme specialist found only in plains killifish (Janovy et al. 1997).

Janovy et al. (1997) documented changes in the parasite community resulting from variations in streamflow over a nine-year period that included several consecutive high water years followed by several low water years. Streamflow conditions were found to have direct and indirect effects on the parasite community by differentially affecting parasite species abundance and

population stability, a result of differences in parasite life cycles and transmission mechanisms.

Janovy et al. (1997) found that the generalist trematode, *Posthodiplostomum minimum*, experienced major fluctuations in prevalence (percentage of hosts infected), average number of parasites per host, and parasite population aggregation in response to changes in streamflow. *Posthodiplostomum minimum* was nearly extirpated during the second and third years of high water, but after extended periods of low flow the population rebounded with nearly 100 percent infection rates of plains killifish and large numbers of parasites per fish. The researchers also reported the effects of variations in streamflow levels on physid snail populations, the intermediate hosts of *P. minimum*, garnered from over 22 years of field observations (Janovy et al. 1997). The authors noted that large snail populations occurred in stream pools during periods of low water following a warm spring. However, during periods of extended high water, snails became rare, presumably having been transported downstream by the increased current in the pools. Furthermore, snail populations took several weeks following flood periods to rebound. Based on these observations, the authors suggested that the strong response of *P. minimum* populations to fluctuations in streamflow was a result of a combination of effects on the abundance of the infective stage of *P. minimum* in the environment. Both the lower abundance of the intermediate host, snails, and the stronger currents the cercariae, the free swimming infective stage, had to swim through to find a host effectively lowered the number of *P. minimum* in the environment. These results suggest that management actions that reduce streamflows have the potential consequence of exposing plains killifish to higher, and potentially harmful, parasite loads.

Janovy et al. (1997) found indications that the parasites had a negative impact on plains killifish populations. In particular, over-winter survival was lower for heavily parasitized fish, with the exception of those infected with *Trichodina* spp. The authors proposed that the apparent decreased over-winter survival rates of heavily parasitized plains killifish could be a result of reduced ability to cope with stress or to avoid predators.

Janovy and Hardin (1988) reported no significant differences in parasite diversity between male and female plains killifish or among size classes.

Brouder and Hoffnagle (1997) and Clarkson et al. (1997) reported the infection of plains killifish

with the Asian fish tapeworm (*Bothriocephalus acheilognathi*) in the Colorado River system, Grand Canyon, Arizona. The Asian fish tapeworm was thought to have been brought to North America with grass carp (*Ctenopharyngodon idella*) and has become established in several fish species in the southern and southeastern United States (Brouder and Hoffnagle 1997). Brouder and Hoffnagle (1997) suggested the restriction of the Asian fish tapeworm to the Little Colorado River was a result of the cooler water temperatures in the mainstem Colorado (from hypolimnetic water releases from reservoirs upstream) isolating the Asian fish tapeworm from other thermally suitable tributaries. Although the chronic effects of Asian tapeworm infection on fish hosts are not well known, emaciation, anemia, reduced growth and reproductive capacity, impairment of swimming ability resulting from muscle fatigue, and secondary bacterial infections are thought to occur (Clarkson et al. 1997). In a laboratory study, Asian tapeworm reduced survivorship among mosquitofish, another cyprinodont (Granath and Esch 1983). The documented infection of plains killifish in the Colorado River system with the Asian tapeworm indicates the potential for this tapeworm to be a threat if introduced into systems with native plains killifish populations.

In Minckley and Klassen's (1969a) study of plains killifish populations in the Smoky Hill River, Kansas, the major ectoparasite was the copepod *Lernaea* spp., which was most often observed attached to fin bases, particularly pelvic fins. The protozoan, *Ichthyophthirius* spp., was another ectoparasite that was reported to occur infrequently but with high infestation rates when present (Minckley and Klaassen 1969a). With the exception of a few fish that appeared emaciated and had three *Lernaea* attached, the plains killifish populations of Smoky Hill River did not appear to be affected by the presence of parasites (Minckley and Klaassen 1969a).

Symbiotic and mutualistic interactions.

None have been documented.

Envirogram of ecological relationships

An envirogram is a useful way of depicting the ecological relationships that influence the survival and reproductive success of a species (Andrewartha and Birch 1984, Hayward and Verner 1994). The envirogram is built around a centrum of four components that together encompass all the major ecological relationships important to the species. These four components are termed resources, malentities, predators, and mates. Environmental (including biotic)

factors that modify the four components form a web extending to several levels of indirect causation. For example, aquatic invertebrates may be important as food for a fish species and thus constitute one of the major categories for the resource component of the centrum. The abundance of aquatic invertebrates, in turn, is determined by a hierarchy of environmental factors that constitute the web. For example, invertebrate abundance is influenced by algal production which, in turn, is determined by water fertility, which, in turn, is determined by watershed geology and land-use.

An envirogram depicting the centrum and web for plains killifish is presented in **Figure 5**. The major resource needed by plains killifish is food, which consists largely of aquatic invertebrates. The abundance of aquatic invertebrates depends on their food sources (e.g., algae and detritus) and these, in turn, depend upon a series of abiotic factors and human modifications of the watershed. The major malentities are summer heat stress, habitat desiccation, water quality and competitors. Piscivorous fish and piscivorous birds are the major predators, with parasites also playing a potential role in determining the abundance of plains killifish. Under mates, suitable spawning habitat and egg hatching success are major determinants of reproductive success. The web indicates how these components of the centrum are modified by a host of abiotic factors, species interactions, and human modifications of the environment.

CONSERVATION

Potential Threats

Although plains killifish do not appear to be declining in the Rocky Mountain Region of the USDA Forest Service, there are factors that could become threats in the future. These include a) water development activities that alter streamflows, cause physical or chemical habitat degradation, and result in stream fragmentation, and b) the introduction of non-native fishes.

Water development activities are a dominant feature of Great Plains watersheds. For example, in the Kansas River system of northeastern Colorado, northern Kansas, and southern Nebraska, 18 large reservoirs and 13,000 small impoundments now control discharge from more than 80 percent of the drainage area (Sanders et al. 1993). For streams fed by a large snowmelt, reservoirs dampen natural flow fluctuations and reduce sediment load, making prairie streams less turbid and more confined in narrower, deeper channels.

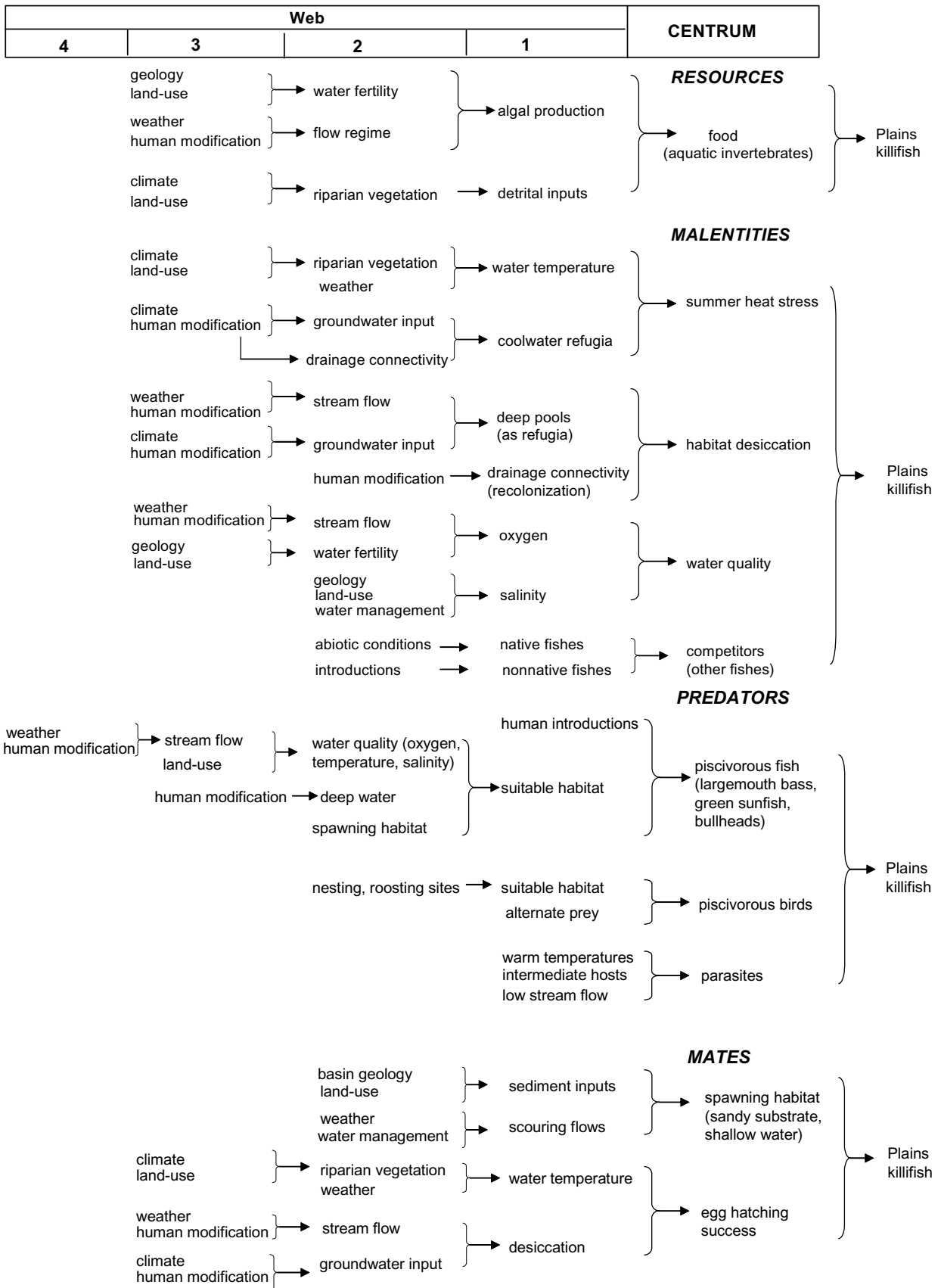


Figure 5. Envirogram for plains killifish.

The result has been replacement of native fishes tolerant of turbid waters, including the plains killifish, flathead chub (*Hybopsis gracilis*), and sturgeon chub (*H. gelida*), with native or introduced fishes characteristic of clearer waters, such as gizzard shad (*Dorosoma cepedianum*) and centrarchids (Cross and Moss 1987). Also, reservoirs act as sediment traps that deprive streams of the gravels needed to replace sediment transported downstream by water currents. This leads to downcutting of the main channel and the subsequent loss of shallow braided channels and backwater areas that are a major habitat for native prairie stream fishes including the plains killifish (Patton and Hubert 1993). In the lower Kansas River system, clear water releases below reservoirs resulted in channel downcutting by as much as 3 m (9.8 feet) within 12 years of operation (Sanders et al. 1993).

Although reservoir releases may enhance summer streamflows in downstream reaches, other water development activities tend to have the opposite effect. Withdrawal of surface water for irrigation can result in dewatering of large stretches of prairie streams. Also, pumping of groundwater can lower water tables and cause streams to become intermittent or dry up completely (Limbird 1993, Sanders et al. 1993). Cross and Moss (1987) reported that a 160 km (99 mile) stretch of the mainstem Arkansas River in Kansas went dry in the summer due to upstream water use and lowering of the water table by irrigation pumping. Because plains killifish tend to be located in headwater and naturally intermittent reaches of prairie streams, they are highly vulnerable to losing habitat from activities that divert water from stream channels or lower the water table.

Physical/chemical habitat degradation can occur due to sewage discharges, feedlot runoff, or pumping of saline groundwater. Sewage and feedlot runoff can cause eutrophication and lead to low oxygen conditions and high ammonia concentrations. The plains killifish is tolerant of high salinities and can live at salinities up to 43 parts per thousand (Echelle et al. 1971b). Nevertheless, discharge of highly saline groundwater from oil or gas field operations could pose a threat to plains killifish populations.

The loss of connectivity in a drainage network exacerbates the loss of plains killifish populations caused by drought, winterkill, or channel dewatering due to irrigation. This species evolved in a disturbance prone system, where recolonization of depopulated stream reaches was probably a common phenomenon. Such source-sink population dynamics have not been examined for the plains killifish but have been

shown to be important in the survival of other prairie stream fishes such as the Arkansas darter (*Etheostoma cragini*). Labbe and Fausch (2000) noted that persistence of the Arkansas darter in two intermittent Colorado streams was dependent on deep pool refuges and the ability of darters to colonize new habitat during high streamflow periods. Of course, such colonization depends on having connected stream systems, which currently is often not the case for Great Plains streams. Instead, recolonization is hampered by fragmentation of watersheds through construction of dams and reservoirs that block fish movement. In some cases, populations of stream fishes have been extirpated after stream reaches became isolated from the rest of the watershed by construction of a dam. Winston et al. (1991) reported that four minnow species were lost due to the damming of a prairie stream in Oklahoma. The species were cut off from downstream populations by the reservoir that formed behind the dam, and when the upstream populations were lost to due natural disturbances, repopulation from downstream sources was no longer possible.

Another potential threat to plains killifish populations involves introduction of non-native fishes. Plains killifish are seldom found in association with larger, piscivorous fish. Historically, piscivorous gamefish such as largemouth bass, green sunfish, and black crappie (*Pomoxis nigromaculatus*) were absent or rare in prairie stream drainages because of the paucity of deepwater habitat. However, construction of stock watering ponds and irrigation reservoirs has created such habitat and led to widespread stocking of piscivorous gamefish. Although the effect of such stocking on native fishes has seldom been evaluated, it appears likely that an abundant population of predators would be detrimental to small prey species, such as the plains killifish. For example, Labbe and Fausch (2000) noted that non-native northern pike (*Esox lucius*) were detrimental to the Arkansas darter in the Arkansas River drainage of Colorado. And Schrank et al. (2001) found that the number of impoundments per hectare in a watershed was positively related to the likelihood that the endangered Topeka shiner (*Notropis topeka*) had been extirpated from sites in Kansas. The likely mechanism was that impoundments promoted an abundance of largemouth bass that eliminated the shiner through predation.

Whether introduction of non-native species that could act as competitors poses a threat to plains killifish is unclear. As noted by Patton (1997) and Nesler et al. (1997), plains killifish often occur in association with small-bodied, native minnow and sucker species

in prairie streams in Wyoming and Colorado. In such assemblages, plains killifish are generally not the most abundant species, suggesting their population size may be depressed by competition with other fishes. Lynch (1988) noted that mosquitofish have been introduced and become established in riverine habitats favored by plains killifish in Nebraska. Because mosquitofish are aggressive toward other fishes, there is the potential for a negative effect on plains killifish. Meffe (1985) reported that introduced mosquitofish extirpated populations of Sonoran killifish (*Poeciliopsis occidentalis*) in the southwestern U.S. However, we found no studies documenting the loss of plains killifish populations following establishment of mosquitofish in the Rocky Mountain Region. Nesler et al. (1997) believed that the lack of negative effects of mosquitofish on native killifishes may reflect the fact that mosquitofish have remained relatively uncommon in most habitats in Colorado and Wyoming. Mosquitofish populations appear to be limited by their intolerance to cold winter water temperature.

Conservation Status of Plains Killifish in the Rocky Mountain Region

The plains killifish is abundant and common in appropriate habitat throughout the Rocky Mountain Region of the U.S. Forest Service. Although individual populations may decline due to drought or to loss of streamflow from water development activities, the species as a whole is secure at present. Plains killifish has been found residing within diverse stream types (intermittent high plains tributaries to main stem rivers) and in varying degrees of water quality (chemical and thermal regimes). No major loss of native geographic range has occurred, and the species has increased its range through anthropogenic introductions in Colorado, South Dakota, and Wyoming (see **Figure 3**). Where management concerns are more localized, there should be an awareness of the need to provide multiple habitat sites (connected and isolated) as a buffer against the possibility of local population extinction. Therefore, it may be important to conserve the natural hydrological processes of plains streams/ rivers where this species occurs.

Potential Management of the Species Region 2

Implications and potential conservation elements

Although the plains killifish is not a conservation concern at present, continued water development in

the naturally arid Great Plains region coupled with natural or climate-change associated drought would be detrimental to this species. Thus, management actions that would help to maintain streamflows, especially in smaller streams that originate on the Great Plains, would be advantageous to this species. For example, securing water rights to maintain instream flows has benefited populations of native salmonids in the Rocky Mountain Region (Annear and Dey 2001). Such a management action also would be of obvious benefit to nongame native fishes in prairie streams.

The species is present on three national grasslands within Region 2 where the distribution range appears stable (**Table 2**). The major land-use on the grasslands, livestock grazing, does not appear to be a major problem for plains killifish, which are tolerant of turbid water conditions.

Plains killifish evolved in stream systems subject to intermittency and other disturbances, such as floods and winterkill. Therefore, dispersal and recolonization after local extirpation are likely important mechanisms allowing regional persistence of the species. Anthropogenic features that impede fish movements, such as impoundments or highway culverts, will be detrimental to the persistence of plains killifish within a given drainage. Impoundments also provide habitat for non-native piscivores (e.g. largemouth bass) that are detrimental to plains killifish. Unknown at this time are the possible effects of coal-bed methane extraction activities on native fishes in plains streams. Coal-bed methane extraction has the potential to produce continuous streamflows within once ephemeral/ intermittent stream channels. Possible problems include reductions in stream temperatures, alterations in water quality (e.g. enhanced salinity), or stabilization of stream flows that favor non-native species that compete with or prey upon native fishes.

It is useful to think of management of plains killifish in terms of management of a group of native Great Plains fishes. The plains killifish is part of an assemblage of small-bodied, warmwater fishes native to streams of the Great Plains. The management actions described above would benefit this entire assemblage of fishes, several species of which are considered to be in need of conservation attention in various portions of Region 2 (See discussions in Nesler et al. 1997, 1999). Management actions aimed at preserving entire assemblages prior to severe imperilment are considered the best approach to conservation of native species. For example, Moyle et al. (1998) described how the return of a more normal flow regime in a

California stream benefited an entire assemblage of native fishes. The case had been in litigation, and the judge ruled that maintaining fish in “good condition” included preserving an assemblage of native, nongame species even though none of the component species were endangered. The major management actions that would benefit native prairie stream fishes are preservation of streamflows, maintenance of stream connectivity, prevention of the establishment of non-native piscivores, and avoidance of introductions of non-native small-bodied fishes from other Great Plains watersheds (Fausch and Bestgen 1997).

Tools and practices

Inventory and monitoring of populations and habitat

Most inventory efforts to date have involved determining the presence or absence of plains killifish at a range of sites across major drainages. Examples include surveys of the South Platte River and Arkansas River drainages in Colorado (Nesler et al. 1997, 1999) and the Missouri River drainage in Wyoming (Patton 1997). These inventories typically involve collecting all species at a site (at least 100 m (325 ft) in length) using seining or electrofishing techniques. Often, the results are compared with earlier inventories to determine which species have decreased and which species have increased their geographic range. For example, the distributions of native fishes in the South Platte River drainage collected in the 1992 survey were compared with distributions reported in earlier surveys starting in 1900 (Nesler et al. 1997). Likewise, Patton et al. (1998) compared species distributions in the 1990s with distributions from a fish survey done in the 1960s. Unfortunately, except for Patton et al. (1998), recent fish surveys rarely involved the same set of sites from earlier surveys, making it difficult to quantify changes in the occurrence of small fishes such as the plains killifish. Although one can determine if a species is still present within a drainage, it is difficult to determine if the species is increasing or decreasing. This makes it difficult to identify species in the early stages of decline, because we often can not recognize declines until a species is lost from a drainage basin. Given that the entire assemblage of small, plains stream fishes can be efficiently and simultaneously sampled, monitoring programs that revisit the same set of sites at regular intervals could be a cost-effective way to determine trends for a number of species within a national forest or grassland. When there is a large number of possible survey sites and one wishes to make inferences involving a spatially-extensive area, a probability-

based sampling design, such as that used in the U.S. Environmental Protection Agency’s EMAP program could be employed (Olsen et al. 1999).

We are aware of only one national grassland within Region 2 where a regular inventory program involving nongame plains fishes is on-going. The Pawnee National Grassland in northern Colorado began a system sampling program involving streams and pothole ponds in 1998.

The little monitoring that has been done for plains killifish has involved determining occurrence (i.e. presence or absence) across relatively large areas. We are not aware of any on-going monitoring being done that would detect population changes for this species. It is likely that individual populations would show considerable fluctuations in population size, given that the species occurs in systems with high naturally hydrological variability. Fausch and Bestgen (1997) surveyed plains killifish at four sites (each 150 m (488 ft) in length) over 12 years in the Cache la Poudre River near Fort Collins. They noted that the species achieved a high abundance at two of the sites for several years but was nearly absent from the sites before and after that period.

There has been virtually no systematic inventorying or monitoring of habitats of plains streams, except for occasional studies involving single streams and time periods seldom exceeding a decade (e.g. Bramblett and Fausch 1991). Although there have been some synoptic papers describing broadscale changes in plains streams during the past century (e.g. Cross and Moss 1987), there is little information available to make quantitative estimates of habitat change, especially for smaller streams. Techniques for assessing aquatic habitats in the Great Plains region were summarized by Osborne et al. (1991) and include the fish habitat rating (FHR) system developed for Wisconsin streams (Simonson et al. 1994) and the warmwater stream assessment (WSA) protocol developed for streams in Wyoming (Wyoming Game and Fish Department 2004). These inventory techniques typically involve measurements of turbidity, intermittence, mean channel width, channel morphology (e.g., proportion of the channel in various depth and substrate categories), and the abundance of woody debris in the channel.

Population or habitat management practices

We did not find any ongoing population or management practices directed specifically at plains killifish. The establishment of preserves for native

plains fishes has lagged behind efforts to preserve native coldwater fish species in the region, especially cutthroat trout (*Oncorhynchus clarki*) (Young 1995). However, management agencies are increasing their interest in the conservation of native nongame fish species (Nesler et al. 1997, 1999, Weitzel 2002). Also, private conservation organizations could play a role in preserving native, plains fishes. For example, The Nature Conservancy has purchased the Fox Ranch on the Arikaree River near Wray, Colorado and is helping to preserve the site as an example of a free-flowing, plains stream (website: <http://nature.org/wherewework/northamerica/states/colorado/preserves/>). This preserve will afford conservation protection for an entire assemblage of native fishes, including the plains killifish.

Managing streamflow for the benefit of fishes, like the plains killifish, that evolved in highly dynamic Great Plains streams is a challenging issue. Probably the best approach is to try to maintain or restore the natural flow regime (Poff et al. 1997). Natural flow regimes produce habitat conditions required by native fishes and often discourage invasions by non-native species (Hubert 1993, Marchetti and Moyle 2001). For Great Plains streams, natural flow regimes usually involve peak streamflows in spring and low or intermittent flows in summer/fall. Complete desiccation would be detrimental to aquatic organisms, but periods of intermittency would likely be tolerated by native plains fishes provided that some refuges exist (e.g. deep pools, springs) and that recolonization is not blocked by movement barriers. Flow enhancements during summer and fall (e.g., through water produced during coal-bed methane extraction) could be detrimental to native fishes if water temperature or water quality are altered, or if increased flow allows non-native fishes such as green sunfish or bass to persist. Small impoundments could be detrimental because they block migratory movements of fish and can be a source of non-native fishes in the drainage basin (Schrack et al. 2001).

Information Needs

Information on the distribution of plains killifish is adequate to indicate that this species is not in need of special conservation attention at the regional level. The species occupies most of its historic range and has expanded its range as a result of anthropogenic introductions in parts of Colorado, Wyoming, South Dakota, Utah, and Arizona (see **Figure 2** and **Figure 3**). This assessment is primarily based on large-scale, synoptic surveys funded by state game and fish agencies (e.g. Nesler et al. 1997, 1999, Patton 1997). However, there are various HUB 4 drainages within

Nebraska and Kansas for which we could not locate information regarding the presence or absence of plains killifish (**Figure 3**). Although none of these drainages are included in national forests or national grasslands, this lack of data represents a gap in our knowledge about the distribution of plains killifish throughout its native range.

There is little information available concerning population trends for plains killifish on individual national grasslands within the Rocky Mountain Region of the USDA Forest Service. As discussed earlier (see section Tools and practices), monitoring populations of plains killifish on national grasslands could be done within the framework of monitoring the entire fish assemblage. Techniques for censusing fish populations are well-developed and include seining, electrofishing, and trapping (Hays et al. 1996, Hubert 1996). Measures of catch-per-unit-effort provide a cost-effective index of fish abundance and are useful for trend monitoring, if the same set of sites is sampled in successive time periods (Ney 1999). Estimates of actual population size can be obtained through mark-recapture or depletion-removal approaches, but these approaches require more effort and would reduce the number of sites that could be sampled.

Much is known about the response of plains killifish to abiotic stressors, such as low oxygen, high temperature, high salinity, and high turbidity. The plains killifish is one of the most physiologically hardy fish species found in the Great Plains region. With the exception of cattle feedlots, land use practices common on national grasslands (primarily livestock grazing) are not likely to degrade water quality to the point where there are major negative effects on this species (assuming these practices are conducted at levels consistent with achieving local riparian objectives). However, reductions in streamflow, construction of small impoundments for livestock watering, and increased intermittency in what were once perennial systems are on-going problems in the arid Great Plains region, and we know little about how plains killifish respond to such disturbances. Thus, a major information need is to understand how plains killifish populations respond to alterations in streamflow (i.e. flows created in once intermittent drainages from coal-bed methane development). This would include knowing where refuges are located during periods of intermittency and determining recolonization pathways following the return of normal flow conditions. It is also important to know if there are barriers to fish movement (e.g., road culverts, impoundments) that prevent populations from returning to suitable habitats. Studies

of movement patterns would answer these questions and provide insight as to whether plains killifish exist as metapopulations or as source/sink populations. Fausch and Bestgen (1997) make the interesting point that, although many sites may be dry when visited during low flow, biologists should not assume that such channels do not provide important spawning or rearing habitat, or dispersal routes, during higher flows.

There is a major gap in our knowledge of vital rates important in understanding and modeling population demographics. Age-specific survival rates have not been determined directly and have to be inferred from the few studies that present size or age-class frequency histograms. There is no information on egg hatching rates in the wild, and this parameter could be determined only by estimating survival rates for other age classes and then back-solving the demographic matrix assuming a stable population size (details in **Appendix A**). Information on the spatial and temporal variability of vital rates is important for modeling

population fluctuations and extinction probabilities.

Finally, there is an important issue regarding management of information on plains killifish as well as other native Great Plains stream fishes. In our phone conversations and e-mail exchanges with biologists from the various national forests and national grasslands within Region 2, it became apparent that much of the data on these species are not in a readily accessible or retrievable form. The biologists we spoke with were extremely cooperative in providing information, but this often involved sifting through old field data sheets or sparsely documented reports whose authors were no longer working in that region. In some cases, there was little information about the exact locations sampled, the level of sampling effort, or the meaning of shorthand notations (e.g., for species abbreviations) used in field notes. Better documentation of sampling locations, sampling effort, and fish catches in formalized reports would ensure that the data remain useful and accessible to future generations of managers and researchers. Such archived data are critical if we are going to detect trends in species abundances or distributions that would signal the need for conservation efforts.

DEFINITIONS

Cyprinodontids are fish species in the order Cyprinodontiformes characterized by small body size, upward facing mouths, and the ability to survive in waters that are too warm, too saline, or have insufficient oxygen for most other fish species.

Egg hatching rates refer to the proportion of eggs that successfully hatch.

Environmental fluctuations are changes in habitat conditions such as temperature, salinity, oxygen concentration, or the amount of water flowing in a stream.

Fecundity is the number of eggs produced by a female fish.

Histogram is a graph showing the number of individuals (or the proportion of the population) that exists in various categories. The categories can be based on age groups or size groups.

Intermittent tributary is a stream that flows into a larger stream and ceases to flow during certain periods of the year. The stream may dry up completely or exist as a series of pools.

Habitat connectivity refers to the degree to which organisms can move throughout the area or system of interest.

Management Indicator Species (MIS) are those species used in land management planning because their population changes indicate the effects of management activities.

Meristic character is an anatomical feature that can be counted, such as the number of spines on the dorsal fin or the number of scales along the lateral line of a fish. Meristic characters are frequently used to identify fish species using a taxonomic key.

Metapopulations are spatially isolated populations that function as independent populations but which can exchange occasional individuals. This exchange allows extirpated populations to become reestablished.

Microhabitats are the localized habitat conditions used by organisms.

Morphometric character is an anatomical feature that can be measured, such as the length of various body parts or ratios of body parts (e.g. the diameter of the eye divided by the length of the head).

Osmoregulation is the maintenance of proper internal body salt concentrations.

Piscivorous means “fish-eating”.

“R-selected” species are species whose life history attributes indicate selection for rapid growth, early age of reproduction, high fecundity, good colonization ability, and a short life span. These species are often termed “weedy species” that are good at finding and living in recently disturbed habitats where there are few competing species.

Sink populations are populations where the death rate exceeds the birth rate. Sink populations require continual immigration from nearby populations if they are to avoid extinction.

Source populations are populations where the birth rate exceeds the death rate and thus these populations are a source of emigrants to nearby areas, including sink populations.

“Species of concern” is a species that has declined in abundance or distribution to the point that management agencies are concerned that further loss of populations or habitat will jeopardize the persistence of the species within that region.

Species viability refers to the likelihood that a species will continue to persist.

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APPENDIX A

Matrix Population Analysis of Population Demographics for Plains Killifish

A life cycle graph (**Figure 4**) was constructed for plains killifish and used as the basis for a matrix population analysis with a post-breeding census (McDonald and Caswell 1993, Caswell 2000). Because virtually no data were available for first-year survival (P_{21}) we used the “missing element” method of McDonald and Caswell (1993) to solve for P_{21} given that the population growth rate (λ) was equal to 1.0. Over the long term λ must be near 1 or the species will go extinct or the population will grow unreasonably large. The model has two kinds of input terms: P_i describing survival rates, and m_i describing fertilities (**Table 4**). **Figure 4** shows the symbolic terms and corresponding numeric values for the projection matrix developed from the life cycle graph. The model assumes female demographic dominance, hence fertilities are given as female offspring per female. The population growth rate (λ), is 1.0 based on the estimated vital rates used for the matrix. Although this suggests a stationary population, the value was used as an assumption for deriving a vital rate, and should not be interpreted as an indication of the general well-being of the population. Other parts of the analysis provide a better guide for assessment. It is important to note that, in contrast to fisheries terminology, the convention here is ordinal numbering beginning with 1 (first, second, third and fourth age-classes). Thus, Age-class 0 in fisheries terminology corresponds to the age class 1 in the matrix model. Each age-class describes a one-year census interval period and the age-class that begins with an egg at the census and proceeds to the first clutch produced by a yearling is described by the self-loop $P_{21}m_1$ in **Figure 4**.

Sensitivity analysis

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. Sensitivity is the effect on population growth rate (λ) of an absolute change in the vital rates (a_{ij} , the arcs in the life cycle graph; **Figure 4**) and the cells in the projection matrix, A (**Figure A1**). Sensitivity analysis provides several kinds of useful information. First, sensitivities show “how important” a given vital rate is to population growth rate (λ) or fitness. For example, one can use sensitivities to assess the relative importance of survival and reproductive transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies.

Inaccuracy will usually be due to paucity of data, but could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing the population growth rate (λ) of an endangered species or the “weak links” in the life cycle of a pest. **Figure A2** shows the “possible sensitivities only” matrix for this analysis (one can calculate sensitivities for non-existent transitions, but these are usually either meaningless or biologically impossible — for example, the sensitivity of λ to moving from Age-class 3 to Age-class 2).

In general, changes that affect one type of age class or stage also will affect all similar age classes or stages. For example, any factor that changes the annual survival rate of Age-class 2 females is very likely to cause similar changes in the survival rates of other “adult” reproductive females (those in Age-classes 3 and 4). It is, therefore, usually appropriate to assess the summed sensitivities for similar sets of transitions (vital rates). For this model, the result is that the summed sensitivity of the population growth rate (λ) to changes in survival is of overriding importance. Plains killifish shows large sensitivity (88 percent of total) to changes in survival, with first-year survival alone accounting for 85 percent of the total. The summed “reproductive” survival sensitivity is just 12 percent of the total. The major conclusion from the sensitivity analysis is that first-year survival is overwhelmingly important to population viability.

Elasticity analysis

Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivities. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. For instance, a change of 0.5 in survival may be a big alteration, e.g., a change from a survival rate of 0.9 to 0.4 corresponds to a reduction in survival from 90 percent to 40 percent. On the other hand, a change of 0.5 in fertility may be a small proportional alteration. e.g., a change from an average clutch size of 100 eggs to 99.5 eggs. Elasticities are the sensitivities of the population growth rate (λ) to proportional changes in the vital rates (a_{ij}) and thus largely avoid the problem of differences in

Age-class	1	2	3	4
1	$P_{21}m_1$	$P_a m_2$	$P_a m_{a3}$	
2	P_{21}			
3		P_a		
4			P_a	

Age-class	1	2	3	4
1	0.73	6.12	8.67	
2	0.04			
3		0.17		
4			0.17	

Figure A1. The top matrix shows symbolic values for the projection matrix. Meanings of the component terms and their numeric values are given in **Table 4**. Symbols refer to those used in the plains killifish life cycle graph of **Figure 4**. The bottom matrix presents the actual numeric values used for the matrix analysis.

Age-class	1	2	3	4
1	0.757	0.027	0.005	
2	5.746			
3		0.233		
4			0.000	

Figure A2. Possible sensitivities only matrix, S_p (blank cells correspond to zeros in the original matrix, A). The three transitions to which the λ of plains killifish is most sensitive are highlighted: first-year survival (Cell $s_{21} = 5.746$), first-year reproduction ($s_{11} = 0.757$), and survival of Age-class 2 ($s_{32} = 0.233$).

units of measurement. The elasticities have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction and survival for a given species.

Elasticities for plains killifish are shown in **Figure A3**. The population growth rate (λ) is most elastic to changes in first-year reproduction ($P_{21}m_1$, the self-loop on the first node in **Figure 4**) followed by first-year survival (P_{21}) and then second-year reproduction ($P_{32}m_2$). The sensitivities and elasticities for plains killifish do not correspond in rank magnitude.

The first and third most elastic transitions involve reproduction, in contrast to the first-year survival so heavily emphasized by the sensitivity analysis. The summed reproductive elasticities account for fully 76 percent of the total (compared to 12 percent for the summed reproductive fertilities). Thus, survival and reproduction in the first year, and to a lesser extent survival and reproduction in the second year, are the data elements that warrant careful monitoring in order to refine the matrix demographic analysis.

Other demographic parameters

The stable age distribution (**Table A1**) describes the proportion of each age-class in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining,

Stage	1	2	3	4
1	0.553	0.164	0.040	0
2	0.204			
3		0.040		
4			0.000	

Figure A3. Elasticity matrix, **E** (remainder of matrix consists of zeros). The λ of plains killifish is most elastic to changes in first-year reproduction ($e_{11} = 0.553$), followed by first-year survival ($e_{21} = 0.204$) and then reproduction by Age-class 2 ($e_{21} = 0.164$). Note the considerably greater relative importance of fertility transitions in the elasticity analysis relative to the sensitivity analysis.

Table A1. Stable age distribution (right eigenvector). At the census, 95.9% of the individuals in the population would be present as eggs. The remaining 4.1% of individuals would be reproductive adults.

Age Class	Description	Proportion
1	Eggs (to yearling)	0.959
2	Second-year females	0.034
3	Third-year females	0.006
4	Fourth-year females	0.001

stationary or increasing. Under most conditions, populations not at equilibrium will converge to the stable age distribution within 20 to 100 census intervals. For plains killifish at the time of the post-breeding annual census (just after the end of the breeding season), eggs represent 96 percent of the population, second-year individuals represent another 3.4 percent, and older fish are extremely rare. Reproductive values (**Table A2**) can be thought of as describing the “value” of a stage as a seed for population growth relative to that of the first (in this case, egg) stage. The reproductive value of the first stage is always 1.0. A female individual in Age-class 2 is “worth” 7.59 eggs, and so on. The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving. The peak reproductive value (8.67) occurs at the third age-class, and these females are an important stage in the life cycle (though they represent <1 percent of the population).

It is important to remember, that the third age-class in the demographic matrix analysis corresponds to Age-class 2 fish using conventional fisheries terminology. The cohort generation time for this fish is 1.3 years (Standard Deviation = 0.6 years).

Stochastic model

We conducted a stochastic matrix analysis for plains killifish. We incorporated stochasticity in several ways, by varying different combinations of vital rates or by varying the amount of stochastic fluctuation (**Table A3**). Under Variant 1 we subjected first-year reproduction ($P_{21}m_1$) to stochastic fluctuations. Under Variant 2 we varied the survival of all age classes, P_i . Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the stable age distribution under the deterministic model. Beginning at the stable age distribution helps

Table A2. Reproductive values (left eigenvector). Reproductive values can be thought of as describing the “value” of an age class as a seed for population growth relative to that of the first (newborn or, in this case, egg) age class. The reproductive value of the first age class is always 1.0. The peak reproductive value (third-year females) is highlighted.

Age Class	Description	Reproductive values
1	Eggs/first-year females	1.00
2	Second-year females	7.59
3	Third-year females	8.67
4	Fourth-year females	0.00

Table A3. Summary of four variants of stochastic projections for plains killifish.

	Variant 1	Variant 2	Variant 3	Variant 4
<u>Input factors:</u>				
Affected cells	F_{11}	P_i	F_{11}	F_{11}
S.D. of random normal distribution	1/4	1/4	1/8	1/16
<u>Output values:</u>				
Deterministic λ	1.00003	1.00003	1.00003	1.00003
# Extinctions/100 trials	98	0	11	0
Mean extinction time	915.8	Not Applicable (NA)	1,587.3	Not Applicable (NA)
# Declines/# survived pop	2/2	87/100	84/89	77/100
Mean ending population size	328.1	5,853.7	1,966.6	8,844.7
Standard deviation	422.8	16,895.0	6,095.5	17,014.5
Median ending population size	328.1	432.2	123.0	3,308.8
Log λ_s	-0.01160	-0.00135	-0.00256	-0.00056
λ_s	0.9885	0.9986	0.9974	0.9994
% reduction in λ	1.156	0.138	0.26	0.059

avoid the effects of transient, non-equilibrium dynamics. The overall simulation consisted of 100 runs (each with 2,000 years). We varied the amount of fluctuation by changing the standard deviation of the random normal distribution from which the stochastic vital rates were selected. The default value was a standard deviation of one-quarter of the “mean” (with this “mean” set at the value of the original matrix entry [vital rate], a_{ij} under the deterministic analysis). Variant 3 affected the same transition as Variant 1 (first-year reproduction; $P_{21}m_1$) but incorporated only one-half the variation (SD was 1/8 of the mean). Variant 4 further reduced variation of $P_{21}m_1$ to 1/16 of the mean. We calculated the stochastic growth rate, $\log \lambda_s$, (see equation 14.61 of Caswell 2000), after discarding the first 1,000 cycles in order to avoid transient dynamics.

The stochastic model (**Table A3**) produced two major results. First, varying first-year reproduction had a greater effect on population growth rate (λ) than did varying all the survival rates. For example, 98 of 100 runs led to extinctions with variable first-year reproduction under Variant 1 from the starting size of 10,000. In contrast, varying the survival rates of all age classes under Variant 2 did not lead to any extinctions. This difference in the effects of stochastic variation is predictable largely from the elasticities. Population growth rate (λ) was more elastic ($e_{11} = 0.553$) to changes in first-year reproduction ($P_{21}m_1$) than it was to changes in the survival rates (summed survival elasticities = 0.24). Second, the magnitude of stochastic fluctuation largely determines the negative effect on population dynamics. This negative effect occurs

despite the fact that the average vital rates remain the same as under the deterministic model — the random selections are from a symmetrical distribution. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2000). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. For plains killifish under the $P_{21}m_1$ Variant 3 with reduced (1/8 vs. 1/4) variability, only 11 (vs. 98 under Variant 1) out of 100 trials of stochastic projection went to extinction. Variant 4 further demonstrates that the magnitude of fluctuation has a potentially large impact on the detrimental effects of stochasticity. Decreasing the magnitude of fluctuation (to SD = 1/16 of the mean) decreased the severity of the negative impacts — the number of extinctions went from 11 in Variant 3 to 0 in Variant 4. Note that Variant 4 is reasonably similar to the outcome of Variant 2 — that is, it takes only larger magnitude fluctuations in survival (SD = 1/4) to have the same detrimental effects produced by even small fluctuations in first-year reproduction (SD = 1/4). These results indicate that populations of plains killifish are vulnerable both to stochastic fluctuations in production of newborns (due, for example, to annual climatic change or to human disturbance) and, to a far lesser degree, to variations in survival (87/100 runs declined under Variant 2). Pfister (1998) showed that for a wide range of life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by

having low variability for sensitive transitions in their life cycles. A possible concern is that anthropogenic impacts may induce variation in previously invariant vital rates (such as annual adult survival), with consequent detrimental effects on population dynamics. For fish with stochasticity having the greatest impact on first-year reproduction, the life history may not allow the kind of adjustment of risk load that may be possible in other species. Variable spawning conditions are likely to be the rule rather than the exception.

Potential refinements of the models

Clearly, the better the data on survival rates are, the more accurate the resulting analysis will be. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability, would allow construction of a series of “stochastic” matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variations in vital rates. Using observed correlations would improve on this assumption by incorporating forces we did not consider. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence.

Summary of major conclusions from the matrix projection models:

- ❖ First-year survival accounts for 85 percent of the total “possible” sensitivity. Any absolute changes in this rate will have major impacts on population dynamics.

- ❖ First-year reproduction ($P_{21}m_1$) accounts for 55 percent of the total elasticity, compared to the 20 percent (next highest value) accounted for by first-year survival. Proportional changes in first-year reproduction will have a major impact on population dynamics.
- ❖ The contrast between the conclusions from the sensitivity and elasticity analyses suggests that survival and reproduction in the first year of life are both critical to the population dynamics of plains killifish.
- ❖ Where the potential exists for survival through to the third year, reproductive values of females in that age-class will be high. Such populations may be important sources of recolonization for other sites or in periods where local conditions improve.
- ❖ Stochastic simulations echoed the elasticity analyses in emphasizing the importance of variation in first-year reproduction to population dynamics. In comparison to life histories of other vertebrates, plains killifish seem vulnerable to local extinction.
- ❖ Management will need to take into account the potential for considerable variability in population trajectories and the need for multiple habitat sites as a buffer against the likelihood of reasonably frequent local population extinctions.

APPENDIX B

Sources of information used to produce the distribution map (**Figure 3**) showing the occurrence of plains killifish within HUB 4 drainages in the five states comprising Region 2 of the USDA Forest Service.

Colorado:

Nesler, T.P., R. VanBuren, J.A. Stafford, and M. Jones. 1997. Inventory and status of South Platte River native fishes in Colorado. Colorado Division of Wildlife, Fort Collins, CO.

Nesler, T.P., C. Bennett, J. Melby, G. Dowler, and M. Jones. 1999. Inventory and status of Arkansas River native fishes in Colorado. Colorado Division of Wildlife, Fort Collins, CO.

Kansas:

Stream Assessment and Monitoring Program Database and 1970's Stream Database, State of Kansas, Department of Wildlife and Parks, Pratt, KS.

Nebraska:

Fisheries survey data supplied by the Nebraska Game and Parks Commission, Lincoln, NE.

Schmulbach, J.C., Gould, G. and Groen, C.L. 1975. Relative abundance and distribution of fishes in the Missouri River, Gavins Point dam to Rulo, Nebraska. Proceedings of the South Dakota Academy of Sciences 54:194-222.

South Dakota:

Backlund, D. Wildlife Biologist, Department of Game, Fish and Parks, Pierre, South Dakota. Personal communication.

Bailey, R.M. and Allum, M.O. 1962. Fishes of South Dakota. Miscellaneous Publications Museum of Zoology, University of Michigan No. 119. Museum of Zoology, University of Michigan, Ann Arbor, MI.

Hampton, D.R. 1998. A survey of the fishes and habitat of the Cheyenne River in South Dakota. Masters Thesis. South Dakota State University, Brookings, SD.

Wyoming:

Lipsev, T.S. B. 2001. Using elevation, channel slope, and stream width to predict the occurrence of native warmwater fish species in the North Platte River drainage in Wyoming. Master's Thesis, University of Wyoming, Laramie, WY.

Patton, T.M. 1997. Distribution and status of fishes in the Missouri River drainage in Wyoming: implications for selecting conservation areas. Dissertation. University of Wyoming, Laramie, WY.

Wyoming Game and Fish Department fisheries data bases. Cheyenne, WY.

The following references were used to determine the status of plains killifish populations as native or introduced:

Baxter, G.T. and M.D. Stone. 1995. Plains killifish, *Fundulus zebrinus*. Pages 212–213 in Fishes of Wyoming. Wyoming Game and Fish Department, Cheyenne, WY.

Hughes, R.M. 1981. The plains killifish, *Fundulus zebrinus* (Cyprinodontidae), in the Colorado River Basin of western North America. The Southwestern Naturalist 26:321-324.

Kreiser, B.R. 1999. Phylogeography of the plains killifish, *Fundulus zebrinus*. Ph.D. Dissertation. Department of Environmental, Population, and Organismic Biology, University of Colorado. Boulder, CO.

- Poss, S.G. and R.R. Miller. 1983. Taxonomic status of the plains killifish, *Fundulus zebrinus*. *Copeia* 1983(1): 55-67.
- Woodling, J. 1985. Plains killifish, *Fundulus zebrinus*. Pages 62-63 in Colorado's little fish; a guide to the minnows and other lesser known fishes in the state of Colorado. Colorado Division of Wildlife, Department of Natural Resources, Denver, CO.

LIST OF ERRATA

06/29/04 Table 2: (1) added “ESA” to the columns titled USFS Status; and (2) changed “1993” to “2003” to all sources that reference “Regional Forester’s Sensitive Species List, USDA Forest Service, Rocky Mountain Region, 1993” in the columns titled Basis of Status.

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