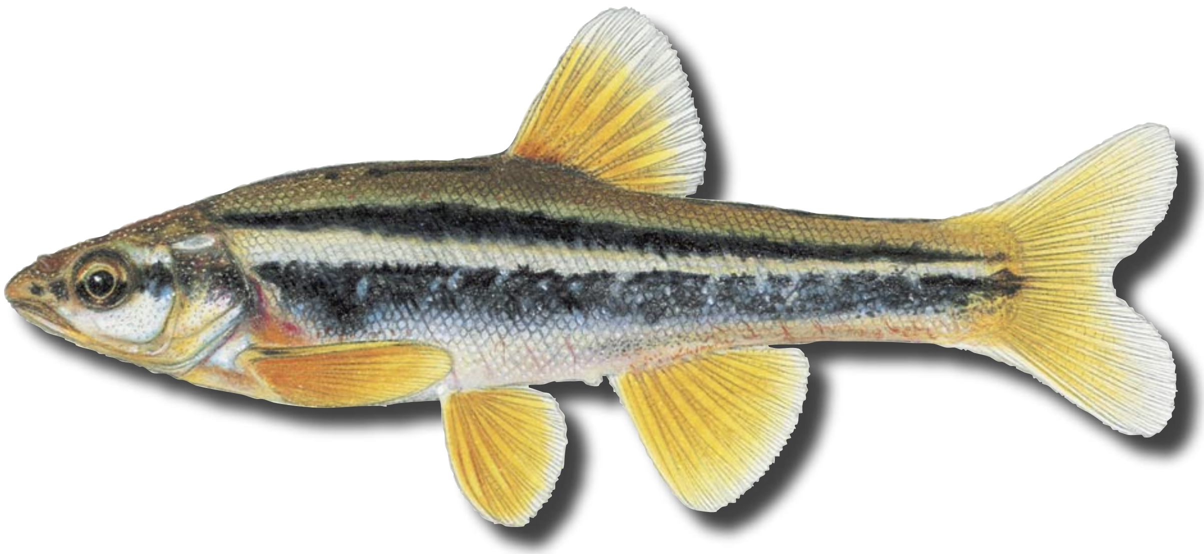
Southern Redbelly Dace (*Phoxinus erythrogaster*): A Technical Conservation Assessment



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AUTHOR'S BIOGRAPHY

Richard H. Stasiak received his Ph.D. from the University of Minnesota. He spent his graduate school days working on the ecology of *Phoxinus* minnows in the bogs and beaver ponds of northern Minnesota. He is currently Professor of Biology at the University of Nebraska at Omaha, where he has spent the past 36 years teaching courses in ichthyology, aquatic ecology, and zoology. Dr. Stasiak was certified as a Fisheries Scientist (#1254) by the American Fisheries Society in 1977. He has been a Fellow of the American Institute of Fishery Research Biologists since 1991. His research interests center around the ecology of fishes found in the Midwest. He has had life-long research interest in the biology of the minnows called "daces."

COVER ILLUSTRATION CREDIT

Southern redbelly dace (*Phoxinus erythrogaster*). © Joseph Tomelleri.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF THE SOUTHERN REDBELLY DACE

Status

The southern redbelly dace (*Phoxinus erythrogaster*) has a range that encompasses most of the Mississippi River Drainage in the United States. It is not considered endangered or threatened at the federal level in the United States, and NatureServe considers it globally secure (G5). This species is, however, uncommon in the Missouri River portion of its range, where it occurs as small, isolated populations in headwater streams. It is found only in three of the five states comprising the USDA Forest Service (USFS) Rocky Mountain Region (Region 2), where it is categorized by NatureServe as critically imperiled (S1) in Colorado and as imperiled (S2) in Kansas. In 2003, this species was reported from a single location in South Dakota, and while it is currently not on the official list of threatened species for South Dakota, it categorized as critically imperiled in the state (S1) by NatureServe. This species has not been reported from any USFS units in Region 2, but its presence in the headwaters of the Arkansas River in Colorado indicates that there may be suitable habitat in small tributaries found on the San Isabel National Forest and the Comanche National Grassland.

Primary Threats

Primary threats to the southern redbelly dace are associated with habitat alteration and introduction of non-native fishes. Water development activities that alter natural spring flow lead to habitat degradation and stream fragmentation. Reservoir construction, groundwater pumping, stream diversions, culverts, and channelization all negatively affect this species. These dace occur in small, low-order streams where the habitat includes permanent springs, seeps, and mats of vegetation, where the natural fish community is highly adapted to the special conditions this habitat presents. Southern redbelly dace depend on relatively clear water; therefore, activities that cause long-term increases in turbidity will be deleterious. Construction projects, forestry practices, and agricultural activities need to be managed so that they do not result in excessive erosion and siltation. Pollution in its many forms, including chemicals such as pesticides and artificial hormones, has the potential to affect this species. Introduced fish species also likely have a negative effect on the dace and other native fishes of this assemblage through the combined pressures of predation, competition, potential for addition of new parasites and disease, and alteration of behavioral components. New predator species would most likely have a negative impact on dace populations. Another threat, which may be of more local concern, is the potential overharvest of dace for private and commercial use as fishing bait or for the aquarium industry.

Primary Conservation Elements, Management Implications, and Considerations

The southern redbelly dace is one of the keystone species of small fishes forming a distinctive community on the Great Plains. In this region, this assemblage of fishes is restricted to low-order (1^{st} to 3^{rd} order) streams near headwater springs of tributaries to the Missouri River. It prefers clear water with sand or gravel substrate, and permanent vegetation. The most important management action for this species is to protect or restore the integrity of its aquatic habitat. Activities that affect the hydrology and the natural flow of streams need to be monitored, as do agricultural practices and construction projects that have the potential to add excessive sediment loads and harmful chemicals to these streams. Non-native fishes, especially piscivores, must necessarily be eliminated in headwater habitats.

Table of Contents

EDITOR: Gary Patton, USDA Forest Service, Rocky Mountain Region

LIST OF TABLES AND FIGURES

Tables:

Figures:

Introduction

This conservation assessment is one of many being produced to support the Species Conservation Project of the USDA Forest Service (USFS) Rocky Mountain Region (Region 2; **Figure 1**). The southern redbelly dace (*Phoxinus erythrogaster* Cope) is the focus of an assessment because concern for the species' viability in the states comprising Region 2 caused the species to be added to the Regional Forester's Sensitive Species List during revision of that list in 2003. Within the National Forest System, a sensitive species is a plant or animal whose population viability is identified as a concern by a Regional Forester because of significant current or predicted downwards trend in abundance and/or habitat capability that would reduce its distribution [FSM 2670.5 (19)]. The southern redbelly dace occurs in three of the five states comprising Region 2 (Kansas, South Dakota, and Colorado) (**Figure 2**), where it is listed as endangered or imperiled either by the states and/or Nature Serve.

This assessment addresses the biology, ecology, and conservation of the southern redbelly dace throughout its range in Region 2. Much of the data, however, comes from research conducted on populations that lie outside Region 2, but make up the major portion of the species' distributional range. The broad nature of this assessment leads to some constraints on the specificity of information for particular locales. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

Species conservation assessments produced for the Species Conservation Project are designed to provide land managers, biologists, and the public with a thorough discussion of the biology, ecology, conservation status, and management of certain species based upon available scientific knowledge. The assessment goals provide critical summaries of scientific

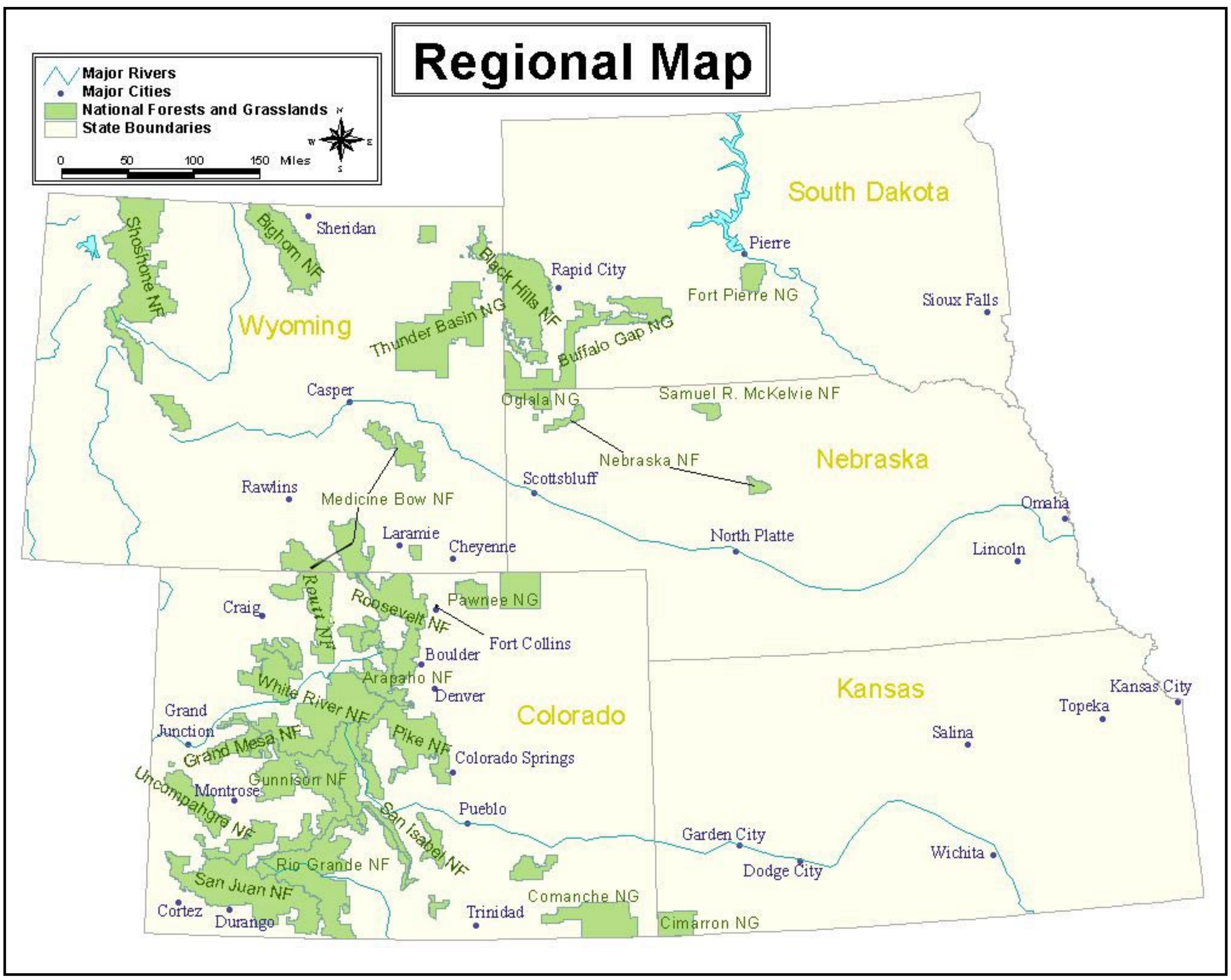


Figure 1. USDA Forest Service Region 2 administrative units.

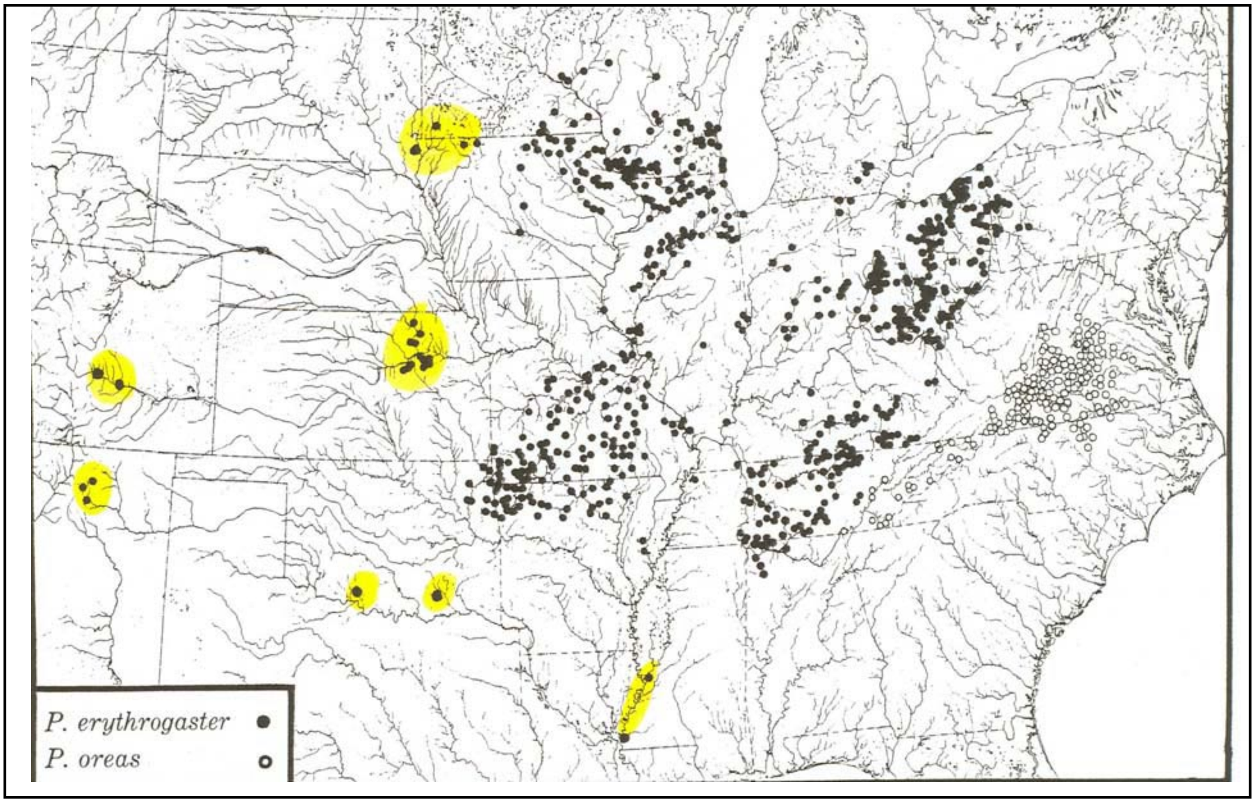


Figure 2. Distribution map for southern redbelly dace. The yellow highlights indicate populations that have been isolated from the main portion of the range for a long period of time, perhaps a thousand years or more. (Modified from Starnes and Starnes 1980).

knowledge, discussion of the broad implications of that knowledge, and outlines of information needs. This assessment does not seek to prescribe management for the USFS. Instead, it provides the ecological background upon which management must be based and focuses on the consequences of changes in the environment that result from management actions (i.e., management implications) and on the conservation needs of the southern redbelly dace.

Scope of Assessment

The southern redbelly dace assessment examines the biology, ecology, conservation status, and management of this species with specific reference to the geographic and ecological characteristics of Region 2. Although much of the literature on this species originates from field investigations outside the region, this document places that literature in the ecological and social contexts of the southern Great Plains and southern Rocky Mountain foothills in Region 2. The evolutionary environment of the species is considered in conducting the synthesis, but it is placed in a context of the current environment.

In producing the assessment, refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies were reviewed. Not all publications on southern redbelly dace are referenced in this assessment, nor were all materials considered equally reliable. This assessment emphasizes refereed literature because this is the accepted standard in science. Some non-refereed literature was used in the report when information was not available in the primary literature. Unpublished data (e.g. Natural Heritage Program Records, internal agency reports) were important in estimating the geographic distribution of the species. Species names used in this account follow those listed in Nelson et al. (2004) for the American Fisheries Society.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference. However, it is difficult to conduct critical experiments in the ecological sciences, and often observations, inference, good thinking, and models must be relied on to guide the understanding of ecological relationships.

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.

Application and Interpretation Limits of this Assessment

Information about the biology of southern redbelly dace was collected and summarized from throughout its geographic range. In general, life history and ecological information collected from a portion of this range should apply broadly throughout the entire distribution. However, certain life history parameters (e.g., time of spawning, growth rates, longevity) could differ along environmental gradients, especially in such a wide-ranging species. Discussion of conservation status was limited to Region 2 and should not be taken to imply conservation status in other portions of the species' overall range.

Publication of Assessment on the World Wide Web

To facilitate their use, species conservation assessments are being published on the Region 2 World Wide Web site (www. fs.fed.us/r2/projects/scp/assessments). Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More importantly, it facilitates updates to and revision of the assessments, which will be accomplished based on protocols established by Region 2.

Peer Review

In keeping with the standards of scientific publication, assessments developed for the Species Conservation Project have been externally peer reviewed prior to their release on the Web. This assessment was reviewed through a process administered by the Society for Conservation Biology, which chose a recognized expert (on this or related taxa) to provide critical input on the manuscript.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

The southern redbelly dace carries no federal status in the United States (http://endangered.fws.gov/), but it does currently reside on the Regional Forester's Sensitive Species List in Region 2 (http://www.fs.fed.us/r2/projects/scp/sensitivespecies/index.shtml).

Using the rating system developed by The Nature Conservancy and NatureServe, the southern redbelly dace is considered critically imperiled (S1) in Colorado (Colorado Natural Heritage Program 1999) and South Dakota (South Dakota Natural Heritage Program 2006), and imperiled (S2) in Kansas (NatureServe Explorer 2005) (**Figure 3**). Despite these ratings, the State of Colorado is the only state in Region 2 that includes the species on its state threatened/endangered species list, ranking it as endangered. A single population of southern redbelly dace has recently been discovered in South Dakota (Springman and Banks 2005). While South Dakota does not currently include this species in its official list of threatened species (Backlund personal communication 2006), the state Natural Heritage Program does classify it as a species of greatest conservation (www.sdgfp.info/wildlife/diversity/comp_plan/). The State of Kansas does not currently list this species, but Haslouer et al. (2005) have proposed it for listing as state threatened. Southern redbelly dace have never been reported in the states of Nebraska or Wyoming (Baxter and Simon 1970, Page and Burr 1991, Cross and Collins 1995).

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

The southern redbelly dace's status as an endangered species in Colorado prohibits the taking, exporting, possessing, processing, selling, delivering, transporting, or shipping of this species except for approved scientific research. This means that any use of this species, such as for fish bait or for the aquarium trade is prohibited in Colorado. In South Dakota and Kansas, the general baitfish regulations provide some protection for the species, by limiting take to licensed anglers and establishing restrictions on how many fish may be possessed and where they can be taken.

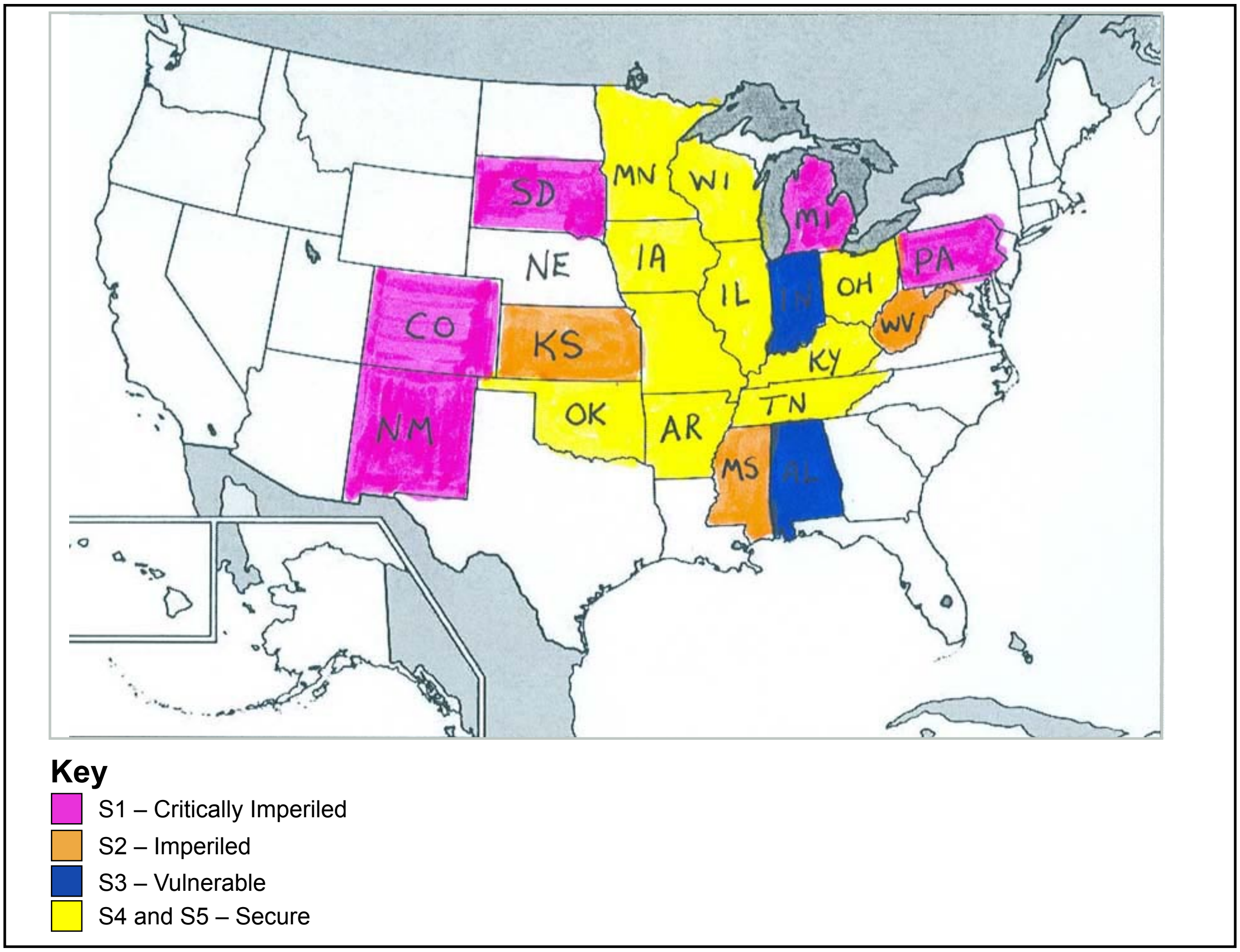


Figure 3. State conservation status for the southern redbelly dace, based on ratings from the Natural Heritage Data Base (NatureServe.org)

The State Wildlife Grants Program created through federal legislation (*Title IX, Public Law 106-553 and Title 1, Public Law 107-63*) is meant to close the funding gap by providing federal dollars for a state to use on conservation projects aimed at preventing wildlife from becoming endangered. Through this program, states develop Comprehensive Wildlife Conservation Strategy (CWCS) plans. The CWCS plans for Colorado and Kansas both include southern redbelly dace as a species in need of conservation; the CWCS for South Dakota was not available at this time. In Kansas, this species is listed under Aquatic – Western Lotic Habitat Species of Greatest Conservation Need, as Tier I (Wasson et al. 2005). Colorado lists the southern redbelly dace under Fish Species of Greatest Conservation Need (Colorado CWCS); here this minnow is covered by the State Recovery Plan and the Arkansas River Native Fish Conservation Plan. The Colorado Water Conservation Board (Department of Natural Resources) has a Water Supply Protection-Native Species Conservation Trust Fund. They proposed using $3.5 million for financing Colorado Division of Wildlife (CDOW) species conservation projects over the next ten years. The recommendations for FY 2006-07 (Blickensderfer et al. 2006) carried $400,000 for projects involving South Platte River/Arkansas River Native Species (southern redbelly dace, northern redbelly dace, lake chub, and Arkansas darter among them).

Biology and Ecology

Systematics

The southern redbelly dace is in the bony fish superclass Osteichthyes, Class Actinopterygii, Order Cypriniformes and minnow family Cyprinidae (Nelson 1994).

Samuel Rafinesque described *Chrosomus erythrogaster*, or what he called the Kentucky RedBelly, from a specimen taken from the Kentucky River (Rafinesque 1820). Edward Drinker Cope

(1867) described *C. eos* (northern redbelly dace) on the basis of specimens from the Meshoppen Creek, Sesquehanna County, Pennsylvania. He noticed the great similarity of the two species, so he included four distinguishing "peculiarities" that separated *C. eos* from *C. erythrogaster*.

Banarescu (1964), writing on the fishes of Romania, listed *Chrosomus* Rafinesque as a American subgenus of *Phoxinus*. This work was essentially a verbatim translation (from Russian) of Berg (1949), who mentioned the similarities of *Phoxinus* and *Chrosomus*. Neither of these works presented any data to support their statements, but the effect of this revision was to merge all of the American *Chrosomus* species into the European genus *Phoxinus*. In this way *Phoxinus* became the only minnow genus with species in Europe, Asia, and North America (Smith-Vaniz 1968). Legendre (1970), Mahy (1972), and Coad (1976) have studied this genus without suggesting taxonomic changes. Others, including Stasiak (1977, 1978), Settles and Hoyt (1978), Gasowska (1979), and Sublette et al. (1990), believed that *Chrosomus* should be the valid genus for North American species of this complex. Until a comprehensive study of the genetics of this entire complex is undertaken, these minnows remain in the genus *Phoxinus* (Jenkins and Starnes 1981, Howes 1985). Currently, the seven North American dace in the subgenus *Chrosomus* include the southern redbelly dace, northern redbelly dace, finescale dace (*P. neogaeus*), mountain redbelly dace (*P. oreas*), blackside dace (*P. cumberlandensis*), laurel dace (*P. saylori*), and Tennessee dace (*P. tennesseensis*) (Nelson et al. 2004).

Species description

The North American dace in the subgenus *Chrosomus* are small to medium sized (70 to 120 mm [3 to 5 inches] total length [TL]) minnows with very small scales (barely visible without magnification). The number of scales in the lateral line is usually greater than 80 (Stasiak 1977). In this genus, the pores of the lateral line organ only extend horizontally along the side from the head to about halfway to the tail fin. These dace have horizontal black bands along their sides with iridescent silvery areas above the main lateral band. Males have bright red and/or yellow bands below the black side band; these color patterns are especially vivid during the breeding seasons (Saphir 1934). While many minnows show sexual dimorphism, the morphological differences between sexes in *Chrosomus* are near the extreme for family Cyprinidae (Balinsky 1948, Pyron 1996). The bold and distinctive markings make the daces easy to recognize and they are considered among the most attractive of the native minnows (**Figure 4**).

Southern redbelly dace reach about 75 mm (3 inches) TL. Pharyngeal arches usually have a 0,5-5,0 tooth formula (Eastman 1970). This means they have only a single row of five teeth on each side of the throat. The intestine of the southern redbelly dace is long and coiled (or looped), much longer than the standard length of the fish. Pearl organs (breeding tubercles) are highly developed on the males during the spring. This species develops a unique pattern of these structures on their fins, on their sides, in front of the pectoral fins, and above the anal fin (**Figure 5**; Maas 1994).

Generally, the distributions of the southern and northern redbelly daces are mutually exclusive, but their ranges do overlap at a few locations, and here these species are syntopic (Greene 1935, Nordlie et al. 1961). Even where they are found together, however, it is fairly easy to distinguish these species. The southern redbelly dace is larger and usually has more prominent (darker and thicker) black lateral bands (**Figure 4**) while the northern redbelly dace is usually smaller and has more slender black lateral bands (Stasiak 2006). When fully colored in the spring, male southern redbelly dace often show bright red coloration on the entire ventral surface while the belly of northern redbelly dace remains white. The snout is longer and the mouth more horizontal in southern redbelly dace (Phillips 1969a). Hill and Jenssen (1968) presented additional meristic data for southern redbelly dace from a spring in Oklahoma, including scales counts.

Distribution and abundance

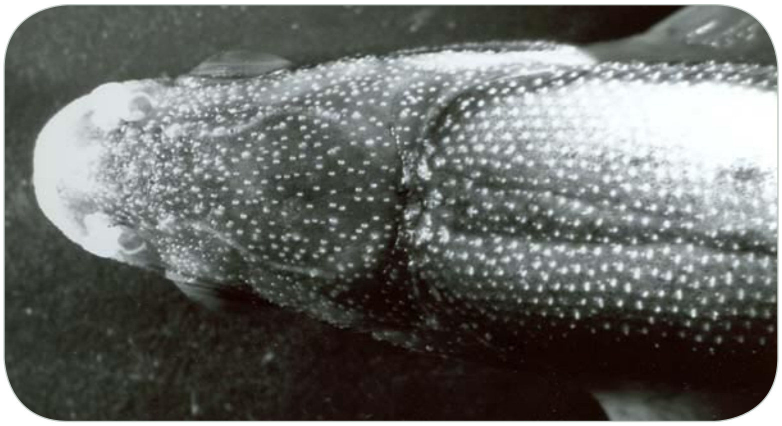
The southern redbelly dace is widely distributed throughout the Mississippi, Ohio, and Missouri River drainages in the United States (**Figure 2**; Starnes and Starnes 1980, Page and Burr 1991). This species is found entirely within the boundaries of the United States, from southern Minnesota and Wisconsin (Underhill 1957, Becker and Johnson 1970, Eddy and Surber 1974, Becker 1983, Underhill 1989) in the north, to Arkansas, southern Mississippi, and Alabama in the south (Hemphill 1957, Cook 1959, Robison and Buchanan 1988), and from western Pennsylvania (Cooper 1983) in the east, to Colorado, New Mexico, and Oklahoma in the west (Koster 1957, Woodling 1985, Gelwick and Gore 1990).

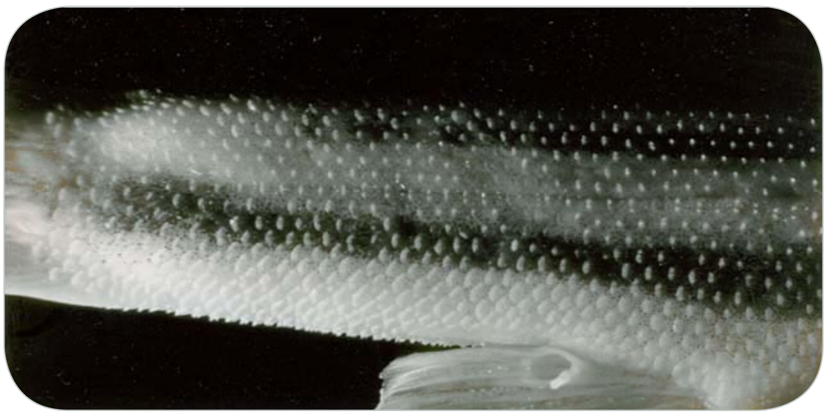
In Region 2, southern redbelly dace are restricted to rather small, scattered populations near the

Figure 4. Male (top) and female (bottom) southern redbelly dace in breeding colors. Photographs by author taken in May 1967 in southeastern Minnesota.

headwaters of tributaries to the Missouri River, forming three isolated clusters. One cluster centers in eastern South Dakota, northwestern Iowa, and southeastern Minnesota in tributaries to the Big Sioux River (Harlan et al. 1987, Hatch et al. 2003); another is found in the Kansas River tributaries in Kansas; and the third is in the headwaters of the Arkansas River in southeastern Colorado and northeastern New Mexico (**Figure 2**; Koster 1957).

The largest population of southern redbelly dace in Region 2 states occurs in the Kansas River system in the Flint Hills of Kansas (Metcalf 1966, Cross 1967, Cross and Collins 1995, Stagliano 2001). In suitable habitat here, they can be considered common (Starnes and Starnes 1980). In Colorado, populations occur in the headwaters of the Arkansas River near Pueblo and Canon City (Loeffler 1982, Woodling 1985, Fausch and Bestgen 1996). From 1979 to 1981, collections near Pueblo totaled 28 specimens, and another 112 specimens were collected between 1993 and 1996 (Nesler et al. 1999). Since then, those original populations have disappeared, while three populations in ponds at Fort Carson, the Pueblo Army Depot, and the Kinney Lake (formerly Hugo) State Wildlife Area in Lincoln County developed from translocations from those historic stocks. For two years, southern redbelly dace were transplanted (294 fish in 1997 and 200 fish in 1998) from the Fort Carson population into three additional waters in the Pueblo State Wildlife Area and Lathrop Park State Recreation Area. These populations still exist and are being monitored (Krieger 2005). Southern redbelly dace are also being raised in the CDOW hatchery facility at Alamosa, and they have been considered for stocking into small streams in the Timpas Creek and Carrizo Creek drainages in the Comanche National Grassland (Nesler et al. 1999, Kreiger 2005). Southern redbelly dace had never been





Field view of lower lateral caudal peduncle just posterior to base of anal fin; all body scales were tuberculate in this species. Number of tubercles per scale increased as a ventral and caudal progression was made.

6-8 sharp conical structures lined the distal edge of each scale in this species. Tubercles were very erect and sharp with a pointed hook or horn like tip, resembling those of the breast and pectoral fin sites. Tips were smooth and uniformly retrorse. (221X)

Figure 5. Breeding tubercles (pearl organs) of southern redbelly dace. Top: dorsal surface of head. Middle: caudal peduncle. Bottom: magnified view of scale edge from flank. (Maas 1994).

reported for the state of South Dakota (Churchill and Over 1938, Bailey and Allum 1962) until 48 specimens were collected in July 2003 in Little Beaver Creek near Canton in Lincoln County (**Figure 6**). This 3rd order stream was about 4 km (2 miles) upstream from its confluence with the Big Sioux River (Springman and Banks 2005).

Despite several state-wide surveys in Nebraska (Johnson 1942, Jones 1963, Bliss and Schainost 1972), southern redbelly dace have never been reported for this state. This is puzzling, as suitable habitat exists in headwaters of the Big Blue River in Nebraska and these fish have been collected in that same stream just across the Kansas border (Cross and Collins 1995). It is possible that Nebraska populations of southern redbelly dace could be discovered with more intensive surveys in Mission, Plum, and Wildcat Creeks in Gage County.

Population trends

In most states with southern redbelly dace, the trend appears to be that the historic range is shrinking (**Figure 7**). For example, Trautman (1981) stated that between 1955 and 1980, Ohio populations of dace known to be present before 1950 became extirpated as the streams were disturbed by channelization, ditching, tree removal along stream banks, and/or increased turbidity. Records over the past century indicate a significant decrease in the range of this species in Kansas (**Figure 7**; Cross 1970, Clay 1975, Cross and Moss 1978, Cross et al. 1986, Haslouer et al. 2005). Although this population center in north-central Kansas the largest and most stable in the region, is the species still is listed in category S2 in the Natural History Data base (**Figure 3**, NatureServe.org, Kansasfish.com). The population centered in the corners of South Dakota, Minnesota, and Iowa is fairly stable, but of limited size (Hatch et al. 2003). The Colorado and New Mexico populations are very restricted and probably represent the last remaining refuges where the species has become isolated (Koster 1957, Loeffler 1982). At least one population near Pueblo, Colorado has disappeared in recent time (Nesler et al. 1999).

Within Region 2, southern redbelly dace are found in the headwaters of low-order streams and in areas of groundwater seepage (Stagliano 2001). The

Figure 6. This male southern redbelly dace represents one of 48 specimens collected in July 2003 from Little Beaver Creek in Lincoln County, South Dakota. This is the first reported population of this species in South Dakota. Photograph courtesy of Deborah Springman.

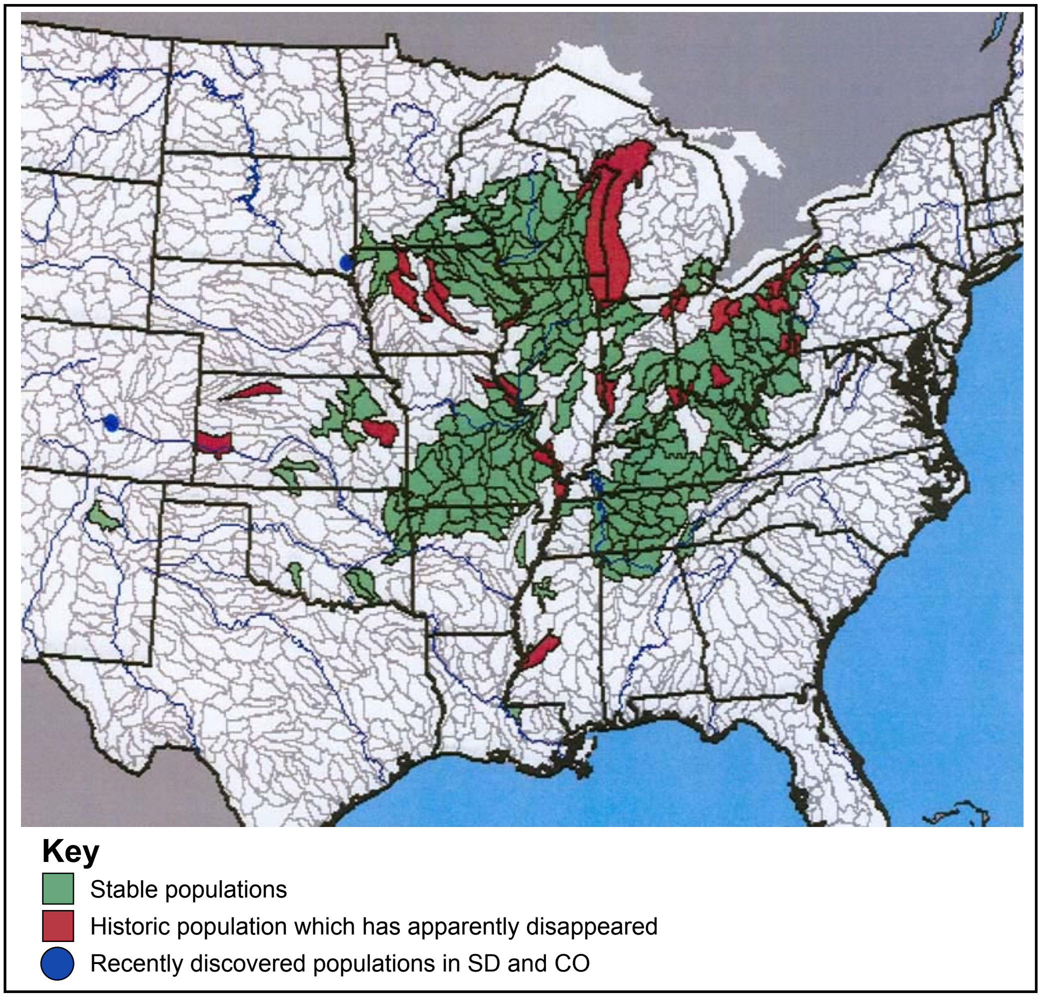


Figure 7. Historic distributional changes for southern redbelly dace. (Modified from NatureServe .org).

cold water provided by these water sources enables the dace to persist under conditions much more similar to the conditions that prevailed thousands of years ago when the southern edge of the glacial shield was much closer to this region (McPhail 1963, Sherrod 1963, Cross 1970, Cross et al. 1986). The warming and drying of the Great Plains region following retreat of the last ice age has led to the natural reduction in suitable habitat for this species (Woodhouse and Overpeck 1998). Human activity that leads to reduction in cold springs or seeps would likely greatly accelerate downward trends in populations. Although populations of southern redbelly dace may be widely scattered, they may still be common or even abundant where preferred habitat exists in adequate quantity and quality (Miller and Robison 1973, Starnes and Starnes 1980).

Activity patterns

Little is known of the activity patterns of the southern redbelly dace. This schooling species prefers the cover of undercut banks and mats of vegetation in clear streams and pools. Occasionally, they can be found in faster current flows in runs and riffles of larger streams (Miller and Robison 1973). This presumably is in conjunction with spawning or feeding on algae-covered rocks. The schooling instinct is strong in this species, and in the presence of predation threats, southern redbelly dace have been reported to form compact shoals in mid-water rather than to scatter and hide (Becker 1983). Phillips (1968) reported that feeding activity was more pronounced during daylight than at night.

Habitat

Southern redbelly dace have a strong habitat preference for sluggish headwaters and upland creeks (usually spring-fed) with vegetation and woody debris (Cross 1967, Cross and Collins 1995). The water is generally clear, and the substrate is sand or gravel (Smith 1908, Forbes and Richardson 1920). Pflieger

(1975) listed Missouri habitat as "small creeks and spring branches having a permanent flow of clear, cool water and silt-free gravelly bottoms. In larger creeks and rivers it occurs only as strays or as highly localized populations in spring pools away from the main channel." Mettee et al. (1996) stated that this species is "frequently found in small pools 1 to 3 feet deep and is often associated with aquatic vegetation." Smith (1979) stated that "schools of dace are often found under bank overhangs among tree roots, especially in clear pools with a muck bottom."

Six sites with southern redbelly dace populations in Mississippi were characterized as narrow, meandering streams with gravel, pebble, and sand substrate, and slow-flowing pools with clear water, and steep banks (Slack et al. 1997). Clear water (with little or no turbidity) is necessary for the sight-feeding dace to find their food and mates. Dissolved organic material can often stain the water a reddish or tea color, but this "dark" water is still transparent. Becker (1983) listed the following percent frequencies for substrate composition where southern redbelly dace were found: gravel 27 percent, rubble 21 percent, silt 19 percent, sand 10 percent, mud 6 percent, boulders 6 percent, clay 5 percent, and bedrock 5 percent. Unlike northern redbelly and finescale dace, southern redbelly dace are often found in mid-channel of moderate-sized (third-order) streams in areas of higher current velocities. Apparently, southern redbelly dace do not occur in ponds or lakes unless they have a connection to a lotic system.

Food and feeding habits

Several studies have indicated that southern redbelly dace are herbivores or omnivores, feeding on small plants and animals (Forbes 1883, Forbes and Richardson 1920, Cahn 1927, Rimsky-Korsakoff 1930, Raney 1969, Reason 1973, Settles and Hoyt 1976, Smith 1979, Becker 1983). As adults, they are primarily sight-feeding particle feeders, selecting relatively small individual items. Phillips (1969b) described their feeding behavior as sucking or nipping slime from rocks, and eating diatoms, other algae, and small invertebrates. He thought they would ingest small detritus or any particles they could find. Etnier and Starnes (1993) described their feeding as opportunistic, including whatever small invertebrates might be present.

Hubbs and Cooper (1936) included the southern redbelly dace as an example of herbivorous or omnivorous minnow species; they characterized these fish as having a long intestine and fine throat teeth. Compared to the other species of *Phoxinus* occurring in Region 2 (finescale dace and northern redbelly dace), the southern redbelly dace has the longest and most severely looped intestine (Miller and Robison 1973, Stasiak 1977, Becker 1983, Cochran et al. 1988). Keast and Webb (1966) described the relationship between the head morphology and feeding preferences of fishes. According to this configuration, redbelly dace should be feeding on small discrete items, as the small and thin pharyngeal teeth (Eastman 1970) of this species are not well-suited for preying on large or hard animal material. All of these studies are consistent with a diet of vegetation and small invertebrates.

Breeding biology

Sexual dimorphism plays a vital role in the reproductive biology of all the North American *Phoxinus*. Female southern redbelly dace usually do not display much of the red and yellow sides and bellies of the breeding males (**Figure 4**). Males attain very bright red and yellow pigmentation on the lateral and ventral portions of the body during the spring; this pattern is obvious even before spawning and is retained to some extent throughout the entire year (Saphir 1934). Males also have fins that are proportionally larger than the same fins of the females; this is especially obvious for the large, paddle-shaped pectoral fins (Phillips 1969a). Cyprinid males have a distinctive pattern of pearl organs (breeding tubercles). These nuptial tubercles develop on the males of most species of cyprinids, and they are usually species-specific in number, size, structure, and location (Reighard 1903, Wiley and Collette 1970, Collette 1977). Southern redbelly dace males have rows of tubercles in front of the pectoral fins, above the anal fin, and on the rays of the paired fins and anal fin (Maas 1994). The colors of the males, the large fins, and the breeding tubercles are all used to stimulate the release of eggs by the females. Spawning occurs in groups of males with single or multiple females; the large pectoral fin of males is used to hold and guide the females into substrate.

Spawning of southern redbelly dace has been described by Smith (1908), Settles and Hoyt (1976, 1978), and Becker (1983) as follows:

> The brilliantly colored males congregate over the spawning area (usually a riffle or gravel bed) with the females staged in the run below. The female darts up into the spawning area, where she is accompanied by two or more males at her side. Males cradle the female with the pectoral fins and caudal peduncle region, which are

heavily endowed with pearl organs; this helps them maintain contact with the female and press her against the substrate. The spawning fish vibrate vigorously, and eggs get buried in the sand or gravel as they are fertilized. This act only lasts for a few seconds and can be repeated many times per hour.

Mature ova ranged from 0.75 mm to 1.44 mm in these studies. Settles and Hoyt (1978) reported an inverse relationship between the standard length of the females and the size of the mature ova. Mean fecundities (number of mature ova) were 267, 401, and 568 for age groups 0, I, and II respectively. Becker (1983) found females in Wisconsin generally produced between 500 and 1,000 eggs; a 68 mm (2 ¾ inch) standard length fish with ovaries 24 percent of the body weight produced 1,020 mature eggs. Phillips (1969c) counted all the ova (even very immature) in the ovaries and obtained a range of 5,000 to 18,888. This count was probably more indicative of the lifetime potential egg production. Laboratory studies report eggs hatch in six days at 20 °C (Sternburg 1992).

Based on field observations and gonosomatic indices, older southern redbelly dace constitute the main reproductive effort in April and May. Some large but mostly younger fish may continue to spawn in shorter and less intensive episodes well into July in some populations. This produces young of the year of varying sizes, depending upon date of hatching.

This breeding behavior is very similar to that described for the northern redbelly dace (Hubbs and Cooper 1936) and the finescale dace (Stasiak 1972, 1978, 2006). The major difference appears to be the southern redbelly dace's preference to spawn in or above clean gravel (in a moderate current) rather than in vegetation (Sternburg 1992). At times, southern redbelly dace have been observed spawning over the top of gravel nests constructed by other minnow species, such as creek chub (*Semotilus atromaculatus*), common shiner (*Luxilus cornutus*), hornyhead chub (*Nocomis biguttatus*), stoneroller (*Campostoma anomalum*), or blacknose dace (*Rhinichthys atratulus*). Hybrids between southern redbelly dace and these species are often the result of this accidental co-mingling of gametes (Raney 1947, Robison and Miller 1972, Greenfield et al. 1973, Grady and Cashner 1988).

Demography

Genetic characteristics and concerns

To date, few genetic studies of southern redbelly dace have been reported. Just as for the other American *Phoxinus* that have been studied, this species has 50 chromosomes in the diploid (2n) condition. Gido and Reeck (2005) at Kansas State are beginning a study of the Heat Shock Proteins (HSP) using quantitative genetic and proteomic approaches. These HSPs are known to play a role in the stress response and thermal tolerance in fishes (Scott 1987).

A priority research need in Region 2 is a population genetics study similar to what was performed for northern plains killifish (*Fundulus kansae*) by Kreiser et al. (2001). They examined the geographic pattern of genetic variation using allozyme loci, mitochondrial DNA restriction fragment length polymorphisms (RFLPs) and the sequencing of the mitochondrial cytochrome oxidase to help understand the roles of dispersal and vicariance. Based upon this study, the northern plains killifish (*F. kansae*) was split into a new species from the plains killifish (*F. zebrinus*). Microarray and microsatellite analysis might also prove useful in this type of study (Billington and Hebert 1991). Because the southern redbelly dace demes in Region 2 occur as widely scattered and isolated entities (**Figure 2**), they may very well each represent a unique evolutionary unit (Beachum et al. 2002). In Region 2, three different populations are located hundreds of river miles from the next closest population (**Figure 2**).

Genetic information takes on additional importance as redbelly dace are being raised in a hatchery facility in Alamosa, Colorado, and consideration is being given to transplanting fish back into wild populations. Normally, it is desirable to maximize the variation and heterozygosity of hatchery-reared fish (Minckley et al. 1989), but in this situation, introducing novel genes may prove damaging to a well-adapted deme. Thus, genetic information would have great significance for conservation, and its current absence represents one of the most important information needs for this species.

Life history characteristics

Age and growth of southern redbelly dace have been recorded by Smith (1908), Phillips (1969a), Reason

(1973), Settles and Hoyt (1976, 1978), and Becker (1983). These studies were the basis for the information summarized as follows. Specimens less than 40 mm (1.5 inches) TL are considered immature, and the sexes are very difficult to distinguish. Most southern redbelly dace attain sexual maturity at age 1, at approximately 50 mm TL (for most fish this is during June in the year after their birth). All 2 and 3 year fish are mature, and few if any individuals survive to 4 years. Unlike the closely related northern redbelly and finescale daces, southern redbelly dace females average slightly smaller than the males, with fish reaching a maximum TL of about 75 mm (3 inches). Where specimens have been collected at spawning locations, males outnumbered females by as much as 6 to 1; in the population as a whole, however, the sex ratio is approximately even. Age 1 fish were observed to be the most numerous in the population and at the spawning sites. Their importance to the overall reproductive effort is apparent from the Life Cycle Matrix (**Appendix**).

Ecological influences on survival and reproduction

Adapting to the environment involves many ecological factors including predators, parasites, disease, food abundance, and competition. Abiotic stressors, such as drought, temperatures, water quality, and habitat availability are important factors controlling reproductive success. Some of these factors are likely to affect different ages and sizes and even sexes of dace unequally. Southern redbelly dace in the Great Plains are restricted to relatively small regions where the entire suite of ecological conditions remains similar to the cooler and wetter conditions that prevailed several thousand years ago (Bleed and Flowerday 1989, Woodhouse and Overpeck 1998). Suitable habitat for this species has been undergoing a natural contraction as the climate has become warmer and more arid (McPhail 1963, Cross 1970, Cross et al. 1986, Cross and Moss 1987). An envirogram developed for this species (**Figure 8**) shows the inter-relationships of ecological factors affecting the species. In this region, the most critical ecological factors are probably a constant flow of cool groundwater, clear unpolluted water, clean gravel substrate, and an unaltered fish community (Becker 1983). The quality of the water supply (i.e., temperature, oxygen, clarity) is important to maintain the proper ranges for spawning and feeding, while a suitable fish community allows the dace to survive in its niche without undue competition and predation.

Social pattern for spacing

Southern redbelly dace do not display territorial behavior, nor do they defend nests or feeding areas. Adult fish are usually observed in tight shoals comprised of individuals of mixed sizes and ages.

Patterns of dispersal

Few studies have dealt directly with dispersal of either young or adult southern redbelly dace. Personal observations indicated that newly hatched fish are usually restricted to areas of heavy cover and reduced current. This is important to reduce predation and to provide the habitat and substrate used by plankton, one of their main food sources at that age. As the fish reach age 1, they become stronger swimmers and gradually move out into more open water. Schools of adult fish are generally mixed with respect to age and size. Flooding and periods of high water are the prime dispersal agents, carrying fish, especially young fish, to downstream areas (Bertrand and Gido 2004). This is an example of an r-selected species, one capable of rapid recolonization when conditions are suitable. Adult fish in streams probably move upstream. They prefer cool springs or seeps with undercut banks, heavy cover, and clear water, conditions that are more likely near the headwaters of low-order streams. Because activity and dispersal patterns have not been studied for the small populations found in most sites in Region 2, this basic life history component should be identified as one of the information needs.

Spatial characteristics of populations

Since the populations of southern redbelly dace are usually restricted to areas of spring seeps, they tend to be found near the headwaters of small streams. The habitat found in large rivers is not suitable for this species, and thus acts as a barrier preventing much contact between dace populations. They can probably be dispersed at times of flooding and high water conditions, but these events have become reduced in the centuries as climate has changed since the last glacial retreat from the Great Plains Region (Woodhouse and Overpeck 1998) and water development projects have altered natural flow patters. Periodic drought conditions on the Great Plains also undoubtedly diminish suitable habitat for these fish. Demes have become reduced and isolated from each other and from populations comprising the main range of this species to the east. The result is

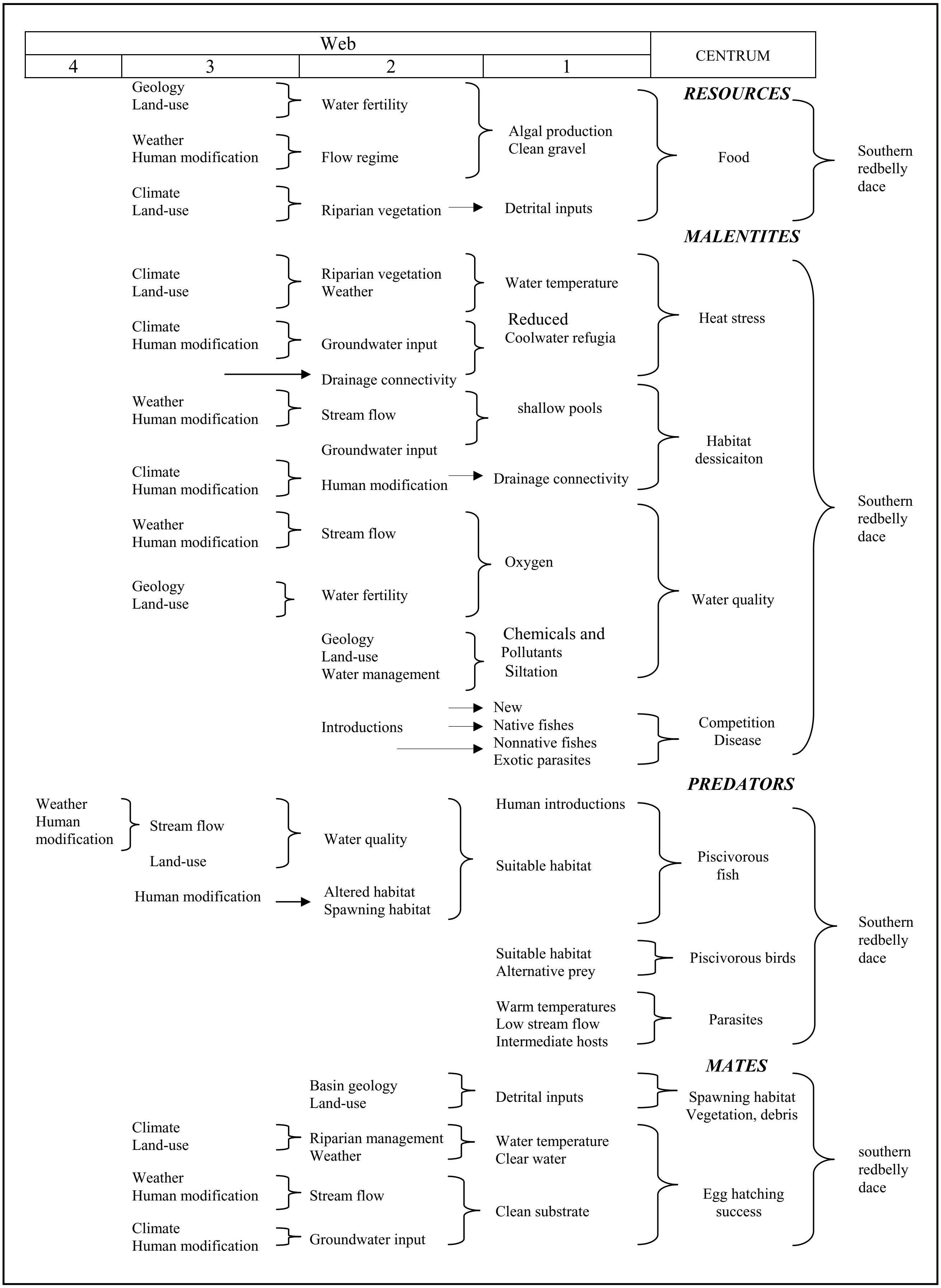


Figure 8. Envirogram for the southern redbelly dace.

little genetic exchange between populations within this region. Population genetics of these isolated populations are hereby identified as perhaps one of the most critical of the future needs assessment in Region 2.

Limiting factors

As with most uncommon fishes, the main factor limiting southern redbelly dace populations in this region is availability of suitable habitat (Andrewartha and Birch 1984). The optimal habitat for these dace is clear-water areas fed by groundwater; heavy vegetation, brush, or undercut banks would be present; and substrate would be sand or gravel. Water flow should be moderate and stable throughout the year, and the natural assemblage of fish species should be present, with few (if any) non-native or large predatory fish species present. As the Great Plains have gradually become warmer and drier over the centuries, conditions have naturally become less suitable for this dace species (McPhail 1963, Cross and Moss 1987, Matthews and Matthews-Marsh 2003), leading to reduced and isolated pockets of spring flows.

Human activities, as they relate to aquatic resources, have accelerated this natural reduction in available habitat. Since the settlement of this region over perhaps the past 150 years, permanent sources of cool, clear groundwater have become highly desired resources for human uses. Much of it is pumped for irrigation or used for domestic or municipal water supplies; in many places, spring seeps have been dammed to form relatively large lakes. Streams have been ditched and channelized, and water control structures and culverts have been constructed. Agricultural practices and construction activities have resulted in increased erosion, siltation, and pollution. Chemicals from pesticides, fertilizers, and artificial hormones have been directly and inadvertently added to streams. Often, the remaining relatively natural small streams have been stocked with "sport species" of large predatory fishes (i.e., trout, pike, bass, or sunfishes) that tend to reduce dace populations (He and Kitchell 1990). Non-native fishes (e.g., mosquitofish) have been stocked in the guise of reducing insect pests (Lynch 1988).

Community ecology

Predators

All classes of vertebrates have aquatic predators capable of feeding directly on southern redbelly dace. Under natural conditions, the main vertebrate predators of northern redbelly dace are probably piscivorous birds (Steinmetz et al. 2003). Belted kingfisher (*Megaceryle alcyon*) and great blue heron (*Ardea herodias*) have been observed actively feeding on schools of the related northern redbelly and finescale dace (Stasiak 1972, Wisenden and Barbour 2004). Kingfishers are especially attracted to habitat favored by the dace; the clear, shallow water and brightly colored minnows provide easy prey for this bird (Hamas 1994). This author has seen kingfishers perch on dead trees in beaver ponds and use them as platforms to dive into schools of dace. Cormorants, loons, and several species of heron also prey upon these minnows.

Carnivorous aquatic invertebrates can also feed heavily on dace (Borror and White 1970). Predacious diving beetles of the family Dytiscidae (larvae are commonly called water tigers) and giant water bugs of the family Belostomatidae (Bobb 1974) were frequently found eating dace of all sizes in Minnesota beaver ponds (Stasiak 1972). These voracious insects can reach 70 mm (2.75 inches) in length and commonly eat aquatic vertebrates such as frogs and tadpoles, snakes, and fishes (Hungerford 1920, McCafferty 1998). Other insects such as dragonfly larvae (Odonata) and smaller bugs (Hemipetra) like water scorpions and backswimmers may also include dace, especially young individuals, in their diet. These insects would be most common in areas of reduced current and heavy cover, where they act as ambush predators.

Some of the fish species that are often associated with southern redbelly dace can occasionally prey on them. Where they have access to deeper pools, sight-feeding predatory fishes such as bass, sunfish, and trout prey upon dace. When they occur together, large creek chubs are very capable of eating small dace (Gilliam et al. 1989). These naturally occurring fish predators play a role in eating very young dace, but their overall effect is probably small compared to the collective effect of predatory insects. Introduced species of large predatory fishes (sport fishes) may have a serious effect on dace because they eat even the largest adults. He and Kitchell (1990) introduced northern pike into a small lake containing the closely related northern redbelly and finescale dace; within weeks there was a significant reduction in the biomass and average size of the dace. The dace also altered their normal activity pattern to try to avoid predation. Dace species are considered the most vulnerable of the minnows. Rahel (1984) reported that *Phoxinus* minnows were absent from bodies of water that contained northern pike and piscivorous centrarchids. The colorful dace species are known to be very attractive as food for game fish. In some regions, southern redbelly dace are used as bait minnows (Becker 1983) and are even advertised for sale online.

Fish-eating snakes and turtles, as well as bullfrogs and salamanders are common predators in pools and streams where dace occur. Mink (*Mustela vison*), martens (*Martes americana*), and raccoons (*Procyon lotor*) will undoubtedly eat southern redbelly dace.

One defense present to some extent in all minnows is the chemical alarm cue. Specialized epidermal cells release this alarm substance (*Schreckstoff*) when the skin is damaged during a predatory attack. The ability to detect and react to this substance has been shown to be acute in northern redbelly dace (Wisenden and Barbour 2004), and it is a sense likely to be well-developed in southern redbelly dace as well. Becker (1983) observed that this species responds to predators by forming a dense shoal in mid-water, as opposed to darting individually into cover. Shoals of this type afford individual fish increased protection from predators, but this behavior makes them especially vulnerable to human collectors with nets.

Competitors

Southern redbelly dace are lively fish that inhabit clear pools and riffles in small to medium-sized streams. They spawn over gravel and feed primarily on algae and small invertebrates associated with the substrate. In these habitats, they are often described as abundant, one of the dominant fish species (Pflieger 1975, Gelwick and Gore 1990, Etnier and Starnes 1993).

Southern redbelly dace are often associated with a regularly occurring small group of other fishes. For example, Slack et al. (1997) found that five species comprised 95 percent of the total number of individuals collected at dace sites. In this Mississippi study, these fishes (in addition to dace) were creek chub, central stoneroller, bluntnose minnow (*Pimephales notatus*), and redfin darter (*Etheostoma whipplei*). In other locations and regions, fishes commonly associated with southern redbelly dace include white sucker (*Catostomus commersoni*), hogsucker (*Hypentilium nigricans*), hornyhead chub, longnose dace (*Rhinichthys cataractae*), blacknose dace, suckermouth minnow (*Phenacobius mirabilis*), common shiner, johnny darter (*Etheostoma nigrum*), rainbow darter (*E. caeruleum*), fantail darter (*E. flabellare*), and bigmouth shiner (*Notropis dorsalis*) (Reason 1973, Settles and Hoyt 1978, Becker 1983). Combinations of these fishes usually represent a well-balanced fish community of small species that can successfully partition the resources available in a relatively confined habitat. Notice that very few strictly piscivorous fishes are part of this community.

Of the minnow species often found with southern redbelly dace, stonerollers and bluntnose minnows probably have the most similar diets. Stonerollers graze on algae growing on rocks at the bottom of streams, and bluntnose minnows eat detritus and small particulate items from the water column. Slack et al. (1997) found that increased standardized abundance of southern redbelly dace was inversely related to abundances of stonerollers and bluntnose minnows, and was highest in absence of those species. They concluded that competition exists between these species, yet they still often co-exist.

Creek chubs are a common associate found in such mixed communities. They are large predatory minnows very capable of eating young dace, as well as large insects. Although they may consume smaller southern redbelly dace, they do not appear to negatively affect dace populations. Occasionally, a small number of larger predators, such as bass, sunfish, or trout, can be present in the fish assemblage (Becker 1983). These are usually small individuals, and dace appear to survive as long as there are not many large predators present. When larger individuals of predatory fish species are introduced into these relatively small and confined habitats, they become direct and important predators on adult dace.

Parasites and disease

Most species of native minnows are parasitized by various protozoans, flatworms (monogenes, trematodes and cestodes), roundworms (nematodes), spiny-headed worms (acanthocephalans), and crustaceans (Hoffman 1970, Schell 1970). Published accounts of the parasites of southern redbelly dace are lacking, but it is probably safe to assume that southern redbelly dace harbor parasites similar to those found on their closest relatives.

The only studies of parasites of *Phoxinus* appear to be Bangham and Venard (1946), Hoffman (1970), Stasiak (1972), Mayes (1976), and Marcoliese et al. (2001). Hoffman (1970) listed three species of protozoans and two species of larval trematodes (*Uvulifer ambloplites* and *Echinochamus donaldsoni*). Marcoliese et al. (2001) listed parasites for the closely related northern redbelly dace. These covered eight taxa, including two monogeneans on the gills, three digenean trematodes in the viscera, a nematode, a myxozoan, and a parasitic copepod on the gills. Encysted trematode flukes are often referred to as "black grub" or "neascus"; the adult is very common as a parasite of the throat of fish-eating birds. The metacercariae are common as tiny black cysts in the skin and muscles of virtually all species of freshwater fishes that are found in shallow water with vegetation. It is common throughout the Midwest to see sport fishes such as pike, bass, perch, and sunfish practically covered with these small black spots. *Phoxinus* species in general appear to be only rarely afflicted with external parasites. Phillips (1968) attributed this to the habit of dace swimming actively in mid-water, thus escaping the swimming cercaria released by snails. The very small scales of *Phoxinus* may also provide good protection from this parasite that actively penetrates through the skin. Personal observations of dace in Minnesota and Nebraska reveal that *Phoxinus* are usually free of other common ectoparasites (such as the "anchor worm" copepod *Lernaea*), which is common in syntopic fishes.

Mayes (1976) described some new species of monogene flukes from the gills of dace collected in Nebraska. Some species of these small worms likely infect southern redbelly dace. The microscopic monogene gill parasites usually do not affect the host fish under normal conditions.

While it appears that parasites and disease do not pose serious threats to southern redbelly dace under normal conditions, this is another ecological study that needs to be carried out as a current information gap for Region 2. There is also the possibility that exotic species of minnow parasites could be carried into the dace populations through introduced fish species.

Conservation

Potential Threats

Populations of southern redbelly dace throughout all but the center of its main range appear to be declining (**Figure 7**; Clay 1975, Trautman 1981, Cross and Collins 1995, Slack et al. 1997, Dodds et al. 2004, NatureServe.org 2006). As is the case for most aquatic organisms, these declines can primarily be attributed to changes in habitat (Warren and Burr 1994, Naiman and Turner 2000). Some habitat changes are a consequence of climatic shift to warmer and drier conditions throughout the Great Plains (McPhail 1963, Cross 1970, Andrewartha and Birch 1984, Briggs 1986, Cross and Moss 1987, Bleed and Flowerday 1989, Jackson and Mandrak 2002). Human activities that alter either the physical or biotic environment then exacerbate the situation (Rapport and Whitford 1999). The following potential threats could jeopardize southern redbelly dace populations:

- ❖ reduction in water flow
- ❖ change in water quality
- ❖ physical modification of stream
- ❖ introduction of non-native species
- ❖ collection for bait or as aquarium fishes
- ❖ loss of genetic integrity.

Reductions in the amount of water in stream systems is an important factor affecting southern redbelly dace populations (Bunn and Arthington 2002). This species requires a rather constant flow of cool water, usually associated with springs, that produces a moderate current and provides clean gravel or pebble substrate. Water withdrawals (both in-stream and from nearby wells) for irrigation or municipal uses can lower flows enough to adversely affect dace habitat (Winston et al. 1991, Mammolitti 2002).

Changes in water quality

Land uses in riparian zones (e.g., crop production, cattle grazing, lumbering, mining, construction) can lead to erosion and siltation (Berkman and Rabeni 1987, Belsky et al. 1999, Gresswell 1999, Jones et al. 2000, Marcogliese et al. 2001, Schrank et a. 2001). Southern redbelly dace require clean gravel substrates for spawning habitat and feeding. Increased turbidity interferes with their reproductive behavior, which depends on recognizing the brilliant color patterns of potential mates (Rieman and Clayton 1997).

Pollution can add many harmful chemicals, including, but not limited to, fertilizers, pesticides, and artificial hormones. Where local land use, especially in the riparian zone, allows crop production and cattle operations, there is danger of increasing amounts of nitrates, phosphates, ammonia, herbicides, and pesticides being released into the watershed. High levels of selenium have been reported in parts of the Arkansas River (Colorado CWCS 2005). Southern redbelly dace are apparently quite sensitive to these changes in water quality (Ward and Irwin 1961, Stagliano 2001). A problem that is just recently gathering attention is the increase in levels of chemicals that can mimic or inhibit estrogens and/or androgens in their effects on fishes and other aquatic animals (Arcand-Hoy and Benson 1998, Ankley et al. 2003). Many of these aquatic species have males that are becoming "feminized", altering their ability to reproduce effectively (Soto et al. 2004, Spano et al. 2004, Alvarez and Fuiman 2005). While this has not been studied directly with respect to southern redbelly dace, endocrine disrupters of this type would probably be especially serious to this species since it depends on marked sexual dimorphisms for proper breeding behavior. This is an area that requires more direct research.

Physical modification of stream

Physical modifications to the stream may also have a harmful effect on southern redbelly dace (Poff and Allan 1995). These may take many forms, such as dams, water control structures, channel straightening, levees, culverts, and ditches and can change the environment into a habitat completely incompatible for this species (Winston et al. 1991). These dace, for example, do not survive well in reservoirs (Mammoliti 2002) and they require a stable, moderate current to provide clean gravel for spawning and oxygen for their buried eggs. Stream-modifying structures also can act as barriers to migration and dispersal, result in changes in channel morphology, and lead to more isolation and fragmentation of the populations (Schlosser and Angermeier 1995, Schrank et al. 2001).

Introduction of non-native species

Invasive non-native species can have a major impact on specialized species, such as these dace (Moyle and Vondracek 1985, Ault and White 1994, Bernot and Whittinghill 2006). This can be due to competition, predation, changes in behavior, or adding new diseases and parasites (Jackson 2002). Moreover, studies indicate that non-native species disrupt drainage network connectivity across the landscape, creating barriers ("dead zones" of unsuitable conditions) to fish migration and affecting recolonization (Minckley and Deacon 1991, Poff and Allan 1995, Fausch and Bestgen 1996) and genetic material exchange. Studies in the region have clearly demonstrated the profound effect that non-native predator fish have on cyprinid communities (He and Kitchell 1990, Findley et al. 2000, MacRae and Jackson 2001). Rahel (1984) and Jackson (2002) identified a set of species (*Phoxinus* among them) as being highly vulnerable to centrarchid (sunfish family) predation.

Another consequence of fish introductions is the effect of potential pathogen or parasite transfer from non-native fish species to the native fish community or other biota within the watershed (Kiesecker et al. 2001). Shields (2004) documented several cases of parasite (nematodes, trematodes, cestodes) transfer from introduced fishes in Oregon, resulting in severe population reductions in native fishes. Although relatively understudied, pathogen transfer among different aquatic taxa may represent an undiagnosed perturbation within aquatic ecosystems that induces stress to a set or sets of aquatic organisms, ultimately affecting survivorship, recruitment, and persistence of these species. Moreover, the introduction of non-native species could alter native aquatic community assemblage patterns, possibly affecting native host-pathogen dynamics (Kiesecker et al. 2001). Thus, mosquitofish or large predatory sportfish such as bass or trout will very likely reduce populations of redbelly dace.

Collection for bait or as aquarium fishes

Southern redbelly dace are desirable minnows for use as bait, and they are a popular species with the aquarium trade (Rice 2006). Occurring in clear water streams, these colorful and active fish are easily observed in mid-channel pools and riffles. At times, they concentrate in spawning areas and have the behavior of gathering into a compact shoal when faced with predation danger. All of these factors make them very susceptible to collection by humans, and since they often are confined to rather small portions of streams, it is easy for a large proportion of the population to be removed this way. For example, Trautman (1957, 1981) observed that in just a few hours, two commercial bait dealers could capture 75 percent of the dace population in a half-mile long segment of a stream. He noted that in streams that were frequently seined, dace populations were very low, even in those brooks with ideal habitat conditions. He further stated, "It was only when visiting a brook protected from seiners and having much suitable habitat, that one realized how numerous this species could be, and how abundant it must have been formerly."

Loss of genetic integrity

Southern redbelly dace in Region 2 are restricted to populations that have been isolated from the main range of this species for a very long time, perhaps several hundred to thousands of years (Cross et al. 1986, Woodhouse and Overpeck 1998, Matthews and Marsh-Matthews 2003). The Colorado southern redbelly dace population is a good example. This period in isolation may easily have allowed these fish to become unique evolutionary units (demes, races, subspecies, true species). This is classic "island biogeography" (Hanfling and Brandl 1998). The danger in these cases is the temptation to add new individuals from other populations, and thus change the genetic make up of what might represent a naturally well-adapted deme (Meffe 1986, Vrijenhoek 1998). Population genetics of isolated groups must be understood before new fish from outside sources are added (Billington and Hebert 1991, Bryant et al. 1999, Watts et al. 2006).

A significant but little studied element in the long-term viability of headwater fish species is the synergistic effects of multiple stressors. Extended severe drought by itself may have only modest effects on the long-term viability of fish assemblages (Matthews and Marsh-Matthews 2003). However, groundwater pumping, irrigation, water diversion, dams, culverts, non-native species, siltation, and chemical pollution combined with extreme disturbance events such as long-term drought may severely deplete a population or extirpate a species on regional basis. Given the already highly fragmented distribution of southern redbelly dace within the Region 2, these combined forces would adversely affect this species.

Conservation Status of Southern Redbelly Dace in Region 2

Although the southern redbelly dace is not considered critically imperiled in most of its range in the Mississippi and Ohio River drainages, historic records indicate a shrinking of the distribution at the margins (**Figure 7**). Declines in dace populations appear to be correlated primarily with changes in land use and habitat alteration. This is especially true for populations in tributaries to the Missouri River in the western portion of its range, where it has always been restricted to rather small areas of clear-flowing, spring-fed streams near the headwaters (**Figure 2**). It can be considered a sensitive species in this region because it is a defining component of the assemblage of fishes that is highly and uniquely adapted to this particular habitat.

The area occupied by southern redbelly dace in states comprising Region 2 is very limited (**Figure 2**). In all three of the states in which this species is found in the region, it is considered a species of greatest conservation concern by the state Comprehensive Wildlife Conservation Strategy plan and listed as S1 or S2 by the Natural Heritage Database (NatureServe.org) (**Figure 3**). Of the Region 2 dace populations, only those found in Kansas might be considered locally common in streams flowing into the Kansas River. Even in this state, several populations peripheral to the core range have declined or disappeared in the past 50 years (Cross 1967, Cross and Moss 1987, Cross and Collins 1995, Haslouer et al. 2005). Southern redbelly dace persist in Kansas primarily in the Flint Hills region, where land use has maintained the virgin prairie and the natural hydrology has been preserved. The primary conservation efforts here would be monitoring the dace populations, protecting against invasive species, and minimizing the fish exposure to toxic chemicals and hormones. Although all three Region 2 states that have southern redbelly dace populations currently designate it at high levels of conservation concern, the species remains vulnerable to extirpation by hydrologic modification of stream systems, presence of non-native species, and various pollutants.

Potential Management of Southern Redbelly Dace in Region 2

Implications and potential conservation elements

Although the southern redbelly dace has not been reported from any National Forest System lands in Region 2, a significant opportunity for conserving the southern redbelly dace in the region may center around the Colorado population distribution in the headwaters of the Arkansas River. Transplanted populations of southern redbelly dace have become established at Fort Carson, the Pueblo Army Depot, and Kinney Lake (Hugo) State Wildlife Area (Kreiger 2006). Certain springs and streams in the Comanche National Grassland have been identified as having habitat suitable for possible translocation of southern redbelly dace (Nesler et al. 1999).

The CDOW has already developed a CWCS plan that includes southern redbelly dace under fish species in greatest need for conservation. This plan lists southern redbelly dace as having a low but stable population in Colorado, and the USFS is one of many agency partners in this plan. Many of the threats they address are the same as discussed in the Potential Threats section of this report. In addition to the activities previously mentioned for the Kansas population, additional conservation actions might include:

- leasing/buying land or water rights
- conserving water and managing water flows to restore natural flow
- acquiring conservation easements.
- identifying and isolating non-point source pollution.
- monitoring and controlling riparian land use (overgrazing) and creating buffer strips
- removing or notching stream barriers
- maintaining genetic databases in conjunction with transplantations.

Conservation of this dace species will require resource managers to consider the unique habitat features that this species utilizes across a mosaic of heterogeneous shifting habitats that are highly dynamic in space and time (Masters et al. 1998). Thus, the management of southern redbelly dace should focus on conserving natural system processes and native fish assemblages in streams and preventing and controlling non-native species introductions (**Table 1**). Resource managers will need to focus their conservation management efforts beyond individual pools to the larger landscape matrix. Terrestrial characteristics across the land-water template within a drainage unit will affect the hydrology, sediments, nutrient inputs, and litter and detritus composition of a stream. Several conceptual models of stream fish population ecology and life history linking key ecosystem processes interacting across multiple scales have been developed (Schlosser and Angermeier 1995, Labbe and Fausch 2000). These could serve as guides for resource managers to use in understanding and assessing the necessary elements for conservation of populations. Ultimately, management actions that recognize and promote natural ecosystem processes will be most successful in meeting conservation needs of this species.

Educating the public and stakeholders to the value of conserving small, poorly known species such as southern redbelly dace should play an important role in management. Given that much of the habitat is on private property, management at the watershed level will require a confederation of federal and state resources agencies, non-profits, and private landowners to develop and implement a sound conservation strategy.

Tools and practices

Inventory and monitoring

The three Region 2 states with southern redbelly dace populations have already been undertaking periodic surveys to inventory their fish fauna (Bestgen 1989, Ashton and Dowd 1991, Bramblett and Fausch 1991, Meester 1998, Nesler et al. 1999, Calamusso 2002, Haslouer et al. 2005). Their CWCS plans call for a more systematic and standardized approach to inventory and monitoring, providing the ability to track changes in population size, instead of simply gathering presence/absence data. Many studies exist that can serve as a framework for establishing such standardized approaches (Loeffler 1982, Green and Young 1983, Hankin and Reeves 1988, Simonson et al. 1994, Angermeier and Smogor 1995, Sclosser and Angermeier 1995, Hays et al. 1996, Hubert 1996, Overton et al. 1997, Mullner et al.1998, Bryant 2000, U.S. Environmental Protection Agency 2001, Quist et al. 2006a).

Any combination of the following procedures can be used to determine the presence of southern redbelly dace. These dace can be captured or detected using a variety of techniques, including seines, traps, electrofishing and snorkeling. Because this species

Table 1. Checklist of conservation options for the southern redbelly dace.

1) Develop watershed based management strategies with partnering organizations and private landowners for connectivity and natural stream ecosystem processes.
2) Protect spring sources flowing into naturally meandering streams. Renovate springs containing non-native fish species and restock with dace from the nearest native source population.
3) Monitor land use in riparian areas, maintain buffer strips to prevent erosion and siltation.
4) Monitor streams for toxic chemicals (selenium, pesticides, excess fertilizers) and artificial hormones.
5) Prohibit the stocking of non-native species within aquatic ecosystems. This would include trout, sunfish, bass, mosquitofish, bullfrogs etc.
6) Restrict harvest of southern redbelly dace for bait or aquarium use. Strictly enforce existing laws and regulations.

often forms shoals in clear water, is very brightly and distinctly marked, it can frequently be observed from stream banks. Southern redbelly dace can be readily captured using seines (Trautman 1981). While many management agencies often employ electrofishing equipment to capture fishes, recent studies have demonstrated potentially harmful long-term effects to fishes, such as injuries to the vertebrae (Snyder 2003). For these reasons, seining may be the preferable method of sampling for presence/absence of southern redbelly dace. Minnow traps are also an effective method for capturing redbelly dace without injury (Stasiak 1972). Bryant (2000) demonstrated that removal counts using minnow traps can present an accurate and fairly simple tool for estimating fish populations.

Probably the two most frequently used methodologies for estimating abundance are removal or depletion estimates and mark-recapture estimates (Lockwood and Schneider 2000). The depletion method compares numbers of fish captured during successive passes. The mark-recapture study involves marking a random sample of the fish, and identifying these fish in a subsequent sample. Rosenberger and Dunham (2005) determined that for fishes in small streams, the latter approach probably gives more accurate results than the depletion method. Alternatively, Mullner et al. (1998) found that day-time snorkeling estimates of trout abundances and size distributions in small streams with little instream cover were highly correlated with results from depletion studies. These findings most likely would apply to southern redbelly dace as well, since they are readily observed by snorkeling in their clear-water habitat (Hankin and Reeves 1988).

Patton et al. (2000) described a method for assessing population trends from presence-absence data. The method also addressed differences in sampling methods and between current and historic data. Population trends were evaluated by comparing data from recently collected sites with data from historic sites (Patton 1997).

It is also important to have a mechanism in place to share information generated from these inventories in a timely fashion, especially between natural resource agencies. In order to coordinate objectives and efforts, the entire scientific community should be able to easily access these data.

Population or habitat management practices

The southern redbelly dace is an excellent Management Indicator Species (MIS) of pristine conditions at the headwaters of spring-fed streams since it is known to be very sensitive to most biotic or abiotic alterations. Habitat elements that have been shown to be important for southern redbelly dace include water temperature, turbidity, stream gradient, presence of aquatic vegetation, substrate composition, availability of cover, and presence/absence of piscivorous fishes. Several guides to the methodology of evaluating and monitoring stream habitat have become available. Recent studies include Platts et al. (1983), Frissell et al. (1986), Richter et al. 1996, Overton et al. (1997), Bain and Stevenson (1999), Pedroli et al. (2002), Labbe and Fausch (2003). Quist et al. (2006b) can be used as model for a habitat assessment protocol that should be appropriate for prairie streams. This details techniques for measuring habitat features important at the reach scale (elevation, turbidity, intermittence), as well as features important at the channel-unit scale (depth, substrate, cover). Richter et al (1996) presented a method for assessing hydrologic alteration attributable to human influence within an ecosystem. This method, called the "Indicators of Hydrologic Alteration", used 32 parameters to provide information on ecologically significant features of surface and ground water regimes influencing aquatic, wetland, and riparian ecosystems. This method can be used in inventories of ecosystem integrity, in planning aquatic management activities, and in setting and measuring progress toward conservation or restoration goals.

Managing habitats to enhance or restore southern redbelly dace populations is fundamentally a matter of restoring stream systems to their natural function (Schlosser 1995). Most of the management practices that will prevent and mitigate negative anthropogenic impacts to southern redbelly dace are covered in the Colorado Comprehensive Wildlife Conservation Strategy (2005) and Calamusso (2002). This involves many possible activities, such as: limiting the spread of invasive animal and plant species; promoting the recovery or reintroduction of native populations; operating dams, canals, diversions, and water retention structures to simulate the natural hydrology; managing road and trail networks to ensure connectivity of aquatic habitats; protecting natural wetlands, and augmenting with engineered wetlands; pretreating water to remove potential contaminants prior to release into riparian systems. One measure that can have almost immediate positive results would be to exclude livestock from the riparian area (Platts 1991, Binns and Remmick 1994, Belsky et al. (1999).

Non-native piscivorous fishes are widely distributed throughout the native range of the southern redbelly dace. Protection of the dace populations requires measures to prevent invasion of these predatory species and monitoring southern redbelly dace populations to ensure that such measures are effective. In some cases, dace populations may have been protected by human activity not designed for fish conservation, such as water diversion structures, dewatering of certain stream reaches, dams, roads, and culverts. In places, it may be necessary to employ artificial barriers of these types to protect or restore southern redbelly dace populations from non-native species (Pritchard and Cowley 2006). Migration barriers must be designed so that fish cannot jump upstream over them or swim around them during high water flows. Mueller (2005) presented information that controlling non-native predators is much more successful in the low-order streams, where southern redbelly dace would be found, than on large rivers.

Information Needs

In compiling this assessment, several areas of information gaps were noted for southern redbelly dace. Activity and dispersal patterns have not been adequately studied for the populations in Region 2. Demographic information has been based on research carried out in other parts of the species' range, and this should be validated for the fish living in the western locations. While the sensitivity of southern redbelly dace to toxic chemicals is generally well known, this species has not been specifically tested for responses to potential threats such as endocrine disrupters or selenium. Exposure to such substances could constitute a serious problem for dace that are concentrated in a relatively confined habitat.

Probably the most important data gap to address is the lack of genetic information on the various populations of southern redbelly dace. All of the individual populations in the headwaters of tributaries to the Missouri River drainage (**Figure 2**) have been isolated for a long time, and they may very well prove to be distinctly separate evolutionary units. This author (Stasiak) was sent some of the original redbelly dace specimens from the Colorado population and confirmed their identity as *Phoxinus erythrogaster*. These specimens, however, did have some slight morphological differences when compared to dace from more easterly locations. Beachum et al. (2002) also reported morphological variation among different southern redbelly dace populations. There is a precedent for this type of careful taxonomic examination. Three new species of *Phoxinus* (*P. tennesseensis*, *P. cumberlandensis*, and *P. saylori*) have been described from populations that, until rather recently, were considered either southern redbelly dace or mountain redbelly dace (Page and Burr 1991, Nelson et al. 2004).

A study similar to the one conducted by Kreiser et al. (2001) for the plainskillifish (*Fundulus kansae*) is needed to understand fully the relationships between these widely scattered and isolated populations. Until that type of study is completed, care should be taken to preserve and monitor the known isolated populations of southern redbelly dace. This genetic concern should be especially noted when considering the use of transplanted dace for restoring or supplementing isolated populations, such as in the case of the Arkansas River demes in Colorado. The popularity of redbelly dace for use as bait minnows also presents the possibility that fishermen can make their own unauthorized transplants (Fausch and Bestgen 1996).

Definitions

Deme – a local population of a species that is more or less reproductively isolated from other populations of the same species.

Fecundity – the total number of ova produced by female fish.

Lotic – running water habitats, such as streams, creeks, brooks, and rivers.

Piscivorous – fish-eating.

"r-selected species" – species whose life history attributes indicate selection for high fecundity, rapid growth, early age of maturation and reproduction, good colonization ability, and a relatively short life span; these species are good at finding and living in new or disturbed habitats where there are few competing species.

Shoal – an aggregation of individual fish in close proximity that form a single entity, almost acting as a single large organism.

Species of Concern – species that have 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.

Sexual dimorphism – when male and female fish of the same species show differences in anatomy or color.

Viability – the likelihood that a species will continue to persist.

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Appendix

Matrix Model Assessment of the Southern Redbelly Dace

Life cycle graph and model development

The life history data described by Settles and Hoyt (1978) for southern redbelly dace provided the basis for an age-classified life cycle graph that had four age-classes (**Figure A1**). From the life-cycle graph, we conducted a matrix population analysis assuming a birth-pulse population with a one-year census interval and a post-breeding census (McDonald and Caswell 1993, Caswell 2001). Beyond this introductory paragraph, rather than using an age-class indexing system beginning at 0, as is the norm in the fisheries literature, we use indexing beginning at 1. Note that Age 0 fish, censused at a pre-reproductive size, will reproduce at the end of the one-year census interval, at which time they will be essentially the same size as the Age 1 census size. In order to estimate the vital rates (**Table A1**), we made the following assumptions and estimates. The fixed points for vital rate estimation were considered to be:

- A stable age distribution based on the age structure of Settles and Hoyt (1978; p. 457)
- Egg production vs. standard length as computed by Settles and Hoyt (p. 293, col. 2)

Because the model assumes female demographic dominance, the egg number used was half the published value, assuming a 1:1 sex ratio. No survival data were available for the species. We therefore adjusted survival rates to produce 1) a stable age distribution matching the age structure described in Settles and Hoyt (1978),

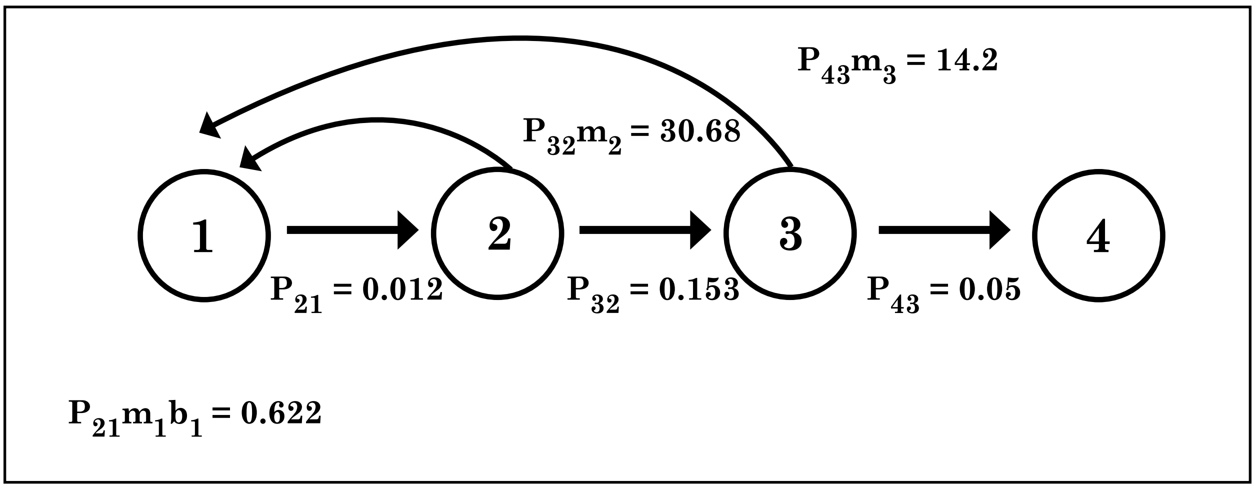

Figure A1. Life cycle graph for southern redbelly dace, consisting of circular *nodes*, describing the four age-classes in the life cycle and *arcs*, describing the *vital rates* (transitions between age-classes). The horizontal arcs are survival transitions (e.g., first-year survival, P_{21} = 0.16). The remaining arcs, pointing back to Node 1, describe fertility (e.g., $F_2 = P_{32} * m_2$). Each of the arcs corresponds to a cell in the matrix of **Figure 2**. Note the extra term, b1, to denote the fact that only 38.85% of first-year fish have mature ova.

Table A1. Parameter values for the component terms (P_i and m_i) that comprise the vital rates in the projection matrix for southern redbelly dace.

Parameter	Numeric value	Interpretation
m_1	133.5	Number of (female) eggs produced by Age-class 1 fish
m_2	200.5	Number of (female) eggs produced by Age-class 2 fish
m_3	284	Number of (female) eggs produced by Age-class 3 fish
b_2	0.3885	Proportion of Age-class 1 fish with mature ova
P_{21}	0.012	Probability of surviving first year (egg to yearling)
P_{32}	0.153	Probability of surviving second year (Age 0 to Age I)
m_{43}	0.05	Probability of surviving third year

and 2) a value of λ (the population growth rate) near 1.0. The long-term value of λ is necessarily near 1.

The model has two kinds of input terms: P_i describing survival rates, and m_i describing fertilities (**Table A1**). **Figure A2a** shows the symbolic terms in the projection matrix corresponding to the life cycle graph. **Figure A2b** gives the corresponding numeric values. Note also that the fertility terms (F_i) in the top row of the matrix include a term for offspring production (m_i) as well as a term for the survival of the mother (P_i) from the census (just **after** the breeding season) to the next birth pulse almost a year later. The population growth rate, λ, was 1.012 based on the estimated vital rates used for the matrix. This should not be taken to indicate a nearly stationary population, because the value was used as a target in estimating the survival rates and was subject to the many assumptions used to derive all the transitions. Nor should the value of λ be interpreted as an indication of the general well-being or stability of the population. Other parts of the analysis provide a better guide for any such assessment.

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 A1**] and the cells in the matrix, **A** [**Figure A2**]). Sensitivity analysis provides several kinds of useful information (see Caswell 2001, pp. 206-225). First, sensitivities show how important a given vital rate is to population growth rate (λ), which Caswell (2001, pp. 280-298) has shown to be a useful integrative measure of overall fitness. One can use sensitivities to assess the relative importance of the survival (P_i) and fertility (F_i) 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 accurate estimation of transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on age-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which age-classes or vital rates are most critical to increasing the population growth (λ) of endangered species or the "weak links" in the life cycle of a pest.

Figure A3 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 will also 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

Age-class	1	2	3	4
1	$P_{21}*m_1$	$P_{32}*m_1$	$P_{43}*m_2$	
2	P_{21}			
3		P_{32}		
4			P_{43}	

Figure A2a. Symbolic values for the matrix cells. The top row is fertility with compound terms describing survival of the mother (P_i) and offspring production (m_i). Empty cells have zero values and lack a corresponding arc in **Figure 1**. Note that the last column of the matrix consists of zeros in order to allow tabulation of the (small) proportion of fourth-year individuals that just completed their final breeding pulse.

Age-class	1	2	3	4
1	0.622	30.68	14.2	
2	0.012			
3		0.153		
4			0.05	

Figure A2b. Numeric values for the projection matrix.

Figure A2. The input matrix of vital rates, **A** (with cells a_{ij}) corresponding to the southern redbelly dace life cycle graph (**Figure A1**). a) Symbolic values. b) Numeric values.

Age-class	1	2	3	4
1	0.709	0.008	0.001	
2	**23.01**			
3		0.18		
4			0.000	

Figure A3. Possible sensitivities only matrix, $\mathbf{S}_p$ (remainder of matrix is zeros). First-year survival, the transition to which λ of southern redbelly dace is overwhelmingly most sensitive, is highlighted.

"adult" reproductive females (those in Age-class 3). 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 sensitivity of λ to changes in first-year survival (23.0; 96.2 percent of total) is overwhelmingly most important. Fertility transitions account for an additional 3 percent of the total sensitivity of λ to changes in vital rates. The major conclusion from the sensitivity analysis is that first-year survival is the key to population viability.

Elasticity analysis

Elasticities are the sensitivities of λ to **proportional** changes in the vital rates (a_{ij}). 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 vital rates (the a_{ij} arc coefficients on the graph or 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 age-classes as well as the relative importance of reproduction (F_i) and survival (P_i) for a given species. It is important to note that elasticity as well as sensitivity analysis assumes that the magnitude of changes (perturbations) to the vital rates is small. Large changes require a reformulated matrix and reanalysis.

Elasticities for southern redbelly dace are shown in **Figure A4**. The λ of southern redbelly dace was most elastic to changes in first-year reproduction, followed by first-year survival and second-year fertility. Overall, fertility transitions accounted for approximately 70.9 percent of the total elasticity of λ to changes in the vital rates. Reproduction, particularly in the first year is a demographic parameter that warrants careful monitoring in order to refine the matrix demographic analysis.

Other demographic parameters

The **stable age distribution** (SAD, **Table A2**) describes the proportion of each a-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, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SAD within 20 to 100 census intervals. For southern redbelly dace at the time of the post-breeding annual census (September in the case of the reference data), fish in the first age-class (Age 0, censused as eggs) should represent 98.6% of the population. **Table A2** also shows the proportions in each age-class excluding eggs, **Reproductive values** (**Table A3**) can be thought of as describing the "value" of an age-class as a seed for population growth relative to that of the first (Age 0 or, in this case, egg) age-class (Caswell 2001). The reproductive value is calculated as a weighted sum of the present and future reproductive output of an age-class discounted by the probability of surviving (Williams 1966). The reproductive value of the first age-class is, by definition, always 1.0. A yearling female (age of first breeding) is "worth" approximately 32.4 female eggs. The cohort generation time for southern redbelly dace is 1.4 years (SD = 0.5 years).

Age-class	1	2	3	4
1	**0.436**	**0.255**	0.018	
2	**0.273**			
3		0.018		
4			0.000	

Figure A4. Elasticity matrix, **E** (remainder of matrix is zeros). The λ of southern redbelly dace is most elastic to changes in first-year reproduction (Cell e11), followed by first-year survival and second-year fertility.

Table A2. Stable age distribution (SAD, right eigenvector). Vital rates were adjusted to yield a stable age distribution in accordance with the observed post-egg age structure [Settles and Hoyt (1978), p. 457] and a λ close to 1.0.

Age-class	Description	Proportion	Proportion excluding eggs
1	First-year females	0.986	—
2	Second-year females	0.012	0.863
3	Third-year females	0.002	0.131
4	Fourth-year females	0.000	0.006

Table A3. Reproductive values for females (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 (Age-class 1, Age 0) age-class, which is always defined to have the value 1. Note that, at the time of the post-breeding census, first-year fish are still eggs. Fourth-year females have no reproductive value because they have just reproduced for the last time and will not survive to breed again.

Age-class	Description	Reproductive values
1	First-year females	1
2	Second-year females	32.44
3	Third-year females	14.04
4	Fourth-year females	0

Potential refinements of the models

Clearly, the better the data on first-year survival and fertility rates, the more accurate the resulting analysis. 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 incorporate forces that 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 matrix projection models

- ❖ First-year survival accounts for 96.2 percent of total "possible" sensitivity. Any absolute changes in this vital rate will have a major impact on population dynamics.

- ❖ First-year fertility accounts for 43.6 percent of the total elasticity, considerably more than any of the other elasticities. Proportional changes in early fertility will have major impacts on population dynamics.

- ❖ The shift in emphasis between the sensitivity analysis (first-year survival) and the elasticity analysis (first-year reproduction) indicate that it may be useful to understand whether variation is generally absolute vs. proportional. Regardless, the first year of life is clearly the critical feature of the population dynamics of southern redbelly dace.

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