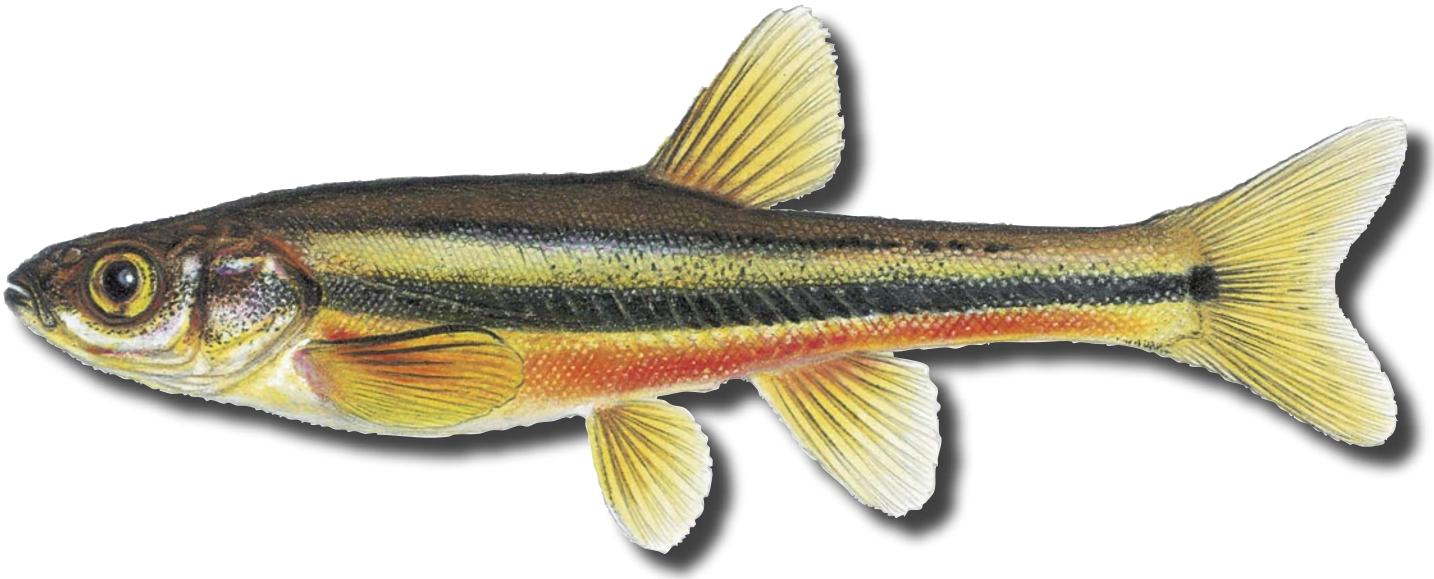
Northern Redbelly Dace (*Phoxinus eos*): A Technical Conservation Assessment



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

February 10, 2006

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Peer Review Administered by
American Fisheries Society

Stasiak, R. (2006, February 10). Northern Redbelly Dace (*Phoxinus eos*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: http://www.fs.fed.us/r2/projects/scp/assessments/northernredbellydace.pdf [date of access].

ACKNOWLEDGMENTS

I would like to offer thanks to David B. McDonald at the University of Wyoming for providing the demographic matrix analysis that appears in the appendix for this species. Without this help, many of the numbers would still be residing in cyberspace! George R. Cunningham provided thoughtful insight into the conservation of this species, especially for South Dakota. I would also like to acknowledge Gary Patton and Richard Vacirca of the USDA Forest Service for all of their help in bringing this report to completion. Comments and suggestions from anonymous reviewers were very much appreciated.

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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-Omaha, where he has spent the past 35 years teaching courses in ichthyology, aquatic ecology, and zoology. 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 PHOTO CREDIT

Illustration of the northern redbelly dace (*Phoxinus eos*) by © Joseph Tomelleri.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF THE NORTHERN REDBELLY DACE

Status

The northern redbelly dace (*Phoxinus eos*) is not considered federally endangered or threatened in the United States. In the Great Plains, however, this species is very uncommon; it is only found in three of the five states comprising USDA Forest Service (USFS), Rocky Mountain Region (Region 2). At the state level, it is ranked as endangered or threatened in Colorado (S1 State endangered), South Dakota (S3 State threatened), and Nebraska (S3 State threatened), where populations occur as small, isolated demes that have been declining steadily since European settlement over 100 years ago. While this dace has not been reported from any National Forest System lands in Region 2, the Black Hills National Forest and Buffalo Gap National Grassland in South Dakota, the Oglala National Grassland and Samuel R. McKelvie National Forest in Nebraska, and the Roosevelt, Arapahoe, and Pike national forests in Colorado are all within the range of the northern redbelly dace.

Primary Threats

The two primary threats to northern redbelly dace in Region 2 include habitat alteration and the introduction of non-native fishes. These dace occur in small, confined places of permanent spring seeps, usually at the extreme headwaters of small streams. Members of the natural fish community in these habitats are highly adapted to the special conditions found there. Water development activities that change natural spring flow (e.g., reservoir construction, groundwater pumping, stream diversions, channelization) lead to habitat degradation and stream fragmentation. Northern redbelly dace populations are strongly correlated to beaver (*Castor canadensis*) pond occurrence, so restrictions on beaver activity will result in reductions in dace populations. These dace are also sight-feeding predators and depend on relatively clear water; therefore any activities that cause long-term increases in turbidity (e.g., construction projects, forestry practices, livestock grazing) will be deleterious. This species is very sensitive to human alterations to its habitat, especially the addition of non-native fishes. Introduced species will negatively affect northern redbelly dace and other native fishes through the combined pressures of predation, competition, potential for addition of new parasites and disease, and altering the behavioral components. Introduction of large sunfish, bass, pike, or trout will have an especially significant negative impact on dace populations. Another threat, which may be of more local concern, would be the potential overharvest of northern redbelly dace for use as fishing bait or for the pet industry.

Primary Conservation Elements, Management Implications and Considerations

The northern redbelly dace is one of the keystone species of small fishes forming a distinctive community in the Great Plains. This assemblage of fishes is restricted to small headwater streams, beaver ponds, and small spring-fed lakes. The major management considerations would be to protect groundwater sources, streamflows, and beaver activity. Introductions of non-native fishes need to be eliminated, controlled, and reduced where they have already become established within this species' habitat. Data gaps exist concerning movement patterns and genetics in populations throughout Region 2.

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INTRODUCTION

This assessment is one of many being produced to support the Species Conservation Project for the USDA Forest Service (USFS) Rocky Mountain Region (Region 2) (**Figure 1**). The northern redbelly dace (*Phoxinus eos*) (**Figure 2**) is the focus of an assessment because it was identified as a sensitive species during the recent revision of the Regional Forester's Sensitive Species List for Region 2. 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 downward trends in abundance and/or habitat capability that would reduce its distribution (FSM 2670.5 (19)). The northern redbelly dace occurs in three of the five states comprising Region 2 (Nebraska, South Dakota, and Colorado). Although this dace has apparently not been reported directly from any USFS Region 2 administrative unit, some of the northern redbelly dace populations are found in adjacent stream systems.

This report addresses the biology, ecology, conservation, and management of the northern redbelly dace throughout its range in Region 2. This introduction defines the goal of the assessment, outlines its scope, and describes the methods used in its production. Scientific and common names of fishes used in this report follow the latest recommendations from the American Fisheries Society (Nelson et al. 2004).

Goal

Species conservation assessments produced as part of the Species Conservation Project are designed to provide forest managers, research biologists, and the public with a thorough discussion

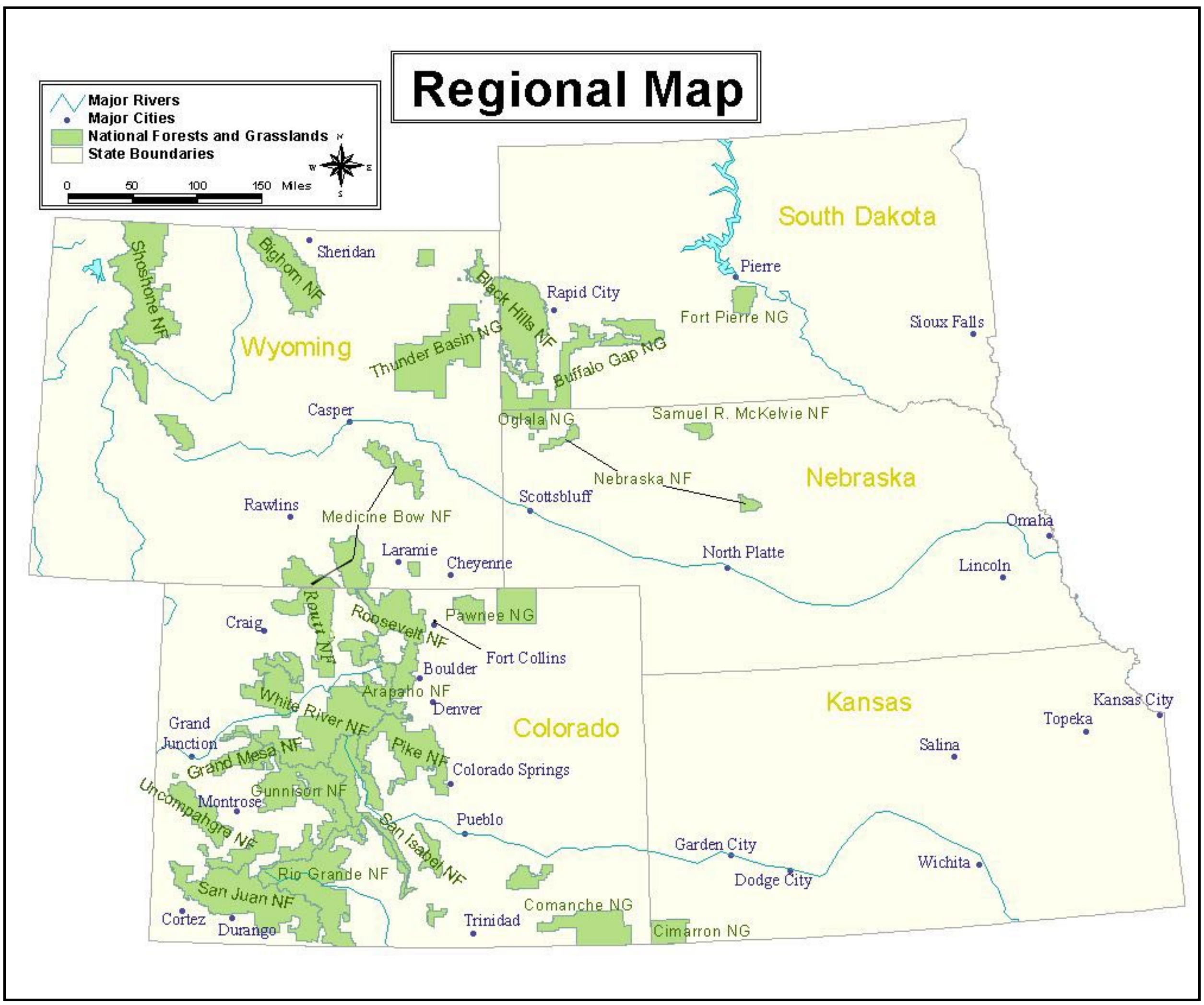

Figure 1. Map of national forests and national grasslands within USDA Forest Service Region 2.

Figure 2. Male northern redbelly dace from the North Platte River in Keith County, NE. June 1979. Photograph by author.

of the biology, ecology, conservation status, and management of certain species based upon available scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of the broad implications of that knowledge, and outlines of information needs. This assessment does not seek to develop specific management recommendations. Rather, 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).

Scope of Assessment

The northern redbelly dace assessment examines the biology, ecology, conservation status, and management of this species with specific reference to the geographic and ecological characteristics of USFS Region 2. While much of the data on this dace comes from research conducted on populations that lie outside Region 2 but within the major portion of the species' range, this document places that literature in the ecological and social context of the central Rocky Mountains and Great Plains. Similarly, this assessment is concerned with reproductive behavior, population dynamics, and other characteristics of the northern redbelly dace in the context of the current environmental rather than historical conditions. The evolutionary environment of the species is considered in conducting the synthesis, but it is placed in a current context.

In producing the assessment, I reviewed the refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on northern 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. I chose to use some non-refereed literature in the report, however, when information was not available in the primary literature. Unpublished data (e.g., Natural Heritage Program records) were important in estimating the geographic distribution of the species.

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 relations. In this assessment, the strength of evidence for particular ideas is noted, and alternative explanations are described when appropriate.

Application and Interpretation Limits of this Assessment

Information about the biology and ecology of the northern redbelly dace was collected and summarized from throughout its geographic range, which extends from Canada south to Colorado and Nebraska, and from British Columbia east to the Atlantic Ocean (**Figure 3**). In general, life history and ecology information collected from a portion of a species' range should apply broadly throughout its entire distribution. However, certain life history parameters (e.g., time of spawning, growth rate, longevity) could differ along environmental gradients, especially in such a wide-ranging species. Information about the conservation status of this species was limited to USFS Region 2 and should not be taken to imply conservation status in other portions of its range.

Publication of Assessment on the World Wide Web

To facilitate the use of species assessments in the Species Conservation Project, they are being published on the Region 2 World Wide Web site (www.fs.fed.us/r2/projects/scp/assessments/index.shtml). Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More important, it facilitates revision of the assessment, which will be accomplished based on the guidelines established by Region 2.

Peer Review

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

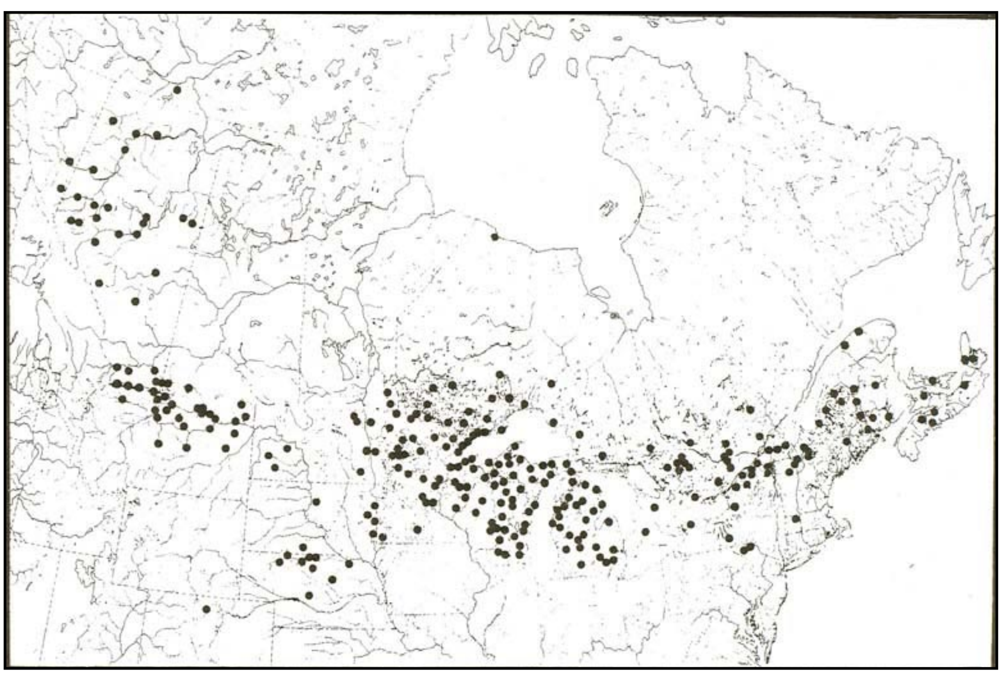

Figure 3. Distribution of northern redbelly dace in North America. (From Stasiak 1980).

Management Status and Natural History

Management Status

As a species, the northern redbelly dace is not considered federally threatened, endangered, or sensitive throughout the major portion of its range (**Figure 3**) in the United States (U.S. Fish and Wildlife Services; http://endangered.fws.gov/). The USFS, Region 2, however, does list it as a sensitive species (Species Conservation Project: Region 2 Regional Forester's Sensitive Species: (http:/www.fs.fed.us/r2/projects/scp/sensitivespecies/index.shtml).

Northern redbelly dace populations historically are known to occur near, if not directly within, National Forest System lands in Colorado (**Figure 4**), South Dakota (**Figure 5**), and Nebraska (**Figure 6**). These three states rank the northern redbelly dace as endangered (S1), threatened (S3), and threatened (S3), respectively. This species is not present in Kansas or Wyoming (Cross 1967, Cross and Collins 1975, Baxter and Simon 1970, Page and Burr 1991, Baxter and Stone 1995, Fertig and Beauvais 1999).

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

The northern redbelly dace is considered endangered or threatened in all three of the states in which it occurs in Region 2 and is given all of the legal protection encompassed by those statuses. This usually prohibits killing or capturing. The State of Nebraska does prohibit the collection of bait minnows from

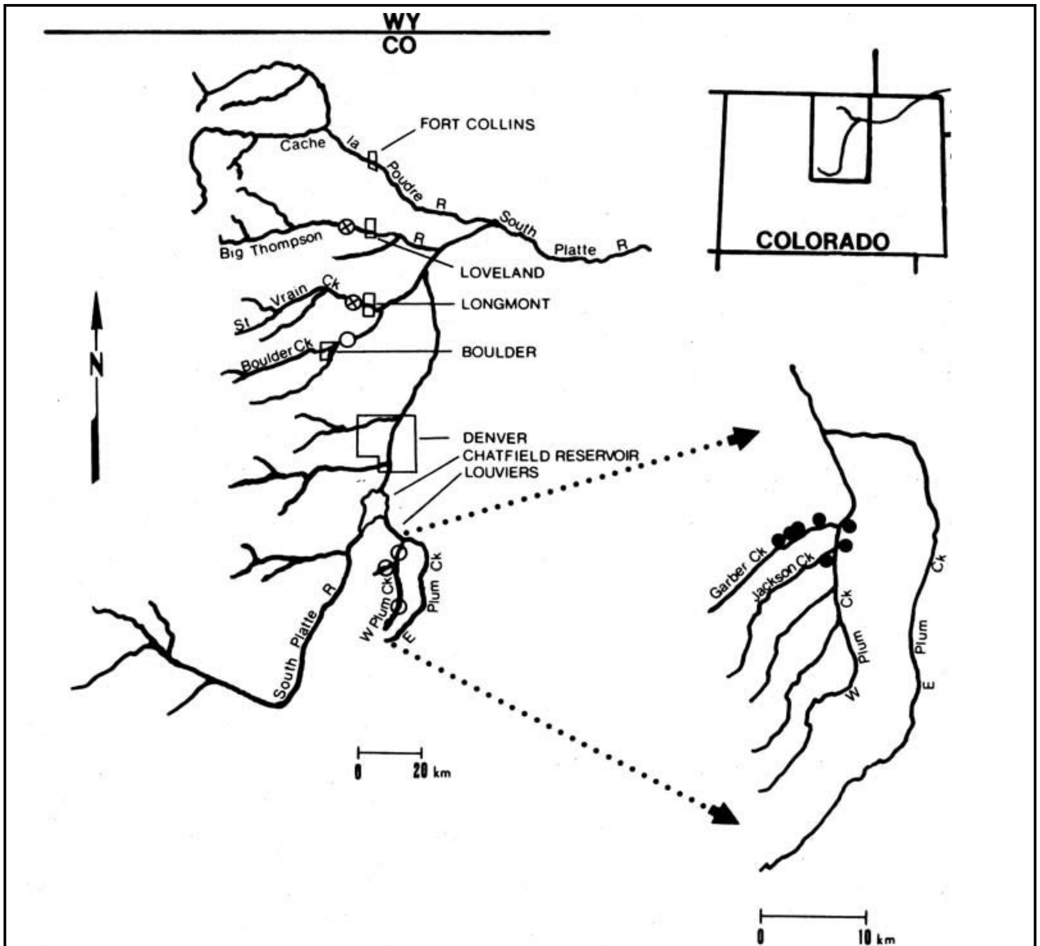

Fig. 1—Map of the upper South Platte River basin and the Plum Creek drainage, Colorado. Solid circles denote *Phoxinus eos* collections made by K. Bestgen in 1985; open circles denote localities prior to 1985; a circled x denotes a hybrid collection site.

Figure 4. Distribution of northern redbelly dace in Colorado. (From Bestgen 1989).

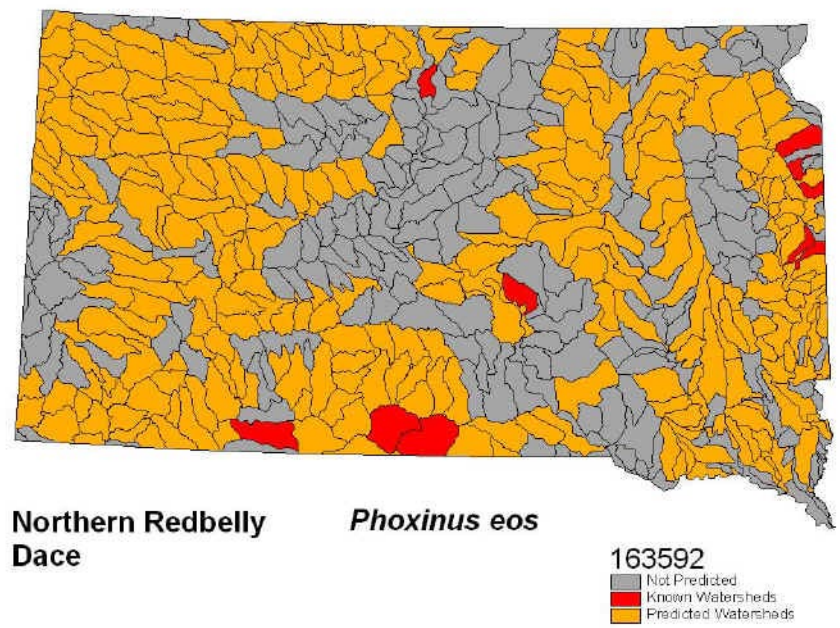

Figure 5. Distribution of northern redbelly dace in South Dakota. (From South Dakota Gap Analysis).

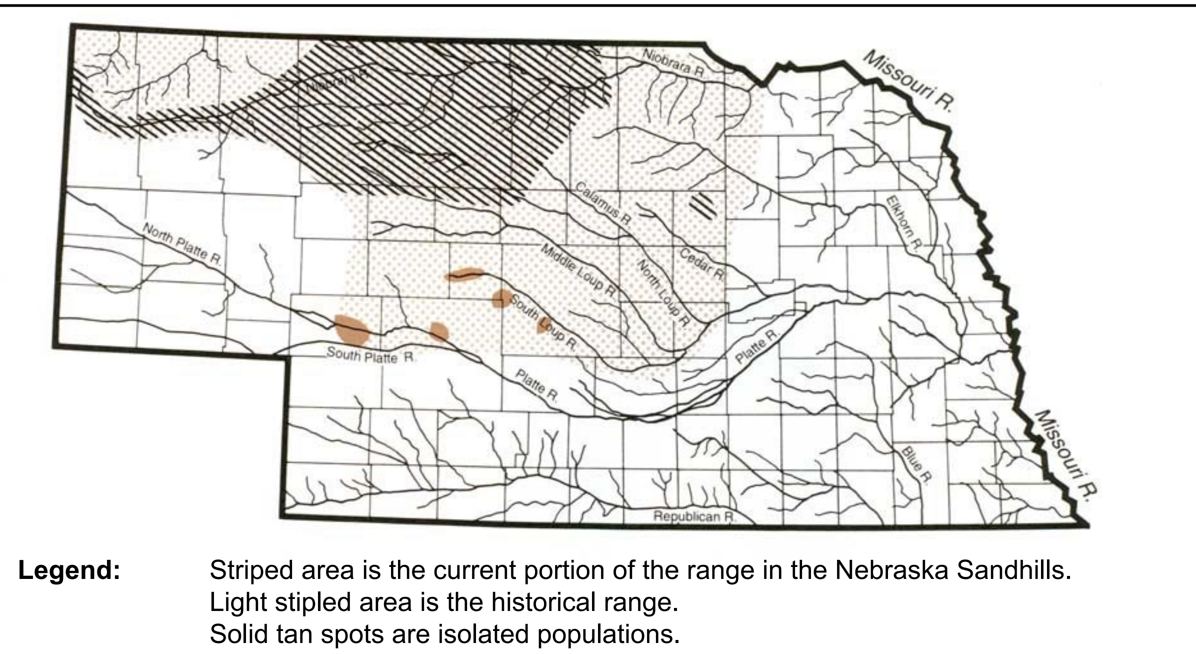

Figure 6. Distribution of northern redbelly dace in Nebraska. (From Clausen and Stasiak 1994).

designated trout waters, and this would include many of the sites where northern redbelly dace are found.

Beyond the state designations, I am aware of only one conservation effort aimed at northern redbelly dace. Each state is currently developing Comprehensive Wildlife Conservation Strategy (CWCS) plans (http://www.teaming.com). Each plan outlines specific action goals for each listed species. Northern redbelly dace will be included will be included in the plans for Nebraska, Colorado, and South Dakota. Other future management options are addressed in the Conservation section of this report.

Biology and Ecology

Systematics and species description

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

Samuel Rafinesque first used the genus name *Chrosomus* when he described *C. erythrogaster*, or what he called the Kentucky RedBelly, from a specimen taken from the Kentucky River (Rafinesque 1820). Edward Drinker Cope (1862) described *C. eos* on the basis of specimens from the Meshoppen Creek, Sesquehanna County, Pennsylvania. He included four distinguishing peculiarities that separated *C. eos* from *C. erythrogaster*.

Hubbs and Brown (1929) were first to report the occurrence of hybrids between *Chrosomus* and *Pfrille* (the finescale dace; now known as *Phoxinus neogaeus*); these were found in Ontario, Michigan, and New York. Jordan (1924) also noticed the great similarity of the two genera. Special mention was given to the similar triangular areas of breeding tubercles anterior to the pectoral fins in both species, a feature attributed only to those two genera. They stated that *Chrosomus* appeared to be a herbivorous modification of *Pfrille*, just as *Hybognathus* appeared to be a herbivorous modification of *Notropis*. This is a clarification of a statement appearing in Hubbs (1926). Only the authors' uncertainty about the fertility of the hybrids apparently prevented them from combining *Pfrille* and *Chrosomus* at that date.

In his work on the fishes of Russia, Berg (1949) listed *Pfrille* Jordan as a questionable species under *Phoxinus*. Banarescu (1964), writing on the fishes of Rumania, went one step further and listed *Chrosomus* Rafinesque together with *Pfrille* Jordan as American species of *Phoxinus*. The effect of this revision was to merge all species of the American *Chrosomus* into the European genus *Phoxinus*. *Phoxinus* became the only minnow genus with species in Europe, Asia, and North America (Mahy 1972, Coad 1976).

Species description

The North American dace in the subgenus *Chrosomus* are small to medium-sized (70 to 120 mm [3 to 6 inches] total length) 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 about half-way from the head toward the tail. These dace have horizontal black bands along their sides with iridescent silvery areas above the main lateral band. Males have bright red, yellow, or red and yellow patterns below the black side band (Stasiak 1972, Scott and Crossman 1973). These bold and distinctive markings, which are especially vivid during the breeding season, make this dace easy to recognize. The northern redbelly dace is, in fact, considered among the most attractive of the native minnows.

In many regions throughout their current range, northern redbelly dace are snytopic with finescale dace (*Phoxinus neogaeus*). Usually it is fairly easy to identify the two different species. The finescale dace is larger and usually has only one prominent black lateral band while the northern redbelly dace is usually smaller, slimmer, and has two black lateral bands (Scott and Crossman 1973). Internal structures, such as the intestine length and pharyngeal tooth pattern, are also distinctive (New 1962, Legendre 1970, Stasiak 1972, 1977, 1978, Becker 1983). Northern redbelly dace reach total lengths of about 75 mm (3 inches). Pharyngeal arches usually have a 0,5-5,0 formula (Eastman 1970, Stasiak 1972). The intestine of the northern redbelly dace is long and coiled (or looped); it is longer than the standard length of the fish. This is in sharp contrast to the intestine of finescale dace, which has a simple S-shape and an overall length of less than the standard length of the fish (Stasiak 1972, 1978). Pearl organs (breeding tubercles) are highly developed on the males during the spring (Reighard 1903). Northern redbelly dace develop a unique and distinctive pattern of these structures on their fins, on their sides, in front of the pectoral fins, and above the anal fin (Maas 1994).

In many situations where finescale dace and northern redbelly dace are found together, hybrids of the species have been reported (Hubbs and Brown 1929, Hubbs 1955, Gilbert 1961, Bailey and Allum 1962, New 1962, Legendre 1969, Brown 1971, Stasiak 1972, 1978, Joswiak et al. 1982, Stasiak 1987, Stasiak et al. 1988, Goddard et al. 1989, Gauthier and Boisclair 1996, Schlosser et al. 1998). These fish apparently represent lineages of clonally reproducing gynogens; they are intermediate in most of the body proportions and other characteristics normally used to identify the two parental species (Joswiak et al.1982, 1985).

In Colorado, northern redbelly dace populations are reported from the headwaters of the Platte River (Hendricks 1947, Propst 1982, Bestgen 1989), and populations of the closely related southern redbelly dace (*Phoxinus erythrogaster* Raf.) occur in the headwaters of the Arkansas River near Pueblo and Canon City (Woodling 1985). These similar species can best be distinguished by referring to Phillips (1969a), who studied sympatric populations of these minnows in Minnesota.

Distribution and abundance

The northern redbelly dace is widely distributed across Canada and the northern portions of the St. Lawrence (Great Lakes), Mississippi, and Missouri River drainages in the United States (**Figure 3**; McPhail and Lindsey 1970, Scott and Crossman 1973, Stasiak 1980, Page and Burr 1991, Campbell 1997). In Canada, it has been taken from the Northwest Territories, British Columbia, and Alberta (Wynne-Edwards 1952, Lindsey 1956, Carl et al. 1959, McPhail and Lindsey 1970, Paetz and Nelson 1970); Saskatchewan (Willock 1969); Manitoba (Hinks 1943, Keleher 1956, Fedoruk 1971); Ontario (Hubbs and Brown 1929, Dymond and Scott 1941, Lindeborg 1941, Brett 1944, Radforth 1944, Ryder et al. 1944, Scott and Crossman 1969, Tyler 1966); Quebec (Legendre 1953, Legendre 1970, McAllister and Coad 1974); and New Brunswick and Prince Edward Island (Scott and Crossman 1959).

In the United States, northern redbelly dace have been found in Maine and New Hampshire (Kendall 1908); New York (Greeley and Bishop 1932, 1933, Smith 1985); Pennsylvania (Cope 1862); Michigan (Hubbs and Lagler 1949, Taylor 1954, Hubbs and Lagler 1964); Wisconsin (Greene 1935, Moore and Roberty 1965, Becker and Johnson 1970, Becker 1983); Minnesota (Smith and Moyle 1944, Underhill 1957, Eddy et al.1963, Stasiak 1972, Hatch et al. 2003); North Dakota (Copes and Tubb 1966, Evenhuis 1969, North Dakota Department of Game and Fish 1994); South Dakota (Evermann 1893, Evermann and Cox 1896, Churchill and Over 1938, Bailey and Allum 1962, Ashton and Dowd 1991, Doorenbos 1998, Isaak et al. 2003); Nebraska (Johnson 1942, Jones 1963, Stasiak 1976, 1980, Madsen 1985, Stasiak 1987, Stasiak et al. 1988); and Colorado (Ellis 1914, Hendricks 1947, Propst 1982, Bestgen 1989). This species apparently reaches its southern-most limit at about 40° N latitude in Colorado (**Figure 4**; Mayden et al. 1992).

In the five states comprising Region 2, northern redbelly dace are found in Colorado, South Dakota, and Nebraska. Specifically, they are found in first order streams of the Niobrara and Platte River systems (**Figure 4**, **Figure 5**, **Figure 6**). None of the populations have been reported directly on National Forest System lands, but in close proximity (Bestgen 1989). All of the northern redbelly dace populations in South Dakota, Nebraska, and Colorado can be considered "glacial relict" populations that have been isolated from the main portion of the species' range in Canada and Minnesota (Cross et al. 1986, Clausen and Stasiak 1994). The hybrid finescale dace-northern redbelly dace has also been reported from all three of the Great Plains states that have northern redbelly dace populations. Region 2 locations with possible populations of northern redbelly dace are the Roosevelt National Forest (northwest of Boulder) and the Pike National Forest (west of Castle Rock) in Colorado (Henricks 1947; Propst 1982; Bestgen 1989).

Population trends

Northern redbelly dace populations are considered stable throughout the main portion of their range in Canada, Minnesota, Wisconsin, Michigan, and New England (Underhill 1957, Nordlie et al. 1961, Becker and Johnson 1970, Paetz and Nelson 1970, Smith 1985, Das and Nelson 1990, Hatch et al. 2003). Where they occur as relict populations following the retreat of the Wisconsin Ice Sheet (this includes the dace populations in Region 2), they are vulnerable. Here they are found in the extreme headwaters of first order streams and in areas of groundwater seepage (McPhail and Lindsey 1970). The cold water provided by these sources enables the dace to persist under conditions that are much more similar to the conditions that prevailed thousands of years ago when the southern edge of the glacier was much closer to this region (McPhail 1963, Sherrod 1963, Cross 1970, Cross et al.1986). The warming and drying of the Great Plains following the retreat of the last ice age several thousand years ago has led to the natural reduction in suitable habitat for this more northern species (Briggs 1986, Clausen and Stasiak 1994). Human activity that leads to reduction in cold springs or seeps will greatly accelerate this process. For more detailed information on documentation of population trends, see the section of this report on Inventory and Monitoring.

Activity patterns

Most of the studies on northern redbelly dace have been conducted in the main portion of their distributional range to the north and east of Region 2 (Emery et al.1997). Little is directly known of the activity patterns of this dace on the Great Plains. Cunningham and Hickey (1995) observed the fish community in a small Nebraska stream using snorkeling and found that northern redbelly dace were generally restricted to the mid-water column, possibly due to niche partitioning. Stasiak (1972) studied populations of northern redbelly dace in a series of beaver (*Castor canadensis*) ponds near the headwaters of the Mississippi River in northern Minnesota. The fish were active throughout the pond during daylight hours, but they were not observed at night. Large schools of dace comprising all sizes and year classes could be observed in open water areas of the ponds in the spring and summer months. Collections made through the ice in December to March indicated that they were active (and feeding) even during the winter months. This is a species that is very well adapted to cold water (Brett 1944, Tyler 1966). Cooper (1936) reported that breeding northern redbelly dace were attracted to filamentous algae along the shoreline in Michigan ponds in early June. In a larger lake situation, Gauthier and Boisclair (1996) observed that hybrid dace (*Phoxinus neogaeus* x *P. eos*) made daily movements offshore to inshore at night, probably in relation to feeding forays (Keast and Welsh 1968).

Habitat

The northern redbelly dace has a very strong habitat preference for sluggish, spring-fed streams with a lot of vegetation and woody debris (Eddy and Surber 1974, Stasiak 1987). They can also be found in small, spring-fed lakes and bogs (Greeley and Bishop 1933, Hubbs and Cooper 1936, Das and Nelson 1990). Perhaps the favorite habitat of this species can be described as a series of beaver ponds filled with a constant supply of cool groundwater (Stasiak 1972, Schlosser 1995, Schlosser and Kallemeyn 2000). This particular habitat is a key to the presence of northern redbelly dace, particularly in the Great Plains region. The water does not need to be deep, but it does need to provide a constant supply of cool, spring water with sufficient oxygen for the fish, even during the hot and dry summer conditions. The vegetation and cover provided by logs and brush supply areas of shade, as well as cover to ambush prey and to avoid predators (Angermeier and Karr 1984).

A critical component of this habitat is the exclusion of large predatory fishes. Brightly colored dace simply do not fare well in the presence of large piscivorous species (Stasiak 1972). Active beaver ponds with their ever-changing dimensions and dams tend to naturally exclude these species of fish. Beaver ponds also usually provide a high amount of organic material, insuring that a large biomass of food organisms is available for all life history stages of the northern redbelly dace (Schlosser 1995). Clear water is necessary for this sight-feeding fish to find their food and their mates. Water can often be stained a reddish or tea color from dissolved organic material (Becker 1983), but this "dark" water is still transparent.

In some first order streams, particularly in the Nebraska Sandhills, northern redbelly dace can be found where the banks are severely undercut, providing deep holes with reduced current and lots of cover (Cunningham 1995). Typical habitat conditions of small streams where the species occurs include:

- ❖ water supplied by clear, cool springs or seeps
- ❖ lack of a strong current
- ❖ cover in the form of undercut banks, heavy vegetation, or brushy debris
- ❖ no large piscivorous fish populations.

This species may also be present in small lakes that can be characterized as spring-fed, clear, with heavy vegetation (at least along the shoreline), and few, if any, species of large predatory fishes in the littoral zone.

Northern redbelly dace are usually associated with a fairly small but distinctive assemblage of other native species that are also adapted to similar habitat requirements. In Sandhill streams, this dace is usually associated with pearl dace (*Margariscus margarita*), brassy minnow (*Hybognathus hankinsoni*), fathead minnow (*Pimephales promelas*), common shiner (*Luxilis cornutus*), blacknose dace (*Rhinichthyes atratulus*), blacknose shiner (*Notropis heterolepis*), creek chub (*Semotilus atromaculatus*), plains topminnow (*Fundulus sciadicus*), white sucker (*Catostomus commersoni*), Iowa darter (*Etheostoma exile*), and brook stickleback (*Culaea inconstans*) (Bailey and Allum 1962, Stasiak 1976, Baxter and Stone 1995, Cunningham 1995). At seven locations where this species was reported in Colorado, the fathead minnow was the most frequent associate (6 sites), followed by the creek chub and white sucker (5 sites each). The central stoneroller (*Campostoma anomalum*), Iowa darter, and common shiner were present at four sites while the plains topminnow, brook stickleback, and green sunfish (*Lepomis cyanellus*) were at two sites (Bestgen 1989).

In the Minnesota beaver ponds, Stasiak (1972) found the northern redbelly dace, finescale dace, fathead minnow, brook stickleback, and central mudminnow (*Umbra limi*). Scott and Crossman (1973) found a similar fish assemblage across much of this species' range in Canada. In Michigan and Wisconsin, the northern redbelly dace has been found with the brassy minnow, pearl dace, common shiner, blacknose shiner, Johnny darter (*Etheostoma nigrum*), white sucker, and mottled sculpin (*Cottus bairdi*). In some eastern streams, brook trout (*Salvelinus fontinalis*) are occasionally found with northern redbelly dace; in these cases the brook trout are native and are apparently quite small in average size (Hubbs and Cooper 1936, Stasiak 1972, Becker 1983).

Food habits

Several studies have indicated that northern redbelly dace are omnivores, feeding on small plants and animals taken from the entire water column (Hubbs and Cooper 1936, Keast and Webb 1966, Phillips 1969b, Stasiak 1972, Becker 1983, He 1986, Cochran et al. 1988, Bestgen 1989). As adults, they are primarily sight-feeding particle feeders, selecting relatively small individual target prey (Stasiak 1972). Hubbs and Cooper (1936) included the northern redbelly dace as an example of a herbivorous or omnivorous minnow species; they characterized this type of fish as having a long intestine and fine throat teeth. The long, coiled intestine of this species was nicely illustrated in Becker (1983). Keast and Webb (1966) described the relationship between the head morphology and feeding preferences of fishes. All of these studies are consistent with a diet of vegetation and small invertebrates for northern redbelly dace.

The herbivorous or omnivorous diet of the smaller northern redbelly dace (and their hybrids) is one of the most obvious differences when compared to the highly predatory finescale dace (Seaburg and Moyle 1964, Stasiak 1972, Naud and Magnan 1988, Bestgen 1989, Trudel and Boisclair 1994, Gauthier and Boisclair 1996). Cochran et al. (1988) compared the diets of finescale dace and northern redbelly dace in a small northern Michigan bog lake. Although both species consumed plant material and invertebrates from the algal mat, the northern redbelly dace ate a much higher proportion of vegetation and smaller invertebrates. Finescale dace ate large insects, but chironomid larvae were the only insects found in northern redbelly dace. Bestgen (1989) examined 10 specimens of northern redbelly dace from Colorado and found that detritus was volumetrically dominant (80 percent), followed by macrophytes (15 percent), and filamentous algae (5 percent). Ostracods were found in 50 percent of the fish, but they represented just a small volume of the diet. Captive studies have demonstrated that northern redbelly dace will eat small active zooplankton as well as small fish fry up to 8 to 9 mm (0.3 to 0.35 inches; Scott and Crossman 1973).

Breeding biology

Spawning of northern redbelly dace was first described by Hubbs and Cooper (1936) in a Michigan lake. Several males chased a single female into dense mats of filamentous algae, and these breeding groups produced five to 30 non-adhesive, fertilized eggs per spawning event. Eggs hatched in eight to 10 days at temperatures ranging from 21 to 26 ºC (70 to 78 ºF.). Captive breeding in aquaria (personal observations) confirms this scenario.

Unlike finescale dace, which have a single spawning period very early in the spring, northern redbelly dace can have two or more spawning periods during the spring into the summer (Hubbs and Cooper 1936), thus ensuring that reproduction is successful at least once each year. The exact spawning period of northern redbelly dace depends on a combination of photoperiod and temperature, so it can be somewhat later in northern Canada (Bullough 1939). McPhail and Lindsey (1970) collected females with large eggs in late August in northern Alberta. Faber (1985) collected early larvae using light traps in a beaver pond in the city of Ottawa; these ranged in size from 7.5 to 10.6 mm (0.3 to 0.4 inches) on June 7, 1979. In Minnesota, Michigan, and Wisconsin, northern redbelly dace began spawning in June and often continued into July (Hubbs and Cooper 1936, Stasiak 1972, Becker 1983). Becker (1983) found ripe females (58 to 60 mm [2.3 to 2.4 inches] total length) in mid-June in Wisconsin with 410 to 435 ripe eggs, which represented 15 to 20 percent of their total weight. Ripe eggs averaged 0.9 to 1.0 mm (0.35 to 0.4 inches), and there were other smaller eggs (0.3 to 0.6 mm [0.01 to 0.02 inches]), which suggested that spawning would also take place later in the summer. The exact number of eggs produced by individual females during a year has never been carefully researched. Preliminary data suggest that each female is capable of producing up to 5,000 eggs each season (Stasiak personal observation).

Northern redbelly dace in the Great Plains states of Region 2 usually spawn from late May to July (Stasiak 1987). Since water temperatures can rise and fall rapidly during this time of year, breeding behavior may commence and then be suspended for periods of time. In locations where substantial groundwater flow is provided, the temperature rise is more gradual and it fluctuates less, providing a more stable breeding situation. Where cool groundwater is not constant, the water temperature can rise much faster and earlier in the season. This perhaps allows the breeding of northern redbelly dace to overlap with the syntopic finescale dace, a situation that can lead to hybridization.

Sexual dimorphism is very apparent in northern redbelly dace. Females are usually larger than males and do not display the red and yellow sides and bellies of breeding males. Some males carry only red color, some have only yellow, and some show both red and yellow (Stasiak 1972, Scott and Crossman 1973). Clear water appears to be a critical ecological component as the females use the colors of the males as a signal to release their eggs. Males also have fins that are proportionally larger than the same fins of the females; this is especially obvious for the large, scoop-shaped pectoral fins. 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 dense aquatic plants (Hubbs and Cooper 1936).

Demography

Genetic characteristics and concerns

Genetic studies of northern redbelly dace populations have concentrated on ways of separating them from the closely related and syntopic finescale dace (Joswiak et al. 1982, 1989). Most of this research has centered on characterizing the genetics of the populations of gynogens in the Great Plains region (Joswiak et al. 1982, 1985, Goddard et al. 1989, Elder and Schlosser 1995). Finescale dace differ from northern redbelly dace at three allozyme loci: PGM (phosphoglucomutase), SOD (superoxide dimutase), and MDH (malate dehydrogenase) (Joswiak et al. 1982). These markers can be used to identify finescale dace from either northern redbelly dace or their hybrids. Little genetic research has been done on the different populations of "pure" northern redbelly dace (Toline and Baker 1994). Since these dace have a very wide range (i.e., from Alberta to Prince Edward Island in Canada, and Wyoming to Maine in the United States), it would be very interesting to compare the genetics of dace from widespread regions.

In the Great Plains populations of Region 2, finescale dace are usually syntopic with northern redbelly dace. This association between two very similar and closely related species often has resulted in hybridization (Hubbs and Brown 1929, Hubbs 1955, New 1962, Brown 1971, Magnin et al. 1976, Stasiak 1978, Joswiak et al. 1982, 1985, Goddard et al.1989, Schlosser et al.1998). These populations of hybrid origin usually exist as all-female gynogens reproducing clonally. Often these fish of hybrid origin can outnumber the parental species. In many Nebraska streams, it is common to find populations of hybrid dace and a small population of parental northern redbelly dace, but no parental finescale dace. Most of these hybrids are diploid ($2n = 50$) with one set of chromosomes from northern redbelly dace and the other from finescale dace; some of these hybrids are triploid ($3n = 75$), however, and some are even mosaics (with some diploid and some triploid cells and tissue in the same fish) (Joswiak et al. 1986, Goddard et al. 1989, Schlosser et al. 1998). Each of these hybrid populations may represent a different self-perpetuating lineage. A few of these hybrid specimens have been collected from Montana (Brown 1971) and Colorado (Woodling 1985); to date no specimens thought to be "pure" finescale dace have been taken in those states. The hybrid populations appear to be most prevalent in habitats that are less than ideal for finescale dace. Hybrids are rare throughout most of the main portion of the range of these syntopic species; for example, Stasiak (1972) found no hybrids present in Minnesota beaver ponds despite abundant populations of both dace species. The presence of any significant number of hybrid individuals can thus be taken as a sign that the habitat may be disturbed somewhat or at least not ideal.

Dace populations were forced south into several different refuges during the last Ice Age advance (McPhail 1963, Cross 1970). Dace followed the melting ice as they dispersed back north via many routes (Cross et al. 1986). Long after the last glacial retreat, we now have isolated populations of northern redbelly dace that exist in springs or seeps in Nebraska, Colorado, and South Dakota. In many cases these populations have been separated and isolated from other dace populations for thousands of years. The dace may have had sufficient time in isolation for selection processes to allow genetic changes, and many of these regional populations may be uniquely adapted to the local ecological conditions. Genetic comparisons of northern redbelly dace populations would be a key to understanding the evolutionary implications, particularly in Region 2. Potential research projects along these lines have been discussed, but few data of this type have been reported. Perhaps this would be one type of research that should be a priority funding measure.

Life history characteristics

Several studies have reported data on the age and growth of northern redbelly dace. In the one study conducted on a population in Region 2, Bestgen (1989) collected data from 247 specimens from Garber Creek in Colorado. He found that the species lived up to three years. The largest female reached 52 mm (2.05 inches) standard length (SL), and the largest male reached 50 mm (2 inches) SL. Northern redbelly dace in Wisconsin lived to a maximum age of 4 years and reached a maximum SL of 62 to 77 mm (2.4 to 2.8 inches) (Becker 1983). Females tended to live longer and reach a greater size than males. The combined data from these reports were used to construct the Matrix Population Analysis of Population Demographics for northern redbelly dace (**Appendix A**). Based on this information, an important conclusion would be that a northern redbelly dace population could withstand a year or two of poor reproductive effort and still recover due to a good number of age II and III fish that would still be present. Likewise, three poor years in a row would be quite detrimental to maintaining the size of the population. This can also be seen from the envirogram (**Figure 7**) and the life cycle diagram and analysis of the demographic matrix performed by David McDonald (**Appendix A**).

Ecological influences on survival and reproduction

Mortality of northern redbelly dace may be due to many conditions including predators, parasites, disease, food abundance, and competition; in some situations, human harvest may take a toll. Abiotic stressors such as drought, temperatures, and habitat availability are also important factors controlling reproductive success. Northern redbelly dace in the Great Plains are restricted to relatively small regions where ecological conditions remain much as they were during the cooler and wetter immediate post-glacial times. Suitable habitat for this species in this region has been undergoing a natural contraction as the climate has warmed and become drier (McPhail 1963). In this region, the most critical ecological conditions for this species are probably a constant flow of cool groundwater and an undisturbed fish community (Stasiak 1972).

Social pattern for spacing

The northern redbelly dace does not display territorial behavior; there is no defense of nests or feeding areas. Adult fish are usually in loose schools comprised of individuals of mixed sizes and ages.

Patterns of dispersal of young and adults

Few studies have dealt directly with dispersal of either young or adult northern redbelly dace. Observations suggest that newly hatched fish are usually restricted to areas of heavy cover and reduced current. This is important to reduce predation and to provide habitat and substrate used by plankton, the main food source for young northern redbelly dace. As the fish mature and reach about one year of age, they become much stronger swimmers and gradually move out into more open water. Schools of adult fish are generally mixed with respect to age and size. In beaver ponds, dispersal occurs when breaks appear in the dam structure, allowing the water in one isolated pool to connect to others in the system. In streams, flooding would be the prime dispersal agent, carrying the young fish especially to downstream areas. Adult fish in streams probably swim upstream; they prefer cool springs or seeps with reduced current flow and heavy cover and the absence of predator fishes, conditions most likely to occur in small streams.

Spatial characteristics of populations

Since the populations of northern redbelly dace are usually in areas of spring seeps, beaver ponds, and small streams, they tend to be very isolated from other demes. They can disperse at times of flooding and high water conditions, but these events probably have become reduced in the centuries since the last glacial retreat from the Great Plains. Periodic drought conditions on the Great Plains undoubtedly diminish suitable habitat for these fish (Cross et al.1986). Demes have become reduced and isolated from each other and from the populations comprising the main range of this species to the north. The result is little genetic exchange between populations in this region. The study of the population genetics of these isolated populations is hereby identified as perhaps one of the most critical of the future needs assessment (Meffe 1986).

Limiting factors

Probably the main factor limiting northern redbelly dace populations in this region is availability of suitable habitat. The optimal habitat for northern redbelly dace would be swampy or marshy, shallow-water areas fed by groundwater with heavy vegetation and brush. Few (if any) large predatory fish species would be present. Beaver ponds in forests with good spring flow at the head of small creeks would be the ideal situation.

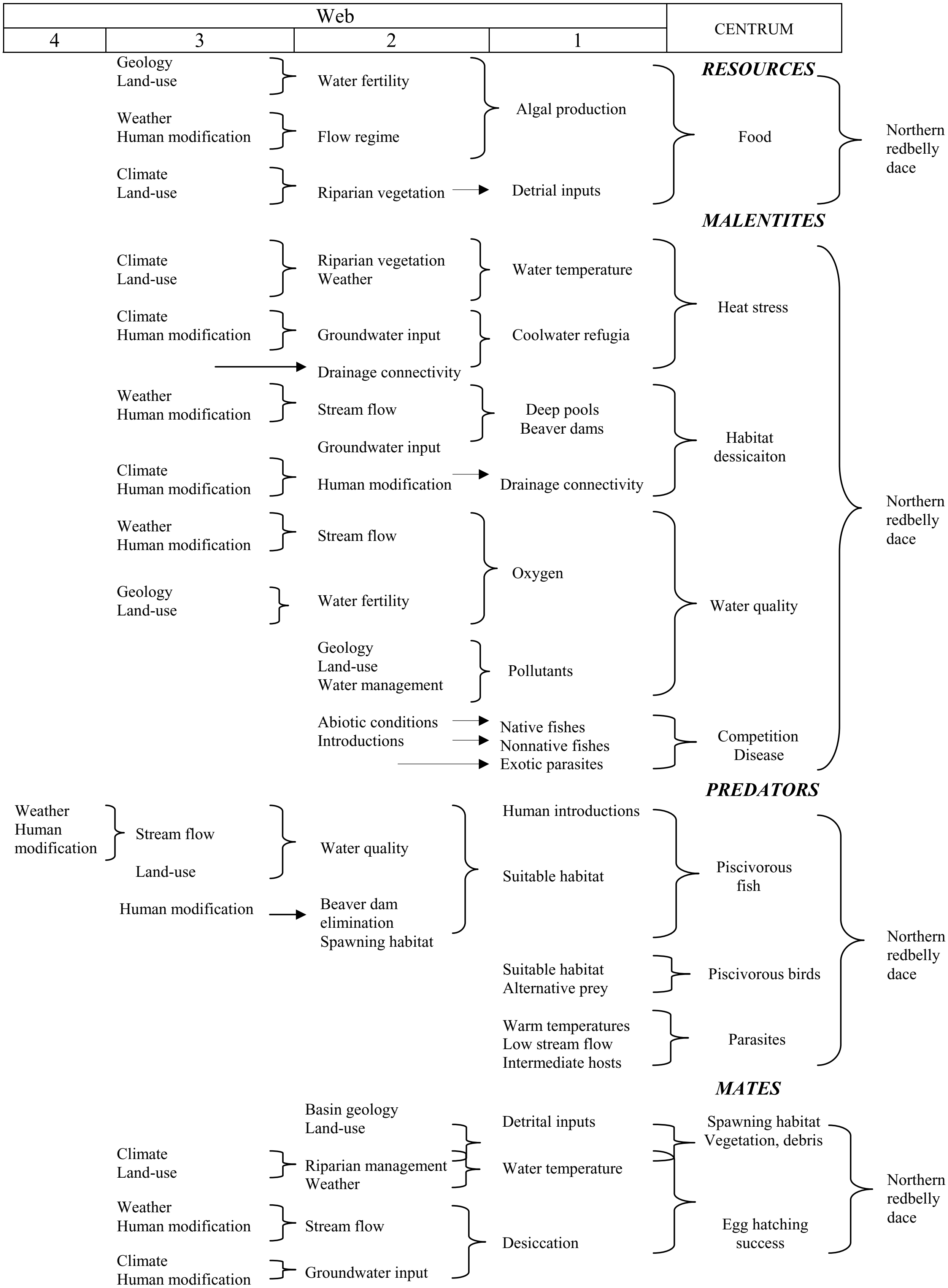

Figure 7. Envirogram for northern redbelly dace describing the complex relationships of food (Resources), threats (Malentities), ecological (Predators) and demographic (Mates) factors influencing populations.

The Sandhills region of Nebraska and South Dakota still contains many permanent groundwater sources, fed by the High Plains Aquifer (Bleed and Flowerday 1989). However, as the Great Plains have gradually become warmer and drier over the centuries since the last glacial retreat from this area, conditions have naturally become less suitable for this dace species (McPhail 1963), and populations have been reduced to isolated, small pockets of spring flows (Clausen and Stasiak 1994). Many of these seeps form the headwaters of small first order streams, or form small seepage lakes. More recently, European settlement of this region has caused high demand for the permanent sources of cool, clear groundwater. Much of it is pumped for irrigation, or used for domestic or municipal water supplies; in many places, spring seeps have been impounded to form relatively large reservoirs. The result of this combination of natural and human activities is a reduction in the aquatic habitat suitable for dace species.

Very frequently the remaining relatively natural small streams have been stocked with game species of large predatory fishes (e.g., trout, pike, sunfish) that will tend to eliminate native minnows; this is especially detrimental to the colorful dace species (Clausen and Stasiak 1994, Whittier et al. 1997).

Community ecology

Predators

Under natural conditions, the chief vertebrate predators of northern redbelly dace are probably piscivorous birds. Belted kingfisher (*Megaceryle alcyon*) and great blue heron (*Ardea herodias*) have been observed actively feeding on schools of these minnows (Stasiak 1972, Steinmetz et al. 2003). The kingfishers are especially attracted to the habitat favored by the dace; the clear, shallow water and brightly colored minnows provide easy prey for this bird (Hamas 1994). Kingfishers perch on dead trees in beaver ponds and use them as platforms from which to dive into schools of dace. Dace are about the ideal size for a kingfisher, but herons of several species can also take these minnows. In deeper lakes, fish-eating birds such as loons, ducks, and cormorants can also quickly reduce dace populations. Fish-eating snakes and turtles, as well as bullfrogs, are common predators in dace ponds and streams. Mink (*Mustela vison*) and raccoons (*Procyon lotor*) will undoubtedly eat northern redbelly dace.

Carnivorous aquatic invertebrates can also feed heavily on dace (McCafferty 1998). Predacious diving beetles of the Family Dyticidae (larvae are commonly called water tigers) and giant water bugs of the Family Belostomatidae 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 total length; they commonly eat aquatic vertebrates such as frogs and tadpoles, snakes, and fishes. Other insects such as dragonfly larvae (Odonata) and smaller bugs (Hemiptera) such as water scorpions and backswimmers will also include dace, especially young individuals, in their diet (Borror and White 1970, Stasiak 1972).

In most situations, the one type of predator that dace do not have to deal with is large predatory fish species. The small and shallow nature of the ponds and streams containing dace generally are not suited for large predatory fish species. The temperature ranges and potential low oxygen levels common to dace habitat also tend to eliminate large fish species. Dace ponds are often subject to heavy ice and snow cover in the winter. Ice may reduce the volume of water substantially, and little oxygen is present in the remaining fluid water. Some of the fish species that are naturally associated with northern redbelly dace, especially mud minnows and green sunfish, can occasionally eat some of the dace. When they occur together, large creek chubs are very capable of eating small dace (Stasiak personal observation). These naturally occurring fish predators will play a role in eating very young dace, but their overall effect is probably very small compared to the collective effect of the predatory insects. However, as discussed in the Threats section of this assessment, introduced species of large predatory fishes (sport fishes) will have a serious effect on dace populations.

Competitors

Northern redbelly dace are hardy fish that can survive environmental extremes of oxygen, pH, annual temperatures, and ice cover conditions that few other species can handle. They are usually associated with a small number of other native fish species that are adapted to similar conditions. In the Great Plains region, northern redbelly dace typically occur with finescale dace, brook stickleback, pearl dace, fathead minnow, and brassy minnow (Baxter and Stone 1995, Isaak et al. 2003). 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.

Northern redbelly dace do not appear to thrive in large streams, large lakes, or any other habitat that harbors a large, diverse fish community. This is most likely due to a combination of predation and competition from other minnow species (Stasiak 1972). Northern redbelly dace do occur, however, in small kettle lakes (such as Deming and Arco in Itasca State Park in Minnesota), where there are extensive mats of vegetation along the shorelines, and no species of large game fish. In lakes large enough to contain permanent populations of large piscivores (e.g., bass, trout, sunfish, pike), small populations of northern redbelly dace may be present if the lake has an extensive shoreline vegetation mat (Stasiak personal observations); dace activity is more or less restricted to this zone.

In their preferred habitat of small ponds and creeks, northern redbelly dace take on the niche of sight-feeding planktivores, selecting individual items of small plants and animals from the plant mat. The other fishes that are commonly found with this species usually feed elsewhere on the food chain. Finescale dace and creek chubs may be found in such "mixed" communities at times. Although they may consume some of the same food items as northern redbelly dace, they do not appear to have a negative impact on northern redbelly dace populations.

In Region 2, another competitive situation needs to be examined. While the feeding niches of finescale and northern redbelly dace generally do not overlap (Stasiak 1972, Litvak and Hansell 1990, Gauthier and Boisclair 1996), the hybrid fish are intermediate and can feed on diverse items that also include much of the diet of both parental species. Therefore, gynogen fish of hybrid origin (*Phoxinus neogaeus* x *P. eos*) may be considered a separate species for matters of competition. Since these fish reproduce clonally, they may also have a reproductive advantage. The result is that pure dace populations are usually absent or very reduced in locations where the hybrid fish exist (Stasiak 1987).

Parasites and disease

Parasites and disease appear to have a minimal impact on northern redbelly dace. Bangham and Venard (1946), Hoffman (1970), Stasiak (1972), and Mayes (1976) have all studied parasites of *Phoxinus* dace. Hoffman (1970) listed three species of protozoans and two species of larval trematodes (*Uvulifer ambloplites* and *Echinochamus donaldsoni*). The former of these worms is often referred to as "black grub" or "neascus"; the adult is very common as a parasite of the throat of fish-eating birds. The larvae are very 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 very common throughout the Midwest to see sport fishes such as pike, bass, perch, and sunfish covered with these small black spots. Stasiak (1972) found that fathead minnows, sticklebacks, and mud minnows in French Creek beaver ponds in Minnesota were very frequently and heavily infected with this parasite. Northern redbelly dace, meanwhile, were rarely infected, with less than 1 percent of the population affected. Affected individuals usually have a light parasite burden and do not appear to be impaired in any way.

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 Nebraska reveal that *Phoxinus* are also almost free of other common ectoparasites such as the copepod *Lernaea*.

Mayes (1976) described some new species of monogene flukes from the gills of dace collected in Nebraska. Upon subsequent examination of the fish host specimens, this author identified the host, and these actually were the hybrid dace (*Phoxinus neogaeus* x *P. eos*). These small worms may infect parental northern redbelly dace. These minute gill parasites usually do not affect the host fish under normal conditions.

Conservation

Threats

Paralleling decreases in terrestrial biodiversity, the principal reasons for fish species decline, in general, are the loss, modification, and fragmentation of habitat, and the introduction of non-native species (Moyle 1976, Cross and Moss 1987, Warren and Burr 1994, Masters et al. 1998). These factors are especially important in the case of northern redbelly dace conservation in Region 2 where we presently face ever-increasing human demands for water resources and continued landscape modification and where streams and ponds fed by cool, clear groundwater are often stocked with sport fish. Furthermore, the CWCS plan for Nebraska identifies the following threats: de-watering, siltation, interruption of stream movement, and introduced species (http://www.teaming.com/state_cwcs/nebraska). The Colorado CWCS plan identifies loss of in-stream flows, pollution causing water quality degradation, overgrazing in riparian areas, and in-stream barriers as threats to native fishes (http://wildlife.state.co.us/WildlifeSpecies/ComprehensiveWildlifeConservationStrategy/). In addition to these anthropomorphic changes, long-term climate change models predict a drier and warmer climate, especially compared to the climate of the past few thousand years.

Unlike most Great Plains stream systems, the headwater streams occupied by northern redbelly dace demonstrate less stochasticity in drying and intermittency (per annum) due to inflows from abundant groundwater sources. These streams have been remarkable in the constancy of their flow (Bleed and Flowerday 1989). Over the last 50 years, however, groundwater pumping and water diversions have occurred extensively across the Great Plains, and such activities may have deleterious consequences for northern redbelly dace viability within Region 2. Fortunately, the ecoregion with multiple extant populations of northern redbelly dace is the Sandhills of Nebraska and South Dakota where groundwater depletion is currently not a threat to stream systems because the edaphic conditions are not suitable for row crop agriculture. However, along the margins of the Sandhills ecoregion, particularly the Upper Niobrara River valley, center pivot irrigation of alfalfa and pasture has increased substantially (Bleed and Flowerday 1989). In addition, groundwater use for agricultural production exists in the sub-watersheds occupied by northern redbelly dace in South Dakota and Colorado. In the future, if groundwater withdrawals exceed annual recharge rates, aquifer-dependent headwater streams and natural lakes will be adversely affected. Maintenance of this hydrologic pathway is critical since the persistence of northern redbelly dace at specific sites during extended dry periods requires groundwater inflows.

Besides direct groundwater pumping, instream diversion units appropriate water for agricultural products or municipal supplies both in the Upper Niobrara River and Platte River drainages in Nebraska and Colorado. These activities modify flow regimes within these drainages and dewater sections of streams. In these drainage systems, decreased flows have reduced channel scour and affected the spatio-temporal heterogeneity of floodplain habitats. Future water diversions in the northern Black Hills will probably fragment remaining populations of this species and most likely cause extirpation of extant northern redbelly dace populations.

Hydrologic alteration has occurred in the Sandhills ecoregion, albeit in a different form. In this ecoregion, the modification of sub-irrigated meadow hydrology by stream channel ditching and water control structure placement and operation has modified nearly every Sandhills stream (Bleed and Flowerday 1989). These activities have contributed to habitat fragmentation and the disruption of stream ecosystem processes. Dace still persist in Sandhills streams despite ditching and water control operations that have created homogeneous instream habitat and incised channel morphology. Most likely species viability has been maintained despite these alterations because of the combination of habitat created by culvert type drop structures, long periods between instream excavation episodes, and late winter-early spring precipitation that occurs every 5 to 7 years, producing overbank flooding. These activities can also modify stream temperatures and trap sediment.

An essential component linked to the abiotic hydrologic process of the headwater systems and spring-fed lakes that northern redbelly dace inhabit is the presence of beaver activity (Olson and Hubert 1994). As has been observed further north in Minnesota, Wisconsin, and Canada (Stasiak 1972, Tonn and Magnuson 1982, Schlosser 1995), *Phoxinus* species readily use beaver pond environments. Where the northern redbelly dace does occur, it is more commonly collected as vegetation is established around the beaver dam and instream vegetative debris accumulates with beaver pond age (Stasiak personal observation). The interaction of beavers with other biotic (predation) and abiotic (physiographic, vicarance) components has a great impact on the assemblage and structure of fish communities (Jackson et al. 2001). These "ecosystem engineers" have strong effects on physical, chemical, and biological attributes within the aquatic ecosystem (Naiman et al. 1988, Schlosser and Kallemeyn 2000). Work in north-temperate beaver bog streams and lakes systems inhabited by northern redbelly dace and other cyprinid dace species conclude that beaver activity is a major factor in fish dispersal (Schlosser 1995), recolonization dynamics (Schlosser and Kallemeyn 2000), and fish community assemblage (Tonn and Magnuson 1982, Angermeier and Karr 1984) in small streams. The mosaic of aquatic patches created by beaver activity is temporally and spatially dynamic, a series of shifting successional habitats of flooded, deep-water, semi-permeable collapsed ponds, and debris-laden streams. Not surprisingly, this phenomenon is observed both in the Sandhills and the northern Black Hills ecoregions, where beaver have only recently returned in significant numbers, but with some interesting adjustments and surrogates.

Interestingly, in the Sandhills ecoregion, the L-shaped culvert drop structures placed in headwater streams appear to be surrogates for beaver dams. Both on the upstream and downstream end of these water control structures, pools form and they are dominated by dace species, particularly the large pools downstream of the structure. Additionally, the small, shallow impoundments or spring-fed lakes fitted with headgates found in the northern Black Hills mimic beaver ponds. Although these anthropogenic structures appear to violate the condition of temporal heterogeneity, at least for the Sandhills streams, the water control structures are designed and used to manipulate water levels, thus varying flows during certain times of the year. Moreover, because of the fine sandy soils of the sub-irrigated meadows, control structures do erode out of place and are occasionally blown-out by high flows. In this way they can mimic the natural changes over time that resulted from beaver activity in these stream systems. While some resource managers may find these anthropogenic structures appealing substitutes for beaver activity, extreme caution should be applied.

Water improvement projects such as channelization and placement of water control structures are very common in the Sandhills ecoregion, and these negatively affect stream hydrology. Conversely, impoundment and reservoir development here is scarce. This is in contrast to the northern Black Hills ecoregion, which has many stock dams, small impoundments, and larger reservoirs. Unfortunately, these larger bodies of water tend to dewater downstream stretches of streams, degrading habitat and further fragmenting fish populations. While they appear to mimic beaver pond areas, these larger bodies of water simply retain too much water and may disrupt groundwater flow and recharge patterns. Perhaps even worse, they provide habitat for non-native fishes, particularly introduced piscivorous sport fishes.

Studies in the north-temperate region clearly demonstrated the profound effect that non-native predator fish have on cyprinid communities in small lakes (He and Kitchell 1990, Findley et al. 2000, MacRae and Jackson 2001). Indeed, Jackson (2002) listed a set of species (northern redbelly dace among them) as being highly vulnerable to centrarchid (sunfish family) predation. Lakes dominated by salmonids (trout) contained significantly more cyprinid species than centrarchid-dominated lakes. This phenomenon is best explained by overlapping habitat between centrarchids and cyprinids, particularly in the littoral zone. Trout have limited overlap in summer habitat with cyprinids, at least in lake environments (Jackson 2002). Thus, impoundments or reservoir development on streams with northern redbelly dace that experience non-native centrarchid introductions can lead to extirpation of this cyprinid species. Although impounding a stream is a modification of natural stream structure and function, northern redbelly dace do reside in some small impoundments and spring-fed lakes in Region 2. The presence and presumed persistence of this species in these artificial environments is due to the absence of centrarchids. The harsh winter conditions (extremely low dissolved oxygen concentrations) found in very small lakes usually prevent centrarchids (particularly bass) from establishing themselves (Schlosser 1995, Jackson 2002).

Non-native predator species also threaten the viability of stream-dwelling populations of northern redbelly dace. Unlike lake populations, the stream populations are equally vulnerable to centrarchids and salmonids. Whether stream systems with cyprinids have been altered by impoundment structures and stocked with centrarchids or whether they have been used as trout-receiving waters by resource agencies, native headwater cyprinids (including northern redbelly dace) are either absent or extremely low in number (Cunningham and Hickey 1995). Northern redbelly dace have been collected in the headwaters of the Niobrara River near the Wyoming border, but they are absent just a few miles downstream at Agate Fossil Beds National Monument (Stasiak 1976, 1989). This is likely due to the presence of stocked brown trout (*Salmo trutta*), pike (*Esox lucius*), bass (*Micropterus salmoides*), and bluegill (*Lepomis macrochirus*). Unlike in lentic systems, trout in lotic environments have a positive habitat association with the headwater cyprinid community (Jackson 2002). Direct trout predation has been observed in some Sandhills streams (Cunningham and Hickey 1995) where trout occupy pool and undercut bank habitats. Indirect effects on northern redbelly dace would include territorial displacement and competition for food resources (Shields 2004).

Clearly, most introductions and modifications of lotic habitat to deeper lentic habitat that allow non-native piscivorous to persist are detrimental to northern redbelly dace populations. Non-native species can affect native species through a number of mechanisms including predation, competition, habitat alteration, pathogen transfer, and behavioral displacement (Ault and White 1994). Jackson (2002) described the risks and consequences of introducing fish to assemblages with small-bodied fishes in greater detail, but these include resource compaction, increased intra- and interspecific competition, and stress. Studies with other cyprinid species in lotic systems strongly link the disappearance of certain cyprinid species and an alteration in small stream fish community assemblage to the presence of introduced piscivorous sport fishes (Winston et al. 1991, Schrank et al. 2001, Mammoliti 2002). Moreover, studies indicate that non-native species disrupt drainage network connectivity across the landscape, creating barriers to fish migration and effecting recolonization (Fausch and Bestgen 1997) and possible exchange of genetic material. Another potential consequence of fish introductions is the effect of potential pathogen transfer from non-native fish species to the native fish community or other biota within the watershed (i.e., amphibians). These non-native species may play a role in the dispersal of pathogens (Kiesecker et al. 2001). Shields (2004) documented several cases of parasite (i.e., nematodes, trematodes, and 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, which ultimately affects 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).

A significant unknown element in the long-term viability of headwater fish species is the synergistic effects of multiple stressors. By itself, extended severe drought may have only modest effects on the long-term viability of fish assemblages (Matthews and Marsh-Matthews 2003). Combined with groundwater pumping, irrigation, and water diversion, however, long-term drought may severely deplete a population or extirpate a species on a regional basis. Couple these phenomena with climate change predictions, and the prospective for long-term survivability is difficult to assess (Jackson and Mandrak 2002). However, given the already highly fragmented distribution of northern redbelly dace within Region 2, this species would be adversely affected by the combined forces of future increased groundwater extraction, water diversion, and climate change-induced, extended dry cycles.

Two other human-related activities are generally cited as common causes of native Great Plains fishes declines: pollution and overharvest. Pollution does not currently appear to be a major problem for northern redbelly dace populations in Region 2, but it is always something that needs to be monitored. It is possible that future mining, logging, and/or agricultural operations could release harmful chemicals into the streams, watersheds, or groundwater. Dace need relatively clear water; anything that would cause sustained turbidity (e.g., frequent erosion, siltation, prolonged use of a water source by cattle) affects their ability to find mates and food items. In terms of direct harvest by humans, anglers often use wild minnows as bait. Northern redbelly dace are known to be an excellent bait species and are relatively easily to find given their small, confined habitats. They are frequently sold by bait dealers in the Ainsworth, Nebraska area. It is possible that this commercial harvest activity could significantly impact small, isolated dace populations. Commercial harvest of northern redbelly dace in Region 2 should probably be prohibited.

Conservation Status of Northern Redbelly Dace in Region 2

Populations of northern redbelly dace throughout Region 2 appear to be declining (Clausen and Stasiak 1994), and given the isolated position of these populations and the unique habitat types required by this relict species, long-term viability is questionable. The area occupied by northern redbelly dace within Region 2 Forest Service units is quite limited. While the streams in the Sandhills ecoregion account for the vast majority of northern redbelly dace populations in Region 2, the species is not present within the Bessey unit of the Nebraska National Forest, the Samuel R. McKelvie National Forest, or the Oglala National Grassland (Cunningham and Hickey 1995). Bestgen (1989) found that the Colorado populations occur close to, but not on, USFS land in the upper Platte River drainage (Garber Creek, Jackson Creek, and Plum Creek). Cunningham (1995) collected this species from the headwaters of the Niobrara River in western Nebraska, but it has never been reported from the state of Wyoming. Clearly, the first attempt at developing a conservation strategy for this species on National Forest System lands is to determine exactly which, if any, potential sites actually have northern redbelly dace populations.

All three of the Region 2 states that have northern redbelly dace populations currently designate this species at high levels of conservation concern. This does confer limited conservation protection, yet the species is still vulnerable to extirpation by hydrologic modification of stream systems and presence of non-native species.

Potential Management of Northern Redbelly Dace in Region 2

Implications and potential conservation elements

Conservation of the northern redbelly dace will require resource managers to consider the unique habitat features utilized by this species across a mosaic of heterogeneous shifting habitats that are highly dynamic in space and time. In addition, the presence of non-native species, particularly piscivores, has a major impact on the persistence of northern redbelly dace populations. Thus, the management of northern redbelly dace should focus on conserving natural system processes in streams and the prevention and control of non-native species introductions. Specific management strategies for this species include:

- ❖ Prohibit the stocking of non-native species within aquatic ecosystems
- ❖ Renovate natural spring-fed lakes containing non-native fish species and restock with northern redbelly dace from the nearest native source population
- ❖ Protect spring sources flowing into naturally meandering streams, particularly if beaver activity is present
- ❖ Manage for the restoration of beaver activity within watersheds
- ❖ Develop watershed-based management strategies with partnering organizations and private landowners for connectivity and natural stream ecosystem processes
- ❖ Restrict commercial harvest of northern redbelly dace by bait dealers

Currently, a vast majority of Great Plains streams of high water quality (cold and clear) are managed for trout at the expense of native fishes, including northern redbelly dace (Erickson et al. 1993). The presence of non-native species (salmonids and centrarchids) has probably been a principal reason for northern redbelly dace decline in aquatic systems in both Nebraska and South Dakota. Resource managers need to be cognizant of the effects of non-native species introductions and their management on aquatic ecosystems (Minckley and Deacon 1991, Whittier et al.1997).

Concurrently, hydrological modifications (e.g., water development projects, sub-irrigated meadow alterations, groundwater pumping) have altered aquatic systems throughout Region 2. Future human water demands and continued drought conditions coupled with the effects of predicted climate change could jeopardize remaining northern redbelly dace populations. Resource managers may be tempted to build habitat for this species by impounding water on sections of streams inhabited by this species. Conceptually, this may be appealing. However, these created ponds would need to be designed to mimic beaver pond morphology, hydrologic retention and flow, and to provide unsuitable habitat for piscivorous fishes. Moreover, simply creating a pond or hole on the landscape is not ecologically sufficient to ensure the viability of northern redbelly dace; connectivity to other habitats and resources is essential for various life history demands such as ontogenetic feeding shifts, spawning habitat, dispersal and segregation of larvae, juveniles, and adults. Resource managers must recognize and understand the spatial arrangement and temporal dynamics of interacting processes at hierarchical scales (Frissell et al. 1986). For example, beaver pond placement, morphology and successional shift within the landscape mosaic will influence northern redbelly dace population establishment and persistence greatly (Schlosser and Kallemeyn 2000). Moreover, the terrestrial characteristics across the land-water template within a drainage unit will affect the hydrology, sediments, nutrient inputs, and litter and detritus composition (Platts et al. 1983, Poff and Allan 1995). Several conceptual models of stream fish population ecology and life history linking key ecosystem process interacting across multiple scales have been developed (Schlosser and Angermeier 1995, Labbe and Fausch 2000). They would serve as ideal guides for resource managers to use in understanding and assessing the necessary and sufficient elements for northern redbelly dace conservation.

Attempts should be made to maintain the natural flow regime in streams where this species resides and to manage for the expansion of beaver activity within these watersheds. The expansion of beaver activity is a difficult one for private landowners since the result of such activity can back water up in unwanted locations or saturate soils. However, on USFS administered lands, expanded beaver activity, in general, should not affect other uses such as grazing and timber harvest. Beaver sites, particularly those areas exhibiting year round spring discharge that flows into a defined meandering stream channel, should be actively managed (Snodgrass and Meffe 1998). For example, absolute unrestricted use of beaver ponds by cattle (particularly during the warm season) could lead to excessive sedimentation, increased turbidity, algal growth, and nutrient concentrations. Managing for only limited temporary access by cattle would be more ecologically sound. However, resource managers must focus their conservation efforts beyond individual pools. Viability of northern redbelly dace populations will require restoring the ecological processes that create and maintain beaver pond habitats across the landscape plus their associated colonization pathways. Ultimately, management actions that recognize and promote natural ecosystem process (i.e., flow regimes, biotic and abiotic interactions) within a landscape context that integrates preservation, maintenance, and restoration will be successful in meeting northern redbelly dace conservation goals.

While northern redbelly dace are present in several states within Region 2, much of the known occupied habitat is outside the national forest boundaries. Efforts are needed to work in conjunction with other federal agencies, state resource agencies, non-profit conservation organizations, and private landowners to develop and manage stream systems within Region 2 on a watershed basis, and these efforts should focus on native fishes (Vanderbush 1999).

Tools and practices

Inventory and monitoring

Apparently systematic inventory and monitoring of northern redbelly dace populations or inhabited watersheds do not occur on National Forest System lands within Region 2. Inventory efforts to date have focused on the presence or absence of this species as part of statewide stream fish surveys or ecoregional sampling efforts. The author of this report has conducted periodic sampling throughout Region 2 for the past four decades.

Although Kansas has had numerous organized fish collection efforts over the last century, the northern redbelly dace has never been documented there. Similarly, fish collections from Wyoming have never recorded this species. Fish surveys in Nebraska, South Dakota, and Colorado have been spotty and limited. Johnson's (1942) survey of Nebraska fishes serves as the baseline for information in this state. Northern redbelly dace have apparently become extirpated in several of his sites in eastern Nebraska (Madsen 1985). Bliss and Schainost (1972) conducted fish surveys for all the major stream systems in Nebraska, but specimens were not saved and much confusion still remains concerning the identities of the sampled fishes. The Sandhills ecoregion was extensively sampled as part of a Nebraska natural heritage program inventory in the 1990s (Cunningham and Hickey 1995, Cunningham et al. 1995). This species was recorded from the headwaters of the Niobrara River in Nebraska during two inventories; however, Patton (1997) has not recorded this species from the springs forming the headwaters of the Niobrara River just across the state line in Wyoming. No systematic, statewide fish survey has been conducted in South Dakota in over fifty years, but smaller projects or inventories have recently recorded northern redbelly dace (Eiserman 1996, Meester 1998). Additional references to surveys were found in the ecoregional conservation plan for the Black Hills (Black Hills National Forest 1996, Hall et al. 2002). Specific survey information post- Bestgen (1989) in Colorado was not found.

Population or habitat management practices

McMahon et al. (1996), Bain and Stevenson (1999), and Hansen (2001) listed some methods for identifying different types of streams for management implications. Attempts at stream or hydrologic restoration are being made in some areas of Region 2. In the Sandhills ecoregion, several sub-irrigated meadow hydrologic restoration projects have been undertaken that involve modifying stream and channel hydrology. (website: http://www.sandhillstaskforce.org). However, the efficacy of these projects to restore and enhance the native headwater fish assemblage is unknown; post-construction research and monitoring has not been conducted at these sites.

Additional opportunities for restoration exist in Nebraska and South Dakota, specifically the removal of non-native species from dace habitat. At the very least, there should be no additional stockings of these sport fish. We are not aware of any attempts, however, within the South Dakota Department of Game, Fish and Parks or the Nebraska Game and Parks Commission to conduct such restoration or to limit the introductions. This type of management for non-game species has traditionally not been popular with anglers.

The restoration and management of natural ecosystem processes to enhance northern redbelly dace populations is needed. Historically, beaver were abundant across the stream and river systems of the Great Plains (Naiman et al. 1988, Parrish et al. 1996), and management strategies should be developed that encourage further expansion of beaver within the

Region 2 (Snodgrass and Meffe 1998). These adopted conservation measures should ultimately allow for the creation of these successional aquatic mosaics across the landscape. Developing conservation strategies to abate such multiple stressors to species viability will need to incorporate the elements of connectivity, spatio-temporal habitat dynamics and life history processes, as well as their associated linkages. How multiple stressors affect these ecological variables must be evaluated.

The Colorado Division of Wildlife has initiated a program to raise rare fishes in a captive breeding program at their Native Aquatic Restoration Facility in Alamosa. Northern redbelly dace have been successfully reared at the facility and stocked into natural waters in at least four locations (Kreiger personal communication 2006, Mix personal communication 2006). These sites include ponds at the Bureau of Land Management Rocky Flats area; wetlands on the Coors property near Golden; some ponds in Denver proper; and wetlands on the Pine Cliff Ranch west of Boulder, which is the original location of the genetic stock of northern redbelly dace in the hatchery. The practice of using hatchery-reared fish to restore natural populations is controversial due to the difficulty of maintaining the genetic integrity of the natural populations (Nelson and Soule 1987). Hatchery rearing may be a necessary tool to restore fishes to native habitat where they have been extirpated, but care must be taken in choosing the genetic stock most similar to the original population. Whenever possible, it would be much better to manage by enhancing habitat for extant populations.

The aquatic conservation assessment portion of the Black Hills ecoregional plan (Hall et al. 2002) has identified areas of biological significance based partly on presence within the watershed. Given that much of the watershed is private property, management at the watershed level will require a partnership of federal and state resources agencies, non-profits, and private landowners working across state boundaries to develop and implement a conservation strategy for northern redbelly dace.

Information Needs

Because of the unique position and habitat requirements that the northern redbelly dace has within a stream system, further inventory targeting this species is relatively straight forward. Additional inventory efforts should target Plum Creek and its associated tributaries to the South Platte River in Colorado, and attempts should be made in conjunction with USFS partners to inventory stream sections on private property in the Plum Creek watershed. Although sampling has been conducted in the USFS units in the Nebraska Sandhills (Cunningham and Hickey 1995), a systematic inventory at spring pool discharge areas in the rivers bordering the Halsey and McKelvie units would close a data gap for this species in the ecoregion.

The Nebraska CWCS plan identifies the need for the following information: determine age structure, recruitment, population dynamics, seasonal movement, and specific habitat use (http://www.teaming.com/state_cwcs/nebraska).

Virtually no data are available regarding the population dynamics of northern redbelly dace in Region 2. Information concerning the distribution, population size, and recruitment success is needed to develop a conservation management plan for this species in streams that flow through National Forest System lands. Basic biological information, such as the total number of eggs produced by a single female dace during the extended breeding season, is needed. Additional information needs for this species are the barriers to fish movement (e.g., impoundments, culverts, non-native species) among habitat types and recolonization areas. Effective conservation planning requires this type of information to ensure the viability of the species.

Northern redbelly dace populations occur in discrete, isolated demes on the Great Plains. Research on the genetic makeup of these populations and how they are related to each other and the fish found in the main portion of the range should be a priority of any conservation effort (Toline and Baker 1994).

Monitoring activities associated with northern redbelly dace are needed throughout Region 2. Various resources and studies are available to serve as a template for designing a monitoring strategy for this species. Fish censusing techniques are well described in Hays et al. (1996) and Hubert (1996), and protocols and methods for assessing aquatic habitat and fish communities are available in Hankin and Reeves (1988), Simonson et al. (1994), and various environmental monitoring and assessment program protocols of the U.S. Environmental Protection Agency (Barbour et al. 1999). Full adoption of these methods is probably unnecessary; rather, a modification of one or a combination of the methods listed above would serve USFS resource managers well.

Information management and document archiving are priority needs. Much of the location and ancillary data recorded at the time of northern redbelly dace collections are recorded in the various natural heritage database systems of individual states comprising Region 2, however location information found in Isaak et al. (2003) is not found in heritage database systems or in the literature. Every attempt should be made to obtain any records detailing any transplant activities (e.g., source of transplants, how many individuals, dates) and to verify with the appropriate biologists involved in these efforts the actions taken at the time. All of this should be placed in the natural heritage database of Colorado and South Dakota given the proximity of state borders and a shared watershed. All notes, field forms, communications, and notations from any state or federal sampling effort undertaken in the past and all future inventories and monitoring should be shared with natural heritage programs for database archival. The CWCS plan for Colorado identifies an overall need for an inventory system to better integrate and share data among all entities conducting species and habitat surveys (http://wildlife.state.co.us/WildlifeSpecies/ComprehensiveWildlifeConservationStrategy/).

Information on some aspects of the life history of Great Plains populations of northern redbelly dace need to be studied. This includes determining the number of eggs that are produced each year; the duration of the spawning season; their day–night activity cycle; and their dispersal mechanisms.

Definitions

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

Edaphic – due to soil or geologic conditions.

Extant – still in existence.

Extirpated – no longer existing in a particular location.

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

Gynogen – a female fish that reproduces asexually by releasing mitotic (usually diploid) eggs, which may develop with or without fertilization. In the case of these dace, the gynogens are often more abundant than the meiotic females.

Keystone species – those whose presence exerts a great effect on the other species in their community.

Lateral line – a fish organ that detects pressure waves; it runs horizontally under the skin along the side of the fish and can often be seen due to surface pores.

Lentic – standing water habitats, such as ponds, bogs or lakes.

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

Pharyngeal teeth – found on the pharyngeal arches (behind the gills) in the throat of minnows; their anatomy is species-specific (related to their diet), so these are of considerable taxonomic interest to ichthyologists.

Piscivorous – "fish eating".

Planktivorous – eating tiny plants and animals.

"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.

Schools – aggregations of individual fish in close proximity that form a single shoal, almost acting as a single large organism.

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

Sexual dimorphism – 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 A

Life Cycle Graph and Model Development

The life history data described by Faber (1985) and Becker (1983) for northern redbelly dace provided the basis for an age-classified life cycle graph that had three 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 (Cochran and Ellner 1992, 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 I 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 Faber (1985)
- Age I egg production of 410 (Becker 1983)

The size of age-classes was based on the Simpson Creek data in Wisconsin (Becker 1983). Because the model assumes female demographic dominance, the egg number used was half the published value, assuming a 1:1 sex ratio. Because the published egg value was only for larger fish (Age I, corresponding to Age-class 2 in the present model), we decremented Age 0 egg production by a factor of 0.397, close to the ratio of egg production between large and small age-classes in the more complete demographic data set available for finescale dace (Stasiak 1972). Because no survival data were available, we adjusted survival rates to produce a stable age distribution matching the age

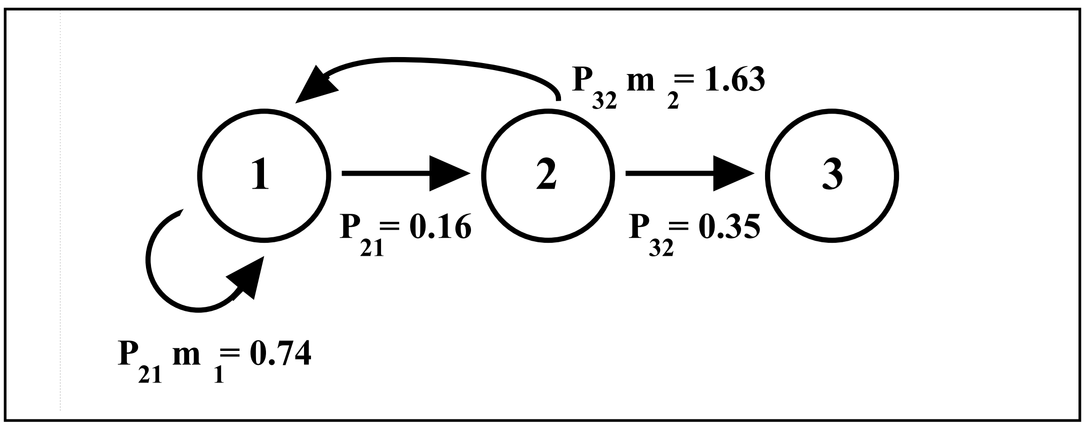

Figure A1. Life cycle graph for northern redbelly dace, consisting of circular *nodes*, describing age-classes in the life cycle and *arcs*, describing the *vital rates* (transitions between age-classes). The horizontal arcs are survival transitions (e.g., first-year survival, P_{21}= 0.16). The remaining 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 A2**.

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

Parameter	Numeric value	Interpretation
Age 1 eggs	205	Number of female eggs produced by Age I fish (Becker 1983)
Age 0 eggs	83.1	Estimated as 0.397 times published Age I egg production value
Egg to Age 0	0.0571	Survival from egg stage to Age 0 census size
m_1	0.744	83.1 x 0.0571 x P21. Eggs x egg survival x maternal survival
m_2	1.63	205 x 0.0571 x P32. Eggs x egg survival x maternal survival
P_{21}	0.144	Probability of surviving first year (Age 0 to Age I)
P_{32}	0.26	Probability of surviving the second year

structure described in Faber (1985). We also made the assumption that the long term value of λ (population growth rate) must be near 1.0.

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 1.004 based on the estimated vital rates used for the matrix. This should not be taken to indicate a 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. Therefore, the value of λ should not 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 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 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 it 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

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

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 A1**. Note that the last column of the matrix consists of zeros in order to allow tabulation of the (small) proportion of third-year individuals that just completed their final breeding pulse.

Age-class	1	2	3
1	0.744	1.63	
2	0.16		
3		0.35	

Figure A2b. Numeric values for the projection matrix.

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

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 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 "adult" reproductive females (those in Age Class 3). Therefore, it is 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 (1.29; 58.3 percent of total) is the most important. First-year fertility accounts for an additional 36 percent of the total sensitivity of λ to changes in vital rates. The major conclusion from the sensitivity analysis is that first-year survival and, to a lesser extent, reproduction are the keys 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 northern redbelly dace are shown in **Figure A4**. The λ of northern 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 79.5 percent of the total elasticity of λ to changes in the vital rates. Reproduction, particularly in the first year is the demographic parameter that warrants most careful monitoring in order to refine the matrix demographic analysis.

Age-class	1	2	3
1	**0.79**	0.13	
2	**1.29**		
3		**0**	

Figure A3. Possible sensitivities only matrix, $\mathbf{S_p}$ (remainder of matrix is zeros). The two transitions to which population growth rate (λ) of northern redbelly dace is most sensitive are in bold. Note the dominance of the value for first-year survival (Cell s_{21}), followed by first-year reproduction and the negligible contribution of second-year values.

Age-class	1	2	3
1	**0.59**	0.21	
2	0.21		
3			

Figure A4. Elasticity matrix, **E** (remainder of matrix is zeros). The population growth rate (λ) of northern redbelly dace is most elastic to changes in first-year reproduction (Cells e_{11}).

Other demographic parameters

The **stable age distribution** (SAD; **Table A2**) describes the proportion of each age-class in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SAD within 20 to 100 census intervals. For northern redbelly dace at the time of the post-breeding annual census (September in the case of the reference data), Age 0 fish should represent 82.3 percent of the population. **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 (newborn or, in this case, Age 0) 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 1.6 first-year females. The cohort generation time for northern redbelly dace is 1.3 years (SD = 0.4 years).

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 and reproduction account for 94 percent of total "possible" sensitivity. Any absolute changes in these rates will have major impacts on population dynamics.

- ❖ First-year fertility accounts for 79.5 percent of the total elasticity, almost twice the total of the elasticities for all the other transitions. 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 northern redbelly dace.

Table A2. Stable age distribution (SAD, right eigenvector). Vital rates were adjusted to yield a stable age distribution in accordance with the observed age structure (Page 228 in Faber 1985).

Age-class	Description	Proportion
1	First-year females (Age 0)	0.823
2	Second-year females	0.131
3	Third-year females	0.046

Table A3. Reproductive values for females. 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 0) age-class, which is always defined to have the value 1. Third-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	Proportion
1	First-year females (Age 0)	1
2	Second-year females	1.62
3	Third-year females	0

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