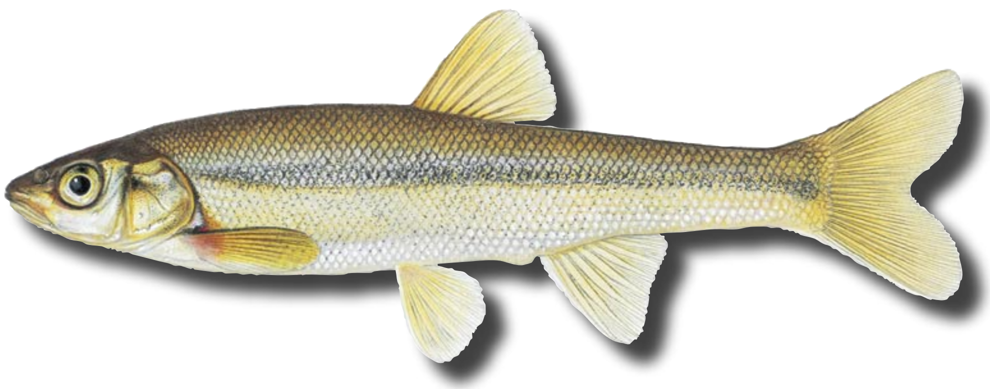
Lake Chub (*Couesius plumbeus*): A Technical Conservation Assessment



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

May 4, 2006

Richard H. Stasiak, Ph.D.
Department of Biology
University of Nebraska at Omaha
Omaha, NE 68182-0040

Peer Review Administered by
American Fisheries Society

Stasiak, R. (2006, May 4). Lake Chub (*Couesius plumbeus*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: http://www.fs.fed.us/r2/projects/scp/assessments/lakechub.pdf [date of access].

ACKNOWLEDGMENTS

Many thanks to David B. McDonald at the University of Wyoming for providing the demographic matrix analysis that appears in the appendix of this species conservation assessment. George R. Cunningham, Doug Backlund, Jeff Shearer, and several others provided thoughtful insight into the conservation of this species in South Dakota. Thanks as well to the many biologists in Colorado, Wyoming, and Nebraska who provided unpublished data from their agencies. The comments and suggestions from anonymous reviewers were very much appreciated. I would also like to acknowledge Gary Patton and Richard Vacirca of the USDA Forest Service for all their help in bringing this report to completion.

AUTHOR'S BIOGRAPHY

Richard H. Stasiak received his Ph.D. from the University of Minnesota. He spent his graduate school days studying the ecology of minnows in the bogs and beaver ponds of northern Minnesota. He is currently Professor of Biology at the University of Nebraska at Omaha, where he has spent the past 35 years teaching courses in ichthyology, aquatic ecology, and zoology. His research interests center around the ecology of fishes found in the Midwest, with a special fondness for native cyprinids.

COVER PHOTO CREDIT

Illustration of the lake chub (*Couesius plumbeus*) by © Joseph Tomelleri.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF LAKE CHUB

Status

The lake chub (*Couesius plumbeus*) has a wide range throughout much of Canada and the northern tier of the United States. While it is not considered federally endangered or threatened in the main portion of its range in the United States, this species is uncommon in the Great Plains. It is found in four of the five states comprising USDA Forest Service (USFS) Rocky Mountain Region (Region 2). Populations in South Dakota, Colorado, and Nebraska occur as small, isolated demes that have been declining steadily since European settlement of this region over 150 years ago. The state of Colorado identifies lake chub as a state endangered species. The national Natural History Database (NatureServe.org) lists the species as critically imperiled (S1) in South Dakota and Nebraska, while ranking the lake chub as secure (S5) in Wyoming. Although the species has a widespread distribution in Wyoming, populations are apparently declining and have become an element of concern. Within Region 2 populations of lake chubs are known to occur on the Black Hills National Forest in South Dakota, The Buffalo Gap National Grassland in South Dakota, the Black Hills, Bighorn and Shoshone national forests in Wyoming, the Thunder Basin National Grassland in Wyoming, the Roosevelt National Forest in Colorado, and administration units of the Nebraska National Forest in Nebraska are within historic lake chub range and may still contain relict populations.

Primary Threats

The primary threats to lake chub in Region 2 include habitat alteration, declining water quality and quantity, and the introduction of non-native fishes. While lake chubs can be found in large rivers and lakes in Canada and in the eastern United States, in the Great Plains these fish usually occur in small, confined habitat in places of permanent spring flow, usually at the headwaters of small streams. The members of the natural fish community in these habitats are highly adapted to the special conditions presented by this environment. Water development activities (e.g., groundwater pumping, stream diversions, channelization) that alter natural flow regimes can lead to both habitat degradation and stream fragmentation and negatively affect lake chub populations. As sight-feeding predators, lake chub depend on relatively clear water, so any activities that cause long-term increases in turbidity will be deleterious. Therefore, construction projects, forestry practices, mining, and livestock grazing activities need to be managed so they do not produce excessive erosion and siltation. The introduction of chemicals (e.g., pesticides, herbicides, fertilizers, hormones, heavy metals) into lake chub habitat can be harmful to this species.

The presence of non-native species can also negatively affect lake chubs and other native fishes through the combined pressures of predation, competition, potential for addition of new parasites and disease, and altering behavioral components of the native fish assemblage. Introduction of large predatory fish species such as largemouth bass (*Micropterus salmoides*), rock bass (*Ambloplites rupestris*), northern pike (*Esox lucius*), or trout (*Oncorhynchus* or *Salvelinus*) could have an especially significant impact on lake chub populations in the Great Plains. An additional threat, which may be of more local concern, would be the potential overharvest of lake chubs for use as fishing bait or for the aquarium trade.

The exact genetic relationships of the lake chub populations in the Great Plains are not well understood at this time. Some of the small isolated populations in Region 2 may represent demes that are genetically unique from those populations in the main part of the range to the north. Until more is known about their genetics, great care must be taken to maintain the genetic integrity of each population.

Primary Conservation Elements, Management Implications and Considerations

The lake chub is one of the species of small fishes forming a distinctive community in the Great Plains. These species can be described as “glacial relicts” as they form scattered populations to the south of the main portions of their overall ranges. This assemblage of fishes is restricted to small streams, beaver ponds, and spring-fed lakes. As the glaciers retreated to the north after the most recent ice age, these remnant habitats remain and still provide suitable conditions for these cold-adapted species.

The major considerations in conserving the lake chub would be to protect groundwater sources, streamflows, and beaver activity. Land use within riparian areas needs to be controlled to prevent erosion and siltation. Chemical pollution in the form of pesticides, fertilizers, and hormones should be monitored. Introductions of non-native fishes need to be eliminated, and where non-native species have already become established in native lake chub habitat, they should be controlled and reduced. Studies should be undertaken to determine the genetic relationships of the lake chub populations in Region 2.

Table of Contents

EDITOR: Richard Vacirca, USDA Forest Service, Rocky Mountain Region

LIST OF TABLES AND FIGURES

Table:

Figures:

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**). Lake chub (*Couesius plumbeus*) occur in four of the five states comprising Region 2 (Wyoming, Nebraska, South Dakota, and Colorado); this species does not occur in Kansas (Cross and Collins 1975). The historical trend of lake chub populations of the Great Plains states is one of general decline. It is considered a sensitive species in Region 2. Within the National Forest System, a sensitive species is a plant or animal whose population viability has been 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)].

This report addresses the biology of the lake chub throughout its range in Region 2. The broad nature of this assessment leads to some constraints on the specificity of information for particular locales. Much of the data used in this assessment comes from research conducted on populations (or even subspecies) that lie outside Region 2 but make up the major portion of the species' range. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

All of the scientific and common names used in this document follow the recommendations found in the 6th edition of the American Fisheries Society names of fishes publication (Nelson et al. 2004).

Goals

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

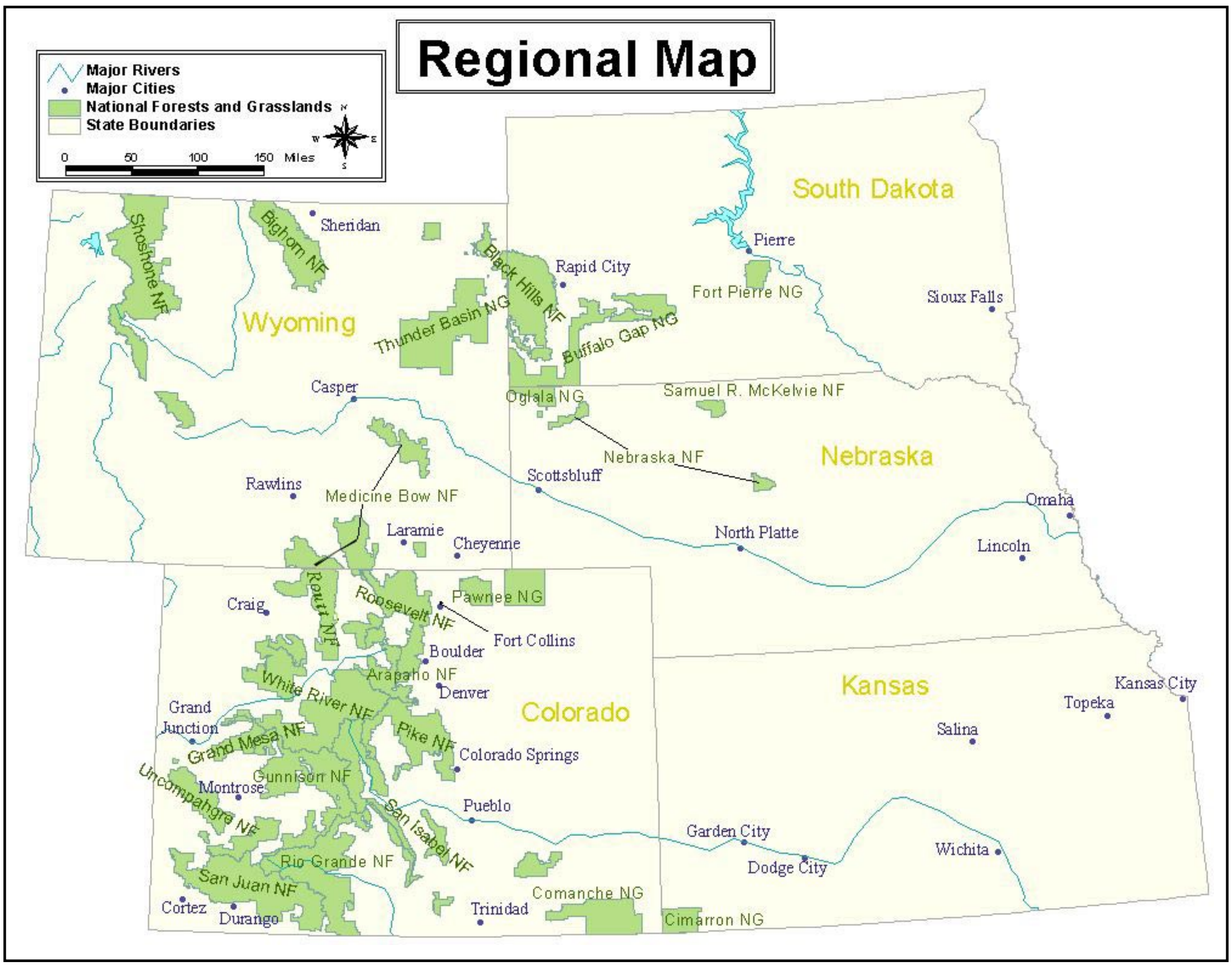


Figure 1. Map of National Forest System lands within USDA Forest Service Region 2.

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

This assessment examines the biology, ecology, conservation status, and management of the lake chub with specific reference to the geographic and ecological characteristics of the USFS Region 2. Although some of the literature on the species originates from field investigations outside the region, this document places that literature in the ecological and social context of the central Rocky Mountains and the Great Plains. Similarly, this assessment is concerned with the reproductive behavior, population dynamics, and other characteristics of the lake chub 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, the refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies were reviewed. Not all publications on the lake chub are referenced in this assessment, nor were all materials considered equally reliable. This assessment emphasizes refereed literature because this is the accepted standard in science. Some non-refereed literature was used in the report, 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. While well-executed experiments represent a strong approach to developing knowledge, it is often difficult to conduct critical experiments in the ecological sciences. Therefore, alternative approaches, such as observations, inference, good thinking, and models, must be relied on to guide our 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 of the lake chub 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 2**). In general, life history and ecological information collected from a portion of this range should apply broadly throughout the entire distribution. However, certain life history parameters (e.g., time of spawning, growth rates, longevity) could differ along environmental gradients, especially in such a wide-ranging species. Information about the conservation status of lake chub was limited to Region 2 and should not be taken to imply conservation status in other portions of the species' overall range.

Publication of Assessment on the World Wide Web

To facilitate the use of species assessments in the Species Conservation Project, they are being published on the Region 2 World Wide Web site (http://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, Web publication facilitates the revision of the assessments, 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 their release on the Web. Peer review for this assessment was administered by the American Fisheries Society, employing at least two recognized experts for the related taxa. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

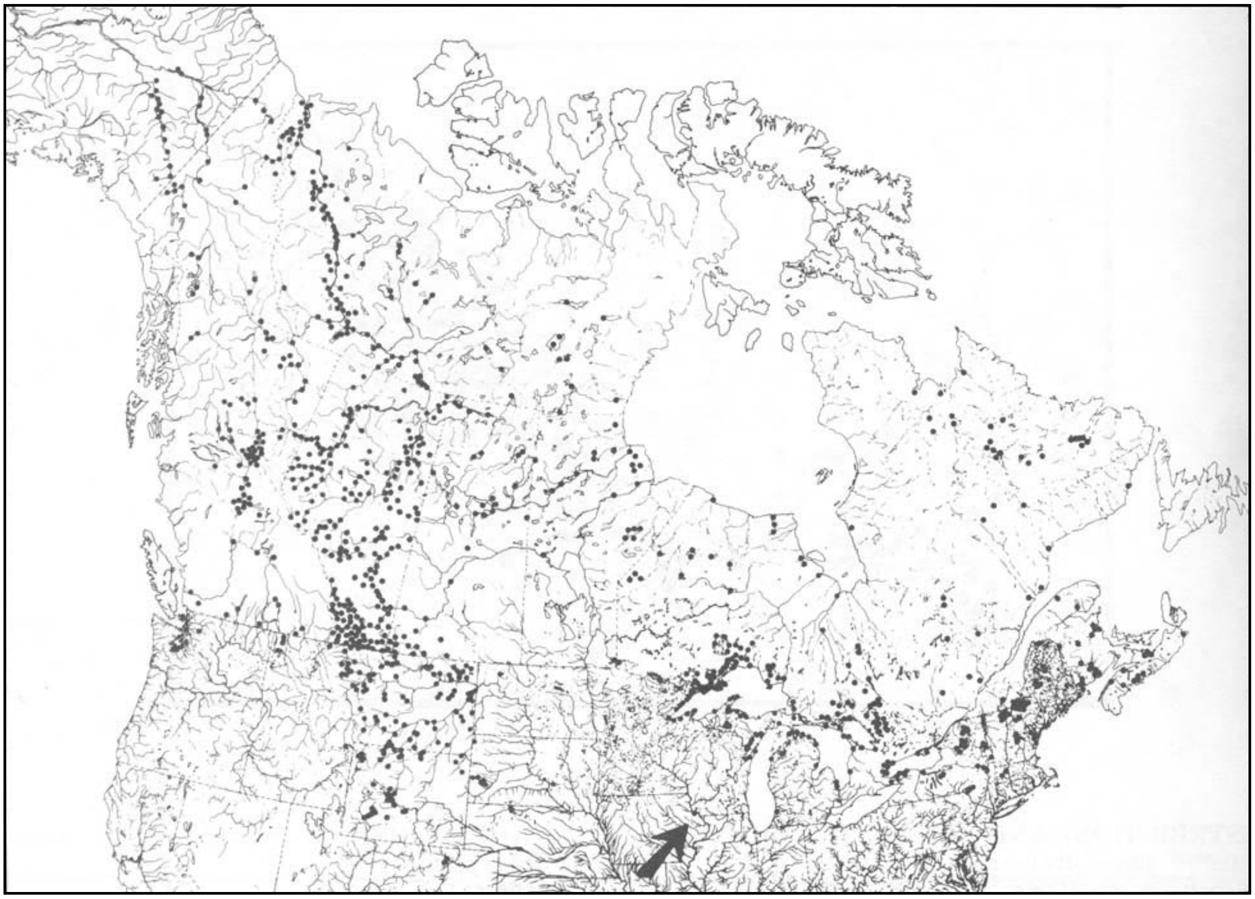


Figure 2. Lake chub distribution in North America. Taken from Wells (1980).

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

The lake chub is not considered a federally threatened, endangered, or sensitive species throughout the major portion of its range (**Figure 2**) in the United States (U.S. Fish and Wildlife Service; http://endangered.fws.gov/). The populations that occur in Region 2 exist as disjunct demes at the southern periphery of the overall range. The USFS has designated the lake chub as a sensitive species in Region 2 (Species Conservation Project: Region 2 Regional Forester's Sensitive Species: http://www.fs.fed.us/r2/projects/scp/sensitivespecies/index.shtml). The Black Hills National Forest is the only administrative unit within Region 2 currently known to contain a population of lake chubs (**Figure 3**). The Buffalo Gap National Grassland in South Dakota, the Black Hills, Bighorn and Shoshone national forests in Wyoming, the Thunder Basin National Grassland in Wyoming (**Figure 4**), the Roosevelt National Forest in Colorado, and administration units of the Nebraska National Forest in Nebraska are within historic lake chub range and may still contain relict populations.

At times the terms "endangered " or "threatened" or "species in need of conservation" can be confusing when applied to an entire range. When a species is not listed as endangered or threatened at the federal level, it may still be listed as such by individual states. Uncommon species for each state can be recognized in three different ways: 1) a species can be officially listed as endangered or threatened and given legal protection under state statues, 2) a species can be included in the state's Comprehensive Wildlife Conservation Strategy (CWCS) plan, and 3) the national Natural History Database Program (NatureServe.org) can rank a species according to its population level in each state (**Figure 5**). Under this latter method, the Natural Heritage Program has ranked the lake chub as critically imperiled (S1) in South Dakota, Colorado, and Nebraska (**Table 1**; NatureServe.org/explorer).

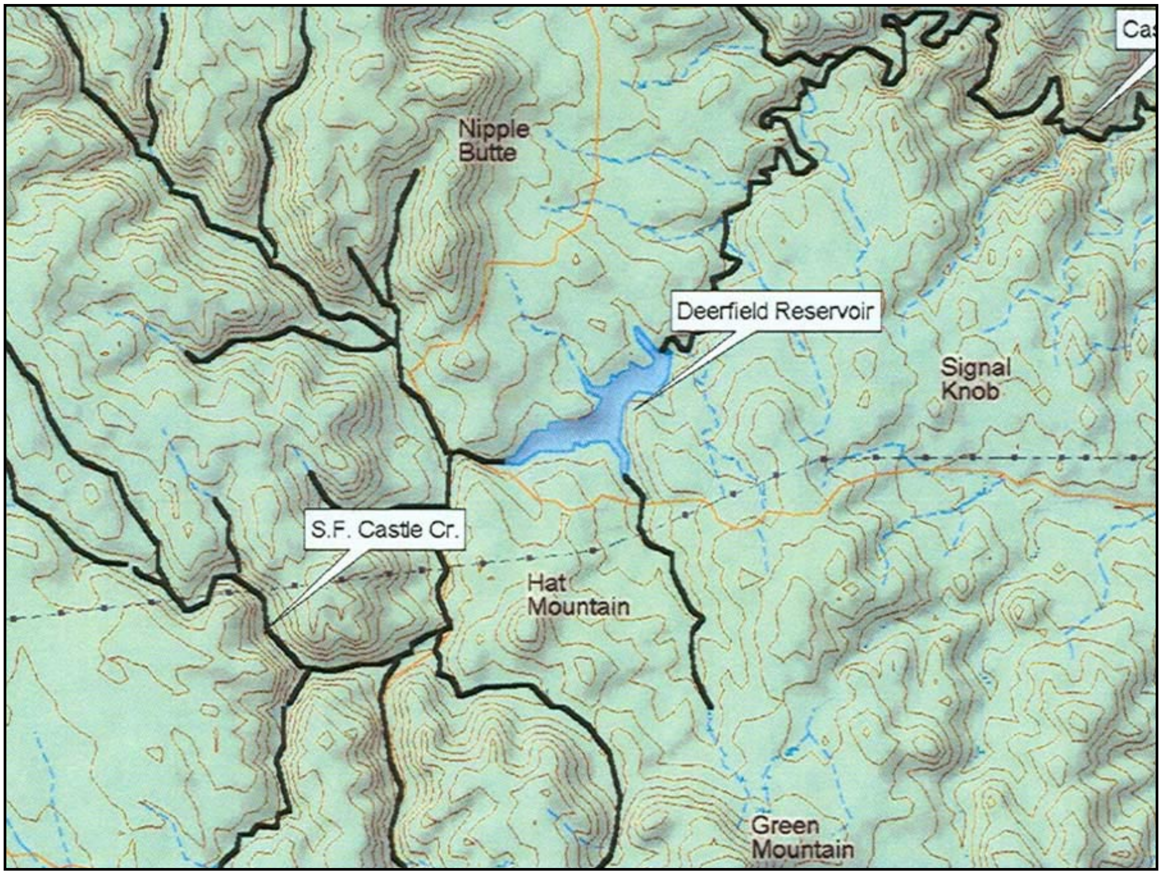


Figure 3. Deerfield Reservoir on the Black Hills National Forest in South Dakota. Lake chub were apparently widespread throughout streams within this area (Evermann 1893), but now are more or less restricted to the impoundment.

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

In Region 2, only Colorado lists the lake chub as an officially endangered species. This designation basically gives the species legal protection from all forms of taking, possessing, and transporting, but it does not address the habitat needs of the species.

The State Wildlife Grants program (*Title IX, Public Law 106-553 and Title 1, Public Law 107-63*), created through federal legislation, is meant to close the funding gap by providing federal dollars for a state to use on conservation projects aimed at preventing wildlife from becoming endangered. Through this program, states are obligated to develop Comprehensive Wildlife Conservation Strategy (CWCS) plans for managing rare species in their jurisdictions. South Dakota, Wyoming, and Colorado each cover lake chub as a Species in Greatest Need of Conservation. The CWCS includes a conservation plan and a list of management actions directed specifically at listed species, including the lake chub.

The Colorado CWCS lists the lake chub as a species of greatest conservation need, with a population status of medium and stable population trend. The plan does not specifically target actions to protect lake chub, but it does address general conservation actions needed to protect rare fishes. This includes performing landscape analyses, acquiring or leasing important streams or water rights, controlling invasive exotic species, and removing dispersal barriers. The Wyoming CWCS plan includes lake chub as a species of declining population trend, and it includes monitoring population levels, studying movement, dispersal, and colonization patterns, and understanding flow requirements as conservation actions. The CWCS plan for South Dakota was not available at the time of writing this report, but the lake chub was included as a species in greatest conservation need by the South Dakota Natural Heritage Program. The lake chub does not appear in the Nebraska CWCS plan, probably because it was

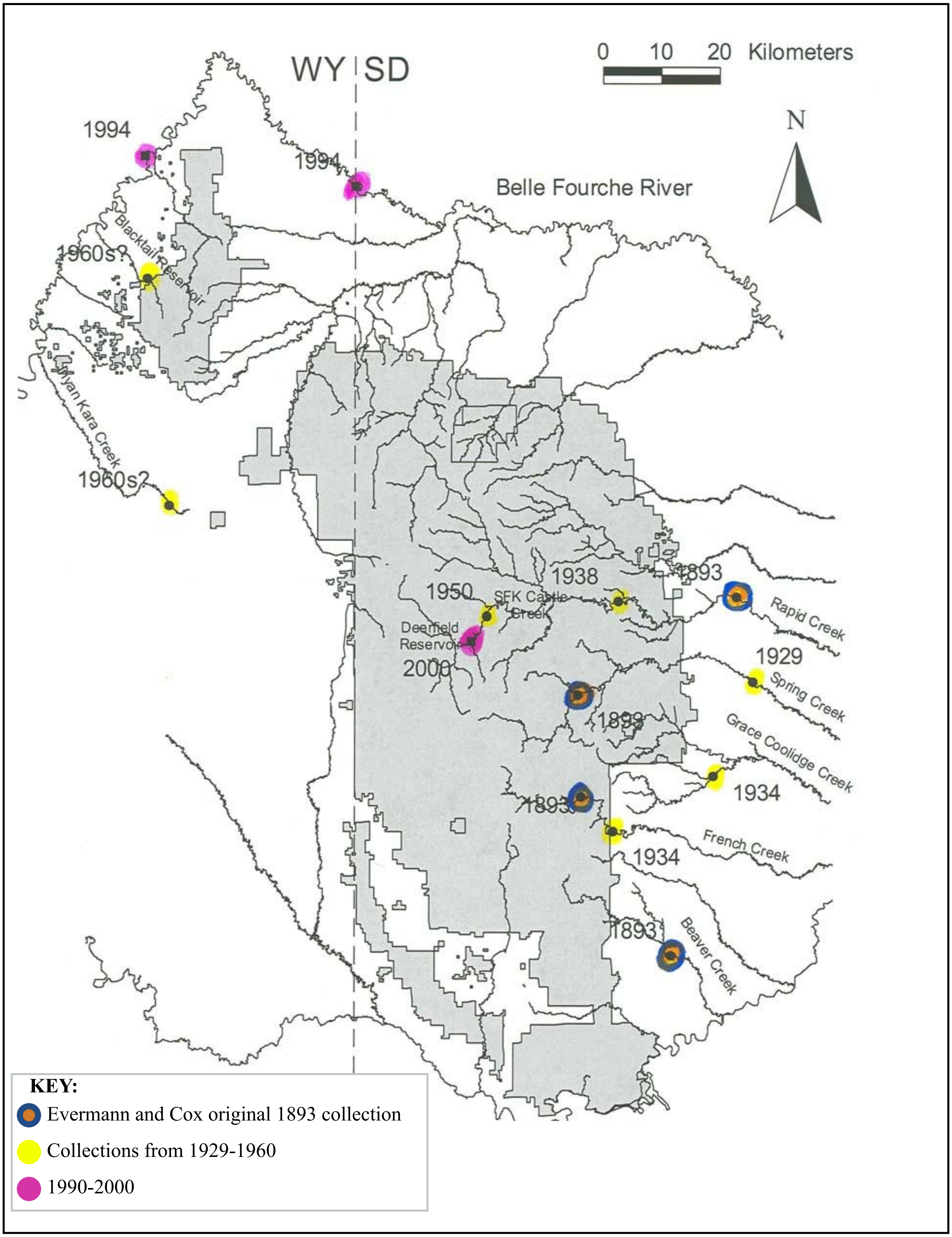


Figure 4. Historic records for lake chub in the Black Hills region of South Dakota and Wyoming. Based on collection data from Evermann and Cox (1896), Bailey and Allum (1962), Eiserman (1966), Patton (1997), Meester (2000), and Wyoming Game and Fish Database. Modified from Isaak et al. 2003.

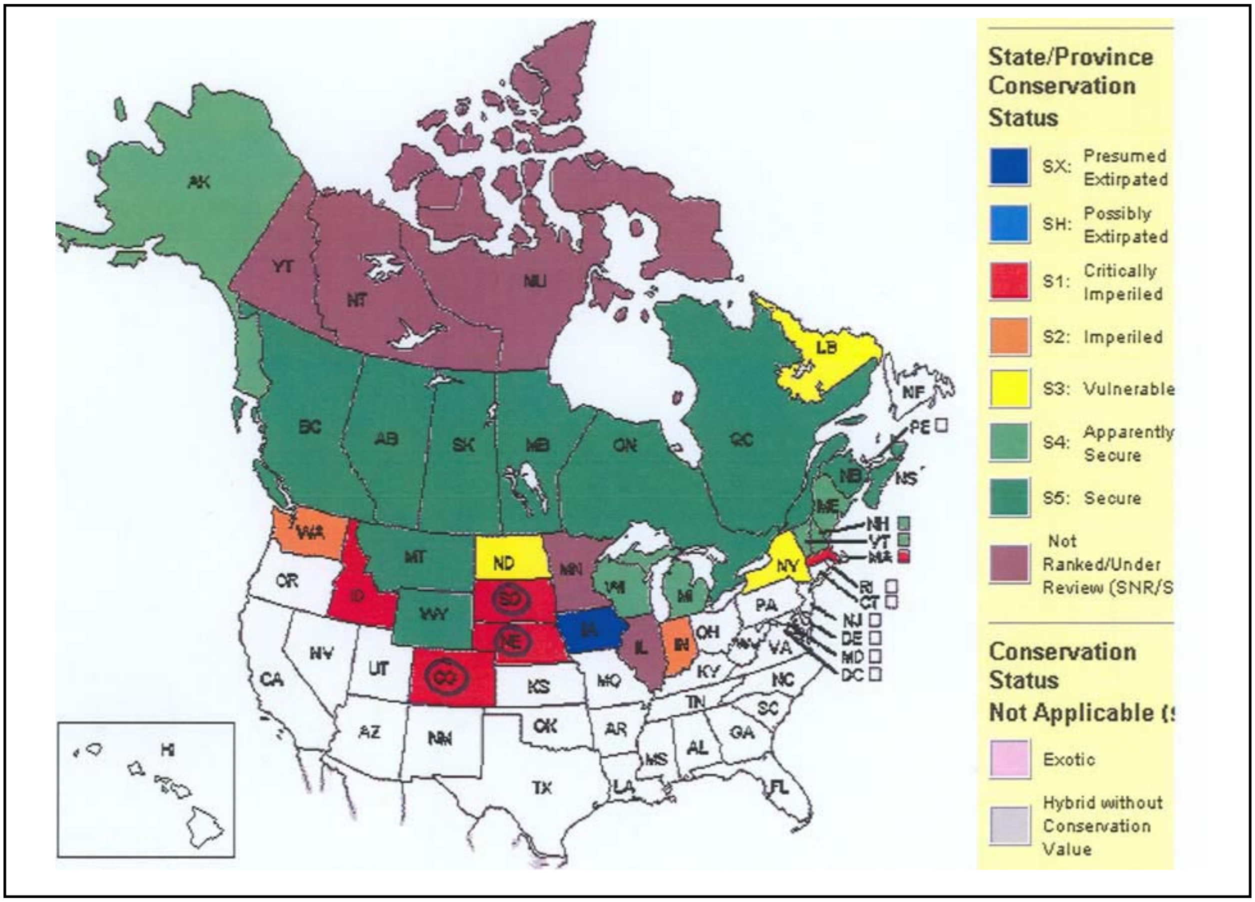


Figure 5. Natural Heritage Database conservation status for lake chub. Note that three of the four states in Region 2 (CO, NE, and SD) are listed as critically imperiled. Nebraska could possibly be considered light blue (possibly extirpated). Modified from NatureServe/explorer.org.

Table 1. Conservation status of lake chub in USDA Forest Service Region 2 states.

State	Legal Listing (State Level)	State CWCS Plan	Heritage Program (NatureServe.org)
Colorado	Endangered	Species in Greatest Need of Conservation: Population medium size and stable	S1; Critically imperiled
South Dakota	None	Species in Greatest Need of Conservation: Tier 1	S1; Critically imperiled
Nebraska	None	None	S1; Critically imperiled
Wyoming	None	Species in Greatest Need of Conservation: Species widely distributed, but populations are declining	S5; Secure
Kansas	Does not occur		

considered extirpated, despite the fact that one was collected in Nebraska in 1985 (**Figure 6**).

The state of South Dakota has been conducting stream surveys in the Black Hills for at least two decades (Ford 1988, Cunningham et al. 1995, Meester 1998). A Black Hills stream management plan was initiated in 1993 (Erickson and Vanderbush 1993). The Black Hills National Forest issued a final environmental impact statement in 1996, and the state of South Dakota implemented a five-year fisheries management plan for Deerfield Reservoir (Vanderbush 1999). Surveys were done under the aegis of the Regional Environmental Assessment Program (REAP). Even still, the conservation status of the lake chub in western South Dakota (the Black Hills National Forest area) is currently unsettled (Backlund 2006, Shearer personal communication 2006). This is based on debate over historical distribution, namely, historic specimens collected from Rapid Creek (Evermann and

Figure 6. Lake chub specimen collected in a headwater spring of Bone Creek in Brown County, Nebraska in 1985. It represented the first lake chub documented in Nebraska in 92 years. Note the large pectoral fin, which indicates it is a mature male. When captured, this fish was in breeding condition. It was bright red at the base of the pectoral fin and behind the operculum, but it blanched just prior to being photographed. It also had a dark horizontal band along the side, which can just barely be discerned in this photo. A barbel was present in the corners of the mouth, and the pharyngeal arches and scale counts were correct for lake chub. Photograph by author.

Cox 1896). The Distribution and Abundance section of this assessment outlines what appears to be resolution concerning this issue.

Biology and Ecology

Systematics and species description

The lake chub is in the bony fish superclass Osteichthyes, Class Actinopterygii, Order Cypriniformes, and minnow family Cyprinidae (Nelson 1994.) In his classic book on Lake Superior, Agassiz (1850) originally described this species as *Gobio plumbeus*. Evermann (1893) described a specimen taken in Rapid Creek near Rapid City in the South Dakota Black Hills as *Couesius dissimilis*. When these were recognized as the same species, the proper name became *C. plumbeus*, with the Great Plains subspecies designated as *C. plumbeus dissimilis*. Bailey (1951) placed the lake chub in the genus *Hybopsis*, but Jenkins and Lachner (1971) split the lake chub back into the unique genus *Couesius* again. Thus for about the past 35 years, the scientific name of the lake chub has been stabilized as *C. plumbeus*.

For many years the lake chub was thought to be represented by three different subspecies: *Couesius plumbeus plumbeus* in eastern North America, *C. plumbeus dissimilis* in the central portion of North America, and *C. plumbeus greeni* of Alaska and the Pacific Slope (Scott and Crossman 1973). Since the merging of the genera *Hybopsis* and *Couesius*, the subspecies have been questioned and are in doubt (Lindsey 1956). In the latest edition of their book on Michigan fishes, Hubbs et al. (2004) used different common names for two of the lake chub subspecies. They called *C. plumbeus plumbeus* the lake northern chub, and *C. plumbeus dissimilis* the creek northern chub. This later subspecies is the one included in this report for Region 2 populations. The change of common name to "northern chub" has not yet been recommended by the American Fisheries Society (Nelson et al. 2004).

Species description

Good descriptions of this species can be found in the McPhail and Lindsey 1970, Scott and Crossman 1973, Becker 1983, Smith 1985, and Page and Burr 1991. The lake chub is a medium to large-sized minnow; adults can reach 227 mm (8.9 inches) total length (TL) (Scott and Crossman 1973, Becker 1983). It has a large terminal mouth with a small barbel near the end of the maxilla (upper jaw). The scales are medium in size, with about 58 to 65 rows along the side. The lateral line pores are complete. The pharyngeal arch has the 2, 4 - 4, 2 dental formula (Eastman 1970). Its color is usually dark olive on the back and silvery or gray on the sides; often there is a horizontal black band along the side from the operculum to the base of the caudal fin. Both sexes develop breeding tubercles during the spring, but these are much more prominent in males (Reighard 1903, 1904, Balinsky 1948, Collette 1977, Maas and Stasiak 1995). Males of the Great Plains subspecies have bright red at the bases of the pectoral fins and on the flanks and operculum; this color is much enhanced during the spawning season. Males also have much larger pectoral fins compared to females.

Distribution and abundance

The lake chub is widely distributed across Canada and the northern portions of the St. Lawrence (Great Lakes), Mississippi, and Missouri River drainages in the United States (McPhail and Lindsey 1970, Scott and Crossman 1973, Wells 1980, Page and Burr 1991). This species apparently reaches its southern-most limit at about 40º N latitude in Colorado (Bestgen et al. 1991). In Canada it has been taken from the Northwest Territories, British Columbia, and Alberta (Wynne-Edwards 1952, Carl et al. 1959, McPhail and Lindsey 1970, Paetz and Nelson 1970), Saskatchewan (Willock 1969, Brown et al. 1970), Manitoba (Hinks 1943, Keleher 1956, Fedoruk 1971), Ontario (Dymond 1926, Hubbs and Brown 1929, Dymond et al. 1929, Dymond and Scott 1941, Lindeborg 1941, Brett 1944, Ryder et al. 1964), Quebec (Legendre 1953 and 1954); McAllister and Coad 1974), and New Brunswick and Prince Edward Island (Scott and Crossman 1959). This is the only minnow (Cyprinidae) species known from Alaska, where it widespread (Morrow 1980).

In the continental United States, lake chubs have been found in Maine and New Hampshire (Kendall 1908), New York (Greeley and Greene 1931, Greeley and Bishop 1932, Greeley and Bishop 1933, Smith 1985), Michigan (Hubbs and Lagler 1949, Taylor 1954, Hubbs 1964), Wisconsin (Greene 1935, Moore and Roberty 1965, Becker and Johnson 1970, Becker 1983), Minnesota (Smith and Moyle 1944, Underhill 1957, Nordlie et al. 1961, Eddy et al. 1963, Underhill and Moyle 1968, Eddy and Surber 1974, Underhill 1986, Hatch et al. 2003), North Dakota (Tubb et al. 1965, Evenhuis 1969), South Dakota (Evermann 1893, Evermann and Cox 1896, Churchill and Over 1938, Bailey and Allum 1962, Ashton and Dowd 1991, Isaak et al. 2003), Nebraska (Johnson 1942, Jones 1963, Madsen 1985, Stasiak 1986, 1987), Colorado (Hendricks 1950, Bestgen et al.1991), and Wyoming (Simon 1951, Baxter and Simon 1970, Baxter and Stone 1995, Patton 1997, Wheeler 1997). A single isolated population is found in Iowa in Twin Springs Creek northwest of Dubuque (Wells 1980, Harlan et al. 1987). Lake chub are widespread in the Missouri and Yellowstone drainages of Montana (Brown 1971, Elser et al. 1980).

Lake chubs were reported in several streams in the South Dakota Black Hills by Evermann and Cox (1896), but recent records indicate that this species is restricted to Deerfield Reservoir (**Figure 3**; Ford 1988, Erickson et al. 1993, Meester 1998, Vanderbush 1999, Isaak et al. 2003, Backlund 2006). The lake chub is now considered a species of special concern in South Dakota (**Figure 5**) in their CWCS plan.

Although lake chub still occur in Deerfield Reservoir in the Black Hills National Forest (**Figure 3**), there is some question about whether they represent a native population. On April 6, 2006 the author examined a collection of specimens (identified as lot 076030; **Figure 7**) from the United States National Museum (USNM) and confirmed their identity as lake chubs. In addition, lot specimens from USNM 076030 were also vouchered to be lake chubs by George Cunningham (Midwestern native fish species expert). These specimens represent some of the original specimens from Rapid Creek collected by B.W. Evermann in 1893. The Evermann and Cox (1896) specimens from Nebraska taken during that same expedition (USNM 076028, 076029, and 008948) were also confirmed as lake chubs (**Figure 4** and **Figure 7**). Lot 076029 was labeled "Beaver Creek, Buffalo Gap, Nebraska", which most likely means they were collected in what is now the Buffalo Gap National Grassland in South Dakota. Apparently there was confusion about the states' borders, as lot 008948 was labeled as coming from "Tongue River, Nebraska" (these probably are from Wyoming). Recent examination of USNM 076030 by the author demonstrates that lake chubs were native to the Black Hills as documented by Evermann and Cox (1896). Lake chubs were certainly native to the South Dakota prairie adjacent to the Black Hills National Forest.

Ellis (1914) reported lake chubs from only two locations in the Platte River drainage west of Boulder, Colorado, and Woodling (1985) has listed the species as extirpated in Colorado. After an 85-year absence in collections, Bestgen et al. (1991) rediscovered a single specimen in the South Fork St. Vrain Creek. Currently this fish is listed as state endangered in Colorado (S1).

A similar situation applies to the Nebraska population. Evermann and Cox (1896) first collected

Figure 7. Lake chub specimens from the Unites States National Museum (used with permission). Above, specimen numbers 858, 859, and 860 that comprise lot USNM 076028. Collected from Minnechaduza Lake, Valentine (Cherry Co.), Nebraska in 1893 by U. O. Cox. Below, specimen numbers 896, 897, and 898 that comprise lot USNM 076030. Collected from Rapid Creek, Rapid City (Pennington Co.), South Dakokta in 1893 by B. W. Evermann for the U.S. Bureau of Fisheries.

lake chubs in four Sandhills streams in Cherry and Brown counties in Nebraska in July 1893; in 1985 (92 years later) a single specimen was recorded from Bone Creek near Ainsworth in Brown County (**Figure 6**; Stasiak 1986). Although it is not on the official state list for Nebraska because it was considered extirpated, the lake chub is now listed as S1 (endangered) by the Nebraska Natural Heritage Program (NatureServe.org/explorer).

Wyoming is the only state in Region 2 with widespread populations of lake chubs (**Figure 4**, **Figure 8**; Simon 1951, Baxter and Simon 1970, Baxter and Stone 1995). Patton (1997) found lake chubs in the Bighorn River, the Tongue River, The Little Missouri River, the Belle Fourche River, Shoshone River, Clark's Fork River, and Popo Agie River in Wyoming. Patton (1997) listed this species as having a declining distribution within the study area. Wheeler (1997) also reported chubs in Yellowstone Lake (apparently introduced), and the Sweetwater River in the Platte Drainage, and in the Green River Basin including Big Sandy Creek.

Population trends (local, regional, and rangewide)

Lake chub populations are considered stable throughout most of the main portion of their range in Canada, Minnesota, Wisconsin, Michigan, and New England (Underhill 1957, Becker and Johnson 1970, Paetz and Nelson 1970, Morrow 1980, Smith 1985, Das and Nelson 1990, Hatch et al. 2003). Where the species occurs as relict populations following the retreat of the Wisconsin Ice Sheet (this includes the populations in Region 2), they are not so stable. 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 in these habitats enables lake chubs to persist under conditions much more

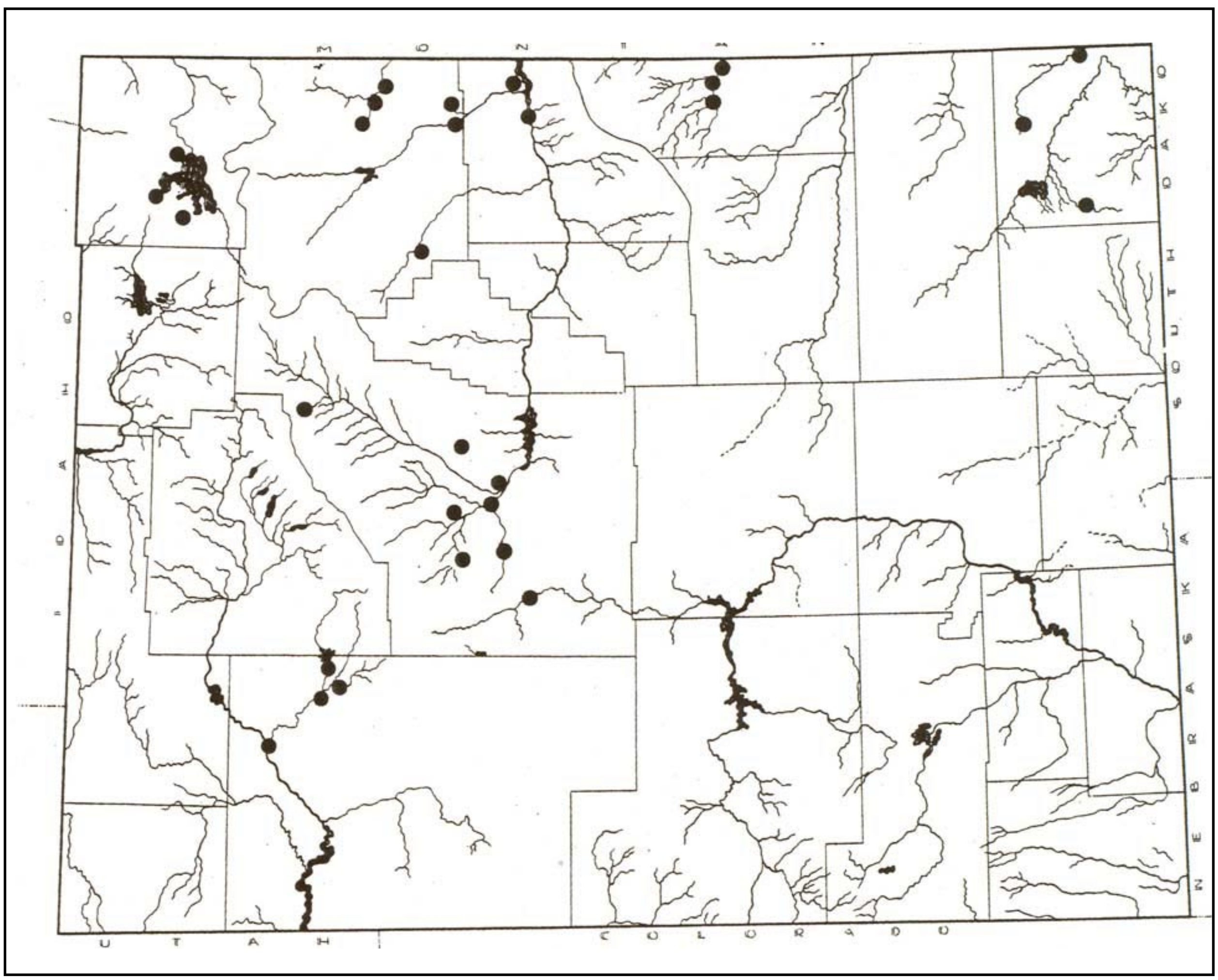


Figure 8. Historic lake chub distribution in Wyoming. Based on Baxter and Simon (1970).

similar to those 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 region following the retreat of the last ice has led to the natural reduction in suitable habitat for this northern species (Woodhouse and Overpeck 1998). Human activity that reduces cold springs or seeps has greatly accelerated this process. Also, since this subspecies prefers clear water with rocky substrate and is a sight-feeding predator, any construction project that leads to soil erosion and siltation could reduce chub habitat and populations.

Population trends in South Dakota, Nebraska, Colorado, and Wyoming indicate that the lake chub is declining. It is becoming restricted to fewer locations and is being sampled in fewer numbers where it is found (Stasiak 1986, Bestgen et al. 1991, Patton 1997, Wheeler 1997). In South Dakota lake chubs were once found throughout the streams of the Black Hills (Evermann 1893); currently they are more or less restricted to Deerfield Reservoir, and even here they are apparently declining (Olson 1998, Doorenbos 1998, Issack et al. 2003).

Lake chub populations at the southern edge of their range occur in such scattered locations that they have been difficult to locate. Evermann (1893) and Evermann and Cox (1896) had sampled lake chubs in north-central Nebraska before the turn of the last century; these specimens still exist in the U.S. National Museum collections and have been confirmed by this author. Ironically, just prior to the lake chub collection in 1986, Madsen (1985) had considered the species extirpated in Nebraska. A very similar situation happened in Colorado. Although not in Region 2, there is a similar single isolated lake chub population in eastern Iowa (**Figure 2**; Wells 1980).

Lake chub populations are more widespread in Wyoming than any of the other Region 2 states, but even here Patton (1997) included lake chubs as among those species with declining populations. The lake chub is considered to be a special concern species (NSS3) in Wyoming due to its declining distribution (Patton 1997, Wheeler 1997, Fertig and Beauvais 1999, NatureServe.org/explorer 2006).

Activity patterns

Most of the studies on lake chub have been conducted in the main portion of their distributional range to the north, east, or west of Region 2 (Emery 1973); little is known of the activity patterns of lake chubs in the Great Plains. Where they are found in lakes and large rivers, this species has been documented making spawning migrations into small tributaries (Brown et al. 1970, Bruce and Parsons 1976, Reebs et al. 1995). Some of these seasonal movements can involve many miles of travel, demonstrating the potential for dispersal. Where they are isolated in small headwater streams, it appears very unlikely that the populations of lake chub in Region 2 undergo any widespread dispersals.

Habitat

Lake chubs are considered common throughout much of Canada and the Great Lakes where they are often found in large lakes (hence their common name) and rivers (Mayden et al. 1992). They prefer clear water and gravel bottoms of glacial scour lakes and tributary rivers that feed into them (Bruce and Parsons 1976, Becker 1983, Patton 1997). Occasionally they are found in turbid water, especially where large rivers empty into lakes. In this type of "big water" habitat, some species of larger predator fish can co-exist with lake chubs. Becker (1983) found that lake chubs were most common in the shallow water of lakes right at the mouths of tributary rivers. They were rarely collected in deep water or very far from the river mouth.

The habitat of the isolated populations of lake chub in the northern Great Plains is quite different; here populations are often confined to small first order streams and cool spring seeps (Stasiak 1986, Bestgen et al. 1991). Headwater streams where lake chubs are present in the Great Plains share the following characteristics: spring-fed with perennial flow regimes; clear and cool water quality; substrate composed of large sand or gravel, not mud; absence of large species of predacious fishes. In this habitat chubs are usually associated with pearl dace (*Margariscus margarita*), finescale dace (*Phoxinus neogaeus*), northern redbelly dace (*P. eos*), 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*) (Stasiak 1986, Bestgen et al. 1991, Cunningham et al. 1995, Patton 1997). In this habitat these species can find constantly cool and clear bodies of water that are small and isolated enough to prohibit most species of large predatory fish from gaining a permanent presence.

Within Region 2, this species can also be found in reservoirs such as Deerfield and Blacktail on the Black Hills National Forest. These smaller impoundments can provide suitable habitat as long as large predatory fish species (especially those in the sunfish family) are not present.

Food habits

The lake chub has the large terminal mouth, strong pharyngeal teeth, and body shape of a predator; it has a short single-loop intestine (Simpson 1941, Eastman 1970). This fish has large eyes, well-developed optic lobes in the brain, and very few external taste buds (Davis and Miller 1967). All of these morphological characteristics indicate that the lake chub is a sight-feeding predator. In terms of ecological niches, the lake chub is probably one of the larger insectivores in its community.

Although few large diet studies have been conducted on lake chub, there is general agreement that the species is a sight-feeding predator on a variety of active animals. Probably the size of the individual fish determines whether they eat large or small prey. McPhail and Lindsey (1970) described their food habits as including mobile aquatic and terrestrial insects and several kinds of zooplankton, especially in small or young chubs. Larger chubs even ate small fishes (sample size is unknown). Simpson (1941) examined the intestinal contents of 11 specimens of lake chub in Wyoming and found that 98 percent of the material by volume was animal related, and the intestines contained virtually no plant material. Stoneflies and caddisflies (Plecoptera and Trichoptera) made up almost 70 percent of the diet, with dragonflies (Odonata), beetles (Coleoptera), and midges (Diptera) comprising most of the rest. Becker (1983) examined 15 lake chubs from Lake Michigan and found that they consumed mayfly, dragonfly, and chironomid larvae. Anderson and Smith (1971) reported that lake chubs in western Lake Superior fed on crustaceans (Mysis, copepods, and cladocerans), large quantities of dipterans, snails, fish, and fish eggs, depending on the size of the fish and the season of the year. Brown et al. (1970) noted that spawning lake chubs would frequently eat their own eggs.

Large lake chubs have been known to take artificial flies and lures as if they were sport fish. The author has personally collected several large lake chubs (225 mm [8 to 9 inches total length) using artificial trout flies in the mouth of the Brule River (where it drains into Lake Superior) in northern Minnesota. The sport fishing potential provided by this species has also been noted by Brown (1971), Scott and Crossman (1973), and Becker (1983).

While there is little doubt about the feeding niche of the lake chub, a diet analysis has not been performed in Region 2. This kind of study is problematic in Region 2, due to the very low numbers of individuals in some of the existing populations.

Breeding biology

Lake chub reproduction has been described by Hubbs and Brown (1929), Greeley and Greene (1931), Dymond (1926), Scott (1954), Geen (1955), Becker (1983), and Ashan (1996). The most comprehensive details of lake chub reproductive biology were reported by Brown et al. (1970) for a lacustrine population of chubs in Lac la Ronge, Saskatchewan. This is a large lake (130,000 hectares [500 square miles]) connected to another lake (Bigstone Lake) by the Montreal River. Although this habitat is quite different from the small headwater streams harboring populations of lake chub in Region 2, it will be used here to summarize the main aspects of breeding biology because it is the most comprehensive study. The data from this study were the main basis for the mathematical data matrix shown in the **Appendix** to this document.

Adult lake chubs were found in the river only during the spring spawning period, which began in early May even before the ice melted on the lake surface. River temperature at this time was 4 ºC (about 39 ºF). Males tended to outnumber females on the breeding grounds 2:1. Spawning occurred in late May when the water temperature in the river rose above 10 ºC (55 ºF). Lake chubs also spawned along the rocky shore of the lake when the water temperature rose above 10 ºC in late June. At both the river and lake spawning sites, males outnumbered females on the spawning grounds, and the activity was polyandrous. No nests were built, and there was no parental guarding of eggs or fry. Several males chased a single female, and eggs were released above stones or gravel beds. Breeding males had orange markings, a darker and more distinct lateral band, larger breeding tubercles, and much larger pectoral fins compared to females. Males used the large pectoral fins to cradle and hold the females under and against rocks while they both released their gametes. These embraces only lasted for about 1 second, and only a small number of eggs were produced each time. The spawning embraces were repeated over a long period of time; they paused at times to feed, and this included feeding on the eggs that were just fertilized. Spawning began early in the morning and often lasted until midnight. Fertilized eggs were non-adhesive and were found on silt and leaf substrates as well as under rocks and gravel.

Breeding was also observed in large aquaria, and the spawning behavior in captivity was consistent with that in the field, with one exception: males in the tank were more aggressive and tended to defend territories; this was thought to represent an artifact due to confinement. Eggs hatched in 8 to 10 days at temperatures ranging from 8 to 19 ºC (46-68 ºF).

Females produced from 800 to 2400 eggs, ranging in diameter between 1.3 and 1.7 mm (0.05 and 0.07 inches); the first fry were observed in early June. Females began spawning at 3 years old, at about 95 mm (3.7 inches). This Age III group contributed over 54 percent of the potential recruitment in terms of fecundity.

Demography

Genetic characteristics and concerns

Genetic information of any kind appears to be lacking for lake chubs. Little information is currently available in the fish genetic data banks, but what does exist includes chromosome numbers (n = 25; 2n = 50). These are typical chromosome numbers for most North American cyprinids (Joswiak et al. 1985). Since there have been as many as three subspecies proposed for this fish (Scott and Crossman 1973), it would seem important to compare the basic genetic profiles of specimens from each population. Because this information does not appear to be available currently, it is hereby listed as a major research priority for this species. Information on genetics would be especially important for the Great Plains populations of the lake chub, which may have been isolated from the main range of the species for a thousand years or more (Underhill 1957, Cross 1970, Briggs 1986, Cross et al. 1986, Cross and Moss 1987). Perhaps there has been sufficient time in isolation for selection processes to allow genetic changes, and many of these regional populations may be uniquely adapted to the ecological conditions in their own habitats.

Life history characteristics

Data on the age and growth of lake chubs has been reported by Geen (1955), Brown et al. (1970), McPhail and Lindsey (1970), Scott and Crossman (1973), Fuiman and Baker (1981), Heufelder and Fuiman (1982), and Becker (1983). These studies were conducted in Canada and the Great Lakes region and probably included mostly the subspecies (*Couesius plumbeus plumbeus*), not the plains subspecies (*C. plumbeus dissimilis*) that is the one found in Region 2. These studies generally agree on the main aspects of lake chub life history characteristics.

Females tend to live longer and attain greater size than males, with some 5-year old individuals reaching about 230 mm (9 inches) total length. At least five age classes have been identified, with Age Class III contributing the greatest fecundity to the reproductive effort. Eggs hatch in about 10 days at temperatures of 50 to 60 ºF, and the first larvae can be observed in June in much of Canada. Early larval development was studied by Fuiman and Baker (1981) and Heufelder and Fuiman (1982). Young of the year juveniles were reported to grow quickly, reaching 44 to 77 mm (2 to 3 inches) by mid-September in Lake Michigan (Becker 1983). The average total length (in mm) at each annulus for Wisconsin lake chubs was as follows: Age I, 77.1; Age II, 114.7; Age III, 148.2; Age IV, 164.6; Age V, 177.8. These sizes were very similar to those reported in Canada by Geen (1955), McPhail and Lindsey (1970), Brown et al. (1970), and Scott and Crossman (1973). Becker (1983) speculated that some of the larger specimens might have been as old as 7 years, but they were hard to age due to scale erosion.

Ecological influences on survival and reproduction

Causes of mortality in lake chub include 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. Some of these factors are more likely to impact different ages and sizes and even sexes of this species unequally (**Figure 9**). Male lake chubs show more orange or red color and have a more distinctive dark color band on their flanks, especially during spawning activity. This possibly exposes them to increased predation, especially since they stay in the shallow water spawning areas for a considerably longer time than the females (Brown et al. 1970). The fact that Age Class III and IV fish are so important to the reproductive effort means that heavy mortality during the first years of life would limit population size (see **Appendix**). Most of the other species of smaller minnows can begin spawning at 1 to 2 years, which is typical of r-selected species that can quickly re-build their populations.

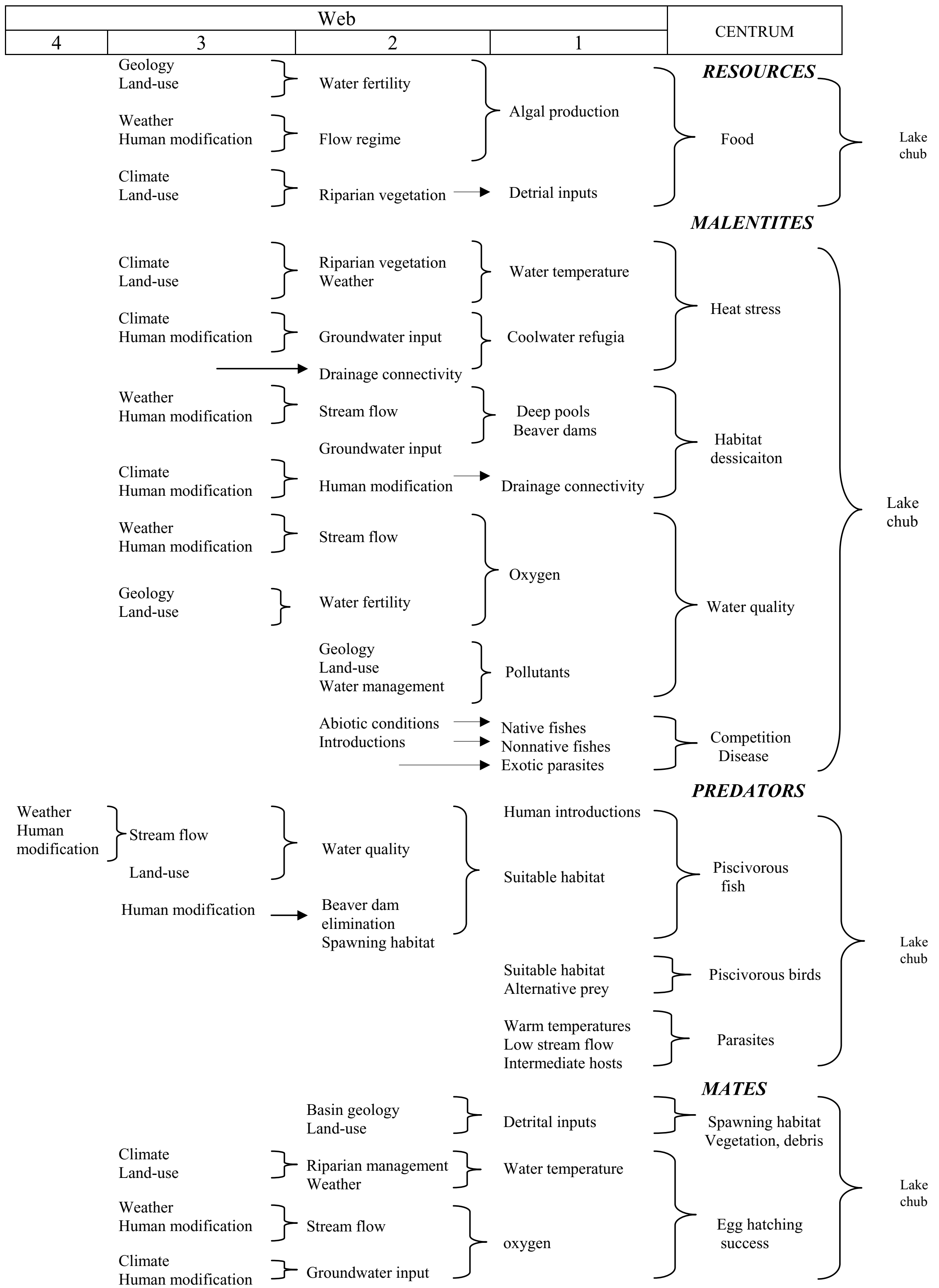


Figure 9. Envirogram for lake chub.

It is possible that this species really requires the conditions associated with larger, more undisturbed bodies of water (similar to the conditions they inhabit in Canada). Becker (1983) reported that lake chubs appear to prefer lakes in the northern part of their range, and rivers in the southern part of their range. As suitable lake chub habitat has slowly diminished on the Great Plains over the past century, they have become much more restricted in the number of sites that have the proper combination of water quality and quantity, substrate composition, and ecological community.

Social pattern for spacing

Lake chubs are usually observed in large schools or shoals. The only report of territoriality was when Brown et al. (1970) confined some fish to an aquarium during the spawning season. Males displayed aggressive behavior and chased other individuals from certain places in the tank. It was thought that this behavior reflected the confined and artificial environment of the fish tank, but perhaps this could become a factor in the much smaller lakes and streams that this species inhabits in Region 2.

Patterns of dispersal of young and adults

Few studies have dealt directly with dispersal of either young or adult lake chubs. In the northern portion of their range (where all of the ecological studies have been carried out), as the fish mature and reach about 1 year of age, they become much stronger swimmers and gradually move out into more open water. Many of the young fish are probably washed into lakes by high water and strong currents in the spring. In streams, flooding would be the prime dispersal agent, carrying the young fish especially to downstream areas. Schools of adult fish are generally mixed with respect to age and size.

Lake chub populations in Canada and the Great Lakes have been known to make spawning migrations of considerable distance (at least a few miles). Movements are generally upstream. In the Colorado and Nebraska populations, chubs appear to prefer cool springs or seeps with reduced current flow and heavy cover as well as the absence of piscivorous fishes (conditions which are most likely at the headwaters of low order streams). Lake chub dispersal mechanisms in these smaller streams have not been studied directly, but flooding probably is important here (Griswold et al. 1982, Jackson et al. 2001, Matthews and Marsh-Matthews 2003, Fritz and Guy 2004).

Spatial characteristics of populations

Since many of the local populations of lake chub are in small lakes, and pools or beaver ponds within low-order streams, they tend to be isolated from other northern lake chub populations (Radforth 1944). They can be dispersed 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 region (Woodhouse and Overpeck 1998). Periodic drought conditions on the Great Plains undoubtedly diminish suitable habitat for lake chub (Poff and Allan 1995). Demes have become reduced and isolated from each other and from populations comprising the main range of this species to the north. The result is little genetic exchange between populations in Region 2.

Limiting factors

As is the case for most aquatic species, the main factor involved in limiting lake chub populations within Region 2 is availability of suitable habitat (Andrewartha and Birch 1984, Fausch and Bestgen 1997, Jackson et al. 2001). 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 species (McPhail 1963, Underhill 1989). In the main portion of their range to the north, this species prefers large glacial scour lakes and large tributary rivers. Populations in Region 2 have been reduced to isolated small pockets of permanent spring discharge, perhaps because this is the last vestige of the cool, clear water quality they require. Many of these springs form the headwaters of small first order streams, or form small seepage lakes. This type of habitat may not be a completely suitable substitute for the larger rivers and gravel-bottomed lakes for which lake chubs are best adapted.

One indication that the Great Plains might represent a disturbed habitat for northern minnows is the common presence of gynogens of the *Phoxinus* complex (New 1962). These all-female populations are of hybrid origin (Joswiak et al. 1985) and probably are the result of mixed environmental signals that allowed frequent interbreeding between northern redbelly and finescale dace. Hybrid dace often outnumber the parental species in Region 2, but they are very uncommon where the species are syntopic in the main portion of their range to the north (Joswiak et al. 1985, Stasiak 1987, Stasiak 2006). The presence of these hybrids in the same pools as the lake chub (as is the case in Nebraska) is an indication that the distribution of these fishes is compressed into a rather confined habitat that may not be entirely suitable (Karr et al. 1986, Fausch et al. 1990, Fausch and Bramblett 1991).

Since European settlement of this region over perhaps the past 150 years, permanent sources of cool, clear groundwater have become highly desired resources for human uses. Much of it is pumped for irrigation or used for domestic or municipal water sources; in some places, spring or seeps have been dammed up to form lakes of marginal water quality. The small streams and lakes in this region are probably more readily subjected to fluctuations in water quality if disturbances such as heavy silt flows, changes in discharge, and increases in toxic chemicals are allowed to happen.

Very frequently the remaining relatively natural small streams have been stocked with game species of large predatory fishes (e.g., trout, pike, sunfishes) that will tend to eliminate species of brightly colored minnows in confined conditions (He and Kitchell 1990, Ault and White 1994, Findley 2000, Jackson 2002). The red or orange males are exposed in clear, shallow water during the spawning season, making them prime targets for sight-feeding predators. The addition of new species of non-native fish predators (game fishes) in small streams may be the last straw that brings the population below the critical level required for survival (Moyle 1976, Moyle and Vondracek 1985).

Community ecology

Predators

In Canada, Scott and Crossman (1973) found several species of large predator fishes feeding on lake chubs. These included pike (*Esox lucius*), lake trout (*Salvelinus namycush*), burbot (*Lota lota*), and walleye (*Sander vitreum*). White (1953) documented kingfishers and mergansers preying on lake chubs in Canada. Probably most other species of piscivorous birds such as loons, herons, and cormorants also will eat lake chubs (Hamas 1994, Steinmetz et al. 2003). Fish-eating mammals (e.g., mink, martens, otters, fishers, raccoons) undoubtedly eat their share of lake chubs as well. In more confined small ponds and headwater streams of Region 2, predatory insects such as diving beetles (Dytiscidae), giant water bugs (Belostomatidae), and dragonfly (Odonata) larvae might actually be some of the prime predators, especially on larval and juvenile lake chubs (Hungerford 1920, Bobb 1974, McCafferty 1998). Fish-eating snakes and amphibians are most likely common inhabitants of the small ponds and streams containing lake chubs in Region 2, and they constitute another source of predation.

The small and shallow nature of ponds and streams containing lake chubs generally are not suited for large predatory fish species. Small ponds are often subject to heavy ice and snow cover in the winter. Dense ice may reduce the volume of water substantially, leaving little oxygen present in the remaining water column. Thus winter conditions may prevent the establishment of large piscivorous fishes in lake chub habitat. Some of the smaller fish species that are often associated with lake chubs, especially mud minnows (*Umbra limi*) and less frequently creek chubs (*Semotilus atromaculatus*), can occasionally eat some of the young lake chubs. Large creek chubs are very capable of eating small fish (Gilliam et al. 1989). These naturally occurring fish predators will play a role in eating very young lake chubs, but their overall effect is probably very small compared to the collective effect of the predatory insects. Introduced species of large predatory fishes would have a serious effect on lake chubs because they can greatly diminish adult chubs that are confined to a relatively small spawning area. There is no doubt that these fish are readily eaten by game fish, and in some regions lake chubs are used as bait minnows (Cooper 1936, Dobie and Meehan 1956, Scott and Crossman 1973, Becker 1983). This practice of using lake chubs as bait also is pointed out by those who favor the “bait bucket theory” to explain the existence of small isolated populations of minnows.

Most, if not all, species of minnows have been shown to produce and respond to chemicals (*schreckstoff*) released from skin cells. The presence of this alarm substance alerts the fish to predator attacks and elicits a fright behavior (Wisenden and Barbour 2004). Each species appears to have its own way of responding to the alarm chemical, and this type of behavior may be important for minnows in small, confined habitats. This type of predator avoidance has not been studied for lake chubs.

Competitors

The lake chub is not usually found in a large, diverse community of other fishes. In Canada and Alaska, it is often the only cyprinid present in its habitat (Morrow 1980). In the Great Plains region, the lake chub typically occurs together with finescale dace, northern redbelly 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 fishes that can successfully partition the resources available in a relatively confined habitat. Some minnows that often occur with lake chubs in the Great Plains are also considered to be sight-feeding insectivores; these are the creek chub, pearl dace, finescale dace, and common shiner. There would undoubtedly be competition for food among these minnows if they all occupied the same pool of a small body of water.

Introduced exotic predators add even more competition, as well as increased predation (Baxter et al. 2004). Shields (2004) has discussed ways that introduced species can alter the behavior and add additional stress factors to native species, above and beyond the negative effects of competition, predation, and disease introduction. This would certainly be true for lake chubs, which appear to be sensitive to interactions with fish species outside of the small group of species with which it has evolved.

Parasites and disease

Lake chubs suffer from the standard array of parasites that typically infect most minnow species in this region. This list would include protozoans, digene and monogene flukes, tapeworms, nematodes, acanthocepalans, leeches, and crustaceans (anchor worms) (Bangham and Venard 1946, Hoffman 1970). Most of these are probably not very host specific and can be readily transferred between individual hosts of different species. Fortunately, most of these parasites probably have a minimal overall effect on the health of lake chub, unless they were to be found in very large numbers.

Bangham (1955) examined lake chubs in Lake Huron, Ontario and found two species of larval trematodes encysted in the livers, as well as adult nematodes and acanthocephalans. Bangham and Adams (1954) examined 161 specimens of lake chub from three different locations on the Columbia River drainage of British Columbia, and from two locations in the Fraser River drainage. They found 160 fish with parasites. These added up to 18 different parasite species, most of which were encysted larval forms of worms that would be passed on to predators of the fish. The majority of these would become adult parasites in fish-eating birds. Probably the most common of these worms is often referred to as "black grub" or "neascus"; the adult is very common as a parasite in 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 common throughout the Midwest to see fishes such as pike, bass, perch, and sunfish practically covered with these small black spots, and apparently they are unaffected (Schell 1970).

Mayes (1976) described many species of parasites that infest Nebraska minnows in habitats similar to those in which lake chubs are found. Some of the new monogenes he described for *Phoxinus* could possibly infect lake chubs. The microscopic monogene gill parasites usually do not have any serious consequences for the host fish under normal conditions (Schmidt and Roberts 1989).

CONSERVATION

Threats

The principal reasons for declines in fish populations are the loss, modification, and fragmentation of habitat and the introduction of non-native species (Cross and Moss 1987, Warren and Burr 1994, Masters et al. 1998, Bunn and Arthington 2002). These factors appear especially important in the case of lake chub conservation in Region 2 (Dodds et al. 2004). Presently we face ever-increasing human demands for water resources and continued landscape modification, and streams and ponds that are fed by cool, clear groundwater are often stocked with sport fish, which can displace lake chubs in small water body habitats. Over the long-term, the climate of this region is expected to become drier and warmer, especially compared to the climate of the past few thousand years (Woodhouse and Overpeck 1998), and this will also have an adverse effect on the species.

Of all the North American minnows, the lake chub has the most northern distribution (Morrow 1980, Wells 1980). In the southern portion of its range, this species persists in areas where cool groundwater keeps the water cool all year. Unlike most Great Plains stream systems, the headwater streams occupied by lake chubs demonstrate less stochasticity in drying and intermittency (perannum) due to inflows from abundant groundwater sources. In fact, these streams have been remarkable in the constancy of their flow (Bleed and Flowerday 1989). However, over the last 50 years, groundwater pumping and water diversions have occurred extensively across the Great Plains, and such activities may have harmful consequences for lake chub viability within Region 2. Along the margins of the Sandhills ecoregion, particularly the Upper Niobrara River valley, center pivot irrigation of forage crops (e.g., alfalfa, pasture) has increased substantially (Bleed and Flowerday 1989). In addition, groundwater use for agricultural production exists in the sub-watersheds occupied by lake chubs on National Forest System lands in Wyoming, South Dakota, and Colorado. In the future, if groundwater withdrawals exceed annual recharge rates, then aquifer-dependent headwater streams and natural lakes will be adversely affected. Maintenance of this hydrologic pathway is critical since the persistence of lake chubs 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 in both the Upper Niobrara River (Nebraska) and Platte River drainages (Colorado). These activities modify flow regimes within these drainages and dewater sections of streams. Future water diversions in the northern Black Hills could fragment remaining populations of this species and most likely cause extirpation of extant lake chub populations. Hydrologic alteration has occurred in the Sandhills ecoregion, albeit in a different form. In this ecoregion, the modification of spring hydrology by stream channel ditching and water control structure placement and operation has modified nearly every Sandhills stream (Bleed and Flowerday 1989). Unquestionably, these activities have contributed to habitat fragmentation and the disruption of stream ecosystem processes (Fausch et al. 2002).

Lake chub population viability has been maintained despite these alterations due to the combination of habitat created by culvert-type drop structures, long periods between instream excavation episodes, and extreme late winter-early spring precipitation that occurs every 5 to 7 years and produces 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 lake chubs inhabit on the Great Plains is the presence of beaver (*Castor canadensis*) activity. The interaction of beavers with other biotic (predation) and abiotic (physiographic) components can greatly impact 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 landscape (Naiman et al. 1988, Schlosser and Kallemeyn 2000). Work in north-temperate beaver bog streams and lakes systems inhabited by lake chubs 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, Schlosser et al. 1998) 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 (Olson and Hubert 1994).

Beaver activity is observed both in the Sandhills and the northern Black Hills ecoregions, but with some interesting adjustments and surrogates. Beaver have only recently returned in significant numbers to both these ecoregions. 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 ends of these water control structures, pools form and are dominated by chub and 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. Like beaver dams, these anthropogenic structures introduce temporal heterogeneity, at least for the Sandhills streams. 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 destroyed by high flows; thus some temporal dimension of habitat and process is expressed in these stream systems.

Water improvement projects such as channelization and placement of water control structures are all too common in the Sandhills ecoregion; these negatively affect stream hydrology. Conversely, impoundment and reservoir development here are 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 by creating migration and dispersal barriers. 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 more significantly, they provide habitat for non-native fishes, particularly introduced piscivorous sport fishes.

Although lake chubs co-exist with species of fish predators in the large rivers and lakes they inhabit in Canada, in the small confined habitats of the Great Plains, they are probably far more vulnerable (He and Kitchell 1990, Findley et al. 2000, MacRae and Jackson

2001). Jackson (2002) indicated that lake chubs and the associated species were highly vulnerable to centrarchid (sunfish family) predation. Minnow species are more likely to survive in lakes containing salmonids (trout species) than in lakes dominated by centrarchid (sunfish and/or bass) predators. This phenomenon is best explained by the large extent to which the habitats of centrarchids and cyprinids overlap, particularly in the littoral zone. Salmonids demonstrate limited overlap in summer habitat with cyprinids, at least in lake environments (Jackson 2002). Thus, impoundments or reservoir developments on streams with lake chubs that experience non-native centrarchid introductions (such as Deerfield Reservoir in the South Dakota Black Hills National Forest) may lead to extirpation of this minnow species (Vanderbush 1999). Although impounding a stream is a modification of natural stream structure and function, lake chubs do reside in some small impoundments and spring-fed lakes in Region 2 (Eiserman 1996). The presence and presumed persistence of this species in these artificial environments is due to the absence of centrarchids. The harsh winter conditions (i.e., extremely low dissolved oxygen concentrations) found in very small lakes usually prevent centrarchids from becoming established (Schlosser 1995, Jackson 2002).

As for the stream-dwelling populations of lake chub, the greatest threat to their viability is from non-native species, but unlike lake populations, the stream populations are equally vulnerable to centrarchids and salmonids. After stream systems with lake chubs have been altered by impoundment structures and later stocked with centrarchids or trout, native headwater cyprinids are either absent or extremely low in number (Cunningham and Hickey 1996). For example, the author has collected northern redbelly dace, pearl dace, and finescale dace (species very similar ecologically to lake chubs) 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 1989). This is undoubtedly due to the presence of stocked brown trout (*Salmo trutta*), pike (*Esox lucius*), bass (*Micropterus salmoides*), and bluegill (*Lepomis macrochirus*).

In lentic systems (lakes), trout and chubs are basically found in different habitats; in streams, however, they share the same microhabitat (Jackson 2002). Direct minnow predation has been observed in some Sandhills streams (Cunningham et al. 1995, Cunningham and Hickey 1996). Here trout occupy pool and undercut bank habitats. Brown trout are present in Bone Creek (just a few miles downstream from the only site in Nebraska at which the lake chub has been recently collected). Probably the only reason that this lake chub population has persisted is that the city of Ainsworth lies between populations of trout and chub, and its pollution acts as a barrier preventing the brown trout from reaching the lake chub at the creek's headwaters.

Indirect effects of non-native fish predators on lake chubs would include territorial displacement and competition for food resources. Jackson (2002) described risks and consequences to small-bodied fishes from introduced fish in greater detail, but these include resource compaction, increased interspecific competition, and behavioral stress. Clearly, most introductions and modifications of lotic habitat to deeper lentic habitat that allow non-native piscivorous fish to persist would be detrimental to lake chub populations in Region 2.

Non-native species can affect native species through a number of mechanisms besides predation; these include competition, habitat alteration, pathogen transfer, and behavioral displacement (Shields 2004). 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, isolating populations (Fausch and Bestgen 1997), and preventing exchange of genetic material. Another potential consequence of fish introductions is the potential pathogen transfer from non-native fish species to the native fish community or other biota within the watershed (i.e., amphibians) (Kiesecker et al. 2001). Shields (2004) documented several cases of parasite (i.e., nematodes, trematodes, cestodes) transfer from introduced fishes to native fishes in Oregon, resulting in severe population reductions in native fish populations. 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 (Kiesecker et al. 2001).

A significant, unknown, and little studied, element in the long-term viability of headwater fish species is the synergistic effects of multiple stressors. For example, extended severe drought by itself may have only modest effects on the long-term viability of fish assemblages (Matthews and Marsh-Matthews 2003), but combined with groundwater pumping, irrigation, and water diversion, it may severely deplete a population or extirpate a species on a regional basis. Couple these negative impacts with climate change predictions, and the potential for long-term viability is difficult to assess.

Two other human-related activities generally cited as common causes of species declines include pollution and overharvest. Many forms of pollutants may find their way into streams. For Region 2, this category includes mostly agricultural pesticides and fertilizers. It is possible that future mining, logging, and/or agricultural operations could release deleterious chemicals into the streams, watersheds, or groundwater (Chamberlin et al. 1991, Gresswell 1999). In addition to purely toxic chemicals, a relatively new concern would be the appearance of endocrine disrupters. These natural and artificial hormones can have a "gender bending" effect on fishes and other aquatic vertebrates, often resulting in diminished reproductive success (Arcand-Hoy and Benson 1998, Alvarez and Fuiman 2005, Milnes et al. 2006).

Lake chubs need relatively clear water; anything that would cause sustained turbidity would most likely limit the population. This includes activities that could lead to frequent erosion and siltation (Berkman and Rabeni 1987). Some examples would be prolonged use of a water source by cattle, overgrazing, row crop agricultural in the riparian zone, and construction projects (Belsky et al. 1999). Pollution in the form of increased siltation and turbidity appears to be a problem for lake chubs in the Black Hills National Forest due to road construction; this is always something that needs to be monitored (Hall et al. 2002).

In terms of direct harvest by humans, people can and do collect wild minnows for use as bait. Lake chubs are known to be a good bait species for lake trout, walleyes, and northern pike (Scott 1957) and are often sold commercially. In Region 2, they are found in small, confined locations that frequently contain other minnow species that are targeted for use as bait. Perhaps all minnow collecting should be restricted in these habitats.

Conservation Status of Lake Chub in Region 2

The area occupied by lake chubs within USFS Region 2 administered lands is quite small. The Colorado populations occur in the South Fork of St. Vrain Creek, in the upper Platte River drainage, near the Roosevelt National Forest, in Boulder County (Bestgen et al. 1991). At one time this species was found in many of the Black Hills streams (Evermann 1893), but it now appears to be very rare in these fluvial systems. In South Dakota, the lake chub population is apparently confined to Deerfield Reservoir in the Black Hills National Forest, and it is declining in abundance (Ford 1988, Eiserman 1996). In the Black Hills in Wyoming, lake chubs can be found in the Bighorn and Shoshone national forests, but even here they appear to have declined in recent years (Parrish et al. 1996, Patton 1997).

The first step at developing a conservation strategy for lake chub on National Forest System lands is to determine exactly which potential sites actually have lake chub populations, and if possible, place this data into a historic framework. It seems that wherever uncommon species of minnow occur, mention is made of the possibility of "bait bucket" introductions or other human transplants to explain their occurrence. Then the claim is made that these are not really native fish, so there is no need to conserve them. In the case of the lake chub, however, the historical records and distributional patterns provide strong evidence to indicate that the small populations represent naturally occurring remnant populations of a species that was once more widespread in Region 2.

Lake chub populations in four of the Region 2 states are currently designated at various levels of conservation concern (**Table 1**). While these designations confer limited conservation protection, the species is still vulnerable to extirpation by hydrologic modification of stream systems and presence of non-native species. Conservation of this minnow species will require resource managers to consider the unique habitat features utilized by this species. Thus, the management of lake chub should focus on conserving natural system processes in streams and the prevention and control of non-native species introductions. Specific conservation actions for lake chub include the following:

- ❖ prohibit the stocking of non-native species within aquatic ecosystems

- ❖ remove non-native fish species from natural spring-fed lakes and restock with lake chubs from 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; regulate land use in the riparian zone
- ❖ restrict minnow harvest in lake chub habitat; strictly enforce existing laws and regulations concerning use of minnows
- ❖ monitor chemical pollutants in water sources; set standards for levels of pesticides and hormones.

Potential Management of Lake Chub in Region 2

Implications and potential conservation elements

Conserving native fish populations is a matter of protecting and restoring the natural aquatic environment (Andrewartha and Birch 1984, Minckley and Deacon 1991, Fausch and Bestgen 1997, Masters et al. 1998, Bunn and Arthington 2002). In the case of lake chub and several other minnow species (e.g., finescale dace, northern redbelly dace, southern redbelly dace, pearl dace), natural changes to a drier and warmer climate (Briggs 1986, Woodhouse and Overpeck 1998) have already reduced their populations within Region 2. Environments suitable for these species are restricted to remnant habitats that depend on stable spring flows (McPhail 1963, Cross 1970). Therefore, protecting underground water supplies and maintaining the natural flow regime are critical for these fishes (Fausch et al. 1990, Dodds et al. 2004).

While lake chub are present in select national forests within Region 2, much of the watersheds in which they occur are outside the national forest boundaries. The USFS should undertake efforts to work in conjunction with its partners (e.g., other federal agencies, state resource agencies, non-profit conservation organizations, private landowners) to develop and manage stream systems on a watershed basis focused on native stream fishes. Currently, a vast majority of Great Plains streams of "high water quality" are managed for various trout species at the expense of native fishes. The presence of non-native species (e.g., trout, pike, walleye, various bass and sunfish) has been a principal reason for lake chub population declines in aquatic systems in both Wyoming 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).

Concurrently, hydrological modifications (e.g., water development projects, sub-irrigated meadow alterations, groundwater pumping, dam building, water diversions) have altered aquatic systems throughout USFS Region 2. Future human water demands and continued drought conditions coupled with climate change could jeopardize remaining lake chub populations.

Resource managers may be tempted to build habitat for lake chub by impounding water on sections of streams inhabited by this species. Conceptually, this may be appealing; however, these artificial ponds would need to be designed to mimic beaver pond morphology, and hydrologic retention and flow. They need to provide unsuitable habitat for piscivorous fishes. Protecting or restoring quality existing habitats is usually more effective than trying to create new ones. Moreover, simply forming a pond or hole on the landscape is not ecologically sufficient to ensure viability of lake chub populations. 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, migration of juveniles and adults. Resource managers must understand and recognize the spatial arrangement and temporal dynamics of interacting processes at hierarchical scales (Frissell et al. 1986, Schlosser and Kallemeyn 2000). Moreover, the quality of land management within a drainage unit will affect the hydrology, sediments, nutrient inputs, and litter and detritus composition. Several conceptual models of stream fish population ecology and life history linking key ecosystem processes interacting across multiple scales have been developed (Schlosser and Angermeier 1995, Labbe and Fausch 2000). These models provide quality insight for resource managers to use in understanding how their land management practices might affect critical habitat required for lake chub conservation.

Attempts should be made to maintain the natural flow regime in the streams were the lake chub resides and to manage for the expansion of beaver activity within these watersheds. Future water diversion, groundwater pumping, and reservoir construction would only further fragment the distribution of the lake chub, disrupting connectivity patterns and possibly leading to additional non-native species establishment. The expansion of beaver activity is a difficult one for private landowners since the result of such activity can back water up into unwanted locations or saturate soils. However, on US FS administered lands, expanded beaver activity should not affect other uses such as grazing and timber harvest. Beaver sites should be actively managed, particularly those areas exhibiting year-round spring discharge that flow into a defined meandering stream channel. 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 (Belsky et al. 1999). Managing for only limited temporary access by cattle would be more ecologically sound, but resource managers must focus their conservation management efforts beyond individual pools. The viability of lake chub 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 lake chub conservation goals.

Tools and practices

Inventory and monitoring

Efforts are needed to inventory and monitor known lake chub populations and areas of potential occupancy within Region 2. To date, inventory efforts have focused primarily on the presence or absence of this species as part of statewide stream fish surveys or ecoregional sampling efforts. It is easy to miss collecting specimens when they occur in very restricted areas and in small populations (Green and Young 1993, Patton et al. 2000). For example, finescale dace and northern redbelly dace were recorded from the headwaters of the Niobrara River in Nebraska during two inventories, but Patton (1997) did not record either species from the springs forming the headwaters of the Niobrara River just across the state line in Wyoming. A fish inventory was conducted in the same headwaters pool of Bone Creek near Ainsworth, Nebraska for 15 years prior to collecting lake chub at this location (Stasiak 1986).

Bennett's (1931) and Johnson's (1942) surveys of Nebraska fishes stand as the baseline for fish distribution information during the past century for this state. The lake chub had apparently become extirpated from most of the previously known sites in Nebraska, since both of these surveys failed to find any lake chubs at all (Madsen 1985); Evermann (1893) had collected them previously from four streams in the Sandhills. Bliss and Schainost (1972) conducted fish surveys for all the major stream systems in Nebraska without collecting lake chub. The Sandhills ecoregion was extensively sampled as part of a Nebraska natural heritage program inventory in the 1990's (Cunningham and Hickey 1996). A new Nebraska stream inventory that re-sampled all of Johnson's (1942) locations was recently conducted by Ed Peters and Steve Schainost. Lake chubs were not collected during this survey.

Several fish surveys have been conducted in South Dakota since the Bailey and Allum report (1962) (Ford 1988, Erickson et al. 1993, Cunningham et al. 1995, Eiserman 1996, Meester 1998, Doorenbos 1998). Additional references to surveys were found in the ecoregional conservation plan for the Black Hills (Hall et al. 2002). Dr. Charles Berry, Jr. at South Dakota State University (in cooperation with the South Dakota Division of Wildlife) has been compiling data on the distribution of all fishes in that state, and a major manuscript is currently in the publication process.

Although Kansas has had numerous organized fish collection efforts over the last century, lake chubs have never been documented in that state.

It would clearly be useful for each service unit in the USFS Region 2 to develop a master plan for conducting surveys and monitoring fish populations. 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 Angermeier and Smogor (1995), Hays et al. (1996), and Hulbert (1996), and protocols and methods for assessing streams 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 (2001). Full adoption of these methods is probably unnecessary; rather a modification of one or a combination of methods would be adequate.

Devising a survey or monitoring plan specifically for lake chubs may prove to be a technically difficult exercise. In streams, standard survey techniques such as seining and electroshocking may be effective, but they could probably add mortality to an already small population. Electroshocking with a boat usually is not very quantitative for minnows (due to their size); however, it may be of some value for inventorying larger age classes of lake chubs (Kruse et al. 1998). Great care must be taken in the handling of the fish to avoid injuries. Perhaps the use of minnow traps, with mesh of the correct size for lake chubs, would allow these to be counted and monitored without as much harm to the fish (Bryant 2000). In large lakes in Canada, gill nets of the correct mesh have proven effective, but these also are usually fatal to the fish. Large beach seines are probably the most effective tool for collecting this species in lakes.

Population or habitat management practices

Water quality data should be monitored in the reservoirs and streams that have known populations of lake chub, with particular attention to increases in siltation, turbidity levels, oxygen levels, temperature changes, and major chemical pollutants. This should include substances that can act as hormones and interfere with the normal reproductive process of this species (Arcand-Hoy and Benson 1998, Ankley et al. 2003, Alvarez et al. 2005, Milnes et al. 2006).

Some attempts at stream or hydrologic restoration are being made in 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 (http://www.sandhillstaskforce.org). However, the efficacy of these projects to restore and enhance the native headwater fish assemblage is unknown, and post-construction research and monitoring need to be conducted at these sites.

Additional opportunities for restoration exist in Nebraska and South Dakota; specifically non-native species could be removed from lake chub habitat. At the very least, there should be no additional stockings of sport fishes, particularly centarchids (sunfish family) and non-indigenous brown trout. Obviously, this type of management for non-game species has traditionally been popular with the fishermen. If consideration is given to transplanting lake chubs to restored or reclaimed habitats, care must be taken to ensure the genetic integrity of the extant populations (Meffe 1986, Billington and Hebert 1991).

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 USFS Region 2. These adopted conservation measures should ultimately allow for the creation of these changing successional stages 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 aquatic conservation assessment portion of the Black Hills ecoregional plan (Hall et al. 2002) has identified areas of biological significance based partly on lake chub 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 common conservation strategies for lake chub.

Information Needs

Lake chub surveys should be continued in the streams of the Black Hills National Forest in South Dakota and Wyoming. These are sites that have historically contained good lake chub populations. Deerfield and Blacktail reservoirs also need to be closely monitored, and any movements of lake chubs into and out of the connecting streams should be documented. Additional inventory efforts within the St.Vrain River and its associated tributaries to the South Platte River in Colorado's Roosevelt National Forest should be conducted. Further, attempts should be made via the USFS partners to inventory stream sections on private property in the Boulder 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 of the Nebraska National Forest would close a data gap for this species in the Sandhills ecoregion. As stated in the state CWCS plan, the Wyoming populations of lake chub need to be monitored.

Virtually no data are available regarding the population dynamics of lake chubs in Region 2 of the USFS. Information concerning distribution, population size, and recruitment success are needed to develop a conservation management plan for this species. Basic biological information (i.e, total number of eggs produced by a female lake chub, spawning habitat, age and growth, dispersal) has been gathered for populations (or possibly different subspecies) in large lakes and rivers in Canada and the eastern United States. Information of this type is also needed for the populations in Region 2, where the data may prove to be quite different.

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. Behavioral studies should be conducted on lake chub response to predators and "alarm substance". There are suggestions that lake chubs in confined areas might become territorial on the spawning sites; this could apply to small headwater pools in Region 2.

Lake chub in Region 2 are restricted to populations that have been isolated from the main range of this species for a very long time, perhaps several hundred to thousands of years (Cross et al. 1986, Woodhouse and Overpeck 1998, Matthews and Marsh-Matthews 2003). This period in isolation may easily have allowed these fish to become unique evolutionary units (i.e., demes, races, subspecies, or even species). It appears that very little genetic research of any type has been performed on this species. An examination of the population genetics for lake chub (similar to what was performed for Plains killifish (*Fundulus zebrinus*) by Kreiser et al. [2001]) is needed. They examined the geographic pattern of genetic variation using allozyme loci, mitochondrial DNA restriction fragment length polymorphisms (RFLPs), and the sequencing of the mitochondrial cytochrome oxidase to help understand the roles of dispersal and vicariance. Microarray and microsatellite analysis might also prove useful. This is classic "island biogeography" (Hanfling and Brandl 1998). The danger here would be the temptation to add new individuals from other populations, and thus change the genetic make up of what might represent a naturally well-adapted deme (Meffe 1986, Vrijenhoek 1998). Population genetics of the isolated groups must be understood before new individuals from outside sources are added (Billington and Hebert 1991, Bryant 2000), Watts et al. 2006). The evolutionary implications of such a genetic study could play a major role in the conservation of lake chubs in Region 2 (Frankham 1996). Perhaps this would be one type of research that should be a priority funding measure.

Information management and document archiving are also important. Inventory and monitoring results should be shared with natural heritage programs for database archival. It is also important for surveys to deposit voucher specimens in major regional collections where they can be readily available to the entire scientific community.

Definitions

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

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

Gynogen – a female fish that reproduces asexually by releasing mitotic (usually diploid) eggs, which develop without fertilization. The dace gynogens are presumed to be the result of a historic cross between finescale dace and northern redbelly dace.

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

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

Pharyngeal teeth – bony projections on the modified 5th gill arch of cyprinid fishes (minnows); these function as teeth, grinding food against a pad at the back of the throat; their number and morphology are species-specific, making them excellent taxonomic tools.

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

Sub-irrigated meadows – grasslands that exist in areas of stable groundwater seepage; even in regions of little precipitation, the plant roots have a constant water supply.

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

Tier 1 species – species that are in need of immediate conservation action and/or research because of extreme rarity, restricted distribution, unknown or decreasing population trends, specialized habitat needs and/or habitat vulnerability. Some species may be considered critically imperiled and at risk of extinction/extirpation.

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

References

Agassiz, J.L.R. 1850. Lake Superior. Its physical character, vegetation, and animals, compared with those of other and similar regions. Gould, Kendall, and Lincoln, Boston, MA.

Alvarez, M.C. and L.A. Fuiman. 2005. Environmental levels of atrazine and its degradation products impair survival skills and growth of red drum. Aquatic Toxicology 74:229-241.

Anderson, E.D. and L.L. Smith. 1971. A syntopic study of food habits of 30 fish species from western Lake Superior. University of Minnesota Agricultural Experimental Station Technical Bulletin 279. 199pp.

Andrewartha, H.G. and L.C. Birch. 1984. The ecological web: more on the distribution and abundance of animals. University of Chicago Press, Chicago, IL.

Angermeier, P.L. and R.A. Smogor. 1995. Estimating number of species and relative abundances in stream-fish communities: effects of sampling effort and discontinuous spatial distributions. Canadian Journal of Fisheries and Aquatic Sciences 52:935-949.

Ankley, G.T., K.M. Jensen, E.A. Makynen, M.D. Kahl, J.J. Korte, and M.W. Hornung. 2003. Effects of the androgenic growth promoter 17-Beta-trenbolone on the fecundity and reproductive endocrinology of the fathead minnow. Environmental Toxicology and Chemistry 22:1350-1360.

Arcand-Hoy, L.D. and W. Benson. 1998. Fish reproduction: an ecologically relevant indicator of endocrine disruption. Environmental Toxicology 17:49-57.

Ashan, S.N. 1996. Effects of temperature and light on the cyclical changes in the spermatogenetic activity of the lake chub, *Couesius plumbeus* (Agassiz). Canadian Journal of Zoology. 44:161-171.

Ashton, D.E. and E.M. Dowd. 1991. Fragile legacy. Endangered, threatened and rare animals of South Dakota. South Dakota Department of Game, Fish and Parks, Report No. 91-04. 56pp.

Ault, T.R. and R.W. White. 1994. Effects of habitat structure and the presence of brown trout on the population density of *Galaxias truttaceus* in Tasmania, Australia. Transactions of the American Fisheries Society 123:939-949.

Backlund, D. 2006. The lake chub. Available online at http://www.sdgfp.info/Wildlife/Diversity/Digest%20Articles/lakechub.htm.

Bailey, R.M. 1951. A check-list of the fishes of Iowa, with keys for identification. Pages 185-237 *in* J.R. Harlan and E.V. Speaker, editors. Iowa Fish and Fishing. Iowa Conservation Commission, Des Moines, IA.

Bailey, R.M. and M.O. Allum. 1962. Fishes of South Dakota. University of Michigan Museum of Zoology, Miscellaneous Publication No. 119. Ann Arbor, MI. 113pp.

Balinsky, B.I. 1948. On the development of specific characters in cyprinid fishes. Proceedings of the Zoological Society of London 118(2):335-345.

Bangham, R.J. 1955. Studies on fish parasites of Lake Huron and Manitoulin Island. American Midland Naturalist 53(1):184-194.

Bangham, R.V. and J.R. Adams. 1954. A survey of the parasites of freshwater fishes from the mainland of British Columbia. Journal of the Fisheries Research Board of Canada 11(6):673-708.

Bangham, R.V. and C.E.Venard. 1946. Parasites of fish of Algonquin Park lakes. Publications of the Ontario Fisheries Research Laboratory No. 65, University of Toronto Studies in Biology Series No. 53.

Baxter, C.V., K.D. Fausch, M. Murakami, and P.L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology 85(10):2656-2663.

Baxter, G.T. and J.R. Simon. 1970. Wyoming fishes. Wyoming Game and Fish Department. Cheyenne, WY.

Baxter, G.T. and M.D. Stone. 1995. Fishes of Wyoming. Wyoming Game and Fish Department Cheyenne, WY.

Becker, G.C. 1983. Fishes of Wisconsin. University of Wisconsin Press. Madison, WI.

Becker, G.C. and T.R. Johnson. 1970. Illustrated key to the minnows of Wisconsin. Department of Biology, Wisconsin State University, Stevens Point, WI.

Belsky, A.J., A. Matzke, and S. Uselman. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. Journal of Soil and Water Conservation 54:419-431.

Bennett, G.A. 1931. A partial survey of the fishes of Nebraska, with comments on fish habitats. M. A. Thesis, University of Nebraska, Lincoln, NE.

Berkman, H.E. and C.F. Rabeni. 1987. Effect of siltation on stream fish communities. Environmental Biology of Fishes 18(4):285-294.

Bestgen, K.R., K.D. Fausch, and S.C. Riley.1991. Rediscovery of a relict southern population of lake chub, *Couesius plumbeus*, in Colorado. The Southwestern Naturalist 36:125-127.

Billington, N. and P. Hebert. 1991. Mitochondrial DNA diversity in fishes and its implications for introductions. Canadian Journal of Fisheries and Aquatic Science 48(Supplement 1).

Black Hills National Forest. 1996. Final environment impact statement, 1996 revised land resource management plan. Black Hills National Forest. Custer, SD.

Bleed, A. and C. Flowerday. 1989. An Atlas of the Sand Hills. Resource Atlas No. 5a. Conservation Survey Division. University of Nebraska, Lincoln, NE.

Bliss, Q. and S. Schainost. 1972. Fish surveys in Nebraska streams. Nebraska Game and Parks Commission, Lincoln, NE.

Bobb, M.L. 1974. The insects of Virginia: No.7. The aquatic and semi-aquatic Hemiptera of Virginia. Research Division, Bulletin 87. Virginia Polytechnic Institute and State University, Blacksburg, VA.

Briggs, J.D. 1986. Introduction to the zoogeography of North American fishes. Pages 1-16 *in* C.H. Hocutt and E.O. Wiley, editors. The Zoogeography of North American Freshwater Fishes. John Wiley and Sons, New York, NY.

Brown, C.D. 1971. Fishes of Montana. Big Sky Books, Montana State University, Missoula, MT.

Brown, J.H., U.T. Hammer, and G. H. Koshinsky. 1970. Breeding biology of the lake chub, *Couesius plumbeus*, at Lac la Ronge, Saskatchewan. Journal of Fisheries Research Board Canada 27:1005-1015.

Bruce, W.J. and R.F. Parsons. 1976. Age, growth, and maturity of lake chub (*Couesius plumbeus*) in Mile 66 Brook, Ten Mile Lake, western Labrador. Fisheries and Marine Service Research Development Technical Report 683.

Bryant, M.D. 2000. Estimating fish populations by removal methods with minnow traps in southeast Alaska streams. North American Journal of Fisheries Management 20:923-930.

Bunn, S.E. and A.H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30(4):492-507.

Carl, G.C., W.A. Clemens, and C. Lindsey. 1959. The freshwater fishes of British Columbia. British Columbia Provincial Museum Handbook No. 5. 192pp.

Chamberlin, T.W., R.D. Harr, and F.H. Everest. 1991. Timber harvesting, silviculture, and watershed processes. Pages 181-206 *in* W.R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Pub. 19. Bethesda, MD.

Churchill, E.P. and W.H. Over. 1938. Fishes of South Dakota. South Dakota Department of Game and Fish, Pierre, SD. 87pp.

Collette, B.B. 1977. Epidermal breeding tubercles and bony contact organs in fishes. Symposium of the Zoological Society of London 39:225-268.

Colorado Comprehensive Wildlife Conservation Strategy. 2005. Available online at http://wildlife.state.co.us/WildlifeSpecies/ComprehensiveWildlifeConservationStrategy/.

Cooper, G.P. 1936. Some results of the forage fish investigations in Michigan. Transactions of the American Fisheries Society 65:132-142.

Cross, F.B. 1970. Fishes as indicators of Pleistocene and recent environments in the Central Plains. University of Kansas Special Publication 3, University of Kansas Press, Lawrence, KS.

Cross, F.B. and J.T. Collins. 1975. Fishes in Kansas. The University of Kansas Museum of Natural History Public Education Series No.3. Lawrence, KS.

Cross, F.B. and R.E. Moss. 1987. Historic changes in fish communities and aquatic habitats in plains streams of Kansas. Pages 155-165 *in* W.J. Matthews and D.C. Heins, editors. Community and Evolutionary Ecology of North American Stream Fishes. University of Oklahoma Press, Norman, OK.

Cross, F.B., R.L. Mayden, and J.D. Stewart. 1986. Fishes in the western Mississippi Basin (Missouri, Arkansas, and Red rivers). Pages 363-412 *in* C.H. Hocutt and E.O. Wiley, editors. The zoogeography of North American freshwater fishes. John Wiley and Sons, New York, NY.

Cunningham, G.R. and S.M. Hickey. 1996. Habitat parameter determination and threatened fish inventory of Sandhills streams. Report to the Nebraska Natural Heritage Program. Nebraska Game and Parks Commission, Lincoln, NE.

Cunningham, G.R., R.D. Olson, and S.M. Hickey. 1995. Fish Surveys of the streams and rivers in south central South Dakota west of the Missouri River. Proceedings South Dakota Academy of Sciences 74:55-64.

Davis, B.J. and R.J. Miller. 1967. Brain patterns in minnows of the genus Hybopsis in Relation to feeding habits and habitat. Copeia 1967:1-39.

Dobie, J. and O.L. Meehan. 1956. Raising bait fishes. U.S. Fish and Wildlife Service Circular No. 35. U.S. Government Printing Office, Washington, D.C. 124pp.

Dodds, M.E., K.B. Gido, M.R. Whiles, K.M. Fritz, and W.J. Matthews. 2004. Life on the edge: ecology of prairie streams. Bioscience 54:205-216.

Doorenbos, R.D. 1998. Fishes and habitat of the Belle Fourche River, South Dakota. M.S. Thesis, South Dakota State University, Brookings, SD.

Dymond, J.R. 1926. The Fishes of Lake Nipigon. University of Toronto Studies in Biology Series 27, Publication of the Ontario Fisheries Research Lab. 27:1-108.

Dymond, J.R. and W.B. Scott. 1941. Fishes of the Patricia portion of the Kenora District, Ontario. Copeia 243-245.

Dymond, J.R., J.L. Hart, and A.L. Pritchard. 1929. The fishes of the Canadian waters of Lake Ontario. University of Toronto Studies in Biology Series 33. Publication of the Ontario Fisheries Research Laboratory 37:1-35.

Eastman, J.T. 1970. The pharyngeal bones and teeth of Minnesota cyprinid and catostomid fishes: functional morphology, variation, and taxonomic significance. Ph.D. Thesis, University of Minnesota. Minneapolis, MN.

Eddy, S., J.B. Moyle, and J.C. Underhill. 1963. The fish fauna of the Mississippi River above St. Anthony Falls as related tot he effectiveness of this falls as a migration barrier. Proceedings of the Minnesota Academy of Science 32(2):111-115.

Eddy, S. and T. Surber. 1974. Northern fishes. Third edition. University of Minnesota Press, Minneapolis, MN. 414pp.

Eiserman, F.M. 1996. A fisheries survey of streams and reservoirs in the Belle Fourche, Cheyenne, Little Missouri, Little Powder and Niobrara River Drainages. Wyoming Game and Fish Commission, Fisheries Technical Report Number 15, Cheyenne, WY.

Ellis, M.M. 1914. Fishes of Colorado. University of Colorado Studies 11:1-136.

Elser, A.A., M.W. Gorges, and L.M. Morris. 1980. Distribution of fishes in southeastern Montana. Montana Department of Fish, Wildlife, and Parks and U.S. Department of the Interior, Bureau of Land Management, Miles City, MT.

Emery, A.R. 1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario Lakes. Journal of the Fisheries Research Board of Canada 30:761-774.

Erickson, J., R. Koth, and L. Vanderbush. 1993. Black Hills Stream Management Plan. Report No. 93-8. Department of Game, Fish, and Parks. Pierre, SD.

Evenhuis, B.L. 1969. A list of fish collected in North Dakota 1964-1968. Report No. A-1011, North Dakota State Game and Fish Department, Bismarck, ND.

Evermann, B.W. 1893. The ichthyological features of the Black Hills region. Proceedings of the Indiana Academy of Science (1892):73-78.

Evermann, B.W. and U.O. Cox. 1896. A report upon the fishes of the Missouri River basin. Report to U.S. Comm. Fish. 20:325-429.

Fausch, K.D. and R.G. Bramblett. 1991. Disturbance and fish communities in intermittent tributaries of a western Great Plains river. Copeia 1991:659-674.

Fausch K.D. and K.R. Bestgen. 1997. Ecology of fishes indigenous to the central and southwestern Great Plains. Pages 131-166 *in* F.L. Knopf and F.B. Samson. editors. Ecology and Conservation of Great Plains Vertebrates. Springer-Verlag, New York, NY.

Fausch, K.D., J. Lyons, J.R. Karr, and P.L. Angermeier. 1990. Fish communities as indicators of environmental degradation. Pages 123-144 *in* S.M. Adams, editor. Biological indicators of stress in fish. American Fisheries Society, Symposium 8, Bethesda, MD.

Fausch, K.D., C.E. Torgersen, C.V. Baxter, and H.W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. Bioscience 52:483-498.

Fedoruk, A.N. 1971. Freshwater fishes of Manitoba: checklist and keys. Province of Manitoba Department of Mines, Resources, and Environmental Management, Winnipeg, Manitoba, Canada.

Ferguson, M. and R. Danzmann. 1998. Role of genetic markers in fisheries and aquaculture: useful tools or stamp collecting? Canadian Journal of Fisheries and Aquatic Science 54:1051-1063.

Fertig, W. and G.B. Beauvais. 1999. Wyoming plant and animal species of special concern. Wyoming Natural Diversity Database, Laramie, Wyoming. Unpublished report.

Findlay, C.S., D.G. Bert, and L. Zheng. 2000. Effect of introduced piscivores on native minnow communities in Adirondack lakes. Canadian Journal of Fisheries and Aquatic Sciences 57: 570-580.

Ford, R.C. 1988. Black Hills stream inventory and classification, 1984 and 1985. Report Number 88-1. South Dakota Department of Game, Fish, and Parks. Pierre, SD.

Frankham, R. 1996. Relationship of genetic variation to population size in wildlife. Conservation Biology 10(6): 1500.

Frissell, C.A., W.J. Liss, C.E. Warren, and M.D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199-214.

Fuiman, L.A. and J.P. Baker. 1981. Larval stages of the lake chub, *Couesius plumbeus*. Canadian Journal of Zoology 59:218-224.

Geen, G.H. 1955. Some features of the life history of the lake chub (*Couesius plumbeus greeni* Jordan) in British Columbia. B.A. Thesis, University of British Columbia.

Gilliam, J.F., D.F. Fraser, and A.F. Sabat. 1989. Strong effects of foraging minnows on a stream benthic invertebrate community. Ecology 70(2):445-452.

Greeley, J.R. and S.C. Bishop. 1932. A biological survey of the Oswegatchie and Black River systems, with annotated list. Supplement to 21st Annual Report, New York State Conservation Department, Albany, NY.

Greeley, J.R. and S.C. Bishop. 1933. Fishes of the upper Hudson watershed with annotated list. Pages 61-101 *in* A biological survey of the upper Hudson watershed. Supplement to 22nd Annual Report, New York State Conservation Department, Albany, NY.

Greeley, J.R. and C.W. Greene. 1931. Fishes of the area with annotated list. Pages 44-94 *in* A biological survey of the St. Lawrence watershed. Supplement to 20th Annual Report, New York State Conservation Department, Albany, NY.

Green, R.H. and R.C. Young. 1993. Sampling to detect rare species. Ecological Applications 3:351-356.

Greene, C.W. 1935. The distribution of Wisconsin fishes. Wisconsin Conservation Commission, Madison, WI. 235pp.

Gresswell, R.E. 1999. Fire and aquatic ecosystems in forested biomes of North America. Transactions of the American Fisheries Society 128:193-221.

Griswold, B.L., C.J. Edwards, and L.C. Woods. 1982. Recolonization of macroinvertebrates and fish in a channelized stream after a drought. Ohio Journal of Sciences 82:96-102.

Hall, J.S., H.J. Marriott, and J.K. Perot. 2002. Ecoregional conservation in the Black Hills. The Nature Conservancy. Arlington, VA. Available online at http://www.conserveonline.org.

Hamas, M.J. 1994. Belted kingfisher (*Ceryle alcyon*). *In*: A. Poole and F. Gills, editors. The birds of North America No. 84. Philadelphia. Academy of Natural Sciences, Washington, D.C. The American Ornithologists Union.

Hanfling, B. and R. Brandl. 1998. Genetic variability, population size, and isolation of distinct populations in the freshwater fish *Cottus gobio* L. Molecular Ecology 7:12, 1625-1632.

Hankin, D.G. and G.H. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Canadian Journal of Fisheries and Aquatic Sciences 45:834-844.

Harlan, J.R., E.B. Speaker, and J. Mayhew. 1987. Iowa fish and fishing. Iowa Department of Natural Resources, Des Moines, IA.

Hatch, J.T., K.P. Schmidt, D.P. Siems, J.C. Underhill, R.A. Bellig, and R.A. Baker. 2003. A new distributional checklist of Minnesota fishes, with comments on historical occurrence. Journal of the Minnesota Academy of Science 67:1-17.

Hays, D.B., C.P. Ferreri, and W.W. Taylor. 1996. Active fish capture methods. Pages 193-220 *in* B.R. Murphy and D.W. Willis, editors. Fisheries Techniques. Second edition. American Fisheries Society, Bethesda, MD.

He, X. and J.F. Kitchell. 1990. Direct and indirect effects of predation on a fish community: a whole-lake experiment. Transactions of the American Fisheries Society 119:825-835.

Hendricks, L.J. 1947. The fishes of Boulder County, Colorado. M.A. Thesis, University of Colorado, Boulder, CO.

Heufelder, G.R. and L.A. Fuiman. 1982. Family Cyprinidae, carps and minnows. Pages 174-344 *in* N.A. Auer, editor. Identification of larval fishes of the Great Lakes basin with emphasis on the Lake Michigan drainage. Great Lakes Fishery Commission, Ann Arbor, Michigan. Special Publication 82-3, 744pp.

Hinks, D. 1943. The fishes of Manitoba. Department of Mines and Natural Resources, Winnipeg, Manitoba, Canada.

Hoffman, G.L. 1970. Parasites of North American freshwater fishes. Second edition. University of California Press, Berkley, CA. 350pp.

Hubbs, C.L. 1964. Fishes of the Great Lakes region. Third edition. Cranbrook Institute of Science Bulletin 26.

Hubbs, C.L. and D.E. Brown. 1929. Materials for a distributional study of Ontario fishes. Trans. Roy. Can. Inst. 17: 1-56.

Hubbs, C.L. and K.F. Lagler. 1949. Fishes of Isle Royale, Lake superior, Michigan. Pennsylvania-Michigan Academy of Sciences, Arts, and Letters 33:73-133.

Hubbs, C.L., K.F. Lagler, and G.R. Smith. 2004. Fishes of the Great Lakes Region, revised edition. University of Michigan Press, Ann Arbor, MI.

Hungerford, H.B. 1920. The biology and ecology of aquatic and semi-aquatic Hemiptera. Kansas University Science Bulletin XI:1-256.

Isaak, D.J., W.A. Hubert, and C.R. Berry. 2003. Conservation assessment for Lake chub, mountain sucker, and finescale dace in the Black Hills National Forest, South Dakota and Wyoming. Report to USDA Forest Service, Rocky Mountain Region, Black Hills National Forest, Custer, SD.

Jackson, D.A. 2002. Ecological impacts of *Micropterus* introductions: the dark side of black bass. *In*: D. Phillip and M. Ridway, editors. Black Bass: Ecology, Conservation and Management. American Fisheries Society, Bethesda, MD.

Jackson, D.A., P.R. Peres-Neto, and J.D. Olden. 2001. What controls who is where in freshwater fish communities – the role of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences 58:157-170.

Jenkins, R.E. and E.A. Lachner. 1971. Criteria for analysis and interpretation of the American fish genera *Nocomis* Gerard and *Hybopsis* Agassiz. Smithsonian Contributions to Zoology No. 90.

Johnson, R.E. 1942. The distribution of Nebraska fishes. Ph.D. Thesis, University of Michigan. Ann Arbor, MI.

Jones, D.J. 1963. A history of Nebraska's fishery resources. Dingell-Johnson Federal Aid in Fisheries Research, Project F-4-R. Nebraska Game, Forest, and Parks Commission, Lincoln, NE.

Joswiak, G.R., R.H. Stasiak, and B.F. Koop. 1985. Diploidy and triploidy in the hybrid minnow, *Phoxinus eos* x *Phoninus neogaeus* (Pisces:Cyprinidae). Experientia 41 (1985):505-507.

Karr, J.R., K.D. Fausch, P.L. Angermeier, P.R. Yant, and I.J. Schlosser. 1986. Assessing biological integrity in running waters: a method and its rationale. Illinois Natural History Survey Special Publication #5, Champaign, IL.

Keleher, J.J. 1956. The northern limits of distribution in Manitoba for cyprinid fishes. Canadian Journal of Zoology 34:263-266.

Kendall, W.C. 1908. Fauna of New England. Part 8. List of the Pisces. Occasional Papers of Boston Society of Natural History No. 7. 152pp.

Kiesecker, J.M., A.R. Blaustein, and C.L. Miller. 2001. Transfer of a pathogen from fish to amphibian. Conservation Biology 15:1064-1070.

Kreiser, B.R., J.B. Mitton, and J.D. Woodling. 2001. Phylogeography of the plains killifish, *Fundulus zebrinus*. Evolution 55(2):339-350.

Kruse, C.G., W.A. Hubert, and F.J. Rahel. 1998. Single-pass electroshocking predicts trout abundance in mountain streams with sparse habitat. North American Journal of Fisheries Management 18:940-946.

Labbe, T.R. and K.D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of threatened fish at multiple scales. Ecological Applications 10:1774-1791.

Legendre, V. 1953. The freshwater fishes of the Province of Quebec: list of the species, ecological groups, history, nomenclature, annotations. Ninth Report Biological Bureau of Game and Fish Department of Province of Quebec. 294pp.

Legendre, V. 1954. Key to game and commercial fishes of the Province of Quebec. First English edition. Volume 1. Society of Canadian Ecology, Montreal Quebec, Canada 180 pp.

Lindeborg, R.G. 1941. Records of fishes from the Quetico Provincial Park of Ontario, with comments on the growth of the yellow pike-perch. Copeia 159-161.

Lindsey, C.C. 1956. Distribution and taxonomy of fishes in the Mackenzie drainage of British Columbia. Journal of the Fisheries Research Board of Canada 13:759- 886.

Maas, M.R. and R.H. Stasiak. 1995. Unique tuberculation analyzed by light and scanning electron microscopy in three species of *Phoxinus* (Pisces:Cyprinidae). Proceeding of the 75th Annual Meeting of the American Society of Ichthyologists and Herpetologists. Edmonton, Alberta, Canada.

MacRae, P.S. and D.A. Jackson. 2001. The influence of smallmouth bass (*Micropterus dolomieu*) predation and habitat complexity on the structure of littoral-zone fish assemblages. Canadian Journal of Fisheries and Aquatic Sciences 58:342-351.

Madsen, T. 1985. The status and distribution of the uncommon fishes of Nebraska. M.A. Thesis, University of Nebraska at Omaha, Omaha, NE.

Mammoliti, C.S. 2002. The effects of small watershed impoundments on native stream fishes: a focus on the Topeka shiner and Hornyhead chub. Transactions of the Kansas Academy of Sciences 105(3-4):219-231.

Masters, L.L., S.R. Flack, and B.A. Stein. 1998. Rivers of Life: Critical Watersheds for Protecting Freshwater Biodiversity. The Nature Conservancy. Arlington, VA.

Matthews, W.J and E. Marsh-Matthews. 2003. Effects of drought on fish across axes of space, time, and ecological complexity. Freshwater Biology 48:1232-1253.

Mayden, R.L., B.M. Burr, L.W. Page, and R.R. Miller. 1992. The native freshwater Fishes of North America. Pages 827-863 *in* Systematics, historical ecology, and North American freshwater fishes. Stanford University Press, Stanford, CA.

Mayes, M. 1976. The adult platyhelminth parasites of Nebraska fishes. Ph.D. Thesis University of Nebraska, Lincoln, NE.

McAllister, D.E. and B.W. Coad. 1974. Fishes of Canada's national capital region. National Museum of Natural Sciences Miscellaneous Special Pub. 24. Ottawa, Ontario, Canada.

McCafferty, A. 1998. Aquatic Entomology. Jones and Bartlett, Boston, MA.

McPhail, J.D. 1963. The postglacial dispersal of freshwater fishes in northern North America. Ph. D. Thesis McGill University.

McPhail, J.D. and C.C. Lindsey. 1970. Freshwater fishes of Northwestern Canada and Alaska. Bull. 173., Fish. Res. Bd. Can. Ottawa.

Meester, R.J. 1998. Statewide Fisheries Surveys, 1997, Part 2 Streams Region 1. Annual Report Number 98-15, South Dakota Department of Game, Fish, and Parks. Pierre, SD.

Meffe, G.K. 1986. Conservation genetics and the management of endangered fishes. Fisheries 11(1):14-23.

Milnes, M.R., D.S. Bermudez, T.A. Bryan, T.M. Edwards, M.P. Gunderson, I.L.V. Larkin, B.C. Moore, and L.J. Gillette Jr. 2006. Contaminant-induced feminization and demasculinization of nonmammalian vertebrate males in aquatic environments. Environmental Research 100 (2006):3-17.

Minckley, W.L. and J.E. Deacon, editors.1991. Battle against extinction: Native fish management in the American West. University of Arizona Press, Tucson, AZ.

Moore, H.H. and B.A. Roberty. 1965. Distribution of fishes in U. S. streams tributary to Lake Superior. U. S. Fish and Wildlife Service, Special Scientific Report No. 516. Washington, D.C.

Morrow, J.E. 1980. The freshwater fishes of Alaska. Alaska Northwest Publishing Co., Anchorage, AK.

Moyle, P.B. 1976. Inland Fishes of California. University of California Press, Berkeley, CA.

Moyle, P.B. and B. Vondracek. 1985. Persistence and structure of the fish assemblage in a small California stream. Ecology 66:1-13.

Naiman, R.J., C.A. Johnston, and J.C. Kelly. 1988. Alteration of North American streams by beaver. Bioscience 38: 753-762.

Nelson, J.S. 1994. Fishes of the World. Third edition. John Wiley & Sons. New York, NY.

Nelson, J.S, E.J. Crossman, H. Espinosa-Rosa, L.T. Findley, C. Gilbert, R. Lea, and J.D. Williams. 2004. Common and Scientific names of fishes from the United States and Canada. Sixth edition. American Fisheries Society Special Publication No. 29. Bethesda, MD.

New, J.G. 1962. Hybridization between two cyprinids, *Chrosomus eos* and *Chrosomus neogaeus*. Copeia 1962. 147-152.

Nordlie, F., J. Underhill, and S. Eddy. 1961. New distributional records of some Minnesota fishes. Minnesota Academy of Sciences 29:255-258.

Olson, R.D. 1997. Lake chub survey. South Dakota Wildlife Diversity Small Grants Results and Reports. Report No. 99-12.

Olson, R. and W.A. Hubert. 1994. Beaver: water resources and riparian habitat manager. University of Wyoming, Laramie, WY.

Paetz, M.J. and J.S. Nelson. 1970. The fishes of Alberta. Queen's Printer, Edmonton, Alberta, Canada.

Page, L.M. and B.M. Burr. 1991. A field guide to the freshwater fishes: North America north of Mexico. Houghton Mifflin, Boston, MA.

Parrish, J.B., D.J. Herman, and D.J. Reyher. 1996. A century of change in Black Hills forest and riparian ecosystems. USDA Forest Service Custer, South Dakota and South Dakota State University Agricultural Experiment Station. Brookings, SD.

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

Patton, T.M., W.A. Hubert, F.J. Rahel, and K.G. Gerow. 2000. Effort needed to estimate species richness in small streams on the Great Plains in Wyoming. North American Journal of Fisheries Management 20:394-398.

Poff, N.L. and J.D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76 (2):606-627.

Radforth, I. 1944. Some considerations on the distribution of fishes in Ontario. Contributions of the Royal Ontario Museum of Zoology No. 25. Toronto, Ontario Canada. 116p.

Reebs, S.G., L. Boudreau, P. Hardle, and R. A. Cunjak. 1995. Diel activity patterns of lake chubs and other fishes in a temperate stream. Canadian Journal of Zoology 73:1221-1227.

Reighard, J. 1903. The function of the pearl organs of the Cyprinidae. Science 17(431):531.

Reighard, J. 1904. Further observations on the breeding habits and the function of the pearl organs in several species of Eventognathi. Science 19(457):211-212.

Ryder, R.A., W.B. Scott, and E.J. Crossman. 1944. Fishes of northern Ontario, north of the Albany River. Royal Ontario Museum of Life Science Contribution 60. University of Toronto, Toronto, Ontario, Canada.

Schell, S.C. 1970. How to know the trematodes. Wm. Brown Co., Dubuque, IA.

Schlosser, I.J. 1995. Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. Ecology 76(3):908-925.

Schlosser, I.J. and P.L. Angermeier. 1995. Spatial variation in demographic processes in lotic fishes: conceptual models, empirical evidence, and implications for conservation. American Fisheries Society Symposium 17: 360-370.

Schlosser, I.J. and L.W. Kallemeyn. 2000. Spatial variation in fish assemblages across a beaver-influenced successional landscape. Ecology 81(5):1371-1382

Schlosser, I.J., M.R. Doeringsfeld, J.F. Elder, and L.F. Arzayus. 1998. Niche relationships of clonal and sexual fish in heterogenous landscape. Ecology 79(3):953-968.

Schmidt, G.D. and L.S. Roberts. 1989. Foundations of Parasitology. Times Mirror/Mosby Publishing, St. Louis, MO.

Schrank, S.J., C.S. Guy, M.R. Whiles, and B.L. Brock. 2001. Influence of instream and landscape level factors on the distribution of Topeka shiners, *Notropis topeka*, in Kansas streams. Copeia 2:413-421.

Scott, W.B. 1954. Freshwater fishes of Eastern Canada. University of Toronto Press, Toronto, Ontario, Canada. 128p.

Scott, W.B. 1957. Distributional records of fishes in western Canada. Copeia (2):160-161.

Scott, W.B. and E.J. Crossman. 1959. The freshwater fishes of New Brunswick: a checklist with distributional notes. Contributions of Royal Ontario Museum No.51.

Scott, W. B. and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184. Ottawa, Canada.

Sherrod, N. 1963. Late Pleistocene fish from lake sediments in Sheridan County, North Dakota. Miscellaneous Series North Dakota Geological Survey 21:32-36.

Shearer, J. 2006. Fishery Biologist, South Dakota Game, Fish and Parks, Rapid City, SD. Personal communication.

Shields, B.A. 2004. Effects of introduced exotic species: Behavioral changes induced upon a native bull trout (*Salvelinus confluentus*) population by introduced brook trout (*Salvelinus fontinalis*) in Oregon. Annual meeting of the Oregon Chapter of the American Fisheries Society.

Simon, J.A. 1951. Wyoming fishes. Revised edition. Wyoming Game and Fish Department Bulletin No. 4. Cheyenne, WY.

Simonson, T.D., J. Lyons, and P.D. Kanehl. 1994. Quantifying fish habitat in streams: transect spacing, sample size, and a proposed framework. North American Journal of Fisheries Management 14:607-615.

Simpson, J.C. 1941. Food analysis of some important species of Wyoming forage fishes. M.S. Thesis, University of Wyoming, Laramie, WY.

Smith, C.L. 1985. The inland fishes of New York. New York State Department of Environmental Conservation, Albany, NY.

Smith, L.L., Jr. and J.B. Moyle. 1944. A biological survey and fishery management plan for the streams of the Lake Superior North Shore Watershed. Minnesota Department of Conservation, Fish and Game Technical Bulletin No.1. Minneapolis, MN.

Stasiak, R.H. 1986. New record of the lake chub (*Couesius plumbeus*) from Nebraska. Proceedings of the Nebraska Academy of Sciences 96:29-30.

Stasiak, R.H. 1987. The minnows and killifish. Pages 56-64 *in* The Fish Book. Nebraskaland Special Publication for January-February 1987. Lincoln, NE.

Stasiak, R.H. 1989. The fishes of Agate Fossil beds National Monument, 1979-1989. Report to the U.S. National Park Service, Scotts Bluff, NE.

Stasiak, R.H. 2006. 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/northern redbellydace.pdf.

Steinmetz, J., S.L. Kohler, and D.A. Soluk. 2003. Birds are overlooked predators in aquatic food webs. Ecology 84: 1324-1328.

Taylor, W.R. 1954. Records of fishes in the John N. Lowe collection from the Upper Peninsula of Michigan. Miscellaneous Publication University of Michigan Museum of Zoology 87:1-50.

Tonn, W.C. and J.J. Magnuson. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology 73:1149-1166.

Tubb, R., F.A. Copes, and C. Johnston. 1965. Fishes of the Sheyenne River of North Dakota. Proceedings of the North Dakota Academy of Science 19:120-128.

USDA Forest Service. 2005. Rocky Mountain Region Species Conservation Project. Region 2 Regional Forester's Sensitive Species. Available online at http://www.fs.fed.us/r2/projects/scp/sensitivespecies/index.shtml.

U.S. Environmental Protection Agency. 2001. Revised protocols for sampling algal, invertebrate, and fish communities as part of the National Water-Quality Assessment Program. Moulton, S.R., J.G. Kennen, R.M. Goldstein, and J.A. Hambrook. Available online at http://www.epa.gov/emap/html/pubs/docs/groupdocs/surfwatr/field/fomws.html.

Underhill, J.C. 1957. The distribution of Minnesota minnows and darters in relation to the Pleistocene Glaciation. Minnesota Museum of Natural History Occasional Papers No. 7.

Underhill, J.C. 1986. The fish faunas of the Laurentian Great Lakes, the St. Lawrence Lowlands, Newfoundland, and Labrador. Pages 105-136 *in* C.H. Hocutt and E.O. Wiley, editors. The Zoogeography of North American Freshwater Fishes. John Wiley & Sons, New York, NY.

Underhill, J.C. and J.B. Moyle. 1968. The fishes of Minnesota's Lake Superior region. Ibid. January-February, 1968.

Vanderbush, L. 1999. Five year fisheries management plan: Deerfield Reservoir. Pages 23-27 *in* D.R. Jost, editor. Statewide fisheries surveys, 1998, management plan. Annual Report Number 99-22, South Dakota Department of Game, Fish and Parks, Pierre, SD.

Vrijenhoek, R.C. 1998. Conservation genetics of freshwater fish. Journal of Fish Biology (1998): 53 (Supplement A) 394-412.

Warren, M.L. and B.M. Burr. 1994. Status of freshwater fishes of the United States: overview of an imperiled fauna. Fisheries 19:6-18.

Watts, P.C., I.J. Saccheri, S.J. Kemp, and D.J. Thompson. 2006. Population structure and the impact of regional and local habitat isolation upon levels of genetic diversity of the endangered damselfly *Coenagrion mercuriale* (Odonata: Zygoptera). Freshwater Biology 51(2):193-205.

Wells, A.W. 1980. *Couesius plumbeus* (Agassiz). Page 150 *in* D.S. Lee, C.R. Gilbert, C.H. Hocutt, R.E. Jemkins, D.E. McAllister, and J.R. Stauffer, editors. Atlas of North American freshwater fishes. North Carolina State Museum of Natural History, Raleigh, NC.

Wheeler, C.A. 1997. Current distributions and distributional changes of fish in Wyoming west of the continental divide. M.S. Thesis, University of Wyoming, Laramie, WY.

White, H.C. 1953. The eastern belted kingfisher in the Maritime Provinces. Fisheries Research Board Canada 22(2): 635-637.

Willock, T.A. 1969. Distributional list of fishes in the Missouri drainage of Canada. Journal of Fisheries Research Canada 26:1439-1449.

Winston, M.R., C.M. Taylor, and J. Pigg. 1991. Upstream extirpation of four minnow species due to damming of a prairie stream. American Fisheries Society Transactions 120(1):98-105.

Wisenden, B.D. and K. Barbour. 2004. Antipredator responses to skin extract of redbelly dace, *Phoxinus eos*, by free-ranging populations of redbelly dace and fathead minnows, *Pimephales promelas*. Environmental Biology of Fishes 00:1-7.

Woodhouse, C.A. and J.T. Overpeck. 1998. 2,000 years of drought variability in the Central United States. Bulletin of the American Meteorological Society 79(12):2693-2714.

Woodling, J. 1985. Colorado's Little Fish. A guide to the minnows and other lesser known fishes in the state of Colorado. Colorado Division of Wildlife, Denver, CO.

Wynne-Edwards, V.C. 1952. Freshwater vertebrates of the Arctic and subarctic. Fisheries Research Board Canada Bulletin 94. 28pp.

Wyoming Game and Fish. 2005. Comprehensive wildlife conservation survey. Available online at http://gf.state.wy.us/wildlife/CompConvStrategy/Species/Fishes/index.asp.

Appendix

Matrix Population Analysis of Population Demographics for Lake Chub

Lifecycle graph and model development

Matrix demographic models facilitate assessment of critical transitions in the life history of a species. A key first step is to create a lifecycle graph, from which to compute a projection matrix amenable to quantitative analysis using computer software (Caswell 2001). The life history data for lake chub described by Brown and Hammer (1970) and Becker (1983; pp. 463-466) provided the basis for a stage-classified lifecycle graph that had five stages (**Figure A1**). The first four stages are age-specific (age-classes), while the fifth includes all fish in their fifth year or later. From the lifecycle 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 stage-based indexing beginning at 1. Note that the breeding pulse comes at the end of each one-year census interval. Individuals are therefore larger when breeding than when they were censused in that stage (almost a year earlier). For example, Stage 2 fish are estimated to be approximately 65 mm in length at the time of the census, but they will have grown to an estimated 95 mm by the time they breed, just prior to the next census (**Table A1**). In order to estimate the vital rates (**Table A2**), we used the following criteria:

- ❖ Egg production by size was estimated from the equation in Figure 4 of Hammer and Brown (1970). Log_{10} [eggs] = -3.2426 + 3.0962 * Log_{10} [length]

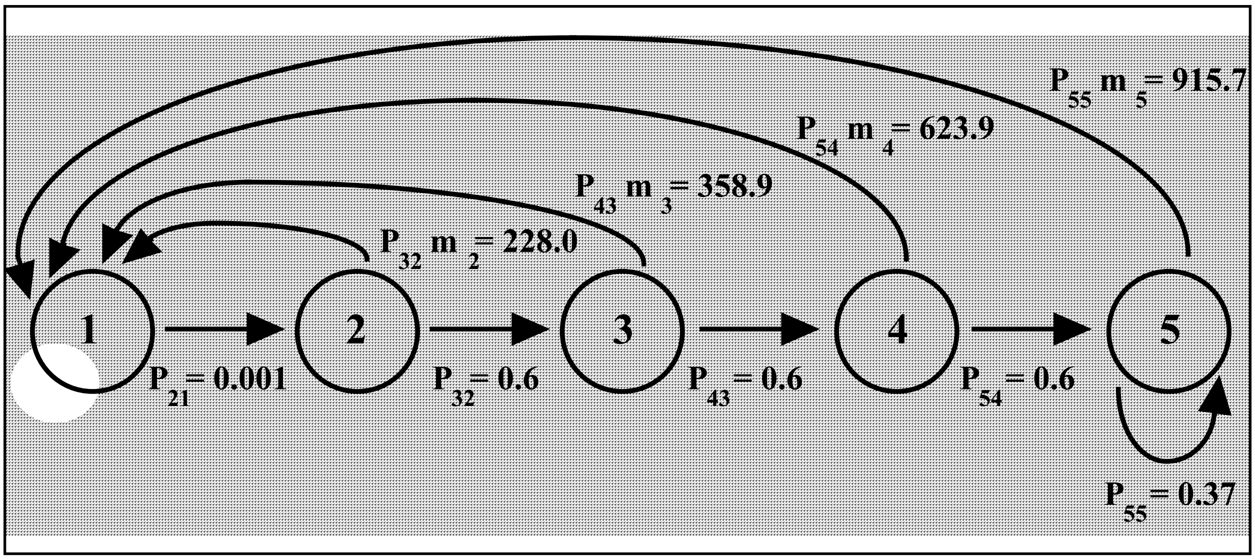


Figure A1. Lifecycle graph for lake chub, consisting of circles (*nodes*), describing stages in the life cycle and *arcs*, describing the *vital rates* (transitions between stages). The horizontal arcs are survival rates (e.g., first-year survival, P_{21}= 0.001). The remaining arcs, pointing back to Node 1, describe fertility (e.g., P_{32} * m_2). Each of the arcs corresponds to a cell in the matrix of **Figure A2**.

Table A1. Relationship between conventional fisheries age categories, life cycle stage and size at beginning and ending of stage, for lake chub.

Age (fisheries convention)	Stage (matrix indexing)	Size range (mm)
0	1	0-64
I	2	65-95
II	3	96-110
III	4	111-131.5
IV+	5	174

Table A2. Vital rates for lake chub, used as inputs for projection matrix entries of **Figure A1** and **Figure A2**.

Vital rate (fertility or survival)	Numerical value	Description
M_2	380.0	Number of female eggs produced by a second-year female
M_3	598.3	Number of female eggs produced by a third-year female
M_4	1,039.9	Number of female eggs produced by a fourth-year female
M_5	2,474.9	Number of female eggs produced by fifth-year and older females
P_{21}	0.00105	First-year survival
P_{32}	0.6	Second-year survival
P_{43}	0.6	Third-year survival
P_{54}	0.6	Fourth-year survival
P_{55}	0.37	Survival in fifth year and beyond

- ❖ The estimated size ranges of the stages were based on a compromise between the rather different age/size data of Becker (1983; p. 466) and those of Brown and Hammer (1970). The values for Age, Stage and their size ranges are shown in **Table A1**

- ❖ Survival rates (not available for this species) were based on those estimated for finescale dace (*Pfrille neogaea*) by Stasiak (1972)

Because the model assumes female demographic dominance, the egg number used was half the published value, assuming a 1:1 sex ratio. We assumed reproduction beginning at two years after hatch (i.e., at the end of Stage 2). We also made a final and major 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_{ij} describing survival rates, and m_i describing fertilities (**Table A2**). **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 was 1.008 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 toward which to adjust estimated fertility rates and was subject to the many assumptions used to derive all the transitions. The value of λ should, therefore, 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 lifecycle graph [**Figure A1**] and the cells in the matrix, **A** [**Figure A2**]). Sensitivity analysis provides several kinds of useful information (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 therefore use sensitivities to assess the relative importance of the survival (P_i) and fertility (F_i) transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to paucity of data, but could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on accurate estimation of transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on age-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages 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 backward in age, from Stage 3 to Stage 2). In this analysis, the sensitivity of λ to changes in first-year survival (252.0; 99.7 percent of total) is overwhelmingly the most important key to population dynamics.

Stage	1	2	3	4	5
1		$P_{32}*m_2$	$P_{43}*m_3$	$P_{54}*m_4$	$P_{55}*m_5$
2	P_{21}				
3		P_{32}			
4			P_{43}		
5				P_{54}	P_{55}

Figure A2a. Symbolic values for the cells of the projection matrix. Each cell corresponds to one of the arcs in the life cycle graph. The top row is fertility, with compound terms describing survival of the mother (P_{ij}) and egg production (m_i). Empty cells have zero values and lack a corresponding arc in **Figure A1**. Note that the matrix differs from a strictly age-classified (Leslie) matrix because of the entry in the bottom right, corresponding to the self-loop on the fifth node in the life cycle graph.

Stage	1	2	3	4	5
1		228.007	358.989	623.935	915.715
2	0.001				
3		0.6			
4			0.6		
5				0.6	0.37

Figure A2b. Numeric values for the projection matrix.

Figure A2. The input matrix of vital rates, **A** (with cells a_{ij}) corresponding to the lake chub lifecycle graph (**Figure A1**). a) Symbolic values. b) Numeric values.

Stage	1	2	3	4	5
1		0.000	0.000	0.000	0.000
2	**252.0**				
3		0.337			
4			0.240		
5				0.139	0.131

Figure A3. Possible sensitivities only matrix, $\mathbf{S_p}$ (remainder of matrix is zeros). The transition to which λ of lake chub is overwhelmingly sensitive is first-year survival.

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 stages 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 lake chub are shown in **Figure A4**. The λ of lake chub was most elastic to changes in first-year survival, followed by second-year and third-year survival. Overall, survival transitions accounted for approximately 73.7 percent of the total elasticity of λ to changes in the vital rates. Survival, particularly in the first year, is the demographic parameter that warrants most careful monitoring in order to refine the matrix demographic analysis.

Other demographic parameters

The **stable stage distribution** (SSD; **Table A3**) describes the proportion of each stage in a population at demographic equilibrium. Under a deterministic model,

Stage	1	2	3	4	5
1		0.062	0.058	0.060	0.083
2	**0.263**				
3		**0.201**			
4			**0.143**		
5				0.083	0.048

Figure A4. Elasticity matrix, **E** (remainder of matrix is zeros). The λ of lake chub is most elastic to changes in first-year survival (Cell e_{21}), followed by second-year survival and then third-year survival.

Table A3. Stable Stage Distribution (SSD, right eigenvector). Because first-year fish (eggs) numerically dominate the population at the time of the census, the proportion of fish excluding eggs are shown in parentheses for Stages 2 to 5.

Stage	Description	Proportion (excluding 1st-year)
1	First-year females	0.998
2	Second-year females	0.001 (0.44)
3	Third year females	0.001 (0.26)
4	Fourth-year females	0.000 (0.16)
5	Fifth-year and older females	0.000 (0.15)

any unchanging matrix will converge on a population structure that follows the stable stage distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SSD within 20 to 100 census intervals. For lake chub at the time of the post-breeding annual census (early summer in this case), eggs should represent 99.8 percent of the population. Second-year fish (hatched the previous breeding season) should constitute 43.8 percent of the non-egg population. **Reproductive values** (**Table A4**) can be thought of as describing the "value" of a stage as a seed for population growth relative to that of the first (newborn or, in this case, egg) stage (Caswell 2001). The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving (Williams 1966). The reproductive value of the first stage is, by definition, always 1.0. For example, a second-year female (age of first breeding) is "worth" approximately 960 eggs. The cohort generation time for lake chub is 3.8 years (SD = 1.5 years).

Potential refinements of the models

Clearly, better data on survival and fertility rates from Region 2 would increase the relevance and accuracy of the analysis. The present analysis should be considered as at best only an approximate guide to the forces acting on the demography of lake chub in Region 2. Data from natural populations on the range of variability in the vital rates would allow modeling 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

Table A4. Reproductive values for females. Reproductive values can be thought of as describing the "value" of a stage as a seed for population growth, relative to that of the first (egg) stage, which is always defined to have the value 1.

Stage	Description	Proportion (excluding 1st-year)
1	First-year females	1
2	Second-year females	960
3	Third year females	1,233
4	Fourth-year females	1,473
5	Fifth-year and older females	1,435

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

- The major purpose of the matrix model is to assess critical stages in the life history (e.g., juvenile vs. adult survival, fertility vs. survival) rather than to make (often unwarranted) predictions about population growth rates, population viability or time to extinction. Because the data are scanty, the model also provides preliminary guidance on which vital rates should be the focus of any future monitoring efforts.

- First-year survival accounts for 99.9 percent of total "possible" sensitivity. Any absolute changes in this vital rate will have major impacts on population dynamics.

- Survival through the first three years accounts for 60.6 percent of the total elasticity. Proportional changes in survival will have major impacts on population dynamics.

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

References

Becker, G.C. 1983. Fishes of Wisconsin. University of Wisconsin Press. Madison, WI.

Brown, J.H., U.T. Hammer, and G. H. Koshinsky. 1970. Breeding biology of the lake chub, *Couesius plumbeus*, at Lac la Ronge, Saskatchewan. Journal of Fisheries Research Board Canada 27:1005-1015.

Caswell, H. 2001. Matrix Population Models: Construction, Analysis, and Interpretation, Second Edition. Sinauer Associates, Sunderland, MA.

Cochran, M.E. and Ellner, S. 1992. Simple methods for calculating age-based life history parameters for stage-structured populations. Ecological Monographs 62:345-364.

McDonald, D.B., and H. Caswell. 1993. Matrix methods for avian demography. Pages 139-185 *in* D. Power, editor. Current Ornithology. Volume 10. Plenum Press, New York, NY.

Williams, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. American Naturalist 100:687-690.