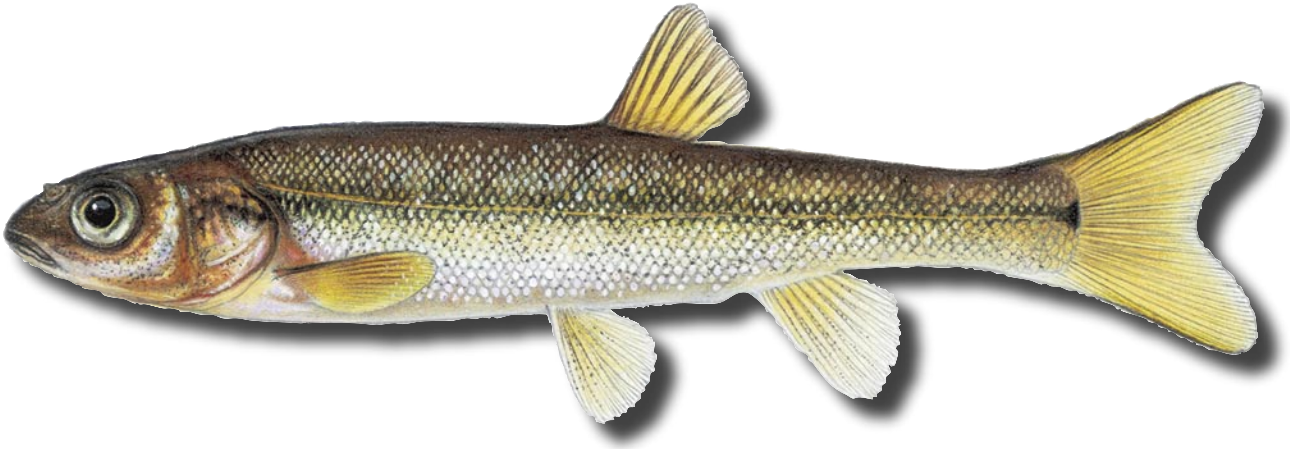
Pearl Dace (*Margariscus margarita*)
A Technical Conservation Assessment



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COVER ILLUSTRATION CREDIT

Pearl dace (*Margariscus margarita*). Illustration by © Joseph Tomelleri.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF PEARL DACE

Status

Pearl dace are not considered federally endangered or threatened in the United States. However, this species is very uncommon in the Great Plains and is found only in three of the five states comprising the Rocky Mountain Region (Region 2) of the USDA Forest Service (USFS). It is listed as endangered or threatened at the state level in Wyoming (S1 - state endangered), South Dakota (S2 - state threatened), and Nebraska (S3 - species of concern). Populations in these three states occur as small, isolated demes that have been declining steadily since settlement of this region over 100 years ago.

Primary Threats

The two primary threats to pearl dace in this region include habitat alteration and introduction of non-native fishes. Water development activities that alter natural spring flow are a concern as they often lead to habitat degradation and stream fragmentation. Reservoir construction, groundwater pumping, stream diversions, and channelization all negatively affect pearl dace populations. Pearl dace populations also somewhat depend on natural beaver activity and the associated hydrological aspects they produce in the landscape; thus, restrictions on beaver activity will result in reductions in pearl dace populations. Pearl dace occur in small, confined habitats in places with permanent spring seeps, usually at the extreme headwaters of small streams. The natural fish community in these habitats is highly adapted to the special conditions presented by this circumstance. Since this species is a sight-feeding predator and depends on relatively clear water, any activities that cause long-term increases in turbidity will be deleterious. Thus, construction projects, forestry practices, and grazing activities need to be managed so that they do not produce excessive erosion and sedimentation. Pearl dace is very sensitive to human alterations to the aquatic system, especially the addition of exotic species of fishes. Introduced species negatively affect pearl dace and other native fishes through the combined pressures of predation, competition, potential for the addition of new parasites and disease, and altering the species' behavioral components. Introduction of large sunfish (i.e., bass species), pike, or trout will have an especially significant negative impact on pearl dace populations. A more localized concern is the potential to overharvest this species for use as fishing bait or for the pet industry.

Primary Conservation Elements, Management Implications and Considerations

The pearl dace is one of the definitive species of small fishes that form distinctive communities in the Great Plains. This assemblage of fishes is restricted to small headwater streams, beaver ponds, and small spring-fed lakes. The most important management actions to conserve this species is to protect groundwater sources, stream flows, and natural hydrogeomorphic processes, as well as ecosystem engineers such as beaver. Introductions of non-native fishes need to be eliminated, and where they have already become established in pearl dace habitat, they need to be controlled.

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INTRODUCTION

This conservation assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2) of the USDA Forest Service (USFS; **Figure 1**). The pearl dace (*Margariscus margarita*) is the focus of an assessment because there was concern for the species' viability in the states comprising USFS Region 2 during the Regional Forester's Sensitive Species List revision process that took place 2001-2003. The pearl dace occurs in three of the five states comprising USFS Region 2 (Nebraska, South Dakota, and Wyoming) (**Figure 2**). Although this species has not been reported from any USFS administrative units, some of the known pearl dace populations are found in adjacent stream reaches in common drainages that flow through national forest and grassland units. Pearl dace also occur in highly disjunct glacial relict populations. It is for these reasons, pearl dace was considered to be a species of concern for USFS Region 2.

This report addresses the biology and ecology of pearl dace throughout its range in Region 2. Also discussed is the history and change of pearl dace habitat in this region. The broad nature of this assessment leads to some constraints on the specificity of information for particular locales. Much of the data come from research conducted on populations outside of Region 2, but that make up the major portion of the species' distributional range. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

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

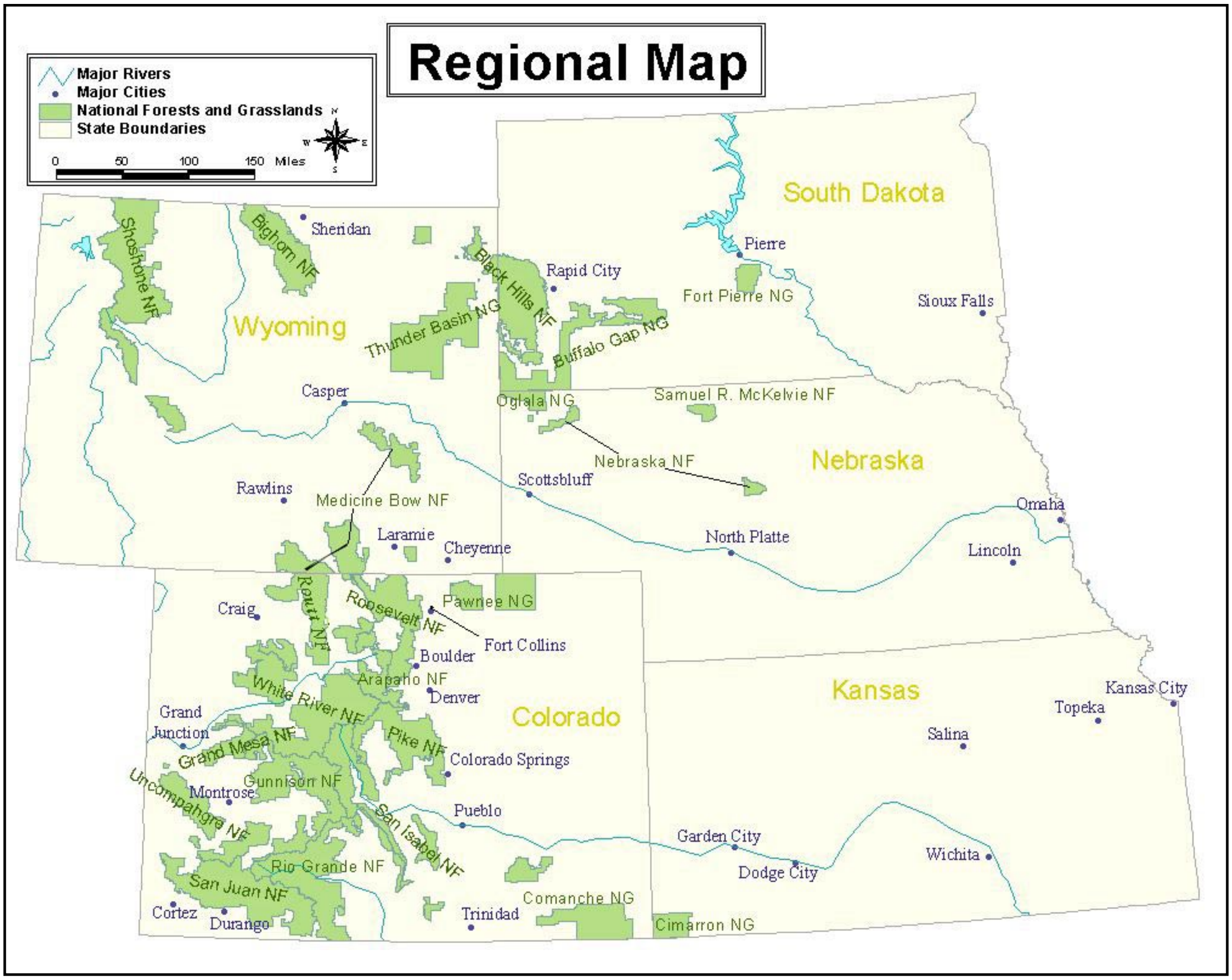

Figure 1. National forests and grasslands within USDA Forest Service Region 2.

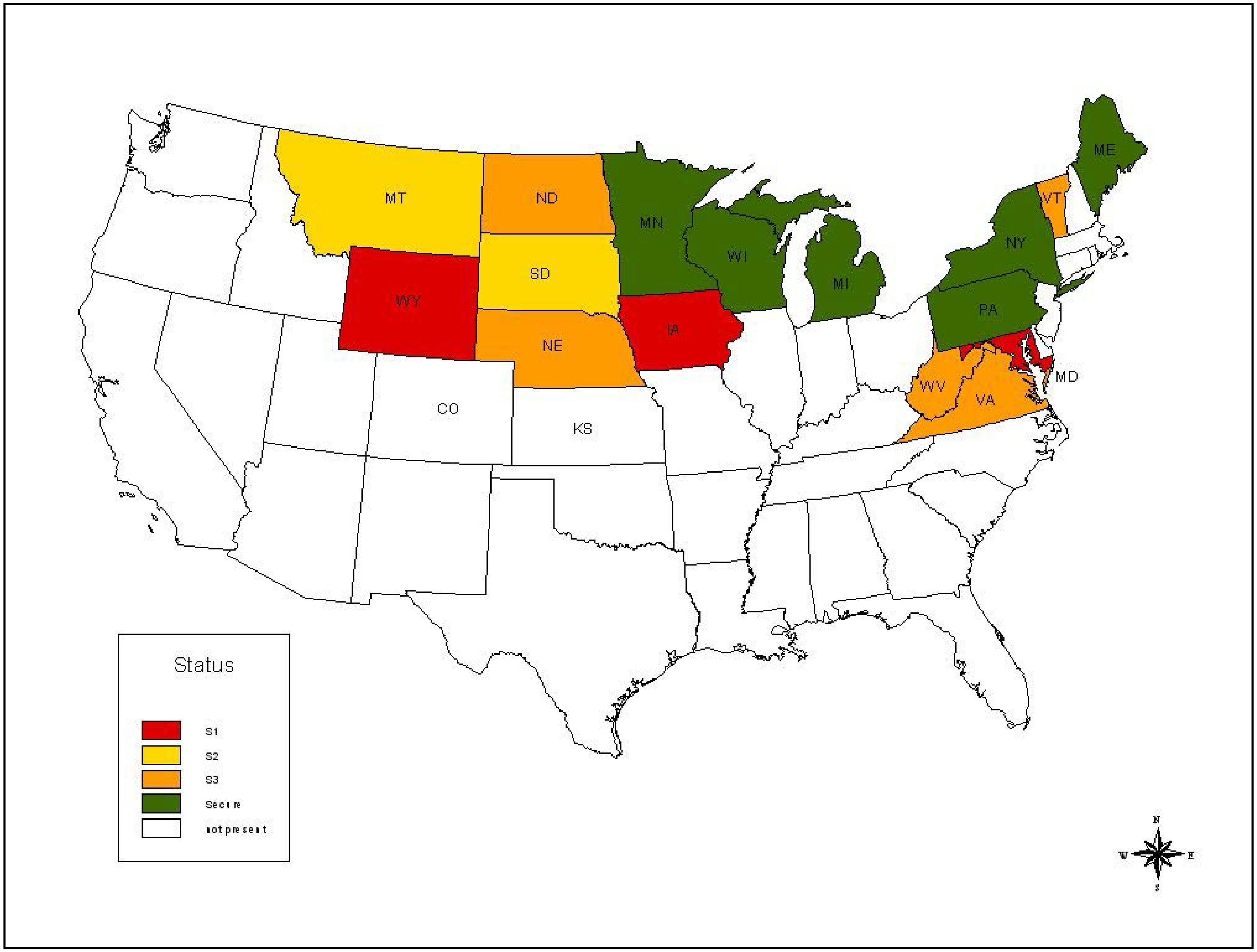

Figure 2. Natural Heritage Program status of pearl dace within the United States.

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 prescribe management but it provides the ecological background upon which management must be based, discusses the consequences of changes in the environment that result from management actions (i.e., management implications), and explores important considerations in the conservation of the species.

Scope of Assessment

The pearl dace assessment examines the biology, ecology, conservation status, and management of this species with specific reference to the geographic and ecological characteristics of the USFS Region 2. Although some of the literature on the species may originate from field investigations outside the region, this document places that literature in the ecological and social contexts 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 pearl dace in the context of the current environment 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, we reviewed the refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on pearl dace are referenced in this assessment, nor were all materials considered equally reliable. This assessment emphasizes refereed literature because this is the accepted standard in science. We chose to use some non-refereed literature, 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 (Platt 1964). However, it is difficult to conduct critical experiments in the ecological sciences, and often observations, inference, good thinking, and models must be relied on to guide the understanding of ecological relations.

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

Application and Interpretation Limits of this Assessment

Information about the biology of pearl dace was collected and summarized from throughout its geographic range, which extends throughout Canada, and from New England, west along the northern Great Lake states and south to disjunct populations in the Sandhills region of Nebraska and South Dakota (**Figure 3**). 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, and longevity) could differ along environmental gradients, especially in such a wide-ranging species. Information about the conservation status of this species was limited to USFS Region 2 and should not be taken to imply conservation status in other portions of its overall range.

Publication of Assessment on the World Wide Web

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

Peer Review

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

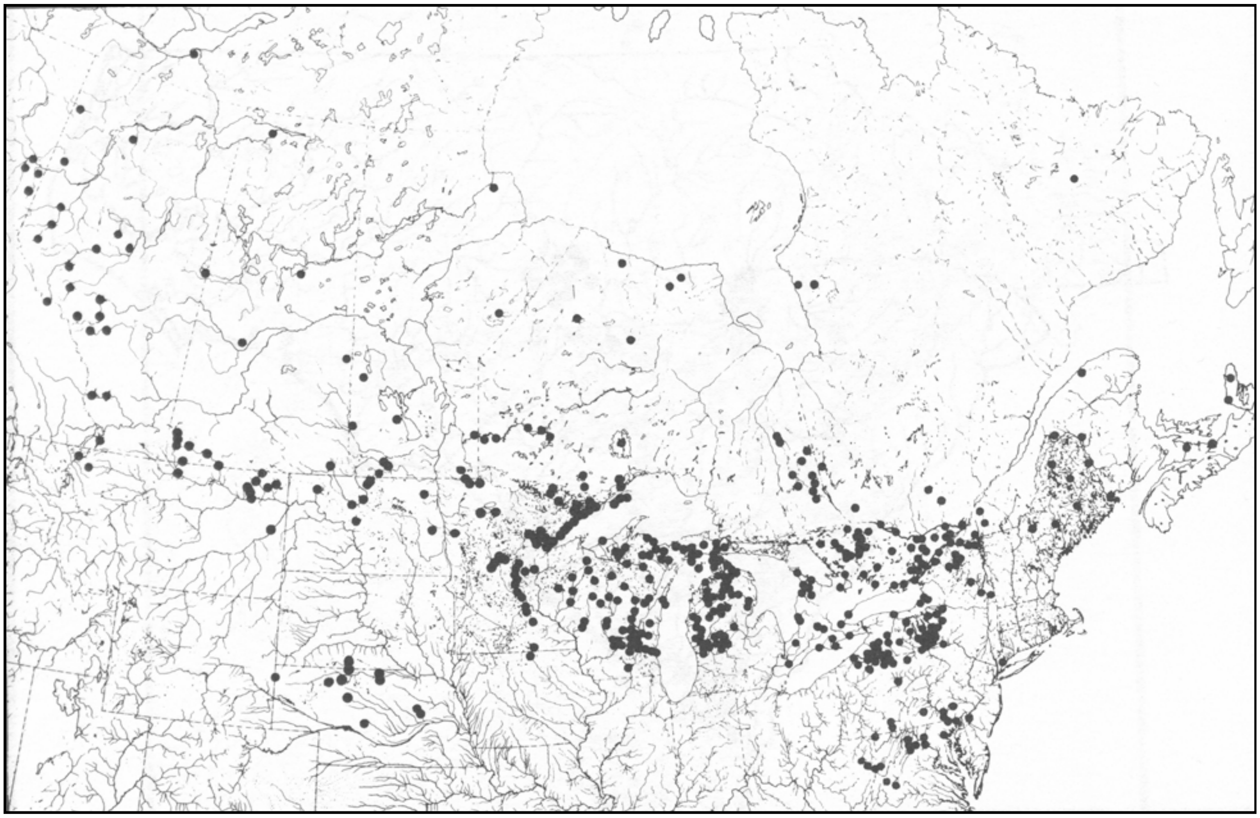

Figure 3. North American distribution of pearl dace. Source: Lee et al. 1980.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

The pearl dace is not federally listed as threatened or endangered in the United States (U.S. Fish and Wildlife Services; http://endangered.fws.gov/). The USFS, however, does list pearl dace 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). At the state level, the pearl dace has a conservation status of some concern in 10 of the 16 states comprising its range in the United States. (**Figure 2**). The species is listed as state endangered in Iowa and Maryland, and it is a species of concern in North Dakota, Vermont, Virginia, and West Virginia. It is considered secure in the remainder of the states that it occupies outside of USFS Region 2. Within USFS Region 2, the pearl dace is listed as state endangered in Wyoming (S1), state threatened in South Dakota (S2), and a species of concern in Nebraska (S3); it has never been reported in Kansas or Colorado (Ellis 1914, Cross 1967, Woodling 1985, Page and Burr 1991). Since pearl dace populations historically are known to occur near USFS administered lands in Nebraska, this species it was added to the Regional Forester's sensitive species list in Region 2 in 2003. Currently, National Forest System (NFS) lands that could harbor populations of pearl dace are Samuel R. McKelvie and Nebraska National Forest units in Nebraska (**Figure 1**). The distribution of this species in Nebraska, South Dakota, and Wyoming is shown in **Figure 3** and **Figure 4**.

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

Pearl dace are given legal protection by the states of Wyoming, South Dakota, and Nebraska, protecting them from take, possession, and transportation. Nebraska also prohibits collections of bait minnows from designated trout waters, and this includes some sites where pearl dace are found. Only Wyoming has developed a conservation plan for the pearl dace with Region 2 (Wyoming Game and Fish Department 2006). This species is one of many used by The Nature Conservancy (2006) for aquatic conservation planning in the Great Plains (Steuter et al. 2003); it is a conservation target in their site conservation plan for the Cherry Ranch Preserve along the headwaters of the

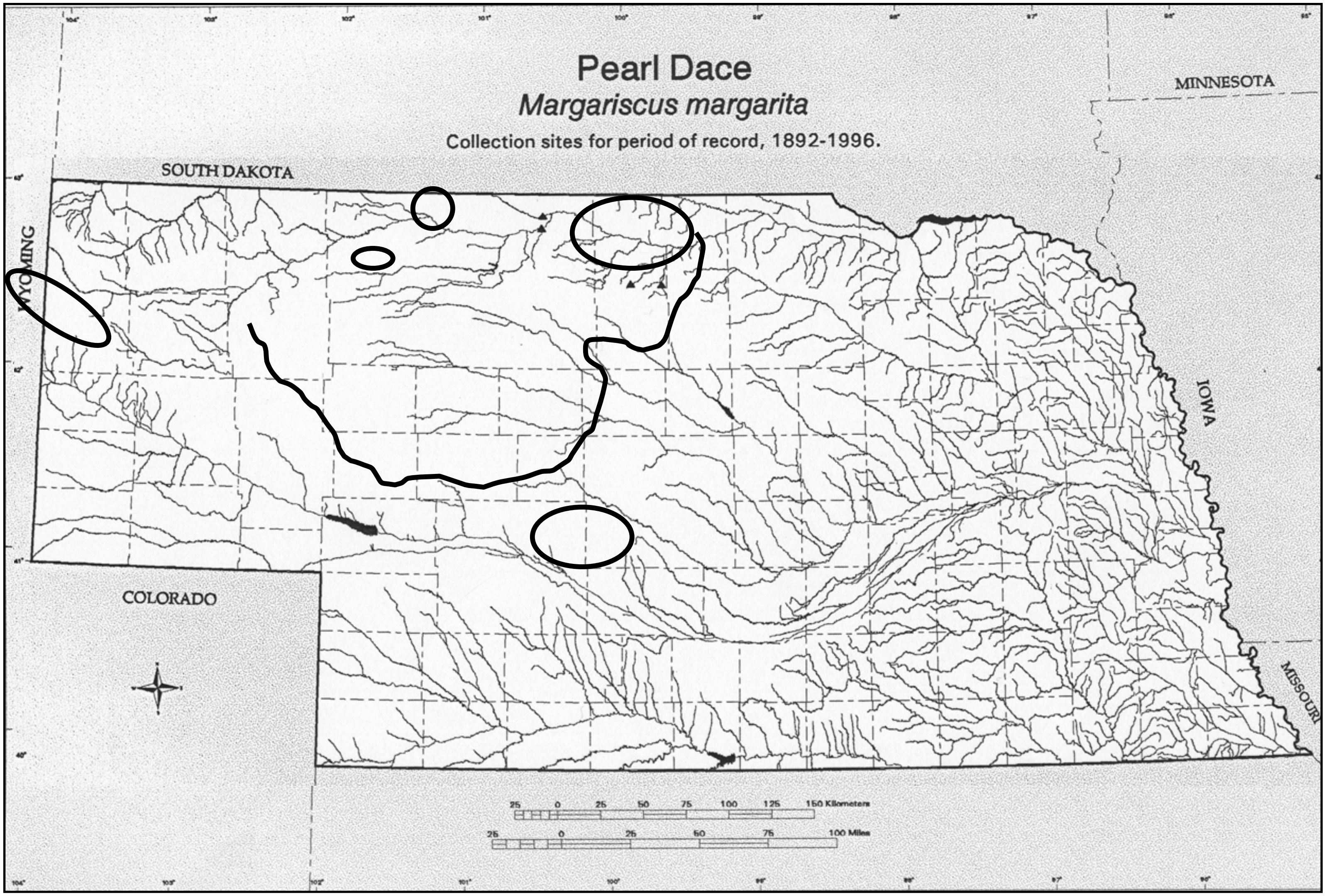

Figure 4. Current distribution of pearl dace within USDA Forest Service Region 2.

Niobrara River in western Nebraska, near the Wyoming border (The Nature Conservancy, 2002). In addition, the pearl dace is one of the species taken into account by the National Park Service in their management plan for the Niobrara National Scenic River (National Park Service 2005). Montana State University is conducting surveys for pearl dace as part of an eastern Montana fish survey funded by Montana Fish, Wildlife, and Parks (Montana State University 2005). The Montana Natural Heritage Program is targeting the pearl dace in its Aquatic Ecosystem Diversity Project (Montana Natural Heritage Program 2005). Potential management options and conservation considerations for this species are addressed in the Conservation section of this report.

Biology and Ecology

Systematics

The pearl dace (**Figure 5**) is in the bony fish Superclass Osteichthyes, Class Actinopterygii, Order Cypriniformes, and minnow Family Cyprinidae (Nelson 1994). Cope (1867) originally described this species as *Clinostomus margarita*, and later Cox (1896) described it as *Leuciscus nachtriebi*. The confusing and complex nomenclatural status of this species continued with several different generic and specific names being applied to subsequent collections (Scott and Crossman 1973). Cockerell (1909) proposed the generic use of *Margariscus*, which Jordan (1924) later supported. However, evidence put forth by Bailey and Allum (1962) and Hubbs and Lagler (1964) rescinded the generic rank of *Margariscus*, and *M. margarita* was placed in the genus *Semotilus*. Later, *M. margarita* was extracted from the genus *Semotilus* and resurrected into the monotypic genus *Margariscus* (Johnson and Ramsey 1990, Cavender and Coburn 1992). Based on osteological evidence, Cavender and Coburn (1992) designated *M. margarita* as a member of the chub clade, which is taxonomically linked with a phyletic group of mostly Nearctic species to form the tribe Phoxinin within the subfamily Leucisinae.

Two subspecies are recognized within *Margariscus* (McPhail and Lindsey 1970, Smith 1985, Jenkins and Burkhead 1994): (1) *Margariscus margarita margarita*

Figure 5. Female pearl dace from Worth County, Iowa (top), and male pearl dace from Cherry County, Nebraska (bottom). Photographs by George R. Cunningham.

(Cope), commonly termed the eastern or Allegheny pearl dace, is located in the southern drainages of New York State south to the Potomac River drainage of Virginia; and (2) *M. m. nachtribei* (Cox), the northern pearl dace, is distributed widely across much of Canada south of the lower Sass River in the Northwest Territories, from British Columbia to Nova Scotia, then southward into the United States through Maine, across the northern sections of the Great Lakes region west to Montana, with disjunct glacial relict populations in South Dakota, Wyoming, and Nebraska (Brown 1971, Nelson and Paetz 1972, Scott and Crossman 1973, Lee et al. 1980). Recently though, Bailey et al. (2004) and Smith (2004) have recognized *M. m. nachtribei* and *M. m. margarita* as valid species (*M. nachtribei* and *M. margarita*), but Nelson et al. (2004) stated that independent conformation is needed before accepting the taxonomic revision.

Species description

Pearl dace are medium-sized (76 to 102 mm total length [TL]) in reproductive individuals (McPhail and Lindsey 1970) with an average TL of 89 mm (Scott and Crossman 1973, Becker 1983). The number of scales in the lateral line varies depending upon the subspecies (Bailey et al. 2004) and latitudinal gradient, with more northern populations exhibiting a higher scale count than southern conspecifics (Scott and Crossman 1973). Lateral line scale counts for the eastern subspecies (*Margariscus margarita margarita*) range from 46 to 60, whereas counts for the northern form (*M. m. nachtribei*), including those populations in USFS Region 2, range from 62 to 75 (Scott and Crossman 1973, Becker 1983, Jenkins and Burkhead 1994). This species has a complete lateral line with the pores of the lateral line extending throughout. Dorsum coloration is olive, usually dark, with the side being pale olive. Below the lateral line, coloration is white to silvery white. The mouth is terminal and slightly oblique, and it extends below the nostril (Becker 1983). The premaxillaries are protracile, the frenum is absent, and in the eastern and northern forms, a small, flap-like barbel in the upper lip groove, slightly above the mouth corner, is usually present. Interestingly, pearl dace from Nebraska and South Dakota rarely possess a barbel (Cunningham 1995). Pharyngeal arches usually have a 2,5-4,2 formula, and are slender and hooked, with a short cutting surface (Becker 1983). The intestine of the pearl dace has a single loop, and it is usually less than the body length. The peritoneum is silvery, with speckling on the dorsal surface (Scott and Crossman 1973).

Males of these species have bright red to orange-red coloration. Females will occasionally develop a faint orange to red stripe, but most often they develop a yellow-gold sheen with red-orange pigment at the base of the pectoral fin (Becker 1983, Jenkins and Burkhead 1994, Cunningham 1995). While these colors are present throughout most of the year, they are more intense during the spring breeding season (**Figure 5**). The ventral surface of both the male and female of this species will be pearl white, particularly the female. In addition, the female will develop a red-orange spot on the upper operculum (Jenkins and Burkhead 1994, Cunningham 1995). Nuptial coloration is vivid and striking, on par with the vibrate coloration of the finescale dace (*Phoxinus neogaeus*) and northern redbelly dace (*Phoxinus eos*).

Pearl organs (breeding tubercles) develop on the males during the spring. Pearl dace develop a unique and distinctive pattern of tubercles on their fins, head, branchiostegal rays, lateral scales, and breast scales (Scott and Crossman 1973, Becker 1983, Cunningham 1995). See the section on Breeding biology for a detailed account of tubercle patterns. This species exhibits sexual dimorphism; females are larger than males, and males develop enlarged, well tubercled fin rays (Fava and Tsai 1976).

Distribution and abundance

Pearl dace are widely distributed across Canada and the northern portions of the St. Lawrence (Great Lakes), Mississippi, and Missouri River drainages in the United States (**Figure 3**; McPhail and Lindsey 1970, Scott and Crossman 1973, Lee et al. 1980, Page and Burr 1991). This species reaches its southern-most limit at about 41 °N latitude in the Nebraska Sandhills (**Figure 4**). In Canada, it has been taken from the Northwest Territories, British Columbia, and Alberta (McPhail and Linsey 1970, Nelson and Paetz 1972, Mayhood 1992); from Saskatchewan (Willock 1969) and Manitoba (Tallman 1980); from Ontario (Chadwick 1976); from Quebec (Legendre 1953); from New Brunswick and Prince Edward Island (Scott and Crossman 1973); and from Newfoundland and Labrador (Bradbury et al. 1999).

In the United States, pearl dace have been found in Maine and Vermont (Lee et al. 1980), Maryland (Tsai and Fava 1982), New York (Smith 1985), Pennsylvania (Cope 1867), Michigan (Hubbs and Lagler 1949, 1964, 2004), Wisconsin (Greene 1935, Becker 1983), Minnesota (Underhill 1957, Eddy et al.1963, Hatch et al. 2003), Iowa (Menzel and Boyce 1973), Montana (Brown 1971, Bramblett and Zale 2004), South Dakota (Bailey and Allum 1962, Cunningham et al. 1995), Nebraska (Johnson 1942, Stasiak 1976, Madsen 1985), North Dakota (Evenhuis 1969, Koel and Peterka 1998), and Wyoming (Baxter 1970).

In the five states comprising USFS Region 2, pearl dace are found in Nebraska, South Dakota, and Wyoming, in first order streams of the Niobrara and Platte River systems (**Figure 4**). While none of the populations have been reported from NFS lands, pearl dace do reside in the headwaters of streams that flow through NFS lands in Nebraska (Cunningham and Hickey 1996, 1997). All pearl dace populations in South Dakota, Nebraska, and Wyoming can be considered "glacial relict" populations that have been isolated from the main portion of the species' range in Canada and Minnesota (Cross et al. 1986).

Boward et al. (1999) determined that the entire pearl dace population throughout Maryland was 500,000. Chadwick (1976) determined from a whole lake piscicide treatment that 1,425 pearl dace occupied a 6.2 ha Precambrian shield lake in Ontario. In Wisconsin, Headrick (1976) estimated a population of over 2,000 pearl dace in a 200-m reach of stream. Through a contract with The Nature Conservancy in Nebraska, Cunningham (1995) estimated 2,256 pearl dace in a 130 m reach of a slightly modified Sandhills stream, and 537 pearl dace in 90 m of a highly altered reach of stream.

Population trends

Across its continental range, pearl dace is ranked S1 to S3 (critically imperiled to vulnerable) in 15 of the 30 state or provinces in its range (**Figure 2**; NatureServe 2006). While pearl dace populations are considered stable throughout much of the main portion of their range in Canada, Minnesota, Wisconsin, Michigan, and New England (McPhail and Lindsey 1970, Scott and Crossman 1973, Becker 1983, Smith 1985, Nelson and Paetz 1992, Campbell 1997, Hatch et al. 2003), they are much less stable where the species occurs as relict populations, including Region 2. In these areas, pearl dace are found in the upper headwaters of first order streams and in areas of groundwater seepage (Bleed and Flowerday 1989, Jenkins and Burkhead 1994). The cold water provided by these water sources enables pearl dace to persist under conditions much more similar to the conditions that prevailed thousands of years ago when the southern edge of the glacial shield was much closer to this region (McPhail 1963, Sherrod 1963, Cross 1970, Cross et al. 1986). The warming and drying of the Great Plains region following the retreat of the last ice advance has led to a natural reduction in suitable habitat for this species. Human activity that likewise leads to reduction in cold springs or seeps will greatly accelerate this process. Pearl dace are currently listed as state endangered in Wyoming, and as state threatened in South Dakota and Montana. For more detailed information on documentation of population trends, see the Inventory and monitoring section of this report.

Activity patterns

Most of the studies on northern pearl dace have been conducted in the main portion of their distributional range to the north and east of Region 2. Little is known of the activity patterns of this species in the Great Plains. Using snorkeling to observe the fish community in a small Nebraska stream, Cunningham (1995) found that pearl dace were generally restricted to the mid-water column, with juveniles occurring high in the water column and closer to instream vegetation, and adults generally found in deeper pools. Tallman (1980) made similar observations in Manitoba. During the winter months, however, all age classes are found in deep pools exclusively (Tallman 1980, Tallman and Gee 1982, Cunningham 1995). This species is active throughout the day and evening, actively foraging at all hours, with the lowest activity period occurring in the early morning daylight hours (Tallman 1980, Johnson and Johnson 1982, Tallman and Gee 1982). Collections made by Tallman (1980) showed this species to actively feed all year; no decrease in activity was seen during winter months. Indeed, the pearl dace is a cold water species preferring a water temperature of 16 ºC (Scott and Crossman 1973, Becker 1983, Stauffer et al. 1984). If temperatures warm significantly, it would be reasonable to expect an increase in movement as the fish seek cooler spring seeps.

Habitat

Pearl dace have a very strong habitat preference for slow moving, spring-fed streams with a sinuous channel, well-vegetated undercut banks, and a diverse array of pool habitats throughout a stream reach (Tallman and Gee 1982, Becker 1983, Smith 1985, Cunningham 1995). This species is also found in smaller glacial lakes throughout Canada (McPhail and Lindsey 1970, Scott and Crossman 1973, Chadwick 1976) and in bog drainage systems (Underhill 1957, Becker 1983, Hatch et al. 2003). Characteristic of these cool, clear headwater and bog drainage systems is the presence of beaver pond complexes that provide pool and undercut bank habitat used by pearl dace (Schlosser et al. 1995, 1998). Although not as essential for pearl dace as they are for *Phoxinus* species, this heterogeneous array of beaver ponds, bend pools, straights, and meandering channels is typical of those streams occupied by the pearl dace. Moreover, this particular heterogeneous habitat is a key predictor to the presence of pearl dace, particularly in the Great Plains region.

The only areas within USFS Region 2 where this type of stream habitat occurs and has pearl dace as a faunal component is the Sandhills region of Nebraska and South Dakota, and the sandy deposits and spring-fed flows of the Upper Niobrara River in Nebraska and Wyoming. Populations of pearl dace in the Sandhills region are restricted to spring-fed headwater streams that offer similar lotic habitat requirements as those in Canada and the Great Lakes region (Scott and Crossman 1973, Chadwick 1976, Tallman 1980, Becker 1983, Smith 1985). These stream systems emanate from springs sustained by seepage of groundwater in sub-irrigated meadow valleys. Because of this groundwater discharge, Sandhills stream flows are relatively persistent, and water temperatures are buffered against extremes in ambient air temperature (Bleed and Flowerday 1990). Accordingly, the preferred habitats of pearl dace in the Sandhills are cool streams with well–vegetated stream banks, abundant aquatic macrophytic growth, undercut banks, a meandering morphology with deep pools at curves, and a sand-gravel and sand-gravel-rubble substrate. In addition, the water is usually tea-colored as a result of leached plant tannins and the presence of peat layers in the marsh-fen complexes present in the wet meadow valleys, which, in turn, are responsible for the slightly acidic stream conditions. Stream disturbance by beaver can also create optimal habitat conditions for pearl dace. Because of beaver dam construction, vegetated areas become inundated and pools develop in depressions, all of which offer additional microhabitat refugia for stream fishes (Schlosser 1982). Stream habitat used by pearl dace in the Great Lakes states appears less restrictive than the obligate headwater habitat of Sandhills populations. Scott and Crossman (1973), Headrick (1976), and Becker (1983) described some populations of pearl dace as occurring in second and occasionally third order streams that were more turbid and had moderately muddy substrates. Extensive collections over the last decade (Cunningham 1996, Cunningham and Hickey 1996, 1997) do not indicate use of this habitat type by pearl dace in USFS Region 2.

A critical component of pearl dace habitat is the absence of large predatory fishes. Small headwater streams within USFS Region 2 were naturally devoid of such fish species, and in areas where a native large piscivore is present, pearl dace and other glacial relict cyprinids are absent. This condition is readily apparent in the Upper Elkhorn River Basin in Nebraska, where grass pickerel (*Esox americanus*) are native and glacial relict cyprinids are absent (Johnson 1942, Stasiak and Cunningham personal observations). Although large piscivores are present in some of the streams inhabited by pearl dace in Canada and in the eastern United States, the zone of sympatry is usually small, with the predators occupying the larger downstream portion of the stream (Lyons 1996). Outside of Region 2, native brook trout (*Salvelinus fontinalis*) that are occasionally found with pearl dace are apparently quite small in average size (Hubbs and Cooper 1936, Stasiak 1972, Becker 1983).

Historically, in the lake environments of Canada and Maine, pearl dace, along with other cyprinids, were found in shallow, spring-fed lakes without large piscivores (Robinson and Tonn 1989, Whittier et al. 1997, Kidd et al. 1999, Jackson 2002). Where this cyprinid assemblage is present in small oligotrophic lakes with large piscivores, many of these lakes possess littoral zone shelves consisting of rock platforms or dense vegetation, creating refugia from predators (Chadwick 1976, Tonn and Magnuson 1982).

Food and feeding habits

Several studies have been conducted on the food resources of pearl dace, all concluding this species feeds principally on aquatic macroinvertebrates and zooplankton (McPhail and Lindsey 1970, Lalancette 1977, Stasiak 1978, Johnson and Johnson 1982, Tallman and Gee 1982), but also on detritus, plant material, and snails. As adults, they are primarily sight-feeding predators. Tallman and Gee (1982) observed spatial segregation during feeding, with younger fish feeding higher in the water column and larger, older fish feeding almost exclusively on the bottom. Variability in food types taken is evident among age classes for this species. Stasiak (1978) found that young pearl dace fed on diptera larvae and zooplankton most frequently while larger fish ate large aquatic macroinvertebrates, snails, and adult beetles. Overall, the most common food item for pearl dace of all sizes was diptera larvae and adults. Tallman and Gee (1982) had similar findings, with diptera larvae accounting for a large percentage of the food items in all age classes. However, larger fish in this Manitoba headwater stream consumed significant quantities of detritus and vegetation. During the winter months, the diets of all age classes were nearly exclusively aquatic macroinvertebrates (Tallman and Gee 1982).

A comparison among the various food studies reveals that unlike the pearl dace from an Adirondack stream (Johnson and Johnson 1982) and Manitoba (Tallman and Gee 1982), pearl dace from a lake in Quebec (Lalancette 1977), from the Experimental Lakes Area in Ontario (Vinebrooke 2001), and a stream in the Sandhills (Stasiak 1978) consumed large quantities of zooplankton. This observation indicates that Region 2 pearl dace possibly utilize a greater diversity of food resources than their counterparts in eastern regions. Johnson and Johnson (1982) compared the diet of pearl dace with the diets of several other minnows and brook trout in an Adirondack mountain stream, and they found that brook trout and pearl dace had similar diets, both primarily consuming Ephemeroptera. However, pearl dace used some food items (i.e., annelids) that brook trout did not. In addition, pearl dace were more active nocturnal feeders than brook trout and made use of drift resources more often than brook trout.

Within the context of littoral food web dynamics, pearl dace are effective omnivores, and able to alter zooplankton biomass and benthic community composition. This has been demonstrated in the Experimental Lakes Area of Ontario, where pearl dace inhabiting lakes recovering from experimental acidification suppressed benthic invertebrate biomass and changed species composition by reducing various families of diptera (Vinebrooke et al. 2001).

Breeding biology

Coker et al. (2001) classify the pearl dace as a non-guarding, open substratum spawning lithophil which deposits eggs on rock, rubble, or gravel bottom where their embryos and larvae develop; there is no parental care of eggs. Spawning occurs only once; they are not multiple clutch spawners. It is not known how many eggs are produced during each spawning act or how long it takes eggs to develop into larva.

Spawning occurs from late March to early May throughout its range when the water temperature reaches 16 to 18 °C (Langlois 1929, Fava and Tsai 1974, Lalancette 1977, Becker 1983, Cunningham 1995). The exact spawning period also depends on the photoperiod; thus, it can be somewhat later in northern Canada. Pearl dace in Region 2 usually spawn from mid to late April to mid May, depending on the water temperature (Cunningham 1995). Since water temperatures can rise and fall rapidly during this time of year, breeding behavior may commence and then be suspended for periods of time. In locations where substantial groundwater flow is provided, the temperature rise is more gradual and it fluctuates less, providing a more stable breeding environment. At sites where cool groundwater is not constant, water temperature can warm up much faster and earlier in the season, and is often associated with early spring rains. Water temperature just before spawning will be 12 to 14 °C, but if heavy rains occur, runoff flows will raise the temperature rapidly to 16 to 17 °C, and spawning will occur (Cunningham 1995). In some years when water temperatures rise above 16 °C in late winter or early spring and low water conditions prevail without spring rainfall runoff, little or no spawning activity was observed (Cunningham 1995).

Spawning of pearl dace has been described only once, by Langlois (1929), from a stream in Michigan. According to this account, males defend a small territory over a gravel and sand substrate and escort intruding males out of the defended area. Gravid females may be driven into the defended area. The act of spawning occurs over the defended territory, but no nest is excavated. A male moves parallel to the female and slides his enlarged tuberculed pectoral fin underneath the female’s body anteriorly. The male then places his caudal fin over the female’s caudal peduncle. A slight bending of the female’s body occurs as the male applies upward pressure with his roughed pectoral fin and downward pressure with his tail. Both the male and female vibrate as a mating pair for about 2 seconds. The female repeats this spawning act many times. Cunningham (1995) attempted to observe the act of spawning in pearl dace, and although he never saw the action described by Langlois (1929), he did observe males and females in parallel formation swimming around a loosely defined area, with the males pushing upward on females with their enlarged pectoral fin. These events were observed near the substrate in deep pools, and at the bottom of undercut bank pools where the male-female companions would dart in and out of instream vegetation and root masses.

Several researchers have collected gravid females in late March to early May. Fava and Tsai (1974) found that age class I – III females collected from January to April in Maryland had 913 to 2,140 ripe eggs. The ripe eggs averaged 1.24 to 1.33 mm in diameter, depending on age class. The calculated maturity index revealed that the eggs of these females represented 12 to 16 percent of their total weight. Lalancette (1977) found females (81 to 102 mm TL) in early May that had 621 to 1322 ripe eggs. Becker (1983) reported gravid females (102 to 123 mm TL) with ovaries 18 to 21 percent of their body weight. The number of ripe eggs averaged approximately 4,000, with egg diameter at 1.35 mm. In the Sandhills streams of Nebraska (Cunningham 1995), age class II fish had ovum diameters of 0.9 mm and ovaries of age class III fish had diameters of 1.1 mm . Clutch size varied between age classes, with age class II females averaging 1,100 eggs and age class III females, 2,800 eggs. Body weight as a percentage of egg mass averaged 15 percent; however, one large age class III female had an egg mass that accounted for 30 percent of her body weight. Estimates of fecundity in Nebraska (mean = 2,845 eggs) are higher than all previous studies except Becker (1983) who reported 4,240 eggs, which was 1,000 more eggs than the highest calculated (3,362 eggs) for pearl dace in Nebraska (Cunningham 1995).

Pearl dace in Region 2 reach reproductive maturity as they enter their second spring after being hatched. Cunningham (1995) found that ova in pearl dace of age class I exhibit significantly different GSI (gonadalsomatic index) values and ovum diameter when compared to age class II and III fish. In addition, the eggs of age class I ova do not have the amber to orange coloration like those of age class II and III. This phenomenon is consistent with Fava and Tsai (1974), Lalancette (1977), and Becker (1983).

Sexual dimorphism is very apparent in this species. Female pearl dace are usually larger than the males and do not display the red and orange sides of the breeding males. Males attain very bright red or red-orange pigmentation on the lateral portions of the body during the spring; they become vividly colored in autumn and remain in color until the next spawning period. Females develop a color pattern intermittently in autumn and may or may not possess brightly colored flanks at the time of spawn (Scott and Crossman 1973, Becker 1983, Cunningham 1995). Males also have scoop-shaped pectoral fins that are proportionally larger than those of females. Cyprinid males have a unique complement of pearl organs (breeding tubercles) that are usually species-specific in number, size, structure, and location (Reighard 1903). These breeding tubercles are most obvious on the enlarged pectoral fin of the males, which possess a double row of tubercles. In the course of examining both males and females for tubercle structures, Cunningham (1995) found pattern differences between Sandhills specimens and those of the eastern subspecies of Allegheny pearl dace (Fava and Tsai 1976) and specimens of northern pearl dace from Minnesota. Fava and Tsai (1976) found tubercles on fins other than the pectoral fin in both males and females, but this condition did not exist in the pearl dace from Sandhills streams. None of the females examined by Cunningham (1995) showed evidence of tubercles on any of the fins. Females in this study did possess tubercles on the apical margins of the breast scales, small tubercles on the posterior edge of the operculum, and on the branchiostegal rays, findings consistent with Fava and Tsai (1976) and visible on the Minnesota specimens. Unlike the eastern subspecies and the specimens from Minnesota, several females from Nebraska possessed minute tubercles on the head. Males from Sandhills streams possessed much larger opercular and branchiostegal ray tubercles than females from the Sandhills; these males also had more tuberculated breast scales than the Sandhills females. These observations are similar to those of Scott and Crossman (1973) and Fava and Tsai (1976). The tuberculated breast scales of the males spread dorsally toward the anterior edge of the pectoral fin, forming several rows of roughened scales, slightly similar to those of *Phoxinus* (Koster 1939, Hubbs 1942, Maas 1994). An additional difference among pearl dace from these different geographic areas included males from the Sandhills having tubercles positioned on the apical margins of side body scales located above the lateral line extending just distal of the caudal peduncle region while males from Minnesota possessed tuberculated side scales extending below the lateral line and continuing into the caudal peduncle area, similar to the findings of Fava and Tsai (1976). A more robust analysis of the breeding tubercle arrangement in *Margariscus* is needed to help clarify the phylogentic relationship among these evolutionary significant units.

Demography

Genetic characteristics and concerns

Few comprehensive genetic studies of pearl dace have been reported. Legendre and Steven (1969) determined the diploid number of chromosomes in this species is 50 As part of their investigation into the phylogenetic relationship of the Phoxinin clade of western North American minnows, Simons and Mayden (1998) placed mitochondrial 12S and 16S ribosomal RNA sequences on GENBANK (National Institute of Health, information that could be used in future taxonomic studies. The National Park Service at Isle Royale in Lake Superior, Michigan indicated that genetic work will take place to look at the relationship among various demes surrounding Isle Royale and the population postulated to be its own subspecies within the park (Hubbs and Lagler 1949, Smith 2004). Since this species is widely distributed and does possess different morphological characteristics across its range, comparative phylogenetic analysis would elucidate the evolutionary relationship among the demes across the North American continent. Given the separation distance from its northern conspecifics, the population of pearl dace within the Sandhills region of Nebraska and South Dakota, as well as the immediate surrounding stream systems, may represent a unique genome warranting specific classification.

Pearl dace populations were forced south into several different refuges during the last glacial advance. As the ice melted, they dispersed back to the north via many routes. Long after the last glacial retreat, we now have isolated populations, along with the other glacial relict dace species including the finescale and northern redbelly. All of these relict species exist in springs or seeps in Nebraska, South Dakota, and Wyoming in sandy headwater streams flowing through eolian deposits. In many cases, populations have been separated and isolated from other dace populations for thousands of years. These species have been sufficiently isolated that genetic changes, through natural selection pressures, may have left these regional populations uniquely adapted to the ecological conditions present in the glacial refugia area. Research has not yet been conducted, but it is key to understanding the evolutionary relationships of this species throughout its range. Several researchers have discussed potential research projects along these lines, but to our knowledge, no data of this type have been reported.

Wells (1981) reported possible hybridization between pearl dace and lake chub (*Couesius plumbeus*), and Becker (1983) mentioned hybridization between pearl dace and northern redbelly dace, as well as pearl dace and central stonerollers (*Campostoma anomalum*). As extensive collections of this species across Nebraska and South Dakota do not appear to include any hybrids, it appears these incidents are extremely rare.

Life history characteristics

Several reports provide data on the age and growth of pearl dace. In the eastern form of the pearl dace, Fava and Tsai (1974) determined that 50 percent of the fish collected were immature (age class 0), followed by age class I (25 percent) and II (18 percent), with only a small fraction of the sampled population consisting of age class III (5 percent) and IV (0.5 percent) fish. The sex ratio was determined at 1.0:2.0 females to males, but in the older age classes, most were females. Both males and females reached maturity at the end of age class I (i.e., start of age class II). Age class size structure in the eastern subspecies (Fava and Tsai 1974) was 37 mm standard length (SL) for age class I, approximately 50 mm SL for age class II, and 60 mm SL for age class III. Life history characteristics were determined for lake dwelling pearl dace in Ontario (Chadwick 1976) and Quebec (Lalancette 1977). The Ontario population possessed a sex ratio of 1.4:1.0 females to males and an age class growth structure of 55 mm TL for age class I, 89 mm TL for age class II, and 114 mm TL for age class III. As with the eastern subspecies, 50 percent of the individuals collected were immature. In the Quebec study, the female to male ratio was nearly 1:1. Both sexes reached maturity at the start of age class II, and the age class growth structure was 60 mm TL for age class I, 82 mm TL for age class II, and 95 mm TL for age class III. Becker (1983) reported similar findings, with slightly higher TLs per age class.

Comparisons of mean SL measurements from pearl dace in the Nebraska Sandhills to pearl dace from Canada and the Great Lakes region indicate that the species attains a slightly larger size per age class in its northern range than in the Nebraska Sandhills (Stasiak 1978, and Cunningham 1995). The smaller average size of pearl dace in the Sandhills probably is attributable to the edge–of–range effect. Those ecological factors determining survivorship may have much more of an impact on Sandhills populations than on Great Lake and Canadian populations. Age structure between males and females in the study by Cunningham (1995) differed from previously reported data. Fourteen age class III males were collected during the course of this study, but data concerning age and sex in both the eastern and northern subspecies indicated that very few males reach age class III. One reason for this difference could also be edge–of–range effect. Since population regulating mechanisms may be more severe in the Sandhills, longevity of males would be an advantage. Collectively, the studies of pearl dace in Nebraska, Canada, and the Great Lakes Region show marked differences from the eastern subspecies. This is one of the reasons that Bailey et al. (2004) and Smith (2004) advocate separation of the pearl dace subspecies into two separate species.

All the studies mentioned herein demonstrate that instantaneous maximum growth in pearl dace occurs in age class 0 fish, and moderate growth takes place between age classes I and II and age classes II and III (approximately 10 to 13 mm of incremental growth) for both sexes. However, females attained greater size than males in age class III. Studies of pearl dace across its range indicate that only a very small number of fish (all females) reach age class IV (Scott and Crossman 1973, Chadwick 1976, Stasiak 1976).

Data taken from Stasiak (1978) were used to construct a Matrix Population Analysis of Population Demographics for pearl dace (Appendix). Based on this information, an important conclusion is that a pearl dace population could withstand a year or two of poor reproductive effort and still recover so long as a good number of age II and III fish remain present. However, three poor years in a row would be quite detrimental to maintaining the size of the population. This can be seen in the life cycle diagram and analysis of the demographic matrix performed by David McDonald (**Figure 6**).

Ecological influences on survival and reproduction

Mortality in pearl dace are cause by many factors, including predators, parasites, disease, food abundance, and competition; in some situations, human harvest may take a toll. Abiotic stressors such as drought, temperatures, and habitat availability are also important factors controlling reproductive success. Some of these factors are more likely to impact different ages and sizes and even sexes of pearl dace unequally.

Social pattern for spacing

There is one account of territorial display behavior in pearl dace (Langlois 1929). Adult fish are usually found in loose schools comprised of individuals of mixed sizes and ages. However, age classes appear to be segregated in pool environments, with larger adults spending considerably more time lower in the water column near the benthos (Cunningham 1995).

Patterns of dispersal of young and adults

No study has dealt directly with dispersal of either young or adult pearl dace. However, our observations of various cyprinid species over several decades allow for these generalizations:

- newly hatched fish are usually restricted to areas of heavy cover and reduced current; this is important to reduce predation and to provide the habitat and substrate used by zooplankton, one of their main food sources at an early age (Stasiak 1978, Vinebrooke et al. 2001)

- as the fish mature and reach about one year of age, they become much stronger swimmers and gradually move out into more open water; schools of adult fish are generally mixed with respect to age and size.

In beaver ponds, dispersal occurs during periodic breaks in the dam structure, allowing the water in one isolated pool to connect to others in the system. In streams, flooding is the prime dispersal agent, allowing young fish access to both upstream and downstream reaches. However, many of the streams inhabited by pearl dace in Region 2 have water control structures that do not allow for upstream migration. Therefore, only under extremely high flow conditions, in which they can go around the structure, does this species have an opportunity to move upstream in Region 2. Adult fish probably move upstream toward cool spring or seep inflow, where they encounter reduced current, heavy cover, and the absence of piscivorous fishes, conditions most often found at the headwaters of first order streams.

Spatial characteristics of populations

Since populations of pearl dace are usually in areas of spring seeps, beaver ponds, sinuous channels with undercut banks, and small first order streams, they tend to be very isolated from each other. While pearl dace may be able to disperse during flooding and high water events, these events probably are reduced since the last glacial retreat from the Great Plains. Periodic drought conditions on the Great Plains undoubtedly diminish suitable habitat for these fish. Demes have been reduced and become increasingly isolated from each other and from those populations comprising the main range of this species to the north. The result is little genetic exchange between populations in this region. The study of population genetics of these isolated populations is perhaps one of the most critical of the future “needs assessment”.

Limiting factors

The main factor limiting pearl dace populations in this region is the availability of suitable habitat, although non-native species interactions may be as important (see Community ecology section). Optimal habitat for pearl dace is streams associated with sub-irrigated meadow valleys fed by groundwater, well-vegetated stream banks, sinuous channels with undercut banks, and few (if any) large predatory fish species. As the Great Plains have gradually become warmer and drier over the centuries since the last glacial retreat, conditions have naturally become less suitable for this species (McPhail 1963). Pearl dace populations in this region have been reduced to isolated small pockets of spring flows. The Sandhills region of Nebraska and South Dakota

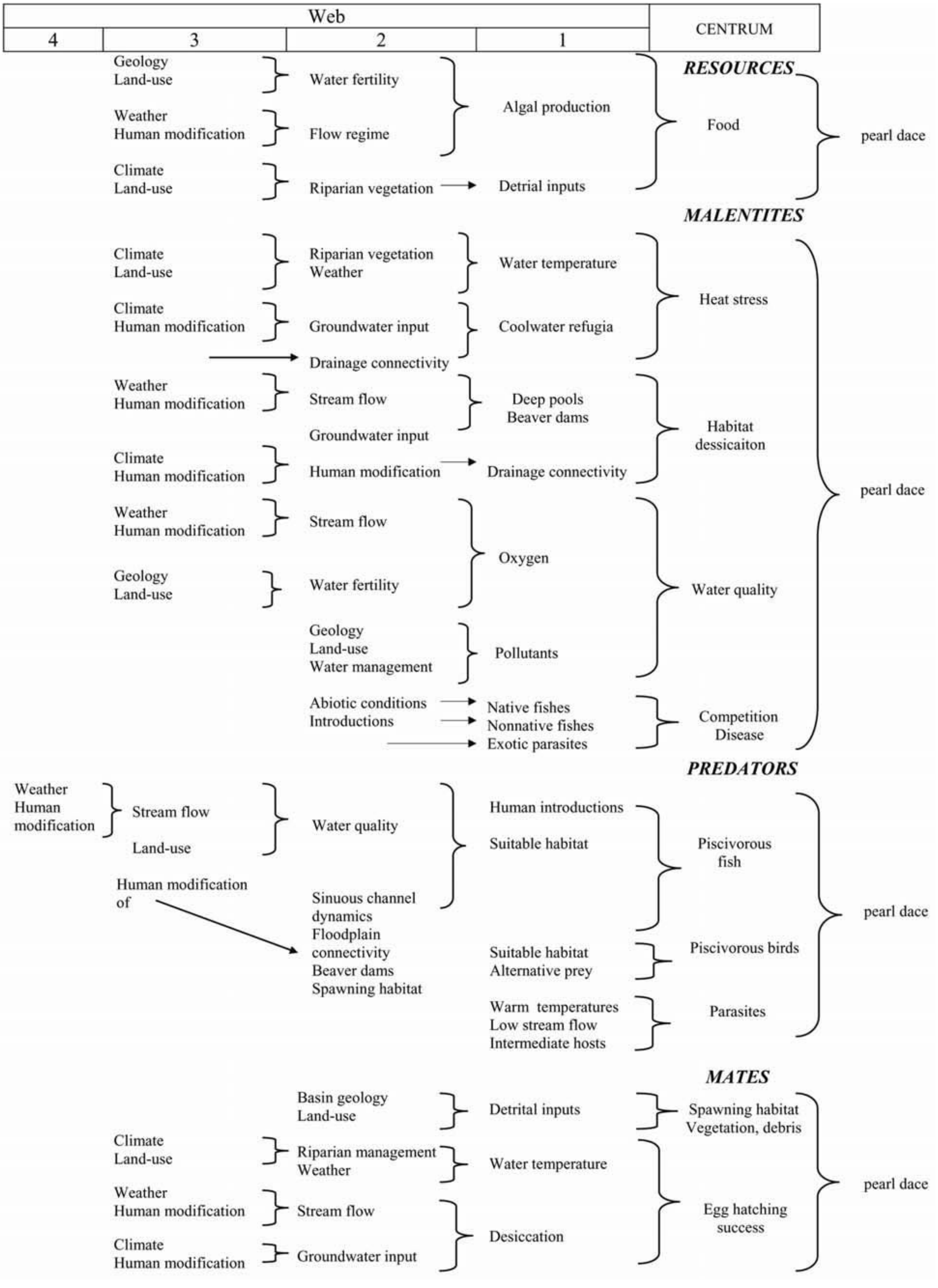

Figure 6. Envirogram for pearl dace.

still contains many of these permanent groundwater sources, where they form the headwaters of small first order streams, or small seepage lakes. However, since the settlement of this region over the past 150 years, permanent sources of cool, clear groundwater have become highly developed for human uses. Much of it is pumped for irrigation or used for domestic or municipal water supplies; in many places, spring seeps have been dammed to form relatively large lakes. The few remaining relatively natural small streams have all too often been stocked with large predatory "game species" (i.e., trout, pike, sunfishes) that often eliminate pearl dace, as well as other members of the glacial relict cyprinid fish community.

Community ecology

Predators

Piscivorous birds, such as belted kingfisher (*Megaceryle alcyon*) and great blue heron (*Ardea herodias*) have been observed actively feeding on schools of these minnows (Stasiak 1972; Cunningham personal observation). In deeper lakes, loons, ducks, and cormorants also consume pearl dace, particularly in lakes in Canada and the Adirondacks. Fish-eating snakes, turtles, and bullfrogs, are also common potential predators in ponds and streams. Mink (*Mustela vison*) and raccoons (*Procyon lotor*) also will undoubtedly eat pearl dace.

Carnivorous aquatic invertebrates can feed heavily on this species. Predacious diving beetles of the family Dyticidae (larvae are commonly called water tigers) and giant water bugs of the family Belostomatidae are known to eat small cyprinids. These voracious insects can reach 70 mm in length and commonly eat aquatic vertebrates such as frogs and tadpoles, snakes, and fishes. Other insects such as dragonfly larvae (Odonata) and smaller bugs (Hemipetra) such as water scorpions and backswimmers may also consume pearl dace, especially young individuals.

Under natural situations, the one type of predator that pearl dace do not have to deal with is a large fish species. The small and shallow nature of the ponds and streams containing this species generally are not suited for large predatory fish species. The temperature ranges and potentially low oxygen levels common to pearl dace habitat also tend to eliminate large fish species. These types of ponds are often subject to heavy ice and snow cover in the winter. The ice may reduce the volume of water substantially, and little oxygen is present in the remaining fluid water. Some of the smaller fish species that are often associated with pearl dace, especially mudminnows (*Umbra limi*) and creek chubs (*Semotilus atromaculatus*) can occasionally eat pearl dace (Schlosser 1982). When they occur together, large creek chubs are very capable of eating small pearl dace (personal observation). These naturally occurring fish predators will play a role in eating very young pearl dace, but their overall effect is probably very small compared to the collective effect of the predatory insects. Stocked species of large predatory fishes (i.e., sport fishes) can have a very deleterious effect on pearl dace populations because they can eat the largest adult pearl dace. There is no doubt that game fish readily eat pearl dace (Whittier et al. 1997, Kidd et al. 1999, Findlay et al. 2000, Jackson 2002).

Competitors

Pearl dace are tolerant of environmental extremes (e.g., variations in oxygen levels, pH, annual temperature extremes, and ice cover conditions) that few other species can handle. They are usually associated with a small number of other native fish species that also are adapted to similar conditions Combinations of these fishes usually represent a well balanced fish community of small species that can successfully partition the resources available in a relatively confined habitat.

Throughout much of its remaining North American range pearl dace are usually associated with a fairly small but distinctive assemblage of other fish native species. In the Sandhills streams of Nebraska and South Dakota, this species is often associated with northern redbelly dace, finescale dace, brassy minnow (*Hybognathus hankinsoni*), fathead minnow (*Pimephales promelas*), creek chub (*Semotilus atromaculatus*), central stoneroller (*Campostoma anomalum*), sand shiner (*Notropis stramineus*), plains topminnow (*Fundulus sciadicus*), white sucker (*Catostomus commersoni*), green sunfish (*Lepomis cyanellus*), Iowa darter (*Etheostoma exile*), and brook stickleback (*Culaea inconstans*). Common shiner (*Luxilis cornutus*) and blacknose shiner (*Notropis heterolepis*) also may be rarely found with pearl dace, and blacknose dace (*Rhinichthyes atratulus*) may be associated in streams in the eastern portion of the Sandhills) (Bailey and Allum 1962, Stasiak 1976, Baxter and Stone 1995, Cunningham 1995). Most of members of this fish assemblage are also present in the headwaters of the Niobrara River in Wyoming and Nebraska, but central stonerollers, sand shiners, and bigmouth shiners are less common, while blacknose shiners and common shiners are absent. Although the pearl dace is always found with the glacial relict *Phoxinus* species in Nebraska and almost always in South Dakota (Cunningham and Hickey 1995, Cunningham et al. 1995, Cunningham and Hickey 1996), this species is not found in those tributaries of the North Platte River that are inhabited by *Phoxinus* species. Moreover, only the pearl dace is found with the two "pure" finescale dace populations (those without northern redbelly dace or the *Phoxinus* hybrid) in Nebraska (Cunningham and Hickey 1995, 1996), but they are not found with the "pure" finescale dace in the northern foothill lakes and streams of the Black Hills region of South Dakota. (Olson 1998, Cunningham personal observation).

In their preferred habitat of small streams, pearl dace are sight-feeding omnivores, selecting a host of aquatic invertebrates as food resources. The other fishes that are commonly found with this species have different food resource niches or only slightly overlap in niche resource use with pearl dace. This separation or compatibility in resource use breaks down when predatory fish species are introduced into pearl dace habitats. When larger predatory fish species (e.g., trout, pike, bass, sunfishes) are introduced into these relatively small and confined habitats, they become direct predators on pearl dace. These non-native predators may reduce pearl dace, as well as other glacial relict cyprinids, by directly preying on the dace, and through competition for critical resources such as space (particularly undercut bank microhabitats) and food resources (Cunningham 1995). Pearl dace do not appear to be able to adapt to the added predation and competition from larger predatory fishes. Shields (2004) 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 pearl dace, which appears to be very sensitive to interactions with fish species outside of the small group of normal associates.

Parasites and disease

Parasites and disease appear to have a minimal impact on pearl dace, although we are not aware of any studies specifically designed to examine parasites in this species. Stasiak (1978) made note of digenetic trematodes attached to the inner lining of the intestine in this species. During a study at a site in Labrador, Canada contaminated with a petroleum-derived hydrocarbon, Khan (1999) found gastrointestinal parasites (tentatively identified as *Bunodera*, *Brachyphallus*, and *Crepidostomum*) in pearl dace taken from the study reference site, but from not the impacted site. This condition is most likely the result of food preferences since preferred food resources at the reference site were not found at the impacted site (Khan 1999). We have rarely observed pearl dace to possess "black spot disease", a condition caused by several digenetic larval trematodes (*Uvulifer*). These larvae are very common as tiny black cysts in the skin and muscles of virtually all species of freshwater fishes found in shallow water with vegetation. While it is very common throughout the Midwest to see sport fishes such as pike, bass, perch, and sunfish practically covered with these small black spots, pearl dace is only rarely afflicted with this external parasite (Steedman 1991). The occurrence of these black cysts on pearl dace has always been noted from streams impacted by high turbidity or stagnant water (Cunningham personal observation). The lack of external parasites has been attributed to the habit of pearl dace swimming actively in mid-water, thus escaping the swimming cercaria released by snails (Phillips 1968). Cunningham (personal observation) has noted the presence of nematodes imbedded in the ventral portion of the ocular cavity of pearl dace in Nebraska.

CONSERVATION

Potential Threats

Populations of pearl dace throughout USFS Region 2 appear to be stable, but they have declined in some areas. The rarity rankings in Wyoming and South Dakota are the result of peripheral populations inhabiting a single drainage basin (Niobrara River in Wyoming) or a landform (Sandhills) just inside the border of the state (South Dakota). However, populations in South Dakota and Nebraska have been lost as a result of the loss, modification, and fragmentation of habitat, and the introduction of non-native fish species (Cross and Moss 1987, Warren and Burr 1994, Masters et al. 1998). Looming as a potential threat to these glacial relict populations is the ever-increasing human demand for water resources and continued landscape modification. Combine these stressors with potential long-term climate change, which is expected to result in drier and warmer conditions in the Great Plains, and pearl dace populations of the Great Plains face an uncertain future. Added to the list of stressors is the intentional or unintentional introduction of predatory "sport fish," which are not compatible with pearl dace. Thus, the factors predicted to have the greatest negative impact on the persistence of this species will be hydrologic alterations of stream systems, resulting in habitat degradation and fragmentation, and the introduction of non-native fish species.

Unlike most Great Plains stream systems, the headwater streams occupied by pearl dace demonstrate less stochasticity in drying and intermittency on an annual basis due to groundwater inflows from abundant groundwater sources. These streams are remarkable in their constancy of their flow (Bleed and Flowerday 1989). However, groundwater pumping and water diversions have occurred extensively across the Great Plains over the past 50 years, and continue to increase, resulting in depletion of ground water. The resulting negative effects on spring inflows to headwater streams is likely to have deleterious consequences for pearl dace viability within Region 2. The Region 2 ecoregion with multiple extant populations of pearl dace is the Sandhills of Nebraska and South Dakota. Fortunately, groundwater depletion is currently not a threat to stream systems in this ecoregion because the edaphic conditions are not suitable for row crop agriculture; range livestock production is the principle land-use practice. However, along the margins of the Sandhills ecoregion (particularly the Upper Niobrara River valley), center-pivot irrigation of forage crops (e.g., alfalfa) has increased substantially (Bleed and Flowerday 1989). In the future, if groundwater withdrawals exceed annual recharge rates, aquifer-dependent headwater streams and natural lakes will be adversely affected. Maintenance of this hydrologic pathway is critical since the persistence of pearl dace at specific sites during extended dry periods is dependent on groundwater inflows.

Besides direct groundwater pumping, instream diversion units appropriate water for agricultural production or municipal water supplies both in the Upper Niobrara River and Platte River drainages in Nebraska. These withdrawals modify flow regimes and dewater sections of streams. In these drainage systems, decreased flows have reduced channel scour and have affected the spatio-temporal heterogeneity of floodplain habitats. Hydrologic alteration has occurred in the Sandhills ecoregion, but in a different form. In this ecoregion, the modification of sub-irrigated meadow hydrology by stream channel ditching and water control structure placement and operation has modified nearly every Sandhills stream (Bleed and Flowerday 1989). These activities have probably contributed to habitat fragmentation and the disruption of stream ecosystem processes. Pearl dace persist in Sandhills streams despite ditching and water control operations that have created homogeneous instream habitat and incised channel morphology. Persistence of pearl dace in these streams has been made possible through a 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 five to seven years and produces overbank flooding.

An important component of the hydrologic processes of those headwater systems and spring-fed lakes inhabited by pearl dace is the presence of beaver activity. Beaver interaction with other biotic (predation) and abiotic (physiographic, vicarance) components of the system greatly influences the assemblage and structure of fish communities (Jackson et al. 2001). These "ecosystem engineers" strongly effect the physical, chemical, and biological attributes of the landscape (Naiman et al. 1988, Schlosser and Kallemyn, 2000). Work in north-temperate beaver bog stream and lake systems inhabited by pearl dace and other cyprinid dace species conclude that beaver activity is a major factor in fish dispersal (Schlosser 1995), recolonization dynamics (Schlosser and Kallemyn 2000), and fish community assemblage (Tonn and Magnuson, 1982, Schlosser and Kallemyn 2000) 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, and plunge pool habitat below dams.

This dynamic is observed in the Sandhills ecoregion where beaver have only recently returned in significant numbers. As has been observed further north in Minnesota, Wisconsin, and Canada (Stasiak 1972, Tonn and Magnuson 1982, Schlosser 1995), pearl dace in this ecoregion are often found downstream and upstream of beaver ponds, unless they are large and deep. Dense, non-woody vegetation becomes established around beaver dams and undercut bank pools become much deeper in beaver modified systems (Cunningham personal observation).

Water improvement projects, such as channelization and placement of water control structures, are all too common in the Sandhills ecoregion, and these negatively affect stream hydrology. Moreover, some governmental agencies and non-government organizations are conducting hydrologic restoration programs in the Sandhills that store water behind grade and water control structures; these may have the unintended consequence of altering fish community structure. While these "solutions" appear to mimic beaver ponds, these larger bodies of water simply retain too much water and may disrupt groundwater flow and recharge patterns, fragmenting fish populations, and more deleteriously, providing habitat for non-native fishes, particularly introduced piscivorous “sport fishes.”

Studies in the north-temperate region clearly demonstrated the profound effect that non-native predator fish have on cyprinid communities in small lakes (He and Kitchell 1990, Findley et al. 2000, MacRae et al. 2001). Introduced non-native centrarchids (e.g., black bass, rock bass) can negatively impact pearl dace in lakes, ponds, or pools of streams, and trout can negatively impact pearl dace in streams. Indeed, Jackson (2002) listed a set of species (pearl dace among them) as being highly vulnerable to centrarchid (sunfish family) predation. Lakes dominated by salmonids (i.e., trout) contained significantly more cyprinid species than centrarchid-dominated lakes. This phenomenon is best explained by overlapping habitat between centrarchids and cyprinids, particularly in the littoral zone. Salmonids demonstrate limited overlap with cyprinids in summer habitat, at least in lake environments (Jackson 2002). Thus, impoundments on streams that experience non-native centrarchid introductions can lead to extirpation of this cyprinid species.

The greatest threat to the viability of stream-dwelling pearl dace populations is from non-native species. Unlike lake populations, however, stream populations are equally vulnerable to centrarchids and salmonids. Whether stream systems are altered by impoundment structures and later stocked with centrarchids or are used as salmonid-receiving waters by resource agencies, glacial relict headwater cyprinids will either be eliminated or persist in extremely low number (Cunningham and Hickey 1996). The authors have collected pearl dace in the headwaters of the Niobrara River near the Wyoming border, but the species is absent just a few miles downstream at Agate Fossil Beds National Monument (Stasiak 1976, 1989, Cunningham personal observation), probably due to the presence of stocked brown trout (*Salmo trutta*), pike (*Esox lucius*), bass (*Micropterus salmoides*), and bluegill (*Lepomis macrochirus*). Unlike lentic systems, salmonids in lotic environments have a positive habitat association with the headwater cyprinid community (Jackson 2002), and predation has been observed in some Sandhills streams (Cunningham and Hickey 1996). Trout have been observed occupying pool and undercut bank pool habitats in these Sandhills streams (Cunningham 1995). Pearl dace could also suffer from territorial displacement and competition for food resources (Shields 2004). Jackson (2002) described the risks and consequences to small-bodied fishes from introduced fishes in greater detail; these include resource compaction, increased intra- and interspecific competition, and stress.

Clearly, most introductions of non-native predacious fishes and modifications of lotic habitat to deeper lentic habitat that allow non-native piscivores to persist are detrimental to pearl dace populations. Non-native species can affect native species through a number of mechanisms including predation, competition, habitat alteration, pathogen transfer, and behavioral displacement. Studies with other cyprinid species in lotic systems strongly link the disappearance of certain cyprinid species, and the alteration of small stream fish community assemblages 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, affecting recolonization capability, and creating barriers to fish migration and (Fausch and Bestgen 1997) and exchange of genetic material. Another potential consequence of fish introductions is the potential for pathogen transfer from non-native fish species to the native fish community or other biota within the watershed (especially amphibians) (Kiesecker et al. 2001). Shields (2004) documented several cases of parasite (i.e., nematodes, trematodes, cestodes) transfer from introduced fishes in Oregon, resulting in severe population reductions in native fishes. Although relatively understudied, pathogen transfer among different aquatic taxa may represent an undiagnosed perturbation. This could induce stress to a set or sets of aquatic organisms, ultimately affecting survivorship, recruitment, and persistence of these species. Moreover, the introduction of non-native species could alter native aquatic community assemblage patterns, possibly affecting native host-pathogen dynamics (Kiesecker et al. 2001).

A significant unknown and little studied element in the long-term viability of headwater fish species is the synergistic effects of multiple stressors. Extended severe drought by itself may have only modest effects on the long-term viability of fish assemblages (Matthews and Marsh-Matthews 2003). However, when combined with groundwater pumping, irrigation, and water diversion, extreme disturbance events such as long-term drought (an element of natural ecosystem processes) may severely deplete a population or extirpate a species on a regional basis. Couple these phenomena with climate change predictions, and the prospective for long-term viability is difficult to assess (Jackson and Mandrak 2002). Given the already highly fragmented distribution of pearl dace within the Region 2, this species could be adversely affected by the combined forces of future increased groundwater extraction, water diversion, and climate change-induced extended dry cycles.

Pollution does not currently appear to be a major problem for pearl dace populations in USFS Region 2, but this is something that needs to be monitored. It is possible that future mining and/or agricultural operations could release deleterious chemicals into the streams or groundwater. Pearl dace need relatively clean, clear water, and anything that would cause sustained turbidity would negatively affect the species. This might include frequent erosion and siltation, and prolonged use of a water source by cattle.

People can and do collect wild minnows for use as bait. In northern Minnesota, minnows are considered good bait for walleye fishing (Dobie and Meehan 1956, Gunderson and Tucker 2000). Commercial bait dealers often sell them under the trade name of "rainbow chub", and pearl dace command premium prices. The author has removed minnow traps and has seen witnessed such exploitive collecting in the Sandhills. It is possible that this type of activity could be highly deleterious to isolated pearl dace populations.

Conservation Status of Pearl Dace in Region 2

The area occupied by pearl dace within USFS Region 2 is relatively small. While the streams of the Sandhills ecoregion account for the vast majority of pearl dace populations in the region, known populations are outside national forest boundaries. The species is not present within the Bessey Unit of the Nebraska National Forest or the Samuel R. McKelvie National Forest, which are located within the ecoregion (Cunningham and Hickey 1995, 1996). Although past surveys have not found pearl dace on NFS lands, populations may exist along the Loup and Dismal rivers that flow through the Bessey Unit; a complete inventory of these parcels has not be conducted and, clearly, the first attempt at developing a regional conservation strategy for this species is to determine exactly which sites with potential to harbor the species actually have pearl dace populations.

Potential Management of Pearl Dace in Region 2

Implications and potential conservation elements

All three states within USFS Region 2 that have pearl dace populations have designated the species as of a high level of conservation concern. While this may confer limited conservation benefit, the species remains vulnerable to extirpation by hydrologic modification of stream systems and the presence of non-native species. Conservation of this species will require resource managers to consider the unique habitat features utilized by this species across a mosaic of heterogeneous habitats that are highly dynamic in space and time. In addition, the presence of non-native species, particularly piscivores, has a major impact on the persistence of pearl dace populations. Thus, the conservation of pearl dace will necessarily focus on preserving or restoring natural system processes in streams and preventing or controlling the establishment of non-native fish species in these systems.

Multi-agency (e.g., federal agencies, state resource agencies, non-profit conservation organizations, private landowners) efforts are needed to develop and manage stream systems on a watershed basis, focusing on native stream fish assemblages. Resource managers need to be cognizant of the effects of non-native species introductions and their management in aquatic ecosystems (Minckley and Deacon 1991). Concurrently, hydrological modifications (e.g., water development projects, sub-irrigated meadow alterations, groundwater pumping) have altered aquatic systems throughout Region 2. Future human water demands and continued drought conditions coupled with climate change effects could jeopardize remaining pearl dace populations. Consequently, every attempt should be made to maintain or reestablish the natural flow regime in drainages where this species resides.

Conservation efforts must necessarily extend beyond individual pools, and focus on maintaining or restoring the ecological processes of stream systems that create and maintain sinuous channel morphology, undercut banks, and bend pools across the landscape. An integral part of these processes is presence of beaver and their hydrologic engineering within watersheds. The reestablishment or expansion of beaver occupancy can go a long way to restoring ecological systems that will benefit pearl dace and other native plains headwaters fish species.

Resource managers may be tempted to build habitat for pearl dace by impounding water on sections of streams inhabited by this species. Conceptually, this may be appealing. However, these created ponds must be designed to mimic beaver pond morphology, hydrologic retention, and flow. Moreover, simply creating a pond or hole on the landscape is not ecologically sufficient to ensure viability of pearl dace. Connectivity to other habitats and resources is essential for various life history demands, such as ontogenetic feeding shifts, spawning habitat, and dispersal and segregation of larvae, 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). For example, beaver pond placement, morphology, and successional shift within the landscape mosaic will influence pearl dace population establishment and persistence greatly (Schlosser and Kallemeyn 2000). Moreover, the terrestrial characteristics across the land-water template within a drainage unit will affect the hydrology, sediments and 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 would serve as ideal guides for resource managers to use in understanding and assessing the necessary and sufficient elements for pearl dace conservation.

Several key considerations in strategically planning for the conservation of pearl dace and other native grasslands headwaters stream fishes include:

- Develop watershed-based management strategies with partnering organizations and private landowners for connectivity and natural stream ecosystem processes.
- Protect spring sources flowing into naturally meandering streams, particularly if beaver activity is present.
- Manage for the restoration of beaver activity within watersheds.
- Avoid stocking of non-native species within these aquatic ecosystems, or remove these species in systems being managed for native cyprinid fish communities.
- Renovate natural spring-fed lakes containing non-native fish species and restock with pearl dace from the nearest native source population.
- Restrict commercial harvest of minnows by bait dealers in waters known to have pearl dace populations.

Tools and practices

Inventory and monitoring

Inventory efforts to-date have focused on the presence or absence of this species during statewide stream fish surveys or ecoregional sampling efforts; however, no systematic statewide surveys have been conducted in Nebraska or South Dakota in over fifty years. Johnson's (1942) survey of Nebraska fishes established a baseline for pearl dace distribution in that state. However, despite many subsequent surveys at locations surveyed by Johnson, the species has not been collected since his early work. Bliss and Schainost (1972) conducted fish surveys for all the major stream systems in Nebraska, but specimens were not saved and much confusion still remains concerning the identities of the sampled fishes. The Sandhills ecoregion was extensively sampled in the 1990's as part of a Nebraska Natural Heritage Program inventory (Cunningham and Hickey 1995, Cunningham et al. 1995, Cunningham 1996), leading to the discovery of several new populations of pearl dace. Currently, Nebraska is undertaking a repeat of Johnson's work (1942), with modifications; and South Dakota has completed major watershed basin surveys throughout much of the state, except north-central South Dakota and small tributaries to the Missouri River. Patton (1997) compared species distributions in Wyoming during the 1990's with distributions constructed from Baxter's 1960's state-wide fisheries survey data (Baxter and Simon 1970), finding no new localities for pearl dace. The author of this report has conducted periodic sampling for pearl dace throughout Region 2 for several decades; the results are included in the distribution maps.

Little if any monitoring of glacial relict cyprinids occurs in Nebraska, South Dakota, and Wyoming. Monitoring would be particularly valuable in the Sandhills region of Nebraska in those streams experiencing "restoration" activities by the U.S. Fish and Wildlife Service and the Sandhills Task Force.

Various resources and studies are available to serve as templates for designing a monitoring strategy for this species. Fish censusing techniques are well described in Hays (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 listed above would serve USFS resource managers well. Due to the nature of habitat occupied by pearl dace, minnow traps and backpack electroshockers are probably the most suitable collecting tools. Sampling efforts using these devices can be quantified and standardized, and they are known to be efficient means of collecting pearl dace. While seines may work in some small streams, the soft bottom and brush associated with many creeks and beaver ponds makes use of these nets problematic. Traps can be transported to the often swampy pearl dace habitat where they can be checked on a standardized schedule (Bryant 2000).

Population or habitat management practices

Population or habitat management practices specifically aimed toward pearl dace appear to be lacking; however, the restoration and management of natural ecosystem processes would greatly benefit pearl dace populations. Attempts at stream or hydrologic restoration are being made in some areas of the Rocky Mountain Region. In the Sandhills ecoregion, several sub-irrigated meadow hydrologic restoration projects have been undertaken that involve modifying stream and channel hydrology (website: http://www.sandhillstaskforce.org). However, because post-construction research and monitoring has not been conducted at these sites, the efficacy of these projects to restore and enhance native headwater fish assemblages is unknown. Additional opportunities for restoration may exist in many of the small spring-fed tributaries to the Niobrara River in Nebraska and the Keya Paha River straddling the Nebraska-South Dakota border. At the very least, there should be no additional stockings of sport fish by resource agencies into headwater streams.

Historically, beaver were abundant across the stream and river systems of the Great Plains (Naiman et al. 1988, Olson and Huburt 1994, Parrish et al. 1996), and management strategies should be developed that reestablish beaver to these systems or encourage their expansion. The establishment of healthy beaver populations will go a long way toward restoring suitable habitat for pearl dace and other grasslands headwater stream cyrinnids. It should be recognized that beaver occupancy can at times generate problems for private landowners where the damming of streams may cause water to back into unwanted locations; and even on public lands beaver activity may affect other land uses, such as livestock grazing and road management. Where stream systems are being managed to bring the benefits of beaver activity to native fish communities and other resources, especially those sites exhibiting year round spring discharge into a meandering stream channel, livestock grazing (particularly during the warm season) and other intensive land uses must be carefully controlled to avoid damage to riparian zone vegetation, damage to stream banks, and the resulting increase in sedimentation, water turbidity, algal growth, and nutrient loading.

Conservation strategies for restoring headwater fish assemblages, including the pearl dace, should strive for the creation of successional aquatic mosaics across the landscape in naturally functioning condition. Successful strategies will incorporate the elements of connectivity, spatio-temporal habitat dynamics, and life history processes, and will seek eliminate or mitigate the negative influences of multiple stressors affecting these systems.

Information Needs

The distribution of pearl dace is well known in some areas of Region 2, particularly the Sandhills ecoregion, but gaps exist. Because of the unique position and habitat requirements of this species within a stream system, further inventory targeting this species is relatively straightforward. Although sampling has been conducted in the NFS units in the Nebraska Sandhills (Cunningham and Hickey 1995, 1996), a systematic inventory at spring pool discharge areas in the rivers bordering the Halsey and McKelvie Units would close a data gap for this species in the Sandhills ecoregion. Moreover, sampling similar unique habitats along the Niobrara River would complete the inventory of that river basin.

Virtually no data are available regarding the population dynamics of pearl dace in Region 2. Within the small area this species is known to inhabit, information concerning distribution, population size, and recruitment success is needed to develop a conservation management plan for the species. Data also are needed concerning barriers to fish movement (e.g., impoundments, culverts, non-native species) among habitats throughout inhabited stream systems.

Pearl dace populations occur in rather discrete, isolated demes on the Great Plains. Research on the genetic makeup of these populations and how they are related to each other and conspecifics in the main portion of their range should be another priority of any conservation effort.

Information management and document archiving are the final needs we mention here. Much of the location and ancillary data recorded at the time of pearl dace collections is recorded in the various natural heritage database systems of individual states comprising USFS Region 2. However, notes, field forms, communications, and notations from state or federal inventory and monitoring efforts (past and future) should also be shared with natural heritage programs for database archival.

DEFINITIONS

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

Edaphic – due to soil or geologic conditions.

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

Gonadosomatic index (GSI) – the fish's ovary weight divided by its total body weight multiplied by 100.

Lentic – standing water habitats (e.g., ponds, bogs, lakes).

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

Piscivorous – "fish eating".

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

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

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

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

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APPENDIX

Matrix Model Assessment of Pearl Dace

Life cycle graph and model development

The life history data described by Stasiak (1978) and Langlois (1929) for pearl dace provided the basis for an age-classified life cycle graph that had five age-classes (**Figure A1**). From the life cycle graph, we conducted a matrix population analysis assuming a birth-pulse population with a one-year census interval and a post-breeding census (Cochran and Ellner 1992, McDonald and Caswell 1993, Caswell 2001). Beyond this introductory paragraph, rather than using an age-class indexing system beginning at 0, as is the norm in the fisheries literature, we use indexing beginning at 1. Note that Age 0 fish, censused as eggs, will reproduce at the end of the second year of life, at which time they will be essentially the same size as the Age II census size. In order to estimate the vital rates (**Table A1**), we made the following assumptions and estimates. The fixed points for vital rate estimation were considered to be:

- a stable age distribution based on the age structure of Stasiak (1978; p. 464; **Table A1**)
- a distribution of ovum size data by age (Stasiak, unpubl. "ovumbysize.xls")
- egg production ranging from 900 eggs at age of first reproduction to a maximum of 4240 eggs at the largest sizes (Web page: www.afs-soc.org/fishdb/fish-list.php)

Because the model assumes female demographic dominance, the egg number used was half the published value, assuming a 1:1 sex ratio. The ovum size data were fit to a logistic curve obeying the following equation:

$$dO/dt = rO(1 - O/O^*)$$

where r was 3.237 and the asymptotic value, O^*, was 0.77 (marginally larger than the observed maximum of 0.769). That equation yielded a good fit (**Figure A2**) to the observed ovum size values presented in **Table A2**. The parameter r = 3.237 (and a zero point of $E_ø$ = 22.2) was then used to generate a logistic curve for egg numbers, passing through the observed lower limit of m_2 = 450 eggs for Age-class 2 and asymptoting at the maximum observed value 2,120. The resulting age-specific fertilities (m_i) are presented as female eggs per female in **Table A2**. Because no survival data were available, we adjusted survival rates to produce a stable age distribution (**Table A1**) matching the age structure described in Stasiak (1978; p. 464). In addition to the constraint of matching the empirical age structure, the survival rates were also set up to be reasonably similar to the more extensive data available for finescale dace

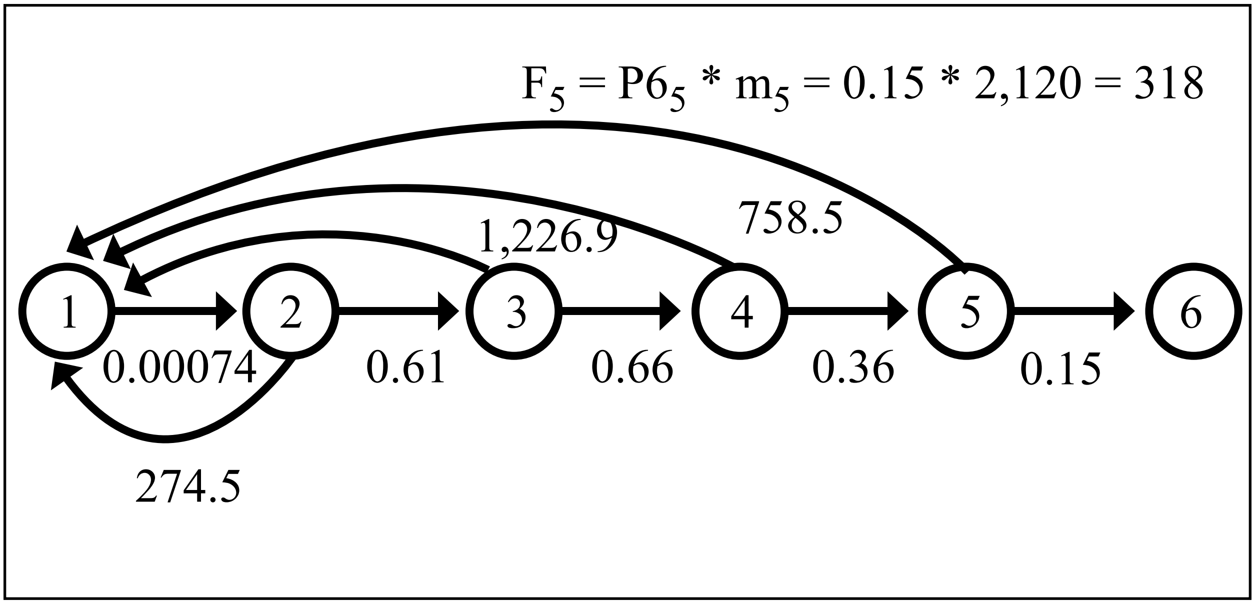

Figure A1. Life cycle graph for pearl dace, consisting of circular *nodes*, describing age-classes in the life cycle and *arcs*, describing the *vital rates* (transitions between age-classes). The horizontal arcs are survival transitions (e.g., first-year survival, P_{21}= 0.16). The remaining arcs, pointing back to Node 1, describe fertility (e.g., $F_5 = P_{65} * m_5$ = 318). Each of the arcs corresponds to a cell in the matrix of **Figure A3**.

Table A1. Observed age distribution of Stasiak (1978) and the modeled stable age distribution (SAD) used in the demographic analysis. Although Stasiak presented the data as 135 Age 0 fish, these were censused in May, just before the breeding season and were therefore considered to represent the size distribution of fish of the next larger age-class (since Age 0 fish are censused as eggs). The stable age distribution values presented omit the contribution of eggs, which represent more than 99.8 percent of the population at the time of the post-breeding census. Survival rates were adjusted to yield a stable age distribution in accordance with the observed age structure and a reasonable fit to the more extensive data available for finescale dace.

Age	Age-class	Description	Observed	Proportion	SAD
0	1	First-year (eggs)	—	—	—
I	2	Second-year	135	0.443	0.462
II	3	Third-year	86	0.282	0.285
III	4	Fourth-year	60	0.197	0.176
IV	5	Fifth-year	21	0.069	0.070
V	6	Sixth -year	3	0.010	0.008

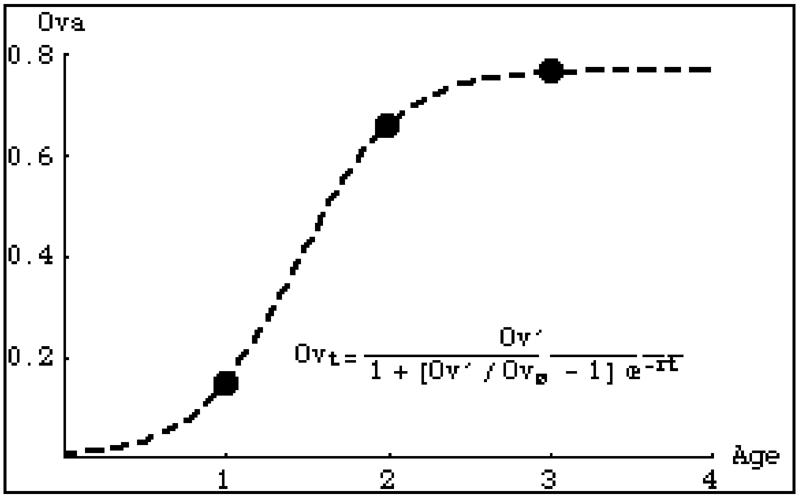

Figure A2. Logistic fit to the ovum size data of Stasiak (ovumbysize.xls). Ov_0 was set at 0.007. The fitted growth parameter, $r = 3.237$, was then used to fit a sigmoid curve for egg number as a function of age.

Table A2. Fertility data for pearl dace. The empirical ovum size by age data were fitted to a logistic equation (**Figure A2**), which was then used to interpolate intermediate values into the observed range of egg production (450 to 2,120).

Age	Age-class	Ovum size	Eggs
0	1	—	—
I	2	0.146	450
II	3	0.657	1,859
III	4	0.769	2,107
IV	5	0.770	2,120
V	6	—	—

(Stasiak 1972). The pearl dace age structure data of Stasiak (1978) were from May, just before the spawning season, and therefore describe fish that should closely approximate the sizes of fish for the next age at the time of the post-breeding census in late May or early June. For example, Stasiak's 135 "Age 0" fish would be essentially the same size as censused Age I fish, rather than at the censused Age 0/Age-class 1 (egg) stage. We also made the assumption that the long term value of λ (population growth rate) must be near 1.0.

The model has two kinds of input terms: P_i describing survival rates, and m_i describing fertilities (**Table A1**). **Figure A3a** shows the symbolic terms in the projection matrix corresponding to the life cycle graph. **Figure A3b** 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 (**Table A3**). The population growth rate, λ, was 1.005 based on the estimated vital rates used for the matrix. This should not be taken to indicate a stationary population, because the value was used as a target in estimating the survival rates and was subject to the many assumptions used to derive all the transitions. The value of 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 population growth rate (λ) of an absolute change in the vital rates (a_{ij}, the arcs in the life cycle graph [**Figure A1**] and the cells in the matrix, **A** [**Figure A3**]). Sensitivity analysis provides several kinds of useful information (see Caswell 2001, pp. 206-225). First, sensitivities show how important a given vital rate is to population growth rate (λ), which Caswell (2001, pp. 280-298) has shown to be a useful integrative measure of overall fitness. One can use sensitivities to assess the relative importance of the survival (P_i) and fertility (F_i) transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to paucity of data, but could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on accurate estimation of transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on age-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which age-classes or vital rates are most critical to increasing the population growth (λ) of endangered species or the "weak links" in the life cycle of a pest.

Figure A3 shows the "possible sensitivities only" matrix for this analysis (one can calculate sensitivities for non-existent transitions, but these are usually either meaningless or biologically impossible – for example, the sensitivity of λ to moving from Age Class 3 to Age Class 2). In general, changes that affect one type of age class or stage will also affect all similar age classes or stages. For example, any factor that changes the annual survival rate of Age-class 2 females is very likely to cause similar changes in the survival rates of other "adult" reproductive females (those in Age-class 3). Therefore, it is usually appropriate to assess the summed sensitivities for similar sets of transitions (vital rates). For this model, the result is that the sensitivity of λ to changes in first-year survival (440; 99.9 percent of total) is the most important. Because survival from the egg stage is so low (0.00074), even the smallest absolute change will have a large proportional effect. For this model, therefore the elasticities are likely to be a more useful guide.

Table A3. Parameter values for the component terms (P_i and m_i) that comprise the vital rates I the projection matrix for pearl dace.

Parameter	Numeric value	Interpretation
m_2 (eggs)	450	Number of female eggs produced by second-year females
m_3	1,859	Number of female eggs produced by third-year females
m_4	2,107	Number of female eggs produced by fourth-year females
m_5	2,120	Number of female eggs produced by fifth-year females
m_{21}	0.00074	Survival from egg through first year
m_{32}	0.61	Second-year survival
m_{43}	0.66	Third-year survival
m_{54}	0.36	Fourth-year survival
m_{65}	0.15	Fifth-year survival

Age-class	1	2	3	4	5	6
1		$P_{32}*m_2$	$P43*m_3$	$P54*m_4$	$P_{65}*m_5$	
2	P_{21}					
3		P_{32}				
4			P_{43}			
5				P_{54}		
6					P_{65}	

Figure A3a. Symbolic values for the matrix cells. The top row is fertility with compound terms describing survival of the mother (P_i) and egg production (m_i). Empty cells have zero values and lack a corresponding arc in **Figure A1**. Note that the last column of the matrix consists of zeros in order to allow tabulation of the (small) proportion of sixth-year individuals that just completed their final breeding pulse (and that will not survive to breed again).

Age-class	1	2	3	4	5	6
1		274.5	1,226.9	758.5	318	
2	0.00074					
3		0.61				
4			0.66			
5				0.36		
6					0.15	

Figure A3b. Numeric values for the projection matrix.

Figure A3. The input matrix of vital rates, **A** (with cells a_{ij}) corresponding to the pearl dace life cycle graph (**Figure A1**). a) Symbolic values. b) Numeric values.

Elasticity analysis

Elasticities are the sensitivities of λ to proportional changes in the vital rates (a_{ij}). The elasticities have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original vital rates (the a_{ij} arc coefficients on the graph or cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and age-classes as well as the relative importance of reproduction (F_i) and survival (P_i) for a given species. It is important to note that elasticity as well as sensitivity analysis assumes that the magnitude of changes (perturbations) to the vital rates is small. Large changes require a reformulated matrix and reanalysis.

Elasticities for pearl dace are shown in **Figure A4** and **Figure A5**. The λ of pearl dace was most elastic to changes in first- and second-year survival, followed by third-year fertility. Overall, survival transitions accounted for approximately 67.6 percent of the total elasticity of λ to changes in the vital rates. Survival, particularly in the first two years is the demographic parameter that warrants most careful monitoring in order to refine the matrix demographic analysis.

Other demographic parameters

The stable age distribution (SAD; **Table A1**) describes the proportion of each a-class in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SAD within 20 to 100 census intervals. For pearl dace at the time of the post-breeding annual census immediately after spawning (May or June), eggs should represent 99.8 percent of the population. Reproductive values (**Table A4**) can be thought of as describing the "value" of an age-class as a seed for population growth relative to that of the first (egg) age-class (Caswell 2001). The reproductive value is calculated as a weighted sum of the present and future reproductive output of an age-class discounted by the probability

Age-class	1	2	3	4	5	6
1		0	0	0	0	
2	440					
3		0.427				
4			0.126			
5				0.03		
6					0	

Figure A4. Possible sensitivities only matrix, $\mathbf{S}_p$ (remainder of matrix is zeos). The λ of pearl dace is overwhelmingly sensitive to changes in first-year survival. Censusing at a slightly later (larval stage would decrease this disproportionate emphasis of first year survival.

Age-class	1	2	3	4	5	6
1		0.065	0.177	0.072	0.011	
2	0.324					
3		0.259				
4			0.082			
5				0.011		
6					0	

Figure A5. Elasticity matrix, **E** (remainder of matrix is zeros). The λ of pearl dace is most elastic to changes in first-year and second-year survival (Cells e_{21} and e_{32}).

Table A4. Reproductive values for females. Reproductive values can be thought of as describing the "value" of an age-class as a seed for population growth, relative to that of the first (Age 0) age-class, which is always defined to have the value 1. Sixth-year females have no reproductive value because they have just reproduced for the last time and will not survive to breed again.

Age-class	Description	Reproductive values
1	First-year females (Age 0)	1
2	Second-year females	1,359
3	Third-year females	1,790
4	Fourth-year females	868
5	Fifth-year females	316
6	Sixth-year females	0

of surviving (Williams 1966). The reproductive value of the first age-class is, by definition, always 1.0. A second-year female (who will breed at the end of the census interval) is "worth" approximately 1,359 eggs. The cohort generation time for pearl dace is 3.1 years (SD = 0.7 years).

Potential refinements of the models.

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

Summary of major conclusions from matrix projection models

- First-year survival account for over 99 percent of total “possible” sensitivity. Any absolute changes in this rate will have major impacts on population dynamics.
- First- and second year survival accounts for 58.3 percent of the total elasticity, greater than the total of the elasticities for all the other transitions. Proportional changes in early survival will have major impacts on population dynamics.

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