Anthropogenic Changes in Biogeography of Great Basin Aquatic Biota

Donald W. Sada and Gary L. Vinyard

ABSTRACT

The Great Basin, the most arid region in North America, has small, widely spaced wetlands compared with those in more mesic regions. These wetland habitats generally support aquatic taxa that are widespread throughout North America. Recent work has complemented the studies of endemic fishes by Carl Hubbs and Robert Miller and has served to identify a diverse fauna of insects and mollusks endemic to the Great Basin. The presence of this fauna in comparatively small wetlands shows that habitat size is not a good indicator of the importance of these wetlands to unique biological communities.

Historical and current records show that anthropogenic activities during the last 120 years have modified the structure of Great Basin aquatic communities by altering habitats and by the translocation of species. Fifty nonnative fish taxa and several invertebrate taxa have been introduced into the region by the public and/or by fishery management agencies. Twenty-four fish taxa endemic to the Great Basin also have been translocated into habitats both within and outside of their native range. Most of these translocations were undertaken to create refuge populations and, thus, to reduce the possibility of extinction.

Within the Great Basin, introductions of nonnative species and habitat modification have caused the extinction of 16 endemic species, subspecies, or other distinctive populations (12 fishes, three mollusks, and one aquatic insect) since the late 1800s. Declines in abundance or distribution were attributable (in order of decreasing importance) to water flow diversions, competitive or predatory interactions with nonnative species, livestock grazing, introductions for sport fisheries management, groundwater pumping, species hybridization, timber harvest, pollution, recreation, and habitat urbanization. Most affected taxa were influenced by more than one of these factors.

The temporal pattern of decline in endemic taxa was examined by determining the calendar decades of first population loss, of major decline (loss of one-half of either a taxon's distribution or abundance), and of extinction for 199 endemic taxa (102 fishes, 85 mollusks, nine aquatic insects, two amphibians, and one fairy shrimp). Population loss has affected approximately 50 percent of taxa for which information was available (135 distinct taxa: 99 fishes, 24 mollusks, and all taxa in the three other aquatic animal groups), and 58 percent of these taxa have suffered major declines. Differences among rates of population loss, major decline, and extinction were not significant (ANCOVA, $p > 0.05$). Declines and extinctions were first recorded in the late 1800s. Rates peaked first after World War I and again in the 1970s after a long increase that began after World War II. Status was comparatively static during both World Wars. This pattern indicates that declines can be attributed to regional economic conditions and increased immigration. Declines slowed in the 1980s and 1990s because most taxa had previously declined, not because threats had diminished.

Declines during the last 120 years have been greatest in the most narrowly distributed and vulnerable populations. All extinct taxa and most taxa suffering major declines (68 percent) had fewer than five populations. If past trends continue into the future, additional extinctions will occur (primarily in narrowly distributed taxa), and extinctions also may begin to affect widespread taxa. These changes will accompany environmental change that characterizes consumption patterns of increasing human populations. Avoiding future changes in Great Basin biogeography that result from declines in taxon status will require new, innovative programs that protect wetland habitats from environmental degradation and the deleterious effects of nonnative species while allowing appropriate human uses of wetland resources.

Donald W. Sada, Division of Hydrologic Sciences, Desert Research Institute, 2215 Raggio Parkway, Reno, Nevada 89512-1095, USA. Gary L. Vinyard (deceased), formerly at the Department of Biology, University of Nevada, Reno, Nevada 89557, USA.

Reviewers: Robert Hershler, Division of Mollusks, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560-0118, USA; W. Ronald Heyer, Division of Herpetology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560-0162, USA; and two anonymous reviewers.

Introduction

The Great Basin, the driest physiographic province in North America, contains fewer small rivers, lakes, streams, springs, and marshes than do more mesic regions, and all of these waterbodies are more widely dispersed in the Great Basin than elsewhere. Aquatic communities in the region include species common to other North American wetlands as well as a diverse fauna of endemic fishes, mollusks, and aquatic insects predominantly associated with springs. Although these unique characteristic have long been recognized (Gilbert, 1893; Brues, 1932), recent surveys have revealed a surprisingly high diversity of additional endemic macroinvertebrates (e.g., Hershler and Sada 1987; Shepard, 1990; Hershler, 1998). We examine herein the major causes of historical change in biodiversity in an effort to understand the predominant ways in which anthropogenic uses of wetlands have affected Great Basin biogeography.

Humans have used Great Basin wetlands since the early Holocene (Janetski and Madsen, 1990). Intermittent settlement near wetlands and daily activities of hunting and gathering naturally tended to focus upon the biotic resources concentrated at these habitats. For a short period before the region was settled by European immigrants, a few indigenous tribes also diverted water to irrigate land and increase production of commonly eaten native plants. The Fremont Tribe diverted water from large rivers near the Wasatch Range (Madsen, 1989), and the Owens River basin Paiutes diverted streams from the east flank of the Sierra Nevada (Steward, 1933). Great Basin wetlands also produced food organisms, such as *Cyprinodon radiosus* (Owens pupfish), *Catostomus tahoensis* (Tahoe sucker), *Chasmistes cujus* (cui-ui), *Oncorhynchus clarki henshawi* (Lahontan cutthroat trout), *Gila bicolor* (tui chub), and *Ephydra hians* (brine fly), which were eaten by Paiutes along the eastern Sierra Nevada (Steward, 1933; Knack and Stewart, 1984). Excavation of sites known to have been inhabited by Fremont Tribe members revealed that their diet included *Catostomus ardens* (Utah sucker), *Gila atraria* (Utah chub), and *Oncorhynchus clarki utah* (a cutthroat trout subspecies) (Janetski, 1990). Greenspan (1990) also documented fish remains from archaeological sites in the Great Basin of Oregon, and Drews (1990) reviewed the dietary role of Great Basin shellfishes.

Although Native Americans used and altered Great Basin wetlands, the major anthropogenically induced changes to aquatic biogeography accompanied habitat alterations and introductions of nonnative taxa during the last 120 years. Since the beginning of the twentieth century, most rivers in the region have been dammed and diverted for irrigation, flood control, or power generation (La Rivers, 1962; Sigler and Sigler, 1987). Many springs and streams have been modified by livestock grazing, water flow diversion, and groundwater use (see Miller, 1961; Dudley and Larson, 1976; Fleischner, 1994). Native aquatic biota also have been affected by the introduction of 50 nonnative fish species for sport, pest management (Sigler and Sigler, 1987), and unspecified recreational or commercial interests (Moyle, 1984). Fisheries management agencies have enhanced nonnative sport fish populations by poisoning thousands of miles of streams, causing the consequent reduction or elimination of native fish and macroinvertebrate populations (Moyle et al., 1986; Rinne and Turner, 1991; Andersen and Deacon, 1996). These habitat modifications and introductions have caused the decline of many populations of native taxa and have driven some species to extinction (Minckley and Deacon, 1968; Williams et al., 1985; Miller et al., 1989; Minckley and Douglas, 1991).

The changing status of fishes and their habitats have been reported as discrete events affecting localized habitats or individual taxa (e.g., Williams et al., 1985; Williams et al., 1989; Moyle et al., 1995). The status of endemic invertebrates and the effects of human activities on smaller aquatic habitats (e.g., springs not occupied by native fishes) have not been examined in detail. We assess herein how habitat modifications and species translocations have affected Great Basin aquatic biogeography by altering the historical distribution of endemic species. This information was then used to examine the temporal pattern of past changes as a means of providing insight into potential future changes in the biogeography of aquatic animals endemic to the Great Basin.

Habitat and Biotic Diversity

Taxonomic studies during the last 140 years have consistently increased recognition of endemic plants and animals in Great Basin wetlands (see Hubbs and Miller, 1948a; Hershler, 1998). Although many taxa have been described, a number of additional populations may qualify for recognition as either endemic species or endemic subspecies (see Hubbs et al., 1974; Deacon and Williams, 1984; Sada et al., 1995; Hamlin, 1996). Recent descriptions of mollusks and insects (e.g., Hershler and Sada, 1987; Shepard, 1990; Hershler, 1998) indicate that additional undiscovered aquatic macroinvertebrates in Great Basin springs may exist. Currently, 118 species (two amphibians, 23 fishes, 84 mollusks, eight insects, and one fairy shrimp) and 45 subspecies (one aquatic insect and 44 fishes) are endemic to the Great Basin. We also studied 36 additional endemic forms that have been identified in published and unpublished reports as morphologically or genetically distinct. All of these described and undescribed forms will be collectively referred to herein as "distinctive taxa."

Distinctive taxa occupy a wide diversity of habitats including rivers, lakes, and streams, as well as cold and thermal springs (La Rivers, 1962; Sigler and Sigler, 1987; Hershler, 1998). Most of these taxa occupy habitats below 2200 m in elevation, where wetlands are most common and the historical use of water by humans has been greatest. Most distinctive taxa occupy specific habitats. Several taxa are primarily lentic but require lotic habitats for spawning (e.g., *Catostomus warnerensis, Chasmistes cujus, Chasmistes liorus*), and some continuously inhabit both lentic and lotic habitats (e.g., *Catostomus ardens, Richardsonius egregius*). Others only inhabit thermal springs (e.g., *Cyprinodon diabolis, Eremichthys acros, Gila boraxobius, Pyrgulopsis militaris*) or cold springs (e.g., *P. ruinosa, P. wongi*). *Cyprinodon radiosus* and *Iotichthys phlegethontis* occupy both lentic and spring habitats. Most endemic macroinvertebrates are restricted to springs, but several are lentic (e.g., *P. nevadensis, Capnia lucustra, Artemia monica*). The primary habitats of most distinctive taxa are springs (153 taxa), followed by lotic (18 taxa) and lentic (10 taxa) habitats; 10 taxa are lentic species that require lotic spawning habitat; and eight taxa are equally abundant in both springs and streams (see Appendix). Many habitats are occupied by a single endemic, and many habitats support several endemics. Communities with the highest diversity of endemics are concentrated in thermal springs of southern Nevada (e.g., Ash Meadows, Pahranagat Valley), which support endemic fishes, mollusks, and aquatic insects (Hershler and Sada, 1987; U.S. Fish and Wildlife Service, 1990; Polhemus and Polhemus, 1994; Hershler, 1998).

The unique aspects of these wetland communities are not limited to the aquatic animals inhabiting them. Great Basin wetlands of Nevada and southeastern Oregon also support 19 endemic plant species and five endemic plant varieties (Nevada Heritage Program Data Base, unpublished; Oregon Heritage Program Data Base, unpublished); four endemic vole subspecies—namely, *Microtus californicus vallicola* (Owens vole), *M. c. scirpensis* (Amargosa vole), *M. montanus fucosus* (Pahranagat vole), and *M. m. nevadensis* (Ash Meadows vole)—inhabit southern Nevada and southern California wetlands (Bailey, 1898; Hall, 1946). No endemic plants or mammals, however, are known from wetlands in the Utah portion of the Great Basin.

Introductions and Translocations

Many nonnative species have been introduced into North American waters, and these introductions have changed the structure of native vertebrate and invertebrate communities and caused extinctions of native biota through predation, hybridization, and competition (see Courtenay and Stauffer, 1984; Mooney and Drake, 1986; Moyle et al., 1986; Johnson and Padilla, 1996). Nonnative aquatic species in the Great Basin were introduced from other parts of North America and from Europe, Asia, Africa, and South America (Deacon and Williams, 1984; Sigler and Sigler, 1987). Many of these introduced species are now widespread, and most Great Basin fish assemblages are dominated by nonnative taxa. Deacon and Williams (1984) and Sigler and Sigler (1987) identified 50 nonnative fish taxa in the region, which exceeds the number of native Great Basin fish taxa (43 species). Most intentional introductions were made to accommodate the recreational sportfishing industry, but some fishes were introduced as biological control agents. Some fish species were released from home aquaria, and others escaped from commercial aquaculture facilities (Courtenay et al., 1985; U.S. Fish and Wildlife Service, 1997a).

Little is known about nonnative invertebrate introductions; several introduced species, however, have become widespread in the region, including *Procambarus* sp. and *Pacifastacus lenusculus* (crayfishes), *Corbicula manilensis* (Asian clam), and *Thiara* (=*Melanoides*) *tuberculata* (red-rimmed thiara, a snail). Crayfish introductions may have reduced refuge populations of *Cyprinodon radiosus* (U.S. Fish and Wildlife Service, 1998a); *T. tuberculata* may have contributed to declines in springsnail populations in southern Nevada (Hershler and Sada, 1987); and the disappearance of *Anodonta californica* (California floater, a bivalve mollusk) from the Owens River basin may have been caused by *Corbicula manilensis*. Disappearance of *Daphnia* sp. (ostracode) from Lake Tahoe is attributed to the introduction of *Mysis relicta* (oppossum shrimp) (Richards et al., 1975; Morgan et al., 1978).

No private or state programs exist to translocate endemic Great Basin macroinvertebrates or amphibians, and no records indicate that these species have been translocated. However, several state and Federal programs have actively translocated 24 endemic Great Basin fishes into refuges both within and outside of their native ranges (Appendix). Most fishes were translocated to expand their distributions and minimize threats, thus reducing the possibility of extinction. Other translocations were conducted to enhance sportfishing opportunities (e.g., *Oncorhynchus clarki henshawi*). Some species were established in single refuges whereas others have been broadly introduced (e.g., *O. c. henshawi* into 33 refuges). Some of these translocations probably prevented imminent extinction (e.g., *Cyprinodon radiosus, Empetrichthys latos latos* (Pahrump poolfish), and *Crenichthys baileyi grandis* (Hiko White River springfish).

Refuge populations may influence biogeography in several ways. They may expand distributions and confound future biogeographic interpretations. Also, many refuges have been established with very few individuals, which presumably represents a comparatively small portion of the genome of the species. These factors suggest that caution should be used when interpreting biogeographic information accumulated from refuge populations. In addition, refuge construction may adversely affect other native taxa. Hershler (1989) reported that *Pyrgulopsis perturbata* (Fish Slough springsnail) disappeared from a spring that had been impounded to create a refuge for *Cyprinodon radiosus*. Effects of refuge development probably have been greatest when construction modified a previously unaltered habitat (e.g., channelized or impounded spring brooks), thus causing functional changes in the aquatic ecosystem's community structure.

Status Changes

We sought to determine the extent of decline for all aquatic taxa endemic to the Great Basin. Status information was gathered from personal communications and from approximately 100 published and unpublished survey reports (undertaken within the private sector and by federal and state agencies) written during the last 120 years. Early records were first prepared before widespread settlement of the region (Frémont, 1845; Beckwith, 1855; Merriam, 1893; Davidson, 1976), and they frequently have been used to compare historical and current distributions of most taxa. Distributional information was also gathered from early taxonomic surveys (e.g., Gilbert, 1893; Hubbs and Miller, 1948a). Most information provided by early records is less comprehensive than that from contemporary records, which frequently describe demography and distribution of extant populations. Early records, however, usually provide baseline distributional information that can be effectively contrasted with current distributions.

For each distinctive taxon, we identified the year in which taxonomic distinction was initially recognized. We then sought to determine the calendar decade(s) in which three possible levels of decline had occurred (if any): the first population loss (loss of first population, i.e., reduced distribution and absolute abundance), a decrease in historical distribution or absolute abundance by at least one-half (a "major decline"), and extinction. Factors that affected the status of each taxon (i.e., threats, when known) were also identified.

All known distinctive aquatic taxa in the Great Basin were considered: 102 fishes, 85 mollusks, nine aquatic insects, two amphibians, and one fairy shrimp. Status surveys, however, had not been conducted for all distinctive taxa (surveys have assessed the status of few recently described taxa), thus status could be reviewed for only 135 taxa—99 fishes, 24 mollusks, and all taxa in the three other aquatic animal groups. By determining the year that each distinctive taxon was identified, we could assess the relationships between changes in status and taxonomic recognition. These dates often predated formal taxonomic descriptions, and they were selected for analysis because Federal and state agencies frequently have initiated status surveys soon after distinctive populations were identified. Relationships between status changes and recognition of distinction may facilitate our understanding of temporal trends in status change. Positive correlation between these factors may indicate that status changes occur quickly after recognition of distinctive taxa. Either a negative correlation or the absence of correlation may suggest that decline rates occur sporadically, regardless of when distinctivenes is recognized. Data for each distinctive taxon are summarized in the Appendix.

The information provided by these records has limitations. Surveys usually have been qualitative, and status changes are rarely quantified. It is also difficult to precisely identify when populations disappeared or declined because surveys have been sporadic as a result of budget limitations and changing agency priorities. Taxonomic studies have also revealed many endemic taxa (approximately 90 mollusks and aquatic insects since 1990) that were uncollected and undescribed until recently (e.g., Shepherd, 1992; Hamlin, 1996; Hershler, 1998). Many of these populations occupy springs that are in poor condition, and traditional human uses of these wetlands have caused several taxon extinctions and population losses in the last five years (Sada and Nachlinger, 1996; Hershler, 1998). Although it is not possible to determine how many extinctions of uncollected taxa have occurred, recent extinctions and population losses suggest that current status information may underestimate the total number of historical Great Basin extinctions. Despite of these limitations, adequate status information was obtained for a sufficient number of taxa such that a meaningful analysis could be conducted.

The status reports identified 10 factors (threats) that influenced abundance and distribution of distinctive endemic aquatic taxa: water flow diversions (affected 90 taxa), nonnative species (78 taxa, which include introductions for fisheries management purposes as well as other other nonnative taxa; e.g., Asian clam and crayfishes, mentioned above in "Introductions and Translocations"), livestock grazing in riparian zones (54 taxa), introductions for sportfisheries management (33 taxa), groundwater pumping (17 taxa), hybridization of species (eight taxa), timber harvest (four taxa), pollution and recreation (three taxa each), and urbanization of habitat (two taxa). Most affected taxa were influenced by more than one factor: two affected 37 taxa, three affected 26 taxa, four affected 12 taxa, and five affected five taxa, whereas 67 taxa were affected by only one factor. This suggests synergistic effects may affect status changes—e.g., the combined effects of degraded habitats and nonnative species on endemic taxa may be greater than the summed effect of individual threats (Moyle and Light, 1996). Nonnative species, water flow diversions, and groundwater use caused most extinctions, whereas livestock grazing and pollution each caused a single extinction. All extinct taxa and most (68%) of the taxa experiencing major decline were narrowly distributed within the Great Basin (<5 populations each); this indicates that taxa with limited distribution are acutely vulnerable to catastrophic changes in status.

Sixty-eight distinct taxa (50% of those reviewed) lost at least one population during the last 140 years, 78 experienced a major decline (58%), and 16 became extinct. Only 28 taxa maintained what is believed to be their approximate historical abundance and distribution. Incidences of first population loss, major decline, and extinction occurred irregularly throughout the period of record (Figure 1). Rates of decline increased and decreased three times since the late 1800s; however, differences among the rates of population loss, major decline, and extinction from the late 1800s through the late 1990s were not significant (analysis of covariance (ANCOVA): slopes, $p > 0.05$; regression, $p < 0.05$), indicating that changes in these rates followed similar temporal trends. The first rate increase began before the turn of the twentieth century, another began during the early decades after the turn of the century, and the third began during the 1950s. Decline rates peaked sharply and then leveled off somewhat for several decades. Both the frequencies of increasing decline rates and amplitudes of the three rates increased with time, indicating that periods of rapid declines have become more frequent.

Several factors may explain general trends in the changes of status. Increases in the rates of decline appear to coincide with periods of human population expansion and economic growth. Status declines were most rapid during the 1890s, 1930s, and 1970s—periods that are associated (respectively) with the greatest revenues from mining and completion of the transcontinental railroad in the late 1800s (Hulse, 1991), the population expansion before the Great Depression, and the growing economy prior to the 1970s recession. Conversely, rates of decline

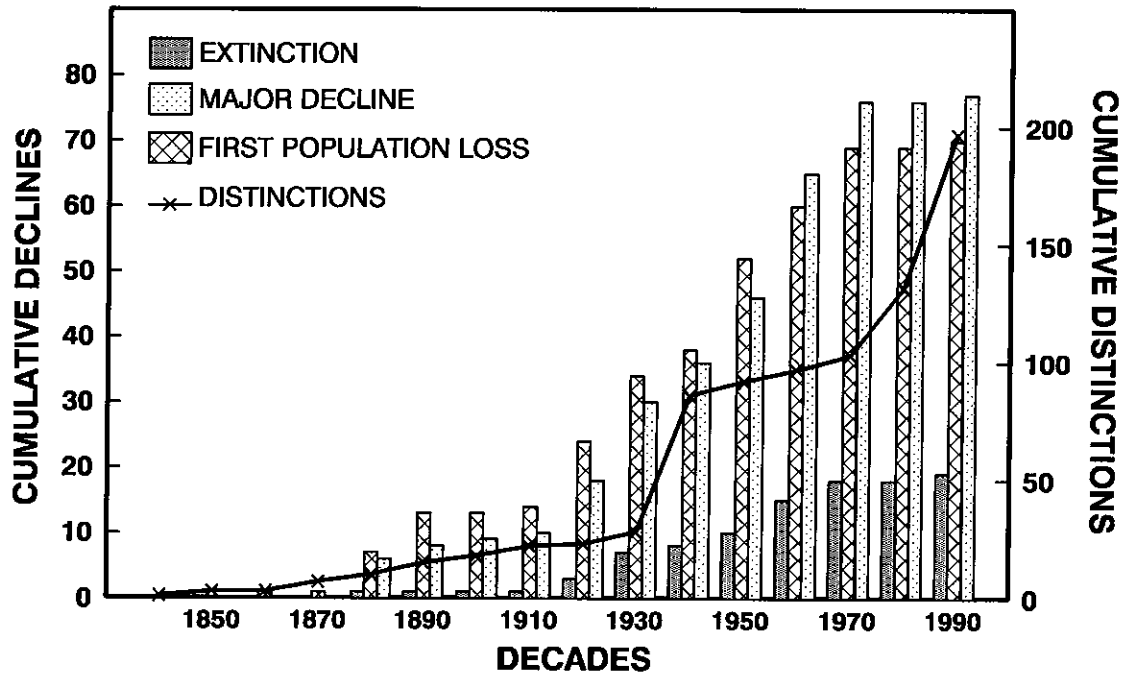

FIGURE 1.—Cumulative percent decline (by calendar decade) of aquatic animals endemic to the Great Basin since the 1850s, as shown by percent of taxa affected by first population loss, major decline (a decrease in historical distribution or abundace by at least one-half), and extinction. Differences among rates of first population loss ($y = 0.516x - 967.0$, $r^2 = 0.88$), major decline ($y = 0.587x - 1101.8$, $r^2 = 0.87$), and extinction ($y = 0.143x - 268.4$, $r^2 = 0.84$) are not significant. "Cumulative distinctions" illustrate the cumulative increases (by decade) in the identifications of 199 endemic taxa determined in published and unpublished taxonomic studies to be distinct within the Great Basin. See "Status Changes" in the text for a description of distinctive taxa.

were slowest during the period before the region was actively settled (pre-1850), during the second decade of the twentieth century (during World War I), and in the 1940s (during World War II). During the last century, status was most stable during both World Wars, when the national economy focused on armament production and when immigration was constrained by fuel shortages and rationing. After World War II, status declines increased through the 1970s to an unprecedented level, and most taxa known in 1980 had either lost one population (68 taxa) or suffered major decline (78 taxa). Rates of decline slowed again during the 1980s and 1990s. This decrease in the decline of taxa coincides with enactment of environmental legislation (i.e., Endangered Species Act, Clean Water Act, National Environmental Policy Act, and many similar state statutes) and with initiation of many state, Federal, and private conservation programs, which seems to suggest these programs are successful. It is problematic, however, to attribute these decreases solely to conservation programs because most distinctive taxa had already declined before these decades, leaving a comparatively smaller portion of endemic taxa to suffer their first population loss and/or major decline. In the future, major declines and the first population loss of a taxon will be recorded mostly for newly discovered taxa. Nonetheless, the high number of extant taxa (199 distinct forms) compared with the numbers of distinct taxa having lost a population (68) and having undergone major decline (78) suggests that these conservation programs may have lowered the extinction rate.

Discussion

Composition and distribution of Great Basin aquatic communities, and the patterns of human resource use, both reflect the influence of regional aridity. Although Great Basin wetlands are small and isolated, they provide most of the water in a dry region and they contain a more diverse flora and fauna than other habitats (Thomas et al., 1979; Brode and Bury, 1984). Riparian vegetation provides nesting, roosting, and migratory habitat for resident and migratory birds and provides food and cover for mammals. Importance of these wetlands to terrestrial wildlife and to the endemic aquatic fauna shows that even small aquatic habitats are important to Great Basin biodiversity. Water has also been a focus for human activities in the Great Basin. Hunter-gatherers frequently placed their settlements near rivers, marshes, and springs (Fowler and Fowler, 1990), and all of the largest contemporary cities are proximal to large water resources (e.g., the Humboldt, Carson, and Truckee Rivers, Utah Lake, etc.).

Anthropogenic use has affected terrestrial and aquatic ecosystems in many ways. Hypotheses relating the extinction of mammals and birds to the arrival of humans approximately 10,000 years ago suggest that some declines were attributed to human predation or climate change (Martin, 1990; Grayson, 1991). A thorough assessment of these impacts is beyond the scope of this paper, and additional evidence is needed to better understand how humans effected Holocene biotic changes in the Great Basin. However, information compiled during the last 120 years shows that historical status declines and extinctions began soon after the region was first settled by European immigrants. Evidence that the impacts of recent human activities on biogeography greatly exceeded those of hunter-gatherers is indicated by archaeological and fossil records and by taxonomic studies.

Wetlands have continuously provided important resources for humans in the Great Basin. Hunter-gatherers did not live in permanent settlements because food resources were frequently scarce and movement was necessary to maximize foraging opportunities that changed seasonally. In wet years, they utilized higher elevations to harvest piñon (*Pinus monophylla* and *P. edulis*) nuts. When food was scarce (e.g., during droughts) they temporarily settled near wetlands (Yellen, 1977; Fowler and Fowler, 1990). Springs and marshes bordering pluvial lakes supported small animals, tubers, and seeds that were foods unavailable in other places (Janetski and Madsen, 1990). Halford (1998) identified a number of edible plant species (e.g., currant, *Ribes* sp.; elderberry, *Sambucus* sp.; and wild rose, *Rosa woodsii*) from pack-rat middens that were located near small springs and an ephemeral lake in the west central Great Basin.

Hunter-gatherers affected endemic aquatic taxa by manipulating habitats and by harvesting fish and shellfish. It is difficult to assess the effects that these activities had on Great Basin biogeography because little information exists that indicates the response of aquatic taxa to human activities. Mehringer and Warren (1976) found that fire was used periodically to clear mesquite (*Prosopis* spp.) bosques and to increase food availability in Ash Meadows, a spring province in southern Nevada. Although fire may dramatically affect riparian vegetation, and fish populations have been extirpated by fire in the southwest (Rinne, 1996), little information suggests that it has been a major cause of extinction. Scoppettone et al. (1998) observed declines in native fish abundances after a fire along spring brooks in southern Nevada, but no extinctions were documented and populations soon recovered to preburn levels. The minimal impact of fire on Great Basin macroinvertebrates was also indicated by the presence of large populations of the springsnail *Pyrgulopsis gibba* in a small, recently burned spring in northern Nevada (Sada, field notes, 1996). Owens Basin Paiutes and the Fremont Tribe manipulated aquatic habitats by diverting streams for irrigation to increase the abundance of edible native vegetation (Steward, 1933; Madsen, 1989). These activities may have affected aquatic taxa by drying streams and by creating barriers that interrupted spawning migrations. The amount of habitat affected by these activities and the abundance and wide distribution of taxa affected by these diversions during early taxonomic surveys indicate that these activities did not cause extinction.

A number of Native American tribes also harvested shellfishes and endemic fishes (Steward, 1933; Knack and Stewart, 1984; Drews, 1990; Greenspan, 1990; Janetski, 1990). The abundance of shellfishes and endemic fishes among midden fossils (Dansie, 1990; Greenspan, 1990; Janetski, 1990; Schmitt and Sharp, 1990) suggests that hunter-gatherers actively harvested aquatic taxa. Harvesting did not cause extinction because the midden fossils are all extant taxa that also were collected during initial taxonomic surveys. The occurrence of extinct taxa in middens would suggest that harvesting or other Holocene events caused extinction. There can be little doubt that harvest and habitat manipulation by hunter-gatherers affected the abundance of aquatic taxa and that similar manipulations since the beginning of the twentieth century have extirpated many populations of aquatic taxa within the Great Basin (Minckley and Deacon, 1968; Williams et al., 1985; Miller et al., 1989; Hershler, 1998); however, no evidence documents extirpations that may have been caused by hunter-gatherer harvesting and habitat manipulations. Early Holocene extinctions of aquatic species are not likely attributable to hunter-gatherers because of their transitory settlement behavior, their limited ability to manipulate large amounts of aquatic habitat, and the large size of habitats that supported harvested populations. Although hunter-gatherers affected the abundance of some endemic aquatic species, it is unlikely that their activities extensively affected aquatic biogeography.

Biogeography could have been affected by hunter-gatherers who transported aquatic species outside of their native range, thus establishing new populations. Translocations may have been inadvertent (e.g., accidental captures in water containers when settlements were moved) or intentional. Effects of these translocations on biogeography are also difficult to determine, but their possible influence is indicated by several factors. If movement was accidental, a wide diversity of taxa (e.g., fishes, mollusks, and aquatic insects) would have been involved because endemic aquatic species occupy many aquatic habitats that would have been encountered because of the transitory lifestyle of hunter-gatherers. These taxa could have been accidentally captured in water jugs or carried in moist clothing and moved to new locations. Intentional translocations would have served a purpose such as broadening the distribution of food fishes, which suggests that a small number of taxa would have been selected. If intentional translocations were common, it is doubtful that they were limited to intrabasin movements. Interbasin translocations from the diverse fish assemblages in surrounding basins (e.g., Colorado River, Klamath River, Sacramento River, and Columbia River basins) would have been likely, and representatives of these faunas would have been recorded in the Great Basin during the early biological surveys.

Evidence that hunter-gatherers translocated aquatic taxa is equivocal. Unintentional capture and movement was highly probable for some taxa, but establishment of viable populations would have been less likely because of differences among aquatic habitats (e.g., water chemistry, water temperature, current velocity, etc.) and competitive interactions that discourage colonization. Translocation of springsnails would have been unlikely; they can persist for several hours in moist, cool conditions but do not appear to survive by rapidly acclimating to waters with chemistries different from their founder habitat (Sada, unpublished data). Unintentional fish translocations likely would have been infrequent because of fish requirements for adequate water and tolerable temperatures and dissolved oxygen concentrations. Water quality differences also may have limited aquatic insect translocation. If unintentional translocation had been common, interbasin genetic differences between populations could not be easily detected and there would be little pattern that could be described by pluvial-period interbasin connectivity.

Evidence for intentional translocations is also weak. Most aquatic taxa of the Great Basin were either too small or too scarce to be used by hunter-gatherers; this suggests that movement of larger fish and invertebrates (e.g., California floater *Anodonta californica*) was more likely. The paucity of large Great Basin taxa also indicates that the efficacy of translocation would have been enhanced if species had been brought in from surrounding basins. There is little evidence, however, that intentional movement was common; the distribution of endemic taxa within the Great Basin can usually be explained by models describing the fluvial connectivity of basins during the Pleistocene (Echelle and Dowling, 1992; Smith, 1992; Hamlin, 1996), and the Great Basin fish fauna has few taxa in common with surrounding basins. Many aquatic species in the Great Basin instead are derived from ancestral taxa occupying surrounding basins (Smith, 1978; Minckley et al., 1991).

Unassisted entrance of aquatic taxa into the Great Basin is shown by the fossil record. Pliocene and Miocene fish and mollusk fossils indicate past connectivity between the Great Basin and its surrounding basins (e.g., Miller and Smith, 1981; Smith, 1981; Taylor and Smith, 1981; Taylor, 1985). Firby et al. (1997) recorded bones of *Oncorhynchus* (trout) and *Catostomus* (subgenus *Pantosteus*) (sucker) from 695,000–725,000 year-old sediments in Owens Lake, California. Neither of these taxa inhabit the Owens Basin today, but closely related taxa are found in the Lahontan Basin to the north and in coastal drainages of southern California (Smith, 1966). Past occurrence and extirpation of these fishes before the arrival of humans indicates that these fish moved into the Great Basin during pluvial periods and became extinct without the influences of hunter-gatherer activity.

European immigrants had an immediate effect on Great Basin aquatic biogeography when they first settled the region during the nineteenth century. Expansion of the livestock industry, which began in the middle 1800s, resulted in some of the first disturbances of many aquatic habitats and riparian communities (Davis, 1977; Mack, 1981). Introductions of nonnative fishes also began in this period, when interest in sportfishing accompanied the expanding population that pursued the silver and gold mining bonanzas then underway (Hulse, 1991; Dill and Cordone, 1997). The resulting effects on biogeography were greater than those caused by hunter-gatherers, because the settlers used technologies that caused large-scale habitat modifications (e.g., pipes, dredging, dams, impoundments) and they introduced species from throughout the world. As a result, many existing wetlands probably bear little resemblance to their condition prior to settlement by the European Americans and immigrants. Water flow diversion and introduced species have degraded most large wetlands, whereas smaller habitats—streams and springs—have been perturbed by water diversion and riparian zone trampling that accompanies pastoral activities. These changes have reduced the distribution and abundance of most endemic aquatic taxa and the aquatic biodiversity within the Great Basin.

Historical declines in Great Basin endemic aquatic taxa can be attributed to a comparatively small number of factors (e.g., water diversion, livestock use, and introduction of nonnative species). The scarcity of proposals for ecologically beneficial changes in future land use, the increasing demands for water, and the changes in abundance and distribution of most endemic species during the last 100 years all indicate that these factors can be expected to cause additional extinctions (primarily in narrowly distributed taxa) and changes in biogeography. Continued declines in abundance and distribution may begin to affect widespread taxa as well, which will limit our ability to interpret pluvial climates and interbasin connectivity; and a natural laboratory will be eliminated wherein the ecology, diversity, and speciation of the aquatic fauna within the Great Basin—almost 20 percent of the area of the United States—can be examined.

The small size of most Great Basin wetlands and the small number of activities causing status declines indicate that stopping the losses of aquatic taxa does not require substantial funding or a large commitment of natural resources. Conserving these habitats requires innovative programs to allow reasonable human uses of wetland areas while protecting Great Basin aquatic ecosystems from further degradation. To meet this challenge, land and resource management strategies must be developed that will allow use of resources while conserving Great Basin biota. This can be accomplished only by increasing ecological knowledge of endemic species and by using this information to create innovative techniques that allow wetland use by humans while providing for conservation of fauna and flora unique to the Great Basin. Experimental work that examines interactions between native and exotic macroinvertebrates is also needed to determine mechanistic causes for interactions between native aquatics and nonnative invertebrates so that effective conservation strategies can be developed.

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Appendix

Primary Habitat and Status of Known Distinctive Aquatic Biota in Great Basin Wetlands

Distinct biota are either described taxa or potential, undescribed taxa whose morphological or genetic distinctiveness has been recognized in published or unpublished reports. Potential taxa are identified by their geographic location in quotes after the taxon name. In parentheses are numbers of translocated populations (if known). The year distinctiveness was first recognized (Distinct); the calendar year or decades of first population loss (First Loss), major decline, and extinction; and the anthropogenic activities causing status change (Threats) are shown for each form. A dash (–) indicates no population loss, major decline, extinction, or threats are known. Threats: 1 = livestock grazing, 2 = nonnative species introduction, 3 = sport fisheries management, 4 = water diversion, 5 = groundwater pumping, 6 = urbanization, 7 = hybridization, 8 = timber harvest, 9 = pollution, 10 = recreation. A question mark (?) denotes instances in which population translocation, status change, or threats are probable but existing information is insufficent for an accurate assessment.

Distinct biota	Habitat	Distinct	First loss	Major decline	Extinct	Threats	References
Amphibians							
Bufo exsul	Spring	1942	–	–	–	1	Szewczak, 1997
Bufo nelsoni	Spring	1893	1980	1980	–	1,2,4	Altig, 1981; Maciolek, 1983; Hoff, 1993; Heinrich, 1996
Fishes							
Catostomus ardens	Lotic/Lentic	1881	1930	–	–	4	Kershner, 1995
Catostomus clarki intermedius	Lotic	1942	1960	1960	–	2,3,4	Courtenay et al., 1985
Catostomus clarki 'Meadow Valley'	Lotic	1948	1950	–	–	2,4	Hubbs and Miller, 1960; Stein, 1997
Catostomus fumeiventris (4)	Lotic	1948	?	1940	–	1,2,3,4	Moyle et al., 1995; USFWS, 1998a
Catostomus occidentalis lacusanserinus	Lotic/Lentic	1948	1940	1940	–	1,2,4,8	J.E. Williams, pers. comm., 1996
Catostomus platyrhynchus lahontan (?)	Lotic	1903	–	–	–	2,3,4	Decker, 1989
Catostomus platyrhynchus platyrhynchus	Lotic	1874	1900	–	–	3,4	Kershner, 1995
Catostomus tahoensis (?)	Lotic/Lentic	1878	1900	–	–	1,2,3,4	La Rivers, 1962
Catostomus warnerensis (1)	Lotic/Lentic	1908	1940	1940	–	1,2,3,4,8	Andraesen, 1975; Kittredge, 1987; Williams et al., 1990
Catostomus 'Wall Canyon'	Lotic	1948	?	?	–	2	Hubbs and Miller, 1948a; Heinrich, 1993
Chasmistes cujus	Lotic/Lentic	1883	–	1930	–	2,3,4,6	Scoppettone and Vinyard, 1991; USFWS, 1992
Chasmistes liorus liorus	Lotic/Lentic	1981	1900	1930	1930	2,3,4	Sharp, 1905; Miller and Smith, 1981
Chasmistes liorus mictus (3)	Lotic/Lentic	1981	–	1950	–	2,3,4	Sharp, 1905; Miller and Smith, 1981; Kershner, 1995
Cottus bairdi 'Mahleur'	Lotic	1948	1960	1940	–	1,2,4,8	Bond, 1974; C.E. Bond, pers. comm. with J.E. Williams, 1996
Cottus echinatus	Lentic	1963	1890	1900	1930	2,4	Heckman et al., 1981; Miller et al., 1989
Cottus extensus (1)	Lentic	1963	–	–	–	–	Sharp, 1905; Holden et al., 1996
Cottus pitensis	Lotic	1963	1940	1890	–	1,2,8	Oregon Department of Wildlife files, 1992
Crenichthys baileyi albivallis	Spring	1981	1970	–	–	1,2,3	Williams and Wilde, 1981; Courtenay et al., 1985
Crenichthys baileyi baileyi (1)	Spring	1981	–	1960	–	1,2,4	Williams and Wilde, 1981; Courtenay et al., 1985; USFWS 1998b
Crenichthys baileyi grandis (1)	Spring	1981	1960	1960	–	1,2,3	Williams and Wilde, 1981; Courtenay et al., 1985; USFWS 1998b
Crenichthys baileyi moapae	Spring	1981	1960	–	–	2,4,5	Williams and Wilde, 1981; Courtenay et al., 1985
Crenichthys baileyi thermophilus	Spring	1981	1960	–	–	2,3,4	Williams and Wilde, 1981; Courtenay et al., 1985; Heinrich, 1993
Crenichthys nevadae (4)	Spring	1932	–	1980	–	2,3,4	Williams and Williams, 1981; USFWS, 1997a
Cyprinodon diabolis (2)	Spring	1930	1970	1970	–	5	Deacon, 1979; Heinrich, 1993
Cyprinodon nevadensis amargosae (3)	Spring	1948	–	–	–	2,4	Moyle et al., 1989; Sada et al., 1997
Cyprinodon nevadensis calidae	Spring	1948	1950	1950	1970	4,7	Miller et al., 1989; Moyle et al., 1995
Cyprinodon nevadensis mionectes (2)	Spring	1948	1960	1970	–	2,4,5	Williams and Sada, 1985; Scoppettone et al., 1995
Cyprinodon nevadensis nevadensis	Spring	1948	–	–	–	–	Deacon and Deacon, 1979; Sada et al., 1997

APPENDIX.—Continued.

Distinct biota	Habitat	Distinct	First loss	Major decline	Extinct	Threats	References
Fishes (continued)							
Cyprinodon nevadensis pectoralis	Spring	1948	1970	–	–	2	USFWS, 1976; Soltz and Naiman, 1978; Scoppettone et al., 1995
Cyprinodon nevadensis shoshone	Spring	1948	1940	1960	1960	2,4	Taylor et al., 1988; Moyle et al., 1995
Cyprinodon radiosus (4)	Spring/Lotic	1948	1930	1940	–	2,4	Miller, 1948; 1961; Miller and Pister, 1971; USFWS, 1998a
Cyprinodon salinus milleri	Spring	1972	–	–	–	–	LaBounty and Deacon, 1972; Sada and Deacon, 1995
Cyprinodon salinus salinus	Spring	1943	–	–	–	–	Miller, 1943; Sada and Deacon, 1995
Empetrichthys latos concavus	Spring	1948	1940	1950	1950	5	Miller, 1948; Sokol, 1954; Miller, 1961
Empetrichthys latos latos (3)	Spring	1948	1970	1970	–	2,5	Miller, 1948; Minckley and Deacon, 1968
Empetrichthys latos pahrump	Spring	1948	1940	1950	1950	5	Miller, 1948; Sokol, 1954; Miller, 1961
Empetrichthys merriami	Spring	1893	1930	1930	1950	2,5	Miller, 1948; Sokol, 1954; Miller, 1961; Miller, 1969
Eremichthys acros	Spring	1948	–	–	–	1,4	Hubbs and Miller, 1948b; Vinyard, 1996; USFWS, 1997b
Gila alvordensis	Spring/Lotic	1972	1960	–	–	1,2,4	Williams and Bond, 1983
Gila bicolor euchila	Spring	1948	–	1970	–	1,2,3,4	Hubbs et al., 1974; Baugh et al., 1986
Gila bicolor eurysoma	Spring	1948	–	1890	–	1	Williams et al., 1980; Williams and Bond, 1981
Gila bicolor isolata	Spring	1948	–	1970	–	1,2,4	Hubbs et al., 1974; Vinyard, 1984; Heinrich, 1993
Gila bicolor mohavensis	Lotic	1938	1930	1940	–	2,4,7	Hubbs and Miller, 1943; USFWS, 1984
Gila bicolor newarkensis	Spring	1948	1950	–	–	1	Hubbs et al., 1974; Hardy, 1980; Haskins, 1996
Gila bicolor obesa	Lotic	1856	1890	1940	–	1,2,3,4	La Rivers, 1962; Snyder, 1917a
Gila bicolor oregonensis	Spring/Lotic	1977	–	1890	–	1,4	Bills, 1977; J.E. Williams, pers. comm., 1997
Gila bicolor pectinifer	Lentic	1917	–	–	–	3,4	La Rivers, 1962
Gila bicolor snyderi (3)	Lotic	1948	1940	1940	–	2,3,4,7	Snyder, 1917b; Miller, 1973; USFWS, 1998a
Gila bicolor vaccaceps	Spring	1948	–	–	–	1,4	Bills and Bond, 1980; Moyle et al., 1995
Gila bicolor 'Big Smokey Valley'	Spring	1948	1960	1980	–	1,2,5	Deacon and Pedretti, 1984; Pedretti et al., 1987
Gila bicolor 'Blue Eagle Spring'	Spring	1948	1970	1970	–	4	J.R. Stein, pers. comm., 1997
Gila bicolor 'Bull Creek'	Spring	1948	–	–	–	–	D.W. Sada, field notes, 1995; J.R. Stein, pers. comm., 1997
Gila bicolor 'Butterfield Spring'	Spring	1948	–	–	–	–	J.R. Stein, pers. comm., 1997
Gila bicolor 'Catlow Valley'	Spring	1948	–	1890	–	1,4	Bills, 1977; J.E. Williams, pers. comm., 1997
Gila bicolor 'Diamond Valley'	Spring	1948	?	?	–	?	Hubbs et al., 1974
Gila bicolor 'Dixie Valley' (2)	Spring	1948	–	–	–	2	Rissler et al., 1991; Vinyard, 1994
Gila bicolor 'Eagle Lake'	Spring	1943	–	1910	–	2,3	Kimsey, 1954; Moyle et al., 1991
Gila bicolor 'Fish Lake Valley'	Spring	1948	1960	1980	–	2,3	D.W. Sada, field notes, 1993
Gila bicolor 'Green Springs'	Spring	1948	–	–	–	–	D.W. Sada, field notes, 1995; J.R. Stein, pers. comm., 1997
Gila bicolor 'High Rock'	Spring	1948	1980	1980	1980	2	Moyle, 1993
Gila bicolor 'Hot Creek Valley'	Spring	1948	1970	–	–	1	J.R. Stein, pers. comm., 1997
Gila bicolor 'Hutton Spring'	Spring	1948	–	–	–	–	Bills, 1977; J.E. Williams, pers. comm., 1997
Gila bicolor 'Kate Springs'	Spring	1948	–	–	–	–	J.R. Stein, pers. comm., 1997
Gila bicolor 'Little Fish Lake Valley'	Spring	1948	–	–	–	–	J.R. Stein, pers. comm., 1997
Gila bicolor 'Pleasant Valley'	Spring	1948	1970	1980	–	2,3	Nevada Division of Wildlife files, 1995
Gila bicolor 'Railroad Valley'	Spring	1948	–	–	–	1,2,3	Williams and Williams, 1981
Gila bicolor 'Summer Valley'	Spring	1948	1930	1960	–	1,2,3,4,7	Bills, 1977; J.E. Williams, pers. comm., 1997
Gila boraxobius (1)	Spring	1980	–	–	–	5	Williams and Bond, 1980; 1983; USFWS, 1987
Gila robusta jordani (1)	Spring	1950	1960	1940	–	2,4	Courtenay et al., 1985; USFWS, 1986, 1998b
Iotichthys phlegethontis (1)	Spring/Lotic	1874	1900	1900	–	2,3,4,6	Kershner, 1995; USFWS, 1995a
Lampetra tridentata 'Goose Lake'	Lentic	1948	–	1940	–	2,4	J.E. Williams, pers. comm., 1997
Lepidomeda albivallis	Spring/Lotic	1960	1960	1970	–	2,4,9	Courtenay et al., 1985; Scoppettone et al., 1992; USFWS, 1994
Lepidomeda altivelis	Spring	1960	1930	1930	1940	2,3,4	Hubbs and Miller, 1960; Miller et al., 1989
Lepidomeda mollispinis pratensis (1)	Spring/Lotic	1960	1950	1950	–	2,4	Hubbs and Miller, 1960; USFWS, 1993
Oncorhynchus clarki henshawi (33)	Lotic	1845	1890	1930	–	1,2,3,4,7	Sumner, 1940; Behnke, 1992; USFWS, 1995b
Oncorhynchus clarki seleniris (4)	Lotic	1933	1920	1920	–	1,2,7	USFWS, 1985; Behnke, 1992
Oncorhynchus clarki utah (23)	Lotic/Lentic	1874	1870	1910	–	1,2,3,4	Kershner, 1995; Duff, 1996; Holden et al., 1996
Oncorhynchus clarki 'Alvord'	Lotic	1934	1890	1890	1940	1,2,3,4,7	Williams and Bond, 1983; Miller et al., 1989; Behnke, 1992
Oncorhynchus clarki 'Humboldt' (?)	Lotic/Lentic	1978	1890	1930	–	1,2,3,4,7	Behnke, 1992; USFWS, 1995b
Prosopium abyssicola	Lentic	1919	–	–	–	–	Sigler and Sigler, 1987
Prosopium gemmifer (1)	Lentic	1919	–	–	–	–	Sigler and Sigler, 1987
Prosopium spilonotus	Lentic	1919	–	–	–	–	Sigler and Sigler, 1987
Relictus solitarius (4)	Spring	1948	1930	1930	–	2,3	Hubbs et al., 1974; Stein and Salisbury, 1994; Haskins, 1995
Rhinichthys osculus lariversi	Spring	1972	–	–	–	1	Pedretti et al., 1987
Rhinichthys osculus lethoporus	Spring	1948	–	1970	–	2,4	Hubbs et al., 1974; Vinyard, 1984
Rhinichthys osculus nevadensis	Spring/Lotic	1893	1971	1970	–	2,4,5	Williams and Sada, 1985; USFWS, 1990; Scoppettone et al., 1995

APPENDIX.—Continued.

Distinct biota	Habitat	Distinct	First loss	Major decline	Extinct	Threats	References
Fishes (continued)							
Rhinichthys osculus oligoporus	Spring	1948	1970	1970	–	1,2,5	Vinyard, 1984
Rhinichthys osculus reliquus	Spring	1948	1940	1950	1969	2	Hubbs et al., 1974; Miller et al., 1989
Rhinichthys osculus robustus (?)	Lotic	1903	1900	–	–	1,3,4	La Rivers, 1962
Rhinichthys osculus velifer	Spring	1893	1969	1969	–	2,3,4	Miller, 1984; Tuttle et al., 1990
Rhinichthys osculus 'Amargosa'	Lotic	1995	–	–	–	2	Williams et al., 1982; Moyle et al., 1995; Sada et al., 1995
Rhinichthys osculus 'Benton Valley'	Spring	1995	1940	1940	–	2,4	Sada, 1989; Sada et al., 1995; USFWS 1998a
Rhinichthys osculus 'Diamond Valley'	Spring/Lotic	1948	?	?	–	?	Hubbs et al., 1974
Rhinichthys osculus 'Foskett Spring' (1)	Spring	1948	–	–	–	1	Andreasen, 1975; Williams et al., 1990
Rhinichthys osculus 'Little Lake'	Spring	1995	1940	1940	1940	2	Sada, 1989; Sada et al., 1995
Rhinichthys osculus 'Long Valley'	Spring	1995	1960	1960	–	2	Sada, 1989; Sada et al., 1995; USFWS 1998a
Rhinichthys osculus 'Meadow Valley'	Lotic	1948	–	–	–	–	Hubbs and Miller, 1960; Stein, 1997
Rhinichthys osculus 'Monitor Valley'	Spring	1948	–	–	–	1	Heinrich, 1991; D.W. Sada, field notes, 1996
Rhinichthys osculus 'Oasis Valley'	Spring	1995	–	1980	–	2,4	Heinrich, 1993; Sada et al., 1995
Rhinichthys osculus 'Pahranagat Valley'	Spring	1984	–	1960	–	1,2	Tuttle et al., 1990
Rhinichthys osculus 'Upper White River'	Spring	1948	1970	1970	–	2,3,4,9	Courtenay et al., 1985; Scoppettone et al., 1992
Richardsonius egregius (?)	Lotic/Lentic	1859	1900	–	–	1,2,3,4	La Rivers, 1962
Mollusks							
Assiminea infima	Spring	1947	1930	–	–	10	Pistrang and Kunkel, 1958; Hershler 1987; Sada, 2001
Fluminicola dalli	Spring	1884	–	–	–	–	Hershler and Frest, 1996
Fluminicola modoci	Spring	1912	–	–	–	–	Hershler and Frest, 1996
Fluminicola turbiniformis	Spring	1865	–	–	–	–	Hershler and Frest, 1996
Pyrgulopsis aardahli	Spring	1989	?	?	–	4	Hershler, 1989
Pyrgulopsis aloba	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis amargosae	Spring	1987	–	–	–	–	Hershler, 1989
Pyrgulopsis anatina	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis anguina	Spring	1998	?	?	–	1	Hershler, 1998
Pyrgulopsis augustae	Spring	1998	?	?	–	4	Hershler, 1998
Pyrgulopsis aurata	Spring	1998	?	?	–	1	D.W. Sada, field notes, 1996; Hershler, 1998
Pyrgulopsis basiglans	Spring	1998	?	?	–	1	Hershler, 1998
Pyrgulopsis bifurcata	Spring	1998	?	?	–	1	Hershler, 1998
Pyrgulopsis breviloba	Spring	1998	?	?	–	4	Hershler, 1998
Pyrgulopsis bryantwalkeri	Spring	1916	?	?	–	?	D.W. Sada, field notes, 1991; Hershler, 1994
Pyrgulopsis cariniata	Spring	1998	?	?	–	4	Hershler, 1998
Pyrgulopsis chamberlini	Spring	1998	?	?	–	10	Hershler, 1998
Pyrgulopsis cruciglans	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis crystalis	Spring	1987	–	1970	–	2,4	Sada, 1985; Hershler and Sada, 1987; D.W. Sada, field notes, 1997
Pyrgulopsis dixiensis	Spring	1998	?	?	–	1	D.W. Sada, field notes, 1991; Hershler, 1998
Pyrgulopsis eremica	Spring	1995	?	–	–	1	Hershler, 1995
Pyrgulopsis erythropoma	Spring	1893	–	1970	–	2,4	Sada, 1985; Hershler and Sada, 1987
Pyrgulopsis fairbanksensis	Spring	1987	–	1970	–	2,4	Hershler and Sada, 1987
Pyrgulopsis fusca	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis gibba	Spring	1995	?	?	–	1,4	Hershler, 1995; Hershler, 1998
Pyrgulopsis gracilis	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis hamlinensis	Spring	1998	?	?	–	1	Hershler, 1998
Pyrgulopsis hendersoni	Spring	1933	?	?	–	?	Hershler, 1994; Hershler, 1998
Pyrgulopsis hovinghi	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis hubbsi	Spring	1998	?	?	–	4	Courtenay et al., 1985; Hershler, 1998
Pyrgulopsis humboldtensis	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis imperalis	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis inopinata	Spring	1998	?	?	–	4	Hershler, 1998
Pyrgulopsis isolata	Spring	1987	–	–	–	–	Sada, 1985; Hershler and Sada, 1987
Pyrgulopsis landeyi	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis lata	Spring	1998	?	?	–	4	Hershler, 1998
Pyrgulopsis lentiglans	Spring	1998	?	?	–	?	Hershler, 1998

APPENDIX.—Continued.

Distinct biota	Habitat	Distinct	First loss	Major decline	Extinct	Threats	References
Mollusks (continued)							
Pyrgulopsis leporina	Spring	1998	?	?	–	1	Hershler, 1998
Pyrgulopsis limaria	Spring	1998	?	?	–	1	D.W. Sada, field notes, 1996; Hershler, 1998
Pyrgulopsis lockensis	Spring	1998	?	?	–	4	Hershler, 1998
Pyrgulopsis longae	Spring	1995	?	?	–	4	Hershler, 1995
Pyrgulopsis longiglans	Spring	1998	?	?	–	1	D.W. Sada, field notes, 1996; Hershler, 1998
Pyrgulopsis marcida	Spring	1998	?	?	–	1	Hershler, 1998
Pyrgulopsis merriami	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis micrococcus	Spring	1893	–	–	–	5	Sada, 1985; Hershler and Sada, 1987; Hershler, 1989
Pyrgulopsis militaris	Spring	1998	?	?	–	1	D.W. Sada, field notes, 1996; Hershler, 1998
Pyrgulopsis millenaria	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis montana	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis nanus	Spring	1987	–	–	–	2,4	Sada, 1985; Hershler and Sada, 1987
Pyrgulopsis neritella	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis nevadensis	Lentic	1883	1890	1890	1890	4	Galat et al., 1981; Hershler, 1994
Pyrgulopsis nonaria	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis notidicola	Spring	1998	?	?	–	1	Hershler, 1998
Pyrgulopsis orbiculata	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis owensensis	Spring	1989	?	–	–	4	Hershler, 1989; Hershler and Pratt, 1990
Pyrgulopsis papillata	Spring	1998	?	?	–	4	Hershler, 1998
Pyrgulopsis peculiaris	Spring	1998	?	?	–	10	Hershler, 1998
Pyrgulopsis pellita	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis perturbata	Spring	1989	–	?	–	4	Hershler, 1989
Pyrgulopsis pictillis	Spring	1998	?	?	–	4	Hershler, 1998
Pyrgulopsis pilcata	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis pilsbryana	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis pisteri	Spring	1987	?	?	–	2,4,5	Hershler and Sada, 1987
Pyrgulopsis planulata	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis ruinosa	Spring	1998	1990	1990	1990	4	D.W. Sada, field notes 1991; Hershler, 1998
Pyrgulopsis sathos	Spring	1998	?	?	–	4	Courtenay et al., 1985; Hershler, 1998
Pyrgulopsis saxatalis	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis serrata	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis steralis	Spring	1998	?	?	–	1	D.W. Sada, field notes, 1992; Hershler, 1998
Pyrgulopsis sulcata	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis transversa	Spring	1998	?	?	–	4	Hershler, 1998
Pyrgulopsis umbilicata	Spring	1998	?	?	–	1	D.W. Sada, field notes, 1996; Hershler, 1998
Pyrgulopsis variegata	Spring	1998	?	?	–	1	Hershler, 1998
Pyrgulopsis villacampae	Spring	1998	?	?	–	4	Hershler, 1998
Pyrgulopsis vinyardi	Spring	1998	?	?	–	?	Hershler, 1998
Pyrgulopsis wongi	Spring	1989	?	–	–	5	Hershler, 1989; Hershler and Pratt, 1990
Pyrgulopsis 'Longstreet Spring'	Spring	1981	1970	1970	1970	5	Taylor, 1980; Sada, 1985
Tryonia angulata	Spring	1987	?	1970	–	2,4	Sada, 1985; Hershler and Sada, 1987
Tryonia elata	Spring	1987	?	1970	–	2,4	Sada, 1985; Hershler and Sada, 1987
Tryonia ericae	Spring	1987	?	1970	–	2,4	Hershler and Sada, 1987
Tryonia margae	Spring	1989	?	?	–	?	Hershler, 1989; Pratt and Hoff, 1992
Tryonia robusta	Spring	1989	1930	–	–	4	Hershler, 1989; Pistrang and Kunkel, 1958
Tryonia rowlandsi	Spring	1989	?	?	–	?	Hershler, 1989
Tryonia salina	Spring	1989	–	–	–	–	Hershler, 1989; Sada and Deacon, 1995
Tryonia variegata	Spring	1987	?	1970	–	2,4	Sada, 1985; Hershler and Sada, 1987; Hershler, 1989
Aquatic insects							
Ambrysus amargosus	Spring	1953	1970	1970	–	4,5	La Rivers, 1953; Scoppettone et al., 1995
Ambrysus funebris	Spring	1948	1930	1930	–	4	La Rivers, 1948; Pratt and Hoff, 1992; Polhemus and Polhemus, 1995
Ambrysus relictus	Spring	1994	–	1970	–	4	Polhemus and Polhumus, 1994
Belostoma saratogae	Spring	1958	–	–	–	–	Pratt and Hoff, 1992; Polhemus and Polhemus, 1995
Capnia lucustra	Lentic	1965	1960	1960	1960	2,9	California Natural History Database (1996 unpublished data)
Microcylloepus formicoideus	Spring	1990	1930	1930	–	4	Shepard, 1990; Pratt and Hoff, 1992
Microcylloepus moapus fraxinus	Spring	1949	?	1960	–	2,4	La Rivers, 1949
Stenelmis calida	Spring	1949	–	1970	–	5	Chandler, 1949; Deacon and Deacon, 1979; Schmude, 1992
Stenelmis lariversi	Spring	1992	–	?	–	?	Schmude, 1992
Fairy shrimp							
Artemia monica	Lentic	1964	–	–	–	4	Jellison et al., 1993; R.S. Jellison, pers. comm., 1997

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