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Distribution and Status of Trout and Char in North America

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Introduction

Trout and char span the continent of North America, hugging its coasts and occupying many catchments throughout the interior of the continent. They have endured and persisted as North America has changed through time, including advances and retreats of glaciers, volcanic eruptions, enormous floods, and the formation of mountain ranges and plateaus. Most trout and char are found in mountainous catchments, requiring specific combinations of flow, temperature, velocity, depth, and cover to thrive. Recent research has led to the revision of the origin and diversification of trout and char. Although common fish names still refer to some of these fishes and others as trout, char, or salmon, recent realignments show that in North America, trout are Pacific trout *Oncorhynchus* spp. (Penaluna et al. 2016) and char encompass all fishes in the genus of *Salvelinus* (Crête-Lafrenière et al. 2012). Fishes in the genus of *Salmo* are also referred to as salmon or trout, and trout species of *Salmo* spp. are native to catchments that drain into the North Atlantic, mainly in Europe and the Atlantic Isles (see Chapters 11, 12, and 13). The taxonomy of North American trout is complicated, changes frequently, and is often under debate. This manuscript represents the best, current understanding of distribution and status but is likely to continue to evolve as the science improves.

Pacific trout are found from the top of the continent in Canada, throughout 12 western states of the United States, and into northern Mexico (Penaluna et al. 2016). They are found in catchments that drain into the Pacific Ocean, but some populations are in closed basins and others drain into the Gulf of Mexico east of the Continental Divide. Pacific trout are optionally anadromous (Rainbow Trout *Oncorhynchus mykiss* and Cutthroat Trout *O. clarkii*), iteroparous spring spawners (except for sea-run forms that also may spawn in winter or summer or holdover for future years to spawn in freshwater), and they can live up to 10 years or more. Different populations of Pacific trout exhibit diverse life histories with respect to demographic characteristics, trophic ecology, and movement. Pacific trout were moved from the genus *Salmo* to *Oncorhynchus* with Pacific salmon in 1989 based on multiple shared traits and both genetic and morphometric characteristics (Stearley and Smith 1993). Although the taxonomy within Pacific trout is still of ongoing debate, the most widely accepted phylogeny assigns six species to their group, including Rainbow Trout (incorporating redband trout and steelhead [anadromous Rainbow Trout]), Cutthroat Trout, and the southern taxa of Golden Trout *O. aguabonita*, Gila Trout *O. gilae*, Apache Trout *O. apache*, and Mexican Golden Trout *O. chrysogaster* in addition to a diverse complex of taxonomically unclassified trout from the Sierra Madre Occidental (SMO) in Mexico (Abadía-Cardoso et al. 2015; Penaluna et al. 2016; see also Chapter 8). Substantial declines in abundance and distributions of many Pacific trout lineages have led to elevated protection in catchments in some or whole portions of their range throughout North America by federal, state, and provincial management agencies (Table 1).

Char *Salvelinus* spp. are naturally found in north temperate and Boreal regions in catchments that drain both into the Pacific and Atlantic oceans in Canada and the United States. Char are freshwater fishes that are iteroparous, fall spawners (except for some populations that also spawn in spring), and they can live up to 15 years or more. Although char may be the most diverse group of salmonid fishes, based on their evolutionary relationships and associated taxonomy, they are the least understood group; the vast majority of these relationships are associated with the Arctic Char *S. alpinus* complex (Crête-Lafrenière et al. 2012). Current understanding describes five main lineages of *Salvelinus* in North America, including Bull Trout *S. confluentus*, Dolly Varden *S. malma*, Brook Trout *S. fontinalis*, Lake Trout *S. namaycush*, and Arctic Char (more details about lineages are provided in Chapter 6). Substantial declines in abundances and distributions of many char species has led to elevated protection in many catchments throughout their range, particularly in the lower United States (Table 1).

This chapter summarizes the status and distribution of native trout and char in North America, with a strong emphasis on the coterminous United States. Behnke (1992, 2002) provides an extensive summary of native trout and char of western North America, including taxonomy, relationships, history, and biology. Consequently, we draw heavily from that treatise and expand using sources that are more current. Similarly, Arctic Char represents one of the most well studied of the salmonids, and the literature describing this species is simply enormous, including books, reviews, and symposium proceedings (e.g., Klemetsen et al. 2003). An entire book is being devoted to Lake Trout (Muir and Krueger, in press). Thus, we note that this chapter is not an exclusive synthesis, but rather a contemporary update on status and distribution on North American trout and reflects upon the areas of expertise (geographic and topical) of the chapter authors.

Table 1. Summary of the genus and species of trout and char in North America, their current legal status, and some notes on their current status, distribution, conservation, or management. Note: taxonomic names and classification are continuously subject to change. Please see text for additional details. ESA = Endangered Species Act.

Genus	Species and subspecies	Common name	Current legal status	Brief comments on mangement and status (please see text for full description)
				***Oncorhynchus mykiss* and their allies**
Oncorhynchus	*mykiss*	Rainbow Trout	No listing	Not currently at imminent risk of extinction because it is still widely distributed with many populations isolated by physical barriers and active conservation efforts are occurring for many populations.
	gilae	Gila Trout	ESA threatened (down-listed in 2006)	Concerted conservation effort re-established some populations previously lost and founded new populations throughout the native range, down-listed from endangered to threatened to allow catch-and-release angling.
	apache	Apache Trout	ESA threatened (down-listed in 1975)	Take regulated to allow angling. 28 populations persisted before fire in 2011. Only 30 populations required for delisting by the ESA.
	aguabonita	Golden Trout	No approved listing	ESA listing not warranted (2011). Cooperation among the federal government, California Department of Fish and Wildlife, Trout Unlimited, California Trout, conservationists, wilderness activists, and the general public have been influential in conservation, but there are still hurdles.
				Coastal
Oncorhynchus	*clarkii clarkii*	Coastal Cutthroat Trout	No approved listing	Series of petitions for their listing under the ESA since 1999. Currently, they are undergoing assessment, likely will be precluded due to their broad presence within watersheds from headwater streams to river mouths.

Table 1. Continued.

Genus	Species and subspecies	Common name	Current legal status	Brief comments on mangement and status (please see text for full description)
		Columbia and Missouri River basins		
Oncorhynchus	*clarkii lewisi*	Westslope Cutthroat Trout	Sensitive by federal agencies. Species of special concern (SOSC) by Idaho	ESA listing not warranted (2003). Determined not at current risk, but pure populations estimated occur in less than 2.5% of stream miles. Conservation efforts include restrictive fishing regulations, habitat restoration, and establishment of captive "introgression free" broodstocks.
		Lahonton Basin forms		
Oncorhynchus	*clarkii henshawi*	Lahontan Cutthroat Trout	ESA threatened (down-listed in 1975)	Reclassification was for the purpose of allowing increased management flexibility for species management and recovery. Recovery plan published in 1995 by the U.S. Fish and Wildlife Service. High levels of extinction risk in many local populations, but diverse and comprehensive conservation efforts underway.
	clarkii seleniris	Paiute Cutthroat Trout	ESA threatened (down-listed in 1975)	Revised recovery plan published in 2004 (U.S. Fish and Wildlife Service) will be reintroduced after the efficacy of completed nonnative fish removals has been determined.
	clarkii alvordensis	Alvord Cutthroat Trout	Extinct	After appropriate evaluation, the Oregon Department of Fish and Wildlife plan to collect spawning pairs of trout exhibiting the phenotype of extinct Alvord Cutthroat Trout and relocate to hatchery for potential future reintroduction.

Table 1. Continued.

Genus	Species and subspecies	Common name	Current legal status	Brief comments on mangement and status (please see text for full description)
		Central and Southern Rocky Mountains		
Oncorhynchus	*clarkii bouvieri*	Yellowstone Cutthroat Trout	No approved listing	Recent petitions to list on ESA. Major efforts underway to ensure existence, including catch and release, no-kill regulations (positive response), improvements to riparian habitat through alternating livestock grazing strategies, restoring fish passage, and nonnative fish removal. Future is encouraging.
	clarkii utah	Bonneville Cutthroat Trout	Multi-partner conservation agreement	ESA listing not warranted (2008). Nonnative Rainbow Trout do not appear to thrive where Bonneville Cutthroat Trout exist in mountainous areas; however, nonnative Brook Trout do thrive and may represent a significant threat. High densities and healthy populations in persisting strongholds.
	clarkii pleuriticus	Colorado River Cutthroat Trout	Species of special concern	ESA listing not warranted (2007). Species of special concern by Colorado, Utah, and Wyoming. Coordinated efforts to shepherd long-term conservation.
	clarkii stomias	Greenback Cutthroat Trout	ESA threatened (down-listed in 1978)	Small population has served as founding source for three new populations via aggressive recovery efforts.
	clarkii virginalis	Rio Grande Cutthroat Trout	Species of special concern	ESA listing not warranted (2014). Robust conversation team composed of state, federal, and tribal agencies to oversee recovery effort.
	clarkii macdonaldi	Yellowfin Cutthroat Trout	Extinct	Appeared to have gone extinct just 17 years after discovery in 1885.

Table 1. Continued.

Genus	Species and subspecies	Common name	Current legal status	Brief comments on mangement and status (please see text for full description)
			Chars	
Salvelinus	*confluentus*	Bull Trout	ESA threatened (1998–1999)	Threatened in the United States. Of special concern or threatened in three of four geographic populations in Canada. Goal in United States to manage threats, with legal challenges underway to challenge this determination.
	malma	Dolly Varden	No listing	Widely distributed and abundant. Primary threats include climate change, potential overharvest, alterations to groundwater or flow, and decreased connectivity.
	fontinalis	Brook Trout	No listing	Distribution within native range is decreasing. Introduced widely across the globe and have displaced native trout in Europe and western North America. Several U.S. states recognize native Brook Trout as a species of conservation concern.
	namaycush	Lake Trout	No listing	Stable at the rangewide scale, but dramatic reductions in the Great Lakes. Established populations in many western U.S. states outside of their native range.
	alpinus	Arctic Char	No listing	Considered stable rangewide and currently a sustainable, subsistence fishery.

Status and Distribution

Southern taxa Oncorhynchus spp.

The southern distribution of native Pacific trout represents the southern-most native distribution of any living trout or char in the world (Figure 1). All of these trout are found in warmer latitudes, thus constraining them to colder, high-elevation headwater streams. The speciation of Pacific trout also likely occurred here because most of the early divergences for living members are concentrated near the southern edge of their distribution in southwestern North America (Cavender and Miller 1982). The only species formally described in the SMO complex of Mexico is Mexican Golden Trout (Hendrickson et al. 2002); however, there are, at least, three more lineages at the species level in the SMO complex (Abadía-Cardoso et al. 2015). Gila Trout and Golden Trout are currently recognized as separate species; however, they have also been proposed as subspecies of Rainbow Trout (Behnke 2002). There is an information gap about how environmental conditions may influence the evolutionary diversity and distribution of trout at their southern-extent in western North America because these populations are likely the most vulnerable to population reductions and range shifts. Continuing exploration and discoveries throughout western North America, but particularly at their southern extent, may lead to formal designations of new taxa.

Rainbow Trout and its allies

Rainbow Trout (including steelhead and redband trout) is the most well-known trout species in North America, with an extensive native distribution spanning the entire west coast of North America from Alaska into Baja California, Mexico (Penaluna et al. 2016; Figures 1 and 2). If its complete distribution is considered, which extends into Asia, it has the broadest range of any Pacific trout. Rainbow Trout display a diversity of life histories, including populations that are sea-run, estuarine, and resident. The current hypothesis for the expression of anadromy or residency of Rainbow Trout is as a response to the combination of absolute water temperature and variation in water temperature, with colder thermal regimes fostering residency via earlier maturation (Kendall et al. 2015; but see Rosenberger et al. 2015). Rainbow Trout seem to have had greater overall mixing relative to Cutthroat Trout, with few distinct lineages at the edges of their distribution.

At their southern edge in northern Mexico, there is a formally recognized subspecies, San Pedro Martir Rainbow Trout *O. m. nelsoni*, in Baja California, Mexico, and there are additional potential lineages in tributaries that drain into the Gulf of California. In both Canada and the United States, there are no officially recognized subspecies of Rainbow Trout. However, in the United States, there are multiple lineages; native Rainbow Trout or steelhead occurring west of the Cascade Range and Sierra Nevada along the Pacific coast are currently classified as Coastal Rainbow Trout *O. m. irideus*. Inland Rainbow Trout groups occurring east of the Cascade Range and

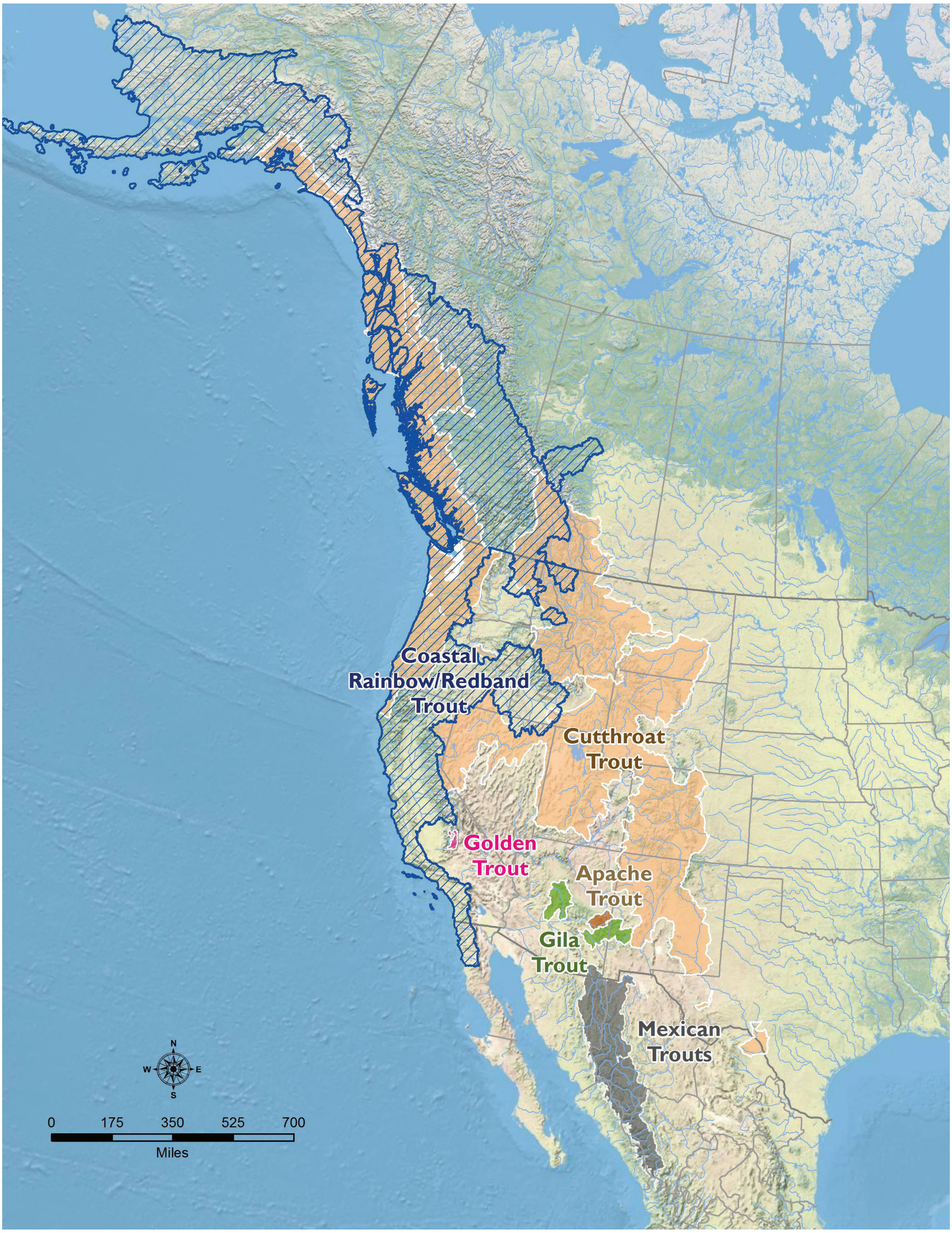

Figure 1. Historical distribution of trout (*Oncorhynchus* spp.) in North America (Matt Mayfield, Trout Unlimited).

Figure 2. Rainbow Trout. Photo: Kevin B. Rogers.

the Sierra Nevada along the Pacific Coast are classified as redband trout (*O. mykiss* ssp; Muhlfeld et al. 2015). Three main lineages of redband trout occur, including (1) Columbia River Redband Trout *O. m. gairdneri*, which occur east of the Cascade Range in the Columbia River and Harney Basin; (2) Klamath Redband Trout *O. m. newberrii* of the northern Great Basin and Klamath region; and (3) McCloud River Redband Trout (also known as Sacramento Redband Trout) *O. m. stonei* of Warner Valley, Goose Lake, and Chewaucan basin (Currens et al. 2009). In general, Rainbow Trout have been extensively introduced within and outside of their range for sportfishing, hatchery, and aquaculture purposes, leading to hybridization with other Pacific trout and displacement of native fishes (Crawford and Muir 2008). Globally, Rainbow Trout has been considered as one of the top 100 most successful invaders (International Union for Conservation of Nature [IUCN]).

Gila Trout.—With a historical range confined to just 600 mi (965.6 km) of stream habitat in the headwaters of the Gila River in New Mexico, including the San Francisco drainage and perhaps the Verde and Agua Fria drainages in Arizona (Behnke 2002; USFWS 2003; Figure 1), the Gila Trout already had one of the smallest native ranges of any salmonid in North America. By the time the species was formally described in 1950, only five populations remained in just 32 km of stream. Declines were due to habitat degradation associated with the effects of livestock grazing, fire suppression, water diversions, competition with nonnative Brown Trout *Salmo trutta*, and hybridization with nonnative Rainbow Trout. Due to increases in fuel loads associated with fire suppression and warming climates (Westerling 2016), the fate of these fish is perhaps more entwined with wildfire than any other native trout of the West (Brown et al. 2001; Dunham et al. 2003).

Interestingly, not only do Gila Trout occur in the United States' first designated wilderness area (Gila Wilderness), it is also likely the first fish in the West to generate conservation interest, with New Mexico's state fish and game agency establishing a policy of not stocking its natal waters with nonnative trout as early as 1920 and building a hatchery to propagate Gila Trout in 1923 (Miller 1950). Along with its sister taxon, the Apache Trout, the Gila Trout was one of 22 fishes threatened with extinction and listed under the Endangered Species Protection Act of 1966, the first piece of comprehensive endangered species legislation (USFWS 1967), which preceded the Endangered Species Act (ESA) of 1973 and the New Mexico Wildlife Conservation Act of 1974 in which Gila Trout were also listed (Propst et al. 1992). By 1987, successful reintroduction efforts led the U.S. Fish and Wildlife Service (USFWS) to consider downgrading the species to threatened under the ESA. Floods and fires in the ensuing years, however, extirpated three populations and led the USFWS to reconsider, ultimately withdrawing their proposal in 1991. Though several more fires ravaged Gila Trout populations in the 1990s, a concerted conservation effort reestablished some of those lost, and founded new populations throughout the native range. Those efforts compelled the USFWS to downgrade the Gila Trout to threatened status in 2006, which allowed for catch-and-release angling (Table 1). When the largest wildfire in recent New Mexico history (121,000-ha [300,000 acres] Whitewater–Baldy Complex Fire) burned through half of the Gila Trout native range in 2012, fish were extirpated from six of the nine streams within the burn area (Wick et al. 2014). Fish were evacuated from three of these streams following the fire to save them from looming toxic ash flows. Currently, 17 populations of Gila Trout occupy 130 km of habitat, with 13 in New Mexico and 4 more in Arizona (J. Wick, New Mexico Game and Fish, personal communication). Ironically, two of those populations were established after the Whitewater–Baldy Complex Fire created an opportunity by clearing the streams of invasive nonnative salmonids.

Apache Trout.—When R. R. Miller of the University of Michigan described *Oncorhynchus gilae* in 1950, he considered the native trout (Apache Trout) of the White Mountains of Arizona to be a separate form of Gila Trout. It was not until 1972, when other biologists noted several distinctions, including fewer and larger spots and a horizontal band across the eye, giving them a masked appearance, that he described them as a separate species (Miller 1972; Behnke 2002, 2007). Behnke lamented the splitting into two full species and argued that based on the distinctive number of chromosomes (only 56) shared by Gila Trout and Apache Trout, and the extremely close genetic relationship between them, that they should be "classified as two subspecies of one species" (Behnke 2007).

The historic distribution of Apache Trout comprised up to 1,320 km of fluvial habitats above 1,800 m in elevation in the headwaters of the Salt River draining the

White Mountains (Behnke 2002, 2007; USFWS 2009a; Figure 1). Prior to reintroduction efforts, only 48 km remained in a few headwater streams, primarily on the Fort Apache Indian Reservation (USFWS 2009a), with grazing, water development, logging, and mining all complicit in their demise. As with other inland trout, competition with nonnative Brown Trout and Brook Trout, as well as hybridization with Rainbow Trout, represents perhaps the greatest threat to their persistence (Rinne and Minckley 1985; USFWS 2009a). Originally listed as endangered in 1967 (USFWS 1967), Apache Trout were downgraded to threatened under the ESA in 1975, a reclassification that allowed the state of Arizona to regulate take and establish angling opportunity for the fish (USFWS 1975; Table 1). Prior to the Wallow Fire in 2011, 28 populations persisted on the landscape in approximately 200 km of streams (USFWS 2009a). The fire was responsible for eliminating at least two small populations, but conservation efforts continue. At least 30 populations are required before the USFWS will consider delisting the subspecies entirely from the ESA (USFWS 2009a).

Golden Trout.—The Golden Trout, often referred to as the California Golden Trout, is formally recognized as its own species, but it has also been proposed as a subspecies of Rainbow Trout native to several headwater tributaries of the Kern River, in the southern Sierra Nevada, California, an area approximately 1,536 km^2 (Hammerson 2013; Skaggs 2013; Figure 1). The Golden Trout is considered one of the most ancestral forms of Rainbow Trout and originated in the late Pleistocene epoch, approximately 12,000 years ago (Behnke 1992). When isolated by natural barriers, it evolved into the Golden Trout (Moyle 2002). Their Latin name comes from the Spanish words *agua bonita* (meaning "beautiful water"), in reference to the waterfall at the mouth of Golden Trout Creek, near the confluence with the Kern River. Golden Trout are notable in expressing the greatest extremes in coloration (hence the common name) and meristic characteristics of all Rainbow Trout forms (Figure 3) and are designated California's state freshwater fish. They express fluvial and adfluvial life histories and thrive in moderately high-elevation, cold (<15°C) oligotrophic alpine lakes and streams (reviewed in Skaggs 2013). There is considerable disagreement about finer scale taxonomy, and they have been considered a complex of two or even three subspecies by some, including *Oncorhynchus mykiss aguabonita*, *O. m. gilberti*, and *O. m. whitei* (Behnke 1992; Stephens et al. 2004). This uncertainty in taxonomic classification complicates status assessments. Golden Trout were also introduced into literally hundreds of lakes and streams outside their native range; however, most of these populations hybridized with Cutthroat Trout and other subspecies of Rainbow Trout and did not persist. Contemporary distribution data may not be completely correct but nonetheless include the states of Arizona, California, Colorado, Idaho, Montana, New Mexico, Nevada, Oregon, Utah, Washington, and Wyoming in the United States and the Alberta Province in Canada (Hammerson 2013).

Figure 3. Golden Trout. Photo: David Lentz.

Almost all populations of Golden Trout have been in steady decline for decades due to threats common to many trout summarized herein (Stephens et al. 2004; reviewed in Skaggs 2013). They have been overexploited, mismanaged, competed with and preyed upon by exotic species (including nontrout), and their habitat has been degraded due to grazing, logging, and roads in addition to synergistic effects of those threats and unpredictable natural disturbance (e.g., drought, fire). Long isolation left them with poor competitive abilities (Behnke 1992). However, hybridization and introgression with stocked Rainbow Trout is probably their most limiting factor (Stephens et al. 2004). As such, they are considered a species of special concern by the California Department of Fish and Wildlife (CDFW) not warranted for listing under the ESA in 2011 due to demonstrated progress on conservation efforts underway (Skaggs 2013; Table 1). The Golden Trout Wilderness was established in 1978 with the goal of protecting their habitat in the upper watersheds of the Kern River. In addition, as part of a comprehensive conservation strategy, the CDFW signed an agreement with federal agencies in 2004 to restore backcountry habitat damaged by overgrazing (Stephens et al. 2004). Millions of U.S. dollars have been spent to build fish migration barriers on the South Fork Kern River to protect Golden Trout from nonnative trout invasions, but nonnative trout eradication remains as a major task for conservation of Golden Trout. Pressure from the federal government, CDFW, Trout Unlimited, California Trout, conservationists, wilderness activists, and the general public has been influential in conservation, but continued pressure, support, and new resources are needed to address nonnative trout and habitat improvement issues for Golden Trout. They are also propagated and are being reintroduced.

Cutthroat Trout subspecies

Cutthroat Trout have the most extensive distribution of all Pacific trout in North America, from California to Alaska, along the coast and interior, occupying both sides of the Rocky Mountains (Behnke 1992, 2002; Penaluna et al. 2016). Cutthroat Trout thrive in cold, clear waters and are thus found in high-elevation lakes, streams, and rivers. They are distinguished by their red or orange marks along the undersides of their gills, hence the name "cut throat" (Figures 4–9). The evolutionary biology and taxonomy of Cutthroat Trout is extensively reviewed in Trotter et al. (2018).

Recent genetic information (Wilson and Turner 2009; Houston et al. 2012; Loxterman and Keeley 2012) has led to renewed interest in reclassification, recovering extensive diversity among the four major lineages proposed by Behnke (1992, 2002). These include (see Table 1) (1) the coastal lineage, including Coastal Cutthroat Trout; (2) the Lahontan Basin lineage, including Lahontan Cutthroat Trout and associated subspecies; (3) Westslope Cutthroat Trout and other lineages from the upper Columbia River and Missouri River drainages; and (4) the Upper Snake/Yellowstone/Bonneville Basin/southern Rocky Mountain lineage (e.g., Figure 4),

Figure 4. Snake River Cutthroat Trout. Photo: Kevin B. Rogers.

Figure 5. Greenback Cutthroat Trout. Photo: Kevin B. Rogers.

Figure 6. Lahontan Cutthroat Trout. Photo: Tim Loux.

Figure 7. Paiute Cutthroat Trout. Photo: William Somer.

including Yellowstone Cutthroat Trout, Bonneville Cutthroat Trout, Colorado River Cutthroat Trout, Rio Grande Cutthroat Trout, Greenback Cutthroat Trout, and other possible groups from the southern Rocky Mountains (Metcalf et al. 2012; Bestgen et al. 2013). The massive diversity in Cutthroat Trout likely resulted from the isolation generated by the Rocky Mountains and the rise of the Continental Divide (Metcalf et al. 2012). However, for the past 40 years, the taxonomic classi-

Figure 8. Bonneville Cutthroat Trout. Photo: Matthew McKell.

Figure 9. Rio Grande Cutthroat Trout. Photo: Kevin B. Rogers.

fication of Cutthroat Trout has included up to 14 subspecies; the primary and contemporary subspecies are described below, including two extinct subspecies (Behnke 1979, 1988, 1992; Trotter 2008).

The subspecies demonstrate many different coloration and spotting patterns, life-history characteristics, and habitat requirements, and organization is equally complex within subspecies (Gresswell et al. 1994). They can be lacustrine, adfluvial, steam resident, anadromous, or fluvial, and often several life-history expressions co-occur. There is also great variation in life-history traits including average size and age, migration strategy, and migration timing. Most Cutthroat Trout are less wary and selective than other trout species, and thus angler success rates are higher and all subspecies support popular sport fisheries (e.g., Gresswell 1995). The earliest propagation efforts for Cutthroat Trout probably occurred in Utah or California as early as 1872 (Behnke 1992). All the western states with native Cutthroat Trout use their own individual propagation programs, which usually rely on a source of "wild eggs." All subspecies of Cutthroat Trout have some level of protected status due to habitat loss and introduction of exotic species, the latter of which has led to hybridization with other *Oncorhynchus* spp. (Table 1). Only Coastal Cutthroat Trout and Westslope Cutthroat Trout naturally co-occur with Rainbow Trout, and when introduced into interior areas, Rainbow Trout typically out-compete and hybridize with Cutthroat Trout (Behnke 1992; Muhlfeld et al. 2014; but see Young et al. 2016).

Coastal Cutthroat Trout.—Coastal Cutthroat Trout have the broadest north–south distribution of any Cutthroat Trout subspecies, extending from Prince William Sound, Alaska, south to the Eel River in northern California and interior a few hundreds of miles from the Pacific coast (Figure 1). Most of their habitat coincides with the Pacific coast coniferous rainforest, extending from Alaska southward into northern California and placing them in rain-dominated catchments; however, they are also found in interior catchments in snow or rain-on-snow catchments. The Coastal Cutthroat Trout is the only *Oncorhynchus clarkii* subspecies that uses the marine environment and also ranges farther upstream into tributaries than other sympatric anadromous salmonids.

Coastal Cutthroat Trout are well known for their diversity of life histories, including sea-run, lake, fluvial, and resident freshwater populations, leading to their wide use of a variety of habitat types from rivers to tributaries, headwater streams, lakes, estuaries, and the nearshore ocean (Goetz et al. 2013). Some landlocked populations of Coastal Cutthroat Trout, although not strongly differentiated genetically, may exhibit novel phenotypic characteristics (e.g., Brenkman et al. 2014). Unlike other subspecies of Cutthroat Trout, Coastal Cutthroat Trout coexists and hybridizes naturally with steelhead across its range. Partial reproductive isolation is believed to occur via spatial segregation, with smaller-bodied Coastal Cutthroat Trout spawning in small tributaries and steelhead spawning in larger streams (Buehrens et al. 2013), but this isolation tends to break down when hatchery steelhead are introduced. Limited evidence suggests that individuals in the marine environment stay much closer to shore than other Pacific salmon or steelhead and reside in marine habitats on only a seasonal basis (Pearcy et al. 1990; Goetz et al. 2013).

Since 1999, there have been a series of petitions for their listing under the ESA due to a decline in some populations from habitat degradation and hybridization from stocking of hatchery steelhead, and currently, they are undergoing assessment (see coastalcutthroattrout.org; Table 1). In their current assessment, it appears as though they will be precluded from being listed due to their broad distribution within watersheds from headwater streams to river mouths. They are generally the salmonid found furthest upstream in a network, and hence, they are often the fish used to determine the upper distribution boundary of fishes throughout their range. Timber harvest is delineated based on this boundary, with fish-bearing reaches receiving greater protection and wider riparian buffers than portions of streams without fish. The complexities of these issues are illustrated by land–water interactions in the Pacific Northwest of North America, where forest harvest practices are regulated to protect these important fisheries. Current conservation plans for Coastal Cutthroat Trout include restoration efforts to maintain cold water in both smaller tributaries and main river channels, as well as enhancing the abundance of pools and instream cover throughout the network by allowing large wood to naturally recruit to streams.

Westslope Cutthroat Trout.—The scientific name of Westslope Cutthroat Trout is derived from explorers William Clark and Meriwether Lewis because they led the expedition where their first specimens were obtained from the Missouri River, Montana. However, their historical distribution covered the broadest area of any Cutthroat Trout subspecies covering five U.S. states and two Canadian provinces, and a considerable portion of their distribution is actually east of the Continental Divide. The Westslope Cutthroat Trout is thought to represent the first divergence of interior Cutthroat Trout from Coastal Cutthroat Trout (Behnke 1979). The Westslope Cutthroat Trout is Montana's state fish. Westslope Cutthroat Trout have three life-history forms, including lake, fluvial, and resident stream populations.

The distribution and abundance of Westslope Cutthroat Trout has contracted severely in recent years, especially in the United States (Penaluna et al. 2016). In Montana, numbers have been reduced by 90% or more from their historical abundances in lakes. In rivers, it has been estimated that pure populations occur in less than 2.5% of their historically occupied stream miles (Behnke 2002), although more recent research has indicated that this may be an overestimate (Young et al. 2016). Much like other species of native trout, their decline is attributed to overexploitation, genetic introgression, competition, and habitat degradation (Liknes and Graham 1988). They hybridize with Rainbow Trout, Golden Trout, and Yellowstone Cutthroat Trout and are highly sensitive to replacement by nonnative kokanee *Oncorhynchus nerka* (lacustrine Sockeye Salmon), Lake Trout, and Lake Whitefish *Coregonus clupeaformis* in lakes, Brook Trout in streams, and Brown Trout in rivers. Consequently, the Westslope Cutthroat Trout is considered sensitive by the U.S. Forest Service and the U.S. Bureau of Land Management and considered a species of special concern by the Idaho Department of Fish and Game (IDFG; reviewed in McIntyre and Rieman 1995). The strongest populations are in Glacier National Park and the Flathead Basin of Montana, but those appear to be declining. Despite persistent threats, however, Westslope Cutthroat Trout remain widely distributed and there are numerous healthy populations in Idaho river drainages in particular (Meyer et al. 2006). The IDFG and the Montana Fish, Wildlife, and Parks (MFWP) have implemented restrictive fishing regulations, MFWP has completed extensive habitat restoration, and both states have established captive broodstocks free of introgression from Rainbow Trout or Yellowstone Cutthroat Trout. Westslope Cutthroat Trout were petitioned for listing as threatened throughout its range under the ESA in 1997 and reassessed in 2002, but in both cases, the listing petition was determined to be not warranted due to currently wide distribution of this subspecies and ongoing conservation measures (USFWS 1999; Shepard et al. 2005; Table 1).

Lahontan group

The evolutionary lineage of Lahontan Cutthroat Trout was most likely derived from the Columbia or Sacramento rivers to the north and west of the Lahontan Basin, respectively (Hubbs et al. 1972; Loxterman and Keeley 2012). Divergence within the Lahontan group is evident, with six uniquely identifiable evolutionary units which correspond largely to the distribution of major catchments nested within the Lahontan Basin, or with geographic dispersal barriers within them (Peacock et al. 2018).

Lahontan Cutthroat Trout.—The range of Lahontan Cutthroat Trout includes a vast swath of the northwestern Great Basin desert (Grayson 1993), including terminal lake basins associated with the Walker, Carson, Truckee, and Susan River systems draining the eastern Sierra Nevada Mountains to the west, and eastward to the Ruby and Jarbidge Mountains in eastern Nevada. The southern limit of the range extends into southern Nevada and north to southeastern Oregon. Currently, most populations of Lahontan Cutthroat Trout exist as isolated enclaves inhabiting small streams in the eastern portion of the species' range.

Historically, populations of Lahontan Cutthroat Trout in the western portion of the subspecies' range were extremely productive, owing to availability of larger fluvial and lacustrine habitats, such as Lake Tahoe, Walker Lake, and Pyramid Lake. In the latter system, it was not uncommon for fish to exceed 15–20 kg (Behnke 1992; Figure 6). By the 1940s, populations in these lacustrine systems were largely extirpated due to heavy exploitation in commercial and recreational fisheries, introductions of nonnative trout, and loss and degradation of tributary spawning habitats. Whereas most lakes have retained their potential to support Lahontan Cutthroat Trout, declining water quality and availability in some (e.g., Walker Lake) still pose threats (Dickerson and Vinyard 1999). In addition to its exceptionally large size in some lacustrine systems (e.g., Pyramid Lake), the Lahontan Cutthroat Trout appears to be unique among subspecies of Cutthroat Trout with respect to tolerance for high levels of dissolved solids (Galat et al. 1985). Current efforts to restore Lahontan Cutthroat Trout have involved control of nonnative species (e.g., Brook Trout) in the handful of systems where natural populations persist (Rissler et al. 2006). In addition, hatchery production (USFWS Lahontan National Fish Hatchery Complex and Pyramid Lake Fisheries of the Pyramid Lake Paiute Tribe) provides support for populations that currently lack access to spawning habitats, as well as reintroductions where reproduction is possible (Al-Chokhachy et al. 2009; Alexiades 2010; Heredia and Budy 2018). Recent confirmation of out-of-basin translocated populations of Lahontan Cutthroat Trout from the Tahoe–Truckee–Pyramid basin to Utah (Hickman and Behnke 1979; Peacock and Kirchoff 2007) has provided new opportunities for hatchery production to restore fish that more closely approximate historical genetic attributes of fish within this system.

Most extant populations of Lahontan Cutthroat Trout currently persist in small, isolated streams in the eastern portion of the subspecies' historical range (Dunham et al. 1999a), where some have proposed new taxonomic subdivisions (Trotter and Behnke 2008; Peacock et al. 2010). Although questions linger regarding the evolutionary history or taxonomic designations appropriate to Cutthroat Trout in this region (Peacock et al. 2018), the ecological situation is more resolved. Fragmentation of these habitats is linked to seasonal patterns of stream drying, unsuitably warm temperatures, presence of nonnative species, and movement barriers (Dunham et al. 1999b, 2003; Neville et al. 2006, 2016). Occupancy models (Dunham et al. 2002), demographic models (Peacock and Dochtermann 2012), and climate projections (Wenger et al. 2011; Warren et al. 2014) all point to moderate to high levels of extinction risk in many local populations. Lahontan Cutthroat Trout were listed as endangered under the Endangered Species Conservation Act of 1969 and later reclassified as threatened under the ESA (USFWS 1975; Table 1). Continued encouraging progress has been made, however, to remove nonnative trout and to improve instream habitat and riparian conditions (USFWS 2009b). Perhaps the main conservation issue with this species, as with many coldwater species at the southern extents of their geographic ranges, is whether current habitats and habitat improvements are enough to support this species in the face of likely future losses attributed to a changing climate in the region.

Paiute Cutthroat Trout.—Genetic and meristic characters suggest that the Paiute Cutthroat Trout are recently diverged from Lahontan Cutthroat Trout (Behnke and Zarn 1976). The lack of spots on the body is a distinguishing characteristic of Paiute Cutthroat Trout (Figure 7). Behnke and Zarn (1976) concluded that the separation of Paiute Cutthroat Trout from Lahontan Cutthroat Trout occurred relatively recently (5,000–8,000 years ago), following the desiccation of Lake Lahontan. However, more recent genetic analyses using restriction-site associated DNA (RAD) sequencing suggest that the two subspecies diverged from each other substantially longer than previously thought (Saglam et al. 2017). Paiute Cutthroat Trout were listed as endangered in 1967 under the Endangered Species Conservation Act of 1966 (USFWS 1967) and later reclassified as threatened under the ESA (USFWS 1975; Table 1). Critical habitat has not been designated for this species. In the most recent 5-year status review, the USFWS concluded that Paiute Cutthroat Trout still meets the definition of threatened and recommended "no change in status" (USFWS 2013).

Paiute Cutthroat Trout are known from a single drainage in the Sierra Nevada range in east-central California located in the Humboldt-Toiyabe National Forest. The presumed historical distribution was limited to 17.8 km (11.1 mi) of habitat in Silver King Creek as well as accessible reaches of three small tributaries. As with other Cutthroat Trout subspecies, nonnative trout were stocked into Silver King Creek in the early 1900s. By the time they were officially described by scientists (Snyder 1933, 1934), Paiute Cutthroat Trout were extirpated from their historical range due to hybridization. Fortunately, Paiute Cutthroat Trout had been moved into previously fishless waters within the Silver King Creek watershed prior to any hybridization event, first by Canadian loggers and then by Basque sheepherders. The progeny of these early transplants within the Silver King Creek watershed were then used to stock other waters outside the Silver King watershed, many of which were unsuccessful. However, these transplants did result in four other stream populations being established, two in the Sierra National Forest and two in the Inyo National Forest. Thus, Paiute Cutthroat Trout now occupy approximately 38 km of habitat, which ironically are all located outside of their historical range.

In 2004, the USFWS published a revised recovery plan (USFWS 2004) that discussed recovery actions in terms of eradicating nonnative salmonids from the historical range and reintroducing Paiute Cutthroat Trout. Since 2004, management agencies have been trying to implement the Paiute Cutthroat Trout Restoration Project; however, legal challenges over the use of piscicides stalled the project. After an injunction was lifted in 2013, the agencies were allowed to move forward (U.S. District Court 2013) and applied piscicides to eradicate nonnative salmonids from the historical range over the period 2013 to 2015. They are now determining the efficacy of those treatments before Paiute Cutthroat Trout are reintroduced.

Alvord Cutthroat Trout (extinct).—Alvord Cutthroat Trout arose in the late Pleistocene after Lahontan Cutthroat Trout invaded ancient Lake Alvord, an inundated area spanning from northeast Nevada to southeast Oregon, north of the Lahontan Basin (Behnke 1992; Trotter 2008). These genetically distinct (subspecies) Cutthroat Trout were restricted to just a few streams in the Lake Alvord drainage as the lake dried. Like other subspecies with long selection for large, lacustrine environments, they appeared to grow quickly and to extremely large sizes. Similar to Yellowfin Cutthroat Trout, they were then unable to resist displacement when occupying small streams with introduced nonnative Rainbow Trout and went rapidly extinct sometime in the 1960s. In 2013, the Oregon Department of Fish and Wildlife released a management plan describing an effort to collect spawning pairs of Cutthroat Trout exhibiting the phenotype of the extinct Alvord Cutthroat Trout and relocate them into the hatchery. Their goal is to reintroduce the Alvord phenotype into a suitable fishless host stream in Oregon, but this will require that specific ecological and genetic criteria have been met.

Yellowstone group

The most diverse clade of Cutthroat Trout is represented by the Yellowstone group that inhabits the heart of the Rocky Mountains. Initially, it was thought they descended from ancestral Cutthroat Trout forms that migrated up the Columbia River basin into Yellowstone country, then invading south into the southern Rocky Mountains where they radiated into Bonneville Cutthroat Trout, Colorado River Cutthroat Trout, Greenback Cutthroat Trout, Rio Grande Cutthroat Trout, and the now-extinct Yellowfin Cutthroat Trout (Behnke 2002). More recent evidence, however, suggests their ancient ancestor may have come from the Truckee River in western Nevada (Stearley and Smith 2016).

Yellowstone Cutthroat Trout.—Yellowstone Cutthroat Trout are native to the Rocky Mountain region, with a native range upstream of Shoshone Falls on the Snake River and tributaries in Idaho and Wyoming, across the Continental Divide in Yellowstone Lake and in the Yellowstone River, as well as its tributaries downstream to the Tongue River in Montana (Varley and Gresswell 1988; MFWP 2013). Yellowstone Lake and the Yellowstone River together historically contained the largest inland population of Cutthroat Trout in the world. The Yellowstone Cutthroat Trout was originally a Pacific drainage species that then traveled (naturally) across the Continental Divide into the Atlantic drainage (Behnke 1992). Yellowstone Cutthroat Trout in Yellowstone Lake became established after the ice melted on the Yellowstone Plateau about 8,000 years ago and grew into the largest population of lake-dwelling Yellowstone Cutthroat Trout. The species is also found in Utah and Nevada (Gresswell 2009; MFWP 2013).

In their native range, Yellowstone Cutthroat Trout are found across a variety of habitats including cold, clear waters of high-elevation, high-gradient tributary streams; larger, main-stem rivers; and lakes (e.g., Yellowstone Lake). Yellowstone Cutthroat Trout are most well known in Yellowstone National Park where they were the dominant fish species prior to Euro-American settlement, and as recently as 1995, the majority of Yellowstone Cutthroat Trout distribution was within the park boundaries (Gresswell 1995). In Yellowstone National Park, they are considered to be a keystone species and provide an important source of food for an estimated 20 species of birds and mammals, including bears, river otters, and mink (Koel et al. 2005; Baril et al. 2013). Yellowstone Cutthroat Trout display a wide variety of life-history forms, including resident, fluvial, and adfluvial and require cold, high-velocity stream habitat for spawning. They are predators, consuming insects and fish, and demonstrate a wide range of adult body sizes, (Gresswell 2011) reaching weights of 5 kg (Gresswell 1995).

Their abundance and range has been reduced by overexploitation by anglers and habitat destruction due to mining, grazing, logging, water storage, and diversions. In addition, their persistence is threatened by competition with nonnative trout introduced in the late 19th and early 20th centuries (Thurow et al. 1988; Varley and Gresswell 1988; Gresswell 1995). The most serious current threats to the subspecies are introgression due to interbreeding with introduced Rainbow Trout in the Greater Yellowstone Area (Gunnell et al. 2008), the presence of exotic Lake Trout (in Yellowstone and Heart lakes in Yellowstone National Park) which prey upon Cutthroat Trout up to nearly 400 mm and 27–33% of their body length (Varley and Schullery 1995; Ruzycki et al. 2003), and several outbreaks of whirling disease in major spawning tributaries (Koel et al. 2006: NPS 2010). Due to a long evolutionary history in the presence of just one other top-predatory fish in Yellowstone Lake, Yellowstone Cutthroat Trout are ill adapted to coexist with other fishes (Behnke 1992). In response to these combined threats, Yellowstone Cutthroat Trout populations have declined dramatically in both abundance and distribution rangewide, and extirpation or introgression has occurred in more than 71% of their historical stream habitat (May et al. 2003).

The strongest primarily allopatric populations of Yellowstone Cutthroat Trout are currently found in the Grand and Black canyons of the Yellowstone River and in the Yellowstone River's major tributary in Yellowstone National Park, the Lamar River and its tributaries, and the Snake River and tributaries to the Snake River throughout Grand Teton National Park and adjacent public lands. In addition, in Idaho, Yellowstone Cutthroat Trout remain widely distributed and appear to have healthy populations in numerous river drainages (e.g., South Fork Snake, Teton, and Blackfoot rivers, despite the presence of nonnative threats [both genetic and competitive; Meyer et al. 2006]). There have been recent petitions to list the Yellowstone Cutthroat Trout under ESA, but the USFWS has deemed listing not warranted because of major efforts already underway to ensure the continued existence of this subspecies.

The Yellowstone Cutthroat Trout is a prized game fish. Because the subspecies feeds primarily on insects, even as adults, it is especially popular among fly-fishing enthusiasts. Today, Yellowstone Cutthroat Trout fisheries support a multimillion U.S. dollar industry in the Greater Yellowstone Area (Kerkvliet and Nowell 2000; Loomis 2006). Yellowstone Cutthroat Trout have been widely propagated, with as many as 800 million eggs taken during annual spawning operations at Yellowstone Lake (Varley and Schullery 1995). They have been successfully established outside their native range in at least seven western U.S. states and two Canadian provinces (Varley and Gresswell 1988). The Wyoming Game and Fish Department still maintains a broodstock and the Idaho Department of Fish and Game collects eggs for replanting as fry.

Bonneville Cutthroat Trout.—Bonneville Cutthroat Trout are native to the Bonneville Basin, which encompasses much of Utah with small sections in northeast Nevada and southeast Idaho. Most of this area was inundated by the late Pleistocene-aged Lake Bonneville. Bonneville Cutthroat Trout are exclusively freshwater, are mid-ranged in longevity (10–15 years), and can be highly mobile, and all freshwater life-history forms exist (Figure 8). Bonneville Cutthroat Trout are imperiled rangewide and have declined to approximately 35% of their historical range due to threats from the usual suspects, including habitat degradation, reduced connectivity, competition with and predation by exotic species, disease, and hybridization (Lentsch et al. 2000; Budy et al. 2007). Exotic Brown Trout were repeatedly and extensively introduced in this region in the 1800s and now likely represent one of the greatest threats to native Cutthroat Trout (summarized in Budy and Gaeta 2018). Nonnative Rainbow Trout were also extensively introduced and compete with and hybridize with almost all Cutthroat Trout (e.g., Allendorf and Leary 1988). When they co-occur, Brown Trout consistently out-compete Bonneville Cutthroat Trout (e.g., McHugh and Budy 2005, 2006). However, Bonneville Cutthroat Trout do appear to be better capable of withstanding replacement by Brown Trout in higher-elevation reaches of streams characterized as high-gradient, cold, and high-velocity (Meredith et al. 2017), and in some cases, nonnative Rainbow Trout also do not always appear to thrive in these mountainous areas. In contrast, nonnative Brook Trout do thrive in smaller streams and mountainous areas and appear to be increasing while Bonneville Cutthroat Trout are decreasing in areas where they are sympatric (Matt McKell, Utah Division of Wildlife Resources, personal communication). Where strongholds persist, there are still some high-density and very healthy populations of Bonneville Cutthroat Trout, and most of these support extremely popular sport fisheries of important economic value (e.g., Budy et al. 2007). A rangewide conservation agreement and strategy for Bonneville Cutthroat

Trout includes a goal of preventing listing under the ESA (Lentsch et al. 2000). Bonneville Cutthroat Trout were petitioned for listing under the ESA but were deemed not warranted (USFWS 2008). Conservation and management efforts have recently been quite successful at both increasing abundance and restoring distribution and include habitat restoration, nonnative fish removal (chemically and opportunistically after wildfire), subsequent reintroduction, and angler education and outreach (Hepworth et al. 1997; Trout Unlimited, www.tu.org/conservation/project-finder; P. Budy, G. P. Thiede, C. Saunders, U.S. Forest Service, and Cache Anglers, unpublished data).

Colorado River Cutthroat Trout—Colorado River Cutthroat Trout are the native trout of the upper Colorado River basin, including the headwaters of the Green River in Utah and Wyoming, south to the headwaters of the San Juan River. Two broad forms have been identified (Rogers 2010; Metcalf et al. 2012; Bestgen et al. 2013), with a more ancestral form occupying the Green, Yampa, and White River basins and a more derived form with fewer spots in the Gunnison River, Dolores River, and headwaters of the Colorado River. Both forms were cultured from wild spawn operations around the turn of the last century and stocked widely around the state of Colorado (Metcalf et al. 2012).

Colorado River Cutthroat Trout now occupy isolated headwater streams where they can escape competition from nonnative Brook Trout and Brown Trout and avoid hybridization with nonnative Rainbow Trout. The Colorado River Cutthroat Trout is listed as a species of special concern by the states of Colorado, Utah, and Wyoming, which inspired the development of a conservation team comprised of state and federal resource agencies to shepherd the long-term conservation of the subspecies. A petition to list Colorado River Cutthroat Trout under the ESA was found to be not warranted in 2007 (USFWS 2007), largely because of the coordinated efforts of the group (Table 1). More than 360 conservation populations (those that are better than 90% pure; UDWR 2000) now reside across the historical range of the subspecies, occupying approximately 11% of historically occupied habitats (Hirsch et al. 2013).

Greenback Cutthroat Trout.—Initially thought to be extinct in the 1930s, presumably due to excessive exploitation and invasion of nonnative trout, the recovery effort for Greenback Cutthroat Trout was launched in the 1960s with what was thought to be the rediscovery of Greenback Cutthroat Trout in several small streams in the South Platte River basin. Listed as endangered under the Endangered Species Protection Act of 1966 and reclassified as threatened under the ESA in 1978, the subspecies was downgraded to threatened in 1978, which then allowed for catch-and-release fishing (Table 1). Greenback Cutthroat Trout became Colorado's state fish in 1996 with strong support from the angling public who relished pursuing them. Dramatic progress had been made toward delisting the taxa entirely when it was determined that the rediscovered populations used in the recovery effort were in fact Colorado River Cutthroat Trout native west of the Continental Divide (Metcalf et al. 2007, 2012). Further research on museum specimens collected in the late 1800s prior to large-scale stocking efforts revealed that a discrete form of Cutthroat Trout did occupy the South Platte River basin prior to European settlement and that a single remnant population still persists on the landscape today (Figure 5) thanks to stocking efforts in 1872 that established them above a natural barrier in what would have been fishless habitat. Despite having endured a significant genetic bottleneck over the past 130 years, this small population has already served as the founding source for three new populations at the time of this writing through an aggressive recovery effort aimed at securing it on the landscape inside its native range.

Rio Grande Cutthroat Trout.—As the southernmost Cutthroat Trout, Rio Grande Cutthroat Trout currently occupy coldwater habitats in the headwaters of the Rio Grande, Pecos, and Canadian River basins in Colorado and New Mexico. Whether these fish are in fact native in the Canadian River basin has been debated (Behnke 2002; Pritchard et al. 2009) since the Pecos is a tributary of the Rio Grande while the Canadian River drains into the Arkansas River basin. Early reports from the Civil War (USA) era suggest that Rio Grande Cutthroat Trout may have historically been found as far south as the Davis Mountains in Texas (Behnke 2002), but no evidence can be found of them there today. The form in the Pecos drainage is both genetically and phenotypically discrete (Pritchard et al. 2009; Bestgen et al. 2013) and has been said to resemble the Greenback Cutthroat Trout (Behnke 2002). However, this similarity is simply a reflection of the Greenback Cutthroat Trout type specimens actually being Rio Grande Cutthroat Trout (Metcalf et al. 2012; Rogers 2012). The Pecos drainage Rio Grande Cutthroat Trout are in fact quite distinct from the true native of the South Platte basin described above (Bestgen et al. 2013; Figure 9).

Without any large natural lakes occurring across the native range, Rio Grande Cutthroat Trout are a fluvial subspecies. Introductions into lotic environments have demonstrated that they are quite adaptable, however, achieving lengths in excess of 60 cm. Like other inland Cutthroat Trout, Rio Grande Cutthroat Trout is vulnerable to competition from nonnative salmonids, with Brown Trout posing one of the more significant threats, as elsewhere.

Recognized by both the states of Colorado and New Mexico as a species of special concern, Rio Grande Cutthroat Trout are perhaps the most litigated of all subspecies of Cutthroat Trout. Rio Grande Cutthroat Trout were first petitioned to be listed under the ESA in 1998 (USFWS 1998). Following a not warranted finding, this decision was appealed in 2001 precipitating a formal status assessment, yet again, listing was determined to be not warranted. After several more appeals and decisions, the USFWS settled and agreed to conduct another status assessment in 2014. Again, listing under the ESA was found to be not warranted (USFWS 2014; Table 1). Like Colorado River Cutthroat Trout, a robust conservation team comprised of state, federal, and tribal agencies oversees the recovery effort. There are currently 120 conservation populations distributed primarily in headwater habitats spread across the historic range, occupying 12% of their native habitats (Alves et al. 2008).

Yellowfin Cutthroat Trout (extinct).—Yellowfin Cutthroat Trout, now extinct, were thought to have been found only in Twin Lakes, Colorado, which formed at the end of the last ice age when boulders and clay moraine blocked off a tributary of the headwaters of the Arkansas River (Figure 10). Though wild spawn operations were conducted in the 1890s in the inlets and outlets of this pair of lotic habitats, progeny from these operations appear to have been simply restocked into them. Twin Lakes represented the only location where two subspecies of Cutthroat Trout allegedly coevolved in the same water, with Greenback Cutthroat Trout and Yellowfin Cutthroat Trout appearing to coexist, isolated via different feeding niches, reproductive timing, and location (Behnke 2002). Recent work (Metcalf et al. 2012) has questioned whether the putative Greenback Cutthroat Trout were native to this system or if they too were introduced prior to surveys conducted in 1889 by David Starr Jordan that found them to be prolific (Jordan 1891). Sharing a mitochondrial DNA clade with Colorado River Cutthroat Trout from west of the Continental Divide rather than the aboriginal fish of the South Platte River basin, a parsimonious explanation might invoke anthropogenic stocking that was beginning to ramp up by the late 1800s. Alternatively, one cannot discount the possibility that the Yellowfin Cutthroat Trout was indeed the ancestral fish of the Arkansas River basin and that the basin was reinvaded after the last ice age by trout from west of the Continental Divide, bringing the two forms together.

The Yellowfin Cutthroat Trout reportedly grew to large sizes in excess of 4.5 kg and were very popular with anglers. By the end of the 19th century, a variety of nonnative salmonids were stocked into Twin Lakes (Lake Trout and Rainbow Trout, in particular), which ultimately spelled the demise of the Yellowfin Cutthroat Trout, with

Figure 10. Yellowfin Cutthroat Trout (extinct). Photo: Kevin B. Rogers.

extensive surveys conducted in 1902 and 1903 failing to recover any (Juday 1906). This species appeared to have gone extinct just 17 short years after its discovery in 1885.

Char Salvelinus spp.

Fishes in the genus *Salvelinus* have a northern circumpolar distribution and are considered to have arisen 5–10 million years ago (Power 2002). Due to evolution in their northern range, char have adapted to life in cold and unproductive environments. In North America, five major lineages exist within the genus *Salvelinus*, covered below (Figure 11). High intraspecific diversity in morphology and life history is a common trait of species in this genus, particularly well known in Arctic Char (Klemetsen 2013) and Lake Trout (Muir et al. 2016). The Brook Trout is the most southern species of *Salvelinus* in North America, with a distribution as far south as Georgia, whereas Arctic Char is the most northern species.

Bull Trout.—Bull Trout are native to the Pacific Northwest and are found throughout British Columbia and much of Alberta, the Northwest Territories, and Yukon in Canada (Reist et al. 2002) and throughout the state of Washington, in large sections of Oregon, Montana, and Idaho, and in southern Alaska in the United States (Figure 11). Bull Trout are a diverse, long-lived, often-migratory species whose range resulted in a scattered, patchy mosaic after the last glaciation (Jonsson and Jonsson 2001; Figure 12). Historically, Bull Trout were known as Dolly Varden but were reclassified as a separate species in 1980 (Suckley 1858; Cavender 1978; Haas and McPhail 1991). Bull Trout require large, unfragmented habitats to persist and are thus highly susceptible to riverscape disturbances as a result of human land practices (Dunham et al. 1999). Generally, juvenile Bull Trout rear 1–3 years in headwater tributaries before moving downstream to larger rivers, lakes, or the ocean (Fraley and Shepard 1989; Swanberg 1997; Brenkman and Corbett 2005). Like other potamodromous salmonids, there can be multiple migratory life histories within the same population, including nonmigratory (i.e., resident), adfluvial, fluvial, and anadromous forms (Homel and Budy 2008; Homel et al. 2008)

In North America, Bull Trout are listed as threatened in the United States and of special concern or threatened for three of four geographic populations in Canada (COSEWIC 2012; USFWS 2015c; Table 1). In the United States, these listings are a result of habitat degradation and fragmentation, overexploitation, reduced water quality, and decreased connectivity (USFWS 2015a). Bull Trout are thermally intolerant and generally prefer water less than 12°C (Dunham et al. 2003; Isaak et al. 2010, 2015c). A warming climate could substantially affect the distribution and abundance of Bull Trout via loss of thermally suitable migratory habitat, which provides connectivity between populations, and decreased availability of spawning and rearing habitat (Rieman et al. 2007; Jones et al. 2014). Due to lost connectivity and poor conditions in the lower river segments where many migratory fish attempt to overwinter (sensu Al-Chokhachy et al. 2016), a declining trend in the abundance and population

Figure 11. Historical distribution of char (*Salvelinus* spp.) in North America (Matt Mayfield, Trout Unlimited).

Figure 12. Bull Trout. Photo: Joel Sartore, Department of the Interior.

growth rate of large, migratory fish, in particular, has been observed in several Bull Trout populations (e.g., Nelson et al. 2002; Budy et al. 2017). This loss of the large migratory form is reason for significant conservation concern. In addition, Bull Trout suffer from introductions of nonnative fishes, including Lake Trout, Brown Trout, and Brook Trout (Al-Chokhachy et al. 2016) and are known to hybridize with Brook Trout (DeHaan et al. 2010).

Many of the large, stable populations of Bull Trout are adfluvial populations where juvenile rearing takes place in large lakes or reservoirs or occur in relatively pristine headwater habitats (Meyer et al. 2014; Kovach et al. 2016). In those systems where Bull Trout are prospering, harvest is allowed and they are a much desired sport fish. In contrast, many of the populations at greater risk of extinction occur at the lower margins of the species' range, in anthropogenically altered habitats, and where invasive species (such as nonnative Brook Trout) are found (Ratliff and Howell 1992; Rieman et al. 1997; Kovach et al. 2016). Bull Trout have been extirpated from California (McCloud River), and a single, isolated population exists in Nevada (Jarbridge River; USFWS 2015c). Bull Trout are affected by all the usual suspects, including invasive species, warming water temperatures, and habitat loss, which individually and synergistically have acted to dictate the reduction in contemporary range and distribution (e.g., Baxter et al. 1999; Wenger et al. 2011). In addition, Bull Trout historically have not been universally appreciated because they preyed upon other salmonids perceived by the public to be of greater value (e.g., Dunham et al. 2008). As late as the 1990s, Bull Trout were considered undesirable and subject to bounty. Nonetheless, Bull Trout represent a popular target for anglers due to both their aggressive nature and large body size, but they must now be released under ESA restrictions.

The ultimate goal of the recovery strategy in the United States is to manage threats and ensure sufficient distribution to improve the status of Bull Trout throughout their extant range in the coterminous United States so that protection under the ESA is no longer necessary (USFWS 2015a). Bull Trout are propagated at several hatcheries in an effort to aid in conservation efforts.

Dolly Varden.—Dolly Varden are members of the char complex and are native to coldwater tributaries of North America (and also Asia) (Figure 13). They often overlap in distribution with Bull Trout and Arctic Char, with which they are closely related but with no evidence of inbreeding (Haas and McPhail 1991). More specifically, they are found in coastal tributaries along the Bering Sea, in the North Pacific from Puget Sound north along the British Columbia Coast to the Alaska Peninsula and into the eastern Aleutian Islands, and in the Arctic Ocean to the Mackenzie River (Figure 11).

Photo Plate K. Dolly Varden. Photo: Stephen Klobucar.

There are two subspecies recognized in Canada, the northern form (*S. malma malma*) and the southern form (*S. m. lordi*). Two different forms of Dolly Varden are also recognized in Alaska, but not as subspecies. The Alaskan northern and southern forms differ in the number of vertebrae, number of chromosomes, and maximum size, with the southern form being capable of attaining a much larger body size (up to 12 kg; ADFG 2017). Dolly Varden have also been introduced into select locations outside their native range in California, Colorado, New Mexico, and Wyoming, but few of these introductions have been successful at developing into reproducing populations (Fuller 2000).

Dolly Varden are true to the genus *Salvelinus* in being difficult taxonomically, and they demonstrate considerable genetic variability common among char (reviewed in Haas and McPhail 1991). The Dolly Varden species was originally identified in 1792 by German taxonomist Johann Julius Walbaum based on type specimens from the Kamchatka Peninsula in Siberia (Kowalchuk et al. 2010). Bull Trout and Dolly Varden were considered the same species (*S. malma*) until 1978. The common name Dolly Varden somewhat ironically comes from a population of char now classified as Bull Trout in the McCloud River, California and derives from an 1800s woman's garment described as "a dress of sheer figured muslin worn over a bright-colored petticoat" (Behnke 2007). When in spawning color, males exhibit brilliant pink, green, and orange and are considered among the more beautiful of the trout.

Many populations are anadromous or partly anadromous, but they also express fluvial and lacustrine life histories. The anadromous or semi-anadromous (also called sea-run) form migrates from freshwater to the ocean or estuaries and spends some time there feeding before returning to freshwater to spawn. The time in salt or estuarine water ranges dramatically, but anadromous Dolly Varden tend to stay close to shore and migrate along the coast (up to 1,600 km). The lacustrine form can also be adfluvial and occupies deep, cold lakes, often migrating to freshwater tributaries to spawn. The fluvial forms tend to occupy moderately large to large freshwater rivers, often migrating to tributaries to spawn. More populations express some degree of anadromy in the north relative to the south. Exclusively freshwater-resident dwarf Dolly Varden are often found in small headwater streams without easy access to the ocean or in other small land-locked water bodies (maturing at 7.5–15 cm). Spawning takes place annually or every other year between September and November, and juveniles remain in the river, migrating to alternative downstream habitat the following spring. Spawning males typically develop a distinct kype not observed in other char. Dolly Varden mature at between 5 and 9 years depending on form and growth rates and can live up to 16 years, whereas 10 years is most common. Dolly Varden are carnivorous generalists and scavengers and therefore associate with and follow salmon migrations upstream (ADFG 2017).

Like Bull Trout, in the 1800–1900s, Dolly Varden held a mixed reputation as undesired because they prey on prized salmonids (primarily eggs and juveniles), and thus they were purposefully exterminated by the state and federal government fishery agencies (Decicco 2005). In Southwest Alaska, there was even a 2.5–5-cent (USA) bounty (accounts vary) for each tail turned in. The Canadian Committee on the Status of Endangered Wildlife in Canada (COSEWIC) considers the northern form (subspecies) of Dolly Varden a species of special concern, the lowest level of risk category. This category is meant to indicate "this species is not presently endangered, but is considered to be sensitive to human activities and natural events, due to biological factors and/or threats." The Canadian southern form is not considered at risk. In Alaska, Dolly Varden are widely distributed and abundant, and there is no legal protection in the United States. Although population abundances are rarely quantified, their numbers can be quite high. Counted at a weir on Eva Creek, on Baranof Island, more than 100,000 Dolly Varden head out to the sea each spring (Armstrong and Hermans 2007). Nonetheless, as with almost all trout, Dolly Varden are threatened by climate change, in particular trends towards drier and warmer climates in the western Arctic are of concern. Other threats include reductions in water levels and groundwater (which can affect spawning and rearing), overfishing, and any offshore and land-based development that reduces connectivity and impacts migration and/or flow and water quality. Dolly Varden support popular sport fisheries and important subsistence fishing throughout their range, and some people in northwestern Alaska depend heavily on harvests of sea-run Dolly Varden for food (ADFG 2017).

Brook Trout.—Brook Trout (also known as Brook Char) are native to eastern North America from the Canadian Shield of northern Québec to the southern Appalachian Mountains of Georgia (USA) (Figure 14). Their native range extends west into the headwaters of the Mississippi, east to Atlantic Ocean, and south to the terminus of the Appalachian foothills in the southern United States (MacCrimmon and Campbell 1969; Behnke 2002; Figure 11). Brook Trout exhibit a broad array of life-history strategies, reflecting the diversity of aquatic habitats across their native range. These include the lake-dwelling and adfluvial populations (coasters), which occupy northern glaciated regions; anadromous populations (salters), which occupy Atlantic Ocean-connected tributaries from New England to Canada; migratory fluvial populations, which occur in stream networks as far south as West Virginia; and resident stream-dwelling populations, which are typical of the southern range. They co-occur with Arctic Char and Lake Trout in portions of their northern range and with Atlantic Salmon *Salmo salar* in portions of their eastern range. However, in their southern range, Brook Trout are the only native salmonid.

Brook Trout typically mature at 2 years of age and spawn during autumn in gravel redds. In addition to summer conditions, flow and temperature conditions during the winter egg incubation period have been recognized as particularly important drivers of Brook Trout population dynamics. Because Brook Trout growth exhibits strong density dependence (Grossman et al. 2010) and overwinter survival increases with age-0 size (Hunt 1969), redd scouring events may be compensated for to some degree

Figure 14. Brook Trout. Photo: Ryan Hagerty, U.S. Fish and Wildlife Service.

by increased per capita survival. However, multiple sequential high-flow winters may cause local extirpations (Kanno et al. 2015) because Brook Trout population persistence is strongly sensitive to juvenile survival rates, given their short life span (Letcher et al. 2007). In their southern range, stream-dwelling Brook Trout populations are typically isolated from larger source populations (Aunins et al. 2015), and therefore, recolonization events are not expected to restore extirpated populations in most cases (Letcher et al. 2007).

The presence of stream-dwelling Brook Trout is often associated with overhead cover and low width-to-depth ratios in forested watersheds (Kozel and Hubert 1989; Petty et al. 2005). However, temperature is more predictive of Brook Trout occurrence than geomorphological features (Rashleigh et al. 2005). Brook Trout typically are absent where daily mean stream temperatures exceed approximately 23°C (Ricker 1934; MacCrimmon and Campbell 1969; Meisner 1990; Wehrly et al. 2007). Brook Trout physiological stress responses occur above 21°C (Chadwick et al. 2015), consistent with observed thresholds for Brook Trout movement into thermal refugia (Petty et al. 2012; Hitt et al. 2017). Thermally moderating effects of groundwater upwelling often accompany spawning redd sites (Webster and Eiriksdottir 1976; Curry and Noakes 1995) and adult overwintering habitats (Cunjak and Power 1986). Mean annual groundwater temperatures of approximately 15°C correspond to the minimum elevation of Brook Trout in the southern range (Meisner et al. 1988), further indicating a limiting effect of temperature and the direct influence of groundwater in this regard. In fact, the word *fontinalis* means "of the fountain or spring," indicating that we have known the importance of upwelling and groundwater since the species was identified and named.

In addition to the importance of groundwater and springs, Brook Trout are sensitive to low pH. The most important source of acidity is sulfuric acid from abandoned underground coalmines in Appalachia. Stream liming programs are being used with success in some locations, although this is a temporary solution to the problem. Low pH diminishes Brook Trout body condition (pH ≈ 5.6; Wesner et al. 2011) and decreases survival (pH < 4; Robinson et al. 1976). Further, survival time of Brook Trout at low pH is inversely related to temperature (Robinson et al. 1976), Brook Trout show movement responses to avoid low pH (Van Offelen et al. 1994), and low pH delays Brook Trout egg development and hatch timing (Hurley et al. 1989). However, acid deposition is decreasing over time in native Brook Trout habitat (Kline et al. 2016), and the tolerance of Brook Trout to low pH may exhibit spatial structure across source populations, suggesting local adaptation (Hurley et al. 1989; Wesner et al. 2011).

Although there is no formal protection in place for Brook Trout, their native distribution has been greatly reduced due to habitat degradation and introduction of nonnative trout (Table 1). Hudy et al. (2008) reported extirpations from 28% of native Brook Trout watersheds and greatly reduced suitable habitat in the majority of remaining watersheds. Forest cover was the strongest predictor of healthy Brook Trout populations. Acidification is also implicated in Brook Trout reductions due to mine drainage (Herlihy et al. 1990) and atmospheric deposition (Baker et al. 1996). Introduced Brown Trout and Rainbow Trout have displaced native Brook Trout due to competitive interactions in many areas (Moore et al. 1983; Larson and Moore 1985; Wagner et al. 2013). Experimental removals of introduced Brown Trout increased native Brook Trout abundance and size (Hoxmeier and Dieterman 2016), further demonstrating the suppressive effects of introduced trout. Anticipated increases in future air temperature are expected to warm groundwater (Meisner et al. 1988) and greatly reduce Brook Trout distributions (Eaton and Scheller 1996; Flebbe et al. 2006), but changes are expected to exhibit complex spatial structure given patchy groundwater–surface water exchange dynamics in Appalachian mountain streams (Snyder et al. 2015). Brook Trout increased their use of areas of high stream temperatures when Brown Trout were removed from experimental streams, suggesting interactive effects of climate change and introduced species (Hitt et al. 2017).

Brook Trout have been introduced widely across the globe and have been moved within their historic range in North America in parks and countless private waters (MacCrimmon and Campbell 1969) and have displaced native trout in Europe (Öhlund et al. 2008) and western North America (Dunham et al. 2002). Displacement patterns may be temperature-dependent (Shepard 2004; Rieman et al. 2007) or habitat-size-dependent (Korsu et al. 2007) rather than stream-gradient-dependent (Adams et al. 2000). Brook Trout hybridization with native Bull Trout presents an important conservation challenge because first generation offspring are fertile (DeHaan et al. 2010), which could result in the loss of locally adapted Bull Trout populations (sensu Muhlfeld et al. 2009). Local adaptation for heat tolerance in Brook Trout has been documented across a set of streams in Newfoundland, Canada (Wells et al. 2016), but the spatial scale of local adaptation across their native range remains unknown.

Lake Trout.—Lake Trout are found in northern North America and occur primarily in Canada. However, its distribution ranges from Alaska in the west to northern New England in the east (Figure 11). Present-day distribution is considered to be shaped by colonization from four main southern refugia (Atlantic, Cascadia, Missouri, and Mississippi) and one northern Wisconsin refugium (Muir et al. 2016). Lake Trout are typically found in cool, deep lentic water bodies but also occur in rivers. This is the largest species of the char in North America, known to grow over 45 kg (Figure 15). Lake Trout most often spawn in the fall, but timing varies with latitude and morphological type. Broadcast spawning occurs primarily on rocky shoals (also referred to as spawning reefs), but riverine spawning populations are also known. Residents of oligotrophic, northern waters are slow growing, with sexual maturity at 6 or 7 years of age and lifespans of up to 60 years (McAllister and Coad 1974; M. Vinson, U.S. Geological Survey, Great Lakes Science Center, personal communication). Four

Figure 15. Lake Trout. Photo: Paul Vecsei/Engbretson Underwater Photography; financial right to publish purchased by the Ecology Center at Utah State University.

morphotypes of Lake Trout are known in Lake Superior, including the siscowet, lean, humper and redfin, and intraspecific diversity of Lake Trout is not uncommon in large lentic habitats (Muir et al. 2014, 2016).

Lake Trout populations are stable at the rangewide scale, but dramatic reductions have been documented in the Great Lakes. Lake Trout were apex predators of these lake food webs and historically supported sizeable commercial, subsistence, and recreational fisheries in the Great Lakes. By the mid-1950s, overfishing and predation by nonnative Sea Lamprey *Petromyzon marinus* led to the collapse of Lake Trout fisheries. The severe decline of Lake Trout triggered trout hatchery stocking and Sea Lamprey control programs, and Lake Trout populations demonstrated signs of recovery by the 1980s in the upper Great Lakes (Gorman and Sitar 2013).

Given the large body size they attain, Lake Trout are a popular sport fish among anglers and have been introduced worldwide, with some negative ecological impacts. A notable example was the illegal introduction of Lake Trout in the 1980s in Yellowstone Lake and an ensuing decline of native Yellowstone Cutthroat Trout. Since the first documented catch of Lake Trout by an angler in 1994, an aggressive Lake Trout removal program has been implemented by the National Park Service, but Lake Trout persist, and consequently the abundance of Yellowstone Cutthroat Trout remains at less than 10% of their historical level in the Yellowstone Lake watershed (Koel et al. 2005; Syslo et al. 2011).

Arctic Char.—Arctic Char are native to alpine lakes and arctic and subarctic coastal waters. They are the freshwater fish found the furthest north (found in Lake Hazen, Ellesmer Island, Northwest Territories, 82°N), and their distribution is holarctic and circumpolar (Figure 11). Their distribution is limited to higher latitudes than most trout because they are adapted and restricted to extremely coldwater habitat (<15°C; Klemetsen et al. 2003). The Arctic Char was first scientifically described in the salmon genus *Salmo* as *Salmo alpinus* by Carl Linnaeus and later separated into *Salvelinus* (California Academy of Sciences 2017). Recent genetic analyses (i.e., mitochondrial DNA) demonstrated five major lineages derived in the early to mid-Pleistocene, determined largely by geographic region and glacial refugia (a comprehensive summary is provided in Brunner et al. 2001). However, the contemporary range of Arctic Char was determined more recently by the last retreat of ice sheets 10,000–20,000 years ago. Of the five lineages identified by Brunner at al. 2001, three are represented in North America: the Bering (including western Alaska), Arctic (Canadian Arctic and northern Alaska), and Acadia lineages (southern Quebec, Canada and New England, USA). Arctic Char are distributed across the Canadian Arctic Ocean, including around the islands of the Arctic Archipelago in Canada. In the United States, Arctic Char are found across Alaska in the Brooks Range, Kigluaik Mountains, and Kuskokwim Mountains, as well as the Alaska and Kenai peninsulas, Kodiak Island, and a small area of Interior Alaska near Denali National Park (ADFG 2017). The southern-most U.S. populations of Sunapee Trout *Salve-*

linus alpinus oquassa (Figure 11) are landlocked in Maine where they were formerly known as both Blueback Trout and Sunapee Trout. In total, there are an estimated 4,000 populations in the United States and Canada combined (Maitland 1995).

Arctic Char are habitat generalists but are most often found in oligotrophic lakes with depauperate fish communities (Figure 16). Arctic Char opportunistically feed on all major prey types, and cannibalism is common and important in structuring populations (basic char biology is extensively reviewed in Johnson 1980 and Klemetsen et al. 2003). Perhaps one of the most notable characteristics of Arctic Char is their ubiquitous and incredible phenotypic plasticity (reviewed in Klemetsen et al. 2003). As a consequence of this plasticity and likely in response to intense competition for resources, multiple morphologies often live in sympatry and occupy different ecological and trophic niches (Jonsson and Jonsson 2001). Arctic Char polymorphisms include lentic and pelagic niches, and extreme differences in coloration, morphology (including trophic differentiation), and size (e.g., giants and dwarfs; Klemetsen et al. 2003, but see also Brunner et al. 2001). Like Bull Trout, they spawn in freshwater, possess diverse life-history expressions, and can be lacustrine, riverine, or anadromous (north of about 65° N). Landlocked populations may migrate within river drainages or can be sedentary and lacustrine. In anadromous populations, juveniles spend their first 1–9

Figure 16 Arctic Char. Photo: Stephen Klobucar.

years in freshwater, then move to the sea where they spend the short arctic summer, returning to overwinter in frozen lakes.

Arctic Char represent an extremely important cultural and economic resource in the Canadian and Alaskan Arctic. They are an important subsistence fishery for indigenous peoples in Canada and Alaska (Boivin et al. 1989; Power et al. 1989). Arctic Char are extensively cultured and farmed in Canada (and in many Nordic countries), support an important commercial fishery (reviewed in Klemetsen et al. 2003), and are considered an environmentally sustainable choice of fish to consume (SFW 2007). In Alaska, wild, lake-dwelling Arctic Char are popular sport fish, but most populations are far from the road, and Arctic Char are thus only lightly fished, with no special regulations (WNTI 2013).

Although they are internationally considered "of least concern" by the IUCN (Freyhof and Kottelat 2008), as a coldwater obligate, they are likely extremely sensitive to the direct effects of climate change (Budy and Luecke 2014). Notably, they dominate some of the northern geographic locations where temperatures are increasing the most on the globe (ACIA 2005; Reist et al. 2006), and as such, the effects of climate change are predicted to exacerbate existing stressors. Metabolically, bioenergetic predictions are that if lake productivity does not also increase in the Arctic, landlocked, lentic char may very well eat themselves out of house and home due to increased consumptive demand under warmer lake temperatures (Budy and Luecke 2014). In Alaska, Arctic Char are also potentially threatened by habitat degradation associated with future oil and gas development (WNTI 2013).

Values

Trout and char are a celebrated group of fishes that have high ecological, economic, social, and cultural value. The connection they have to their native ecosystems and to people in general is profound and complex. In addition, throughout North America, trout and char hold a distinct place in the culture, nutrition, and economy of the indigenous people. In fact, the names of many trout and char come from names given by or linked to indigenous people. Apache Trout and Paiute Cutthroat Trout are named after North American tribes; the scientific name of Rainbow Trout, *mykiss*, is derived from the Koryak Tribe of Kamchatka; and the scientific name of Lake Trout, *namaycush*, is derived from the Eastern Cree. Trout and char were also historically important for food and as trade. However, they continue to be an important symbol for the culture and commerce for various groups of people in the places where they live. Many trout and char are designated as state fishes in the United States, emphasizing their wide-ranging social and cultural importance and symbology, including Apache Trout in Arizona; Golden Trout in California, Rainbow Trout (including steelhead and redband trout) in Washington; Cutthroat Trout in the states of Colorado, Idaho, Montana, Nevada, New Mexico, Utah, and Wyoming; and Brook Trout in Michigan, New Hampshire, New Jersey, New York, North Carolina, Pennsylvania, Vermont, Virginia, and West Virginia.

Trout and char have important recreational and economic value, with 7.2 million Americans fishing for them in 2011 (USFWS 2015b). Trout anglers spent approximately US\$3.6 × 10^9 on fishing equipment and trip expenses in 2011, which translated into an overall estimated economic impact of \$8.6 × 10^9. Trout and char continue to be among the most popular freshwater recreational fishes in the United States along with bass *Micropterus* spp., catfish *Ictalurus* spp., and crappies *Pomoxis* spp. However, despite an increase of 26% from 1991 to 2011 in the U.S. population aged 16 years and older, the number of trout anglers simultaneously declined 21% from 9.1 million to 7.2 million. Reversal of this trend, both through efforts to revitalize enthusiasm for outdoor leisure in nontraditional markets (e.g., urban fisheries) and habitat improvement and population restoration programs, could result in substantial economic development at the local and state levels (Jackson et al. 2012).

Because of their popularity as game fish, trout and char enjoy broader management support than most species of fish and wildlife, particularly among those that are imperiled. Such support is not without controversy because of apparently conflicting mandates for management. For example, the USFWS recognizes hundreds of conservation populations of Colorado River Cutthroat Trout when evaluating the viability of the subspecies and whether listing is warranted under the ESA. However, the hundreds of lakes that are managed for recreational fishing with aerial stocking of pure Colorado River Cutthroat Trout fingerlings are not subject to listing deliberations since these are not self-sustaining populations. On one hand, we sometimes foster robust conservation efforts designed to protect native trout, imposing stringent environmental regulations related to land-use and angling pressure, while on the other, we encourage angling and liberal harvest.

Throughout their ranges in North America, trout and char have been intertwined with subsistence and various industries and activities, including the fur trade, mining, agriculture, forestry, urbanization and development, hydropower and flood control, hatchery and aquaculture, and illegal drug activities. The value of trout to society has been recognized by laws and regulations designed to protect them. For example, forestry has been strongly regulated to protect water quality as well as habitat for trout and char in forested headwater streams, and instream flow regulations typically take into account ecological needs of native trout (Armstrong et al. 2001; Beauchene et al. 2014).

But in addition to legal mechanisms, many imperiled species, for example certain subspecies of Cutthroat Trout (e.g., Bonneville Cutthroat Trout; Lentsch et al. 2000), are protected under multi-partner conservation agreements, which typically are signed by state, federal, and private partners and are aimed at encouraging activities that work to prevent listing under the ESA. These agreements demonstrate the widespread and diverse value placed on trout species of concern and provide recommendations for maintaining and improving their status. Similarly, many trout anglers across North America participate in voluntary catch and release, further demonstrating the value they place on native and wild trout.

Management

There is a long history of trout and char management in North America (e.g., Gresswell and Varley 1988; Behnke 1992). In the earlier days of the 19th and 20th centuries, management focused on establishing or supplementing populations through hatchery propagation and stocking. Although the recreational importance of trout and char remains unchanged or perhaps has increased since the early days, contemporary management also emphasizes conservation and restoration of native populations. Management actions vary depending on whether the goal is to manage for recreation or conservation, and management that works to achieve one goal can negatively affect another (e.g., stocking of a nonnative species for recreational angling resulting in hybridization with a native species). Consequently, many management agencies have adopted contemporary policies whereby existing native wild stocks in particular have greater priority for management (e.g., Yellowstone Cutthroat Trout and Brook Trout preference for native strains; Thurow et al. 1988).

Although declining in some regions, demand for recreational angling is partly met by propagation and stocking programs of federal and state agencies responsible for fisheries management. These efforts are particularly important in areas where trout and char abundance has substantially decreased, such as the southern Appalachian Mountains, the Rocky Mountains, and the Intermountain West. Fishing regulations are common and include size and possession limits, seasonal restrictions, delayed harvest, and bait and tackle restrictions. Types of fishing regulations may vary depending on water bodies, with hatchery-supported trout waters having more liberal restrictions than wild trout waters. Catch-and-release regulations are frequently used, particularly in smaller water bodies not capable of supporting a large trout or char population. Yellowstone Cutthroat Trout, for example, have responded positively to catch-and-release, no-kill regulations in many cases (Varley and Gresswell 1988).

Many contemporary management actions are targeted for conservation and restoration of native trout and char populations. Instream and riparian habitat has been managed for trout, and the addition of large woody debris is a common technique of habitat restoration in streams lacking physical complexities (Gowan and Fausch 1996; Hilderbrand et al. 1998; Flebbe 1999). Riparian areas regulate sediment loading, stream temperature, flow regime, and channel sinuosity (Gregory et al. 1991) and play an important role in mediating trout and char habitat. The importance of high-quality habitat is demonstrated, for example, by the few strongholds of Westslope Cutthroat Trout, which are all located in wilderness areas or national parks where habitat degradation is minimal (Liknes and Graham 1988). Because streams are influenced by surrounding land use, cooperation with stakeholders to apply best management practices is important in minimizing the impact on stream habitats. As such, using properly designed livestock grazing strategies, for example, has substantially improved riparian habitats for Cutthroat Trout (reviewed in Varley and Gresswell 1988; Saunders and Fausch 2007, 2012). Similarly, management standards for lands adjacent to streams often include the protection of riparian buffers, with the widest buffer requirements for fish-bearing streams on federal land (e.g., Boisjolie et al. 2017).

Restoration of stream habitat connectivity is another management action that can benefit trout and char populations at the watershed scale. A large proportion of non-anadromous trout and char individuals typically move within a watershed and help reconnect local populations (Gowan and Fausch 1996; Letcher et al. 2007; Petty et al. 2012). In response to this need to maintain metapopulation connectivity for Brook Trout in their native range, culvert replacement or removal has been prioritized by the Eastern Brook Trout Joint Venture and Trout Unlimited. Similarly, fish screens on irrigation diversions have been successful for restoring passage and reducing losses of Yellowstone Cutthroat Trout (Thurow et al. 1988). Acquisition of property, conservation easements, and water rights are frequently listed as management goals for the conservation of trout (e.g., Gresswell 1988) and are becoming more important as human demand for land and water increases. Maintaining sufficient stream flows is increasingly becoming a critical issue for trout and char particularly in arid regions. For example, in Montana, the earliest legal protections of Blue Ribbon trout streams came in 1969 with a bill that created 12 instream water rights held by the Montana Department of Fish, Wildlife, and Parks. Additional legislation provided further vital protections to hundreds of miles of streams from new water withdrawals. However, it is the ability to transfer a senior irrigation right to an instream purpose and retain the right's priority date that has provided restoration flows to dewatered rivers and streams across Montana. Every western state now recognizes instream flow rights, and progress is being made in addressing the legal and administrative challenges of obtaining and holding instream rights across the West, increasing their effectiveness as habitat restoration tools (Ziemer et al. 2016). Abundant public land in the western United States also provides plentiful water and habitat and thus will continue to serve as a foothold for these species (e.g., 66% of the water supply comes from federal lands; Brown et al. 2008).

Management of nonnative trout and char and the threat of predation, competition, and hybridization is critical in the conservation of native species and has been identified as the most limiting factor to the persistence of many native trout populations (the management paradox of trout is reviewed in Chapter 19). For example, physical barriers have been installed to isolate threatened Cutthroat Trout populations from invasion by downstream dwelling nonnative species. This isolation strategy, however, comes with the cost of making the typically small populations more vulnerable to local extirpation due to stochastic demographic and genetic effects (Fausch et al. 2009). Removals of nonnative trout species have been successfully implemented with electrofishing and piscicides across the range of Cutthroat Trout (e.g., Thurow et al. 1988; Saunders et al. 2014) and char (Moore et al. 1986, 2005; Hoxmeier and Dieterman 2016) and other nonnative removals are underway using commercial fishing techniques to remove nonnative Lake Trout from Yellowstone Lake (Syslo et al. 2011). However, with current technology, eradications of nonnative species are expensive and often simply not feasible (Meyer et al. 2006; Hoxmeier and Dieterman 2016). Innovative alternative approaches including the release of YY male Brook Trout are being tested in Idaho to reduce and eventually eradicate invasive Brook Trout populations by creating populations composed solely of males (Schill et al. 2016). To eliminate straying, sterile triploids are being used more frequently and becoming popular sport fishes (e.g., Winters et al. 2017).

Native trout and char have also been reintroduced in their former range as a management and conservation approach. For example, efforts are underway to reintroduce Greenback Cutthroat Trout after a recent genetic study identified a single remaining population of Greenback Cutthroat Trout persisting outside of its native range (Metcalf et al. 2012). Brook Trout populations in the southern Appalachian Mountains streams harbor a mix of genetically pure southern strains and those with signs of hatchery introgression (Hayes et al. 1996). Reintroduction of Brook Trout in the region aims to restore southern strains and is usually preceded by removals of nonnative Rainbow Trout (Kanno et al. 2016). Cutthroat Trout have been successfully reintroduced and have re-established after nonnative Brown Trout and Brook Trout were removed mechanically, chemically, or after intense wildfire (e.g., Hepworth et al. 1997; Saunders et al. 2014). Actions such as these will help ensure these diverse iconic fish persist long into the future.

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