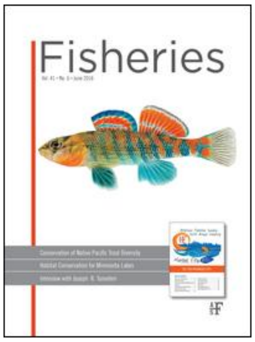

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FEATURE

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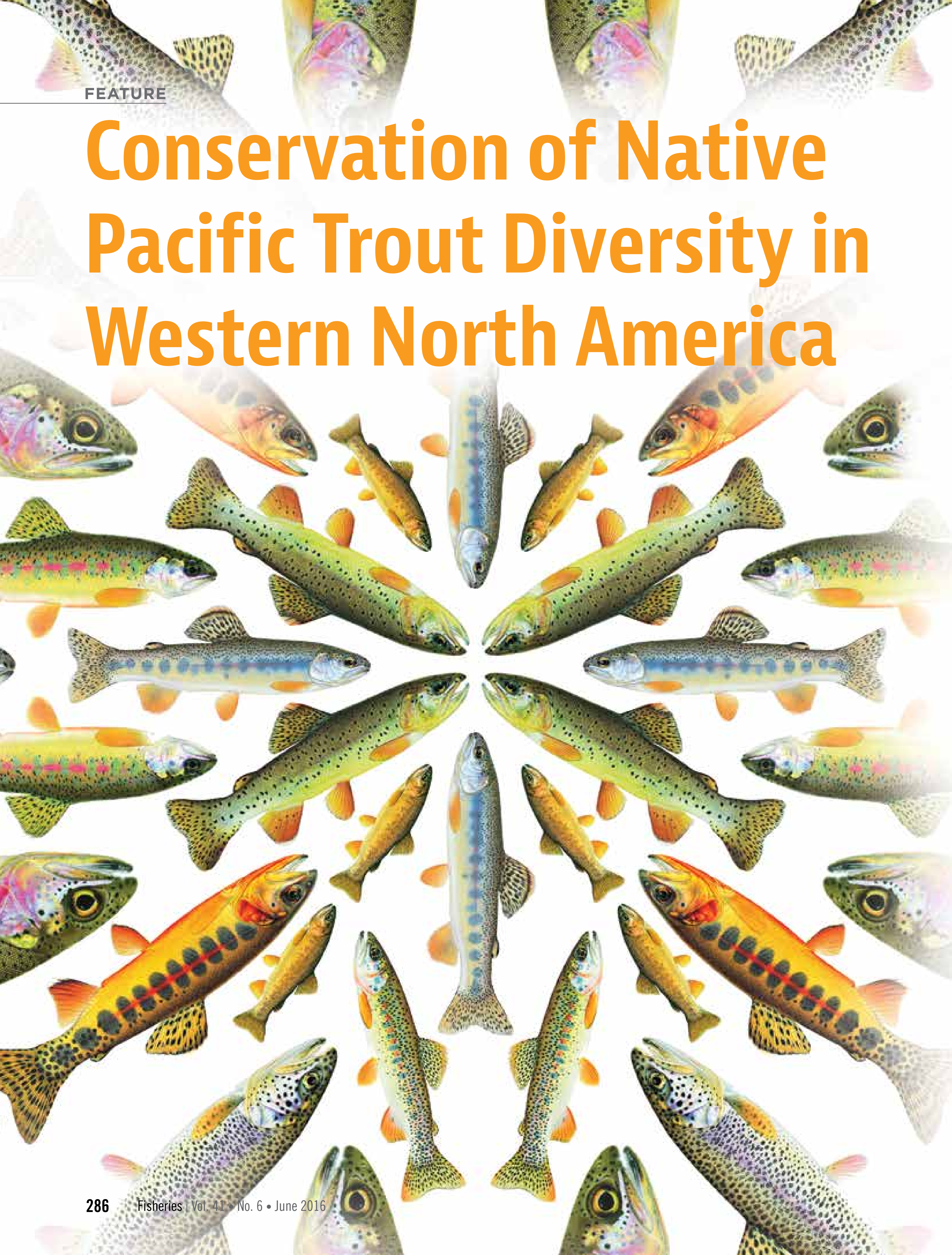

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Pacific trout *Oncorhynchus* spp. in western North America are strongly valued in ecological, socioeconomic, and cultural views, and have been the subject of substantial research and conservation efforts. Despite this, the understanding of their evolutionary histories, overall diversity, and challenges to their conservation is incomplete. We review the state of knowledge on these important issues, focusing on Pacific trout in the genus *Oncorhynchus*. Although most research on salmonid fishes emphasizes Pacific salmon, we focus on Pacific trout because they share a common evolutionary history, and many taxa in western North America have not been formally described, particularly in the southern extent of their ranges. Research in recent decades has led to the revision of many hypotheses concerning the origin and diversification of Pacific trout throughout their range. Although there has been significant success at addressing past threats to Pacific trout, contemporary and future threats represented by nonnative species, land and water use activities, and climate change pose challenges and uncertainties. Ultimately, conservation of Pacific trout depends on how well these issues are understood and addressed, and on solutions that allow these species to coexist with a growing scope of human influences.

Conservación de la diversidad de truchas nativas del Pacífico en el oeste de Norteamérica

La trucha del Pacífico *Oncorhynchus* spp. en el oeste de Norteamérica tiene un alto valor desde el punto de vista ecológico, socioeconómico y cultural, y ha sido objeto de importantes esfuerzos de conservación e investigación. A pesar de ello, el conocimiento que se tiene sobre su historia evolutiva, diversidad general y retos de conservación sigue siendo incompleto. Se hace una revisión del estado del conocimiento sobre estos puntos, con énfasis en la trucha del Pacífico dentro del género *Oncorhynchus*. Si bien la mayor parte de los estudios hechos sobre salmónidos se enfocan al salmón del Pacífico, aquí nos enfocamos en la trucha del Pacífico ya que ambos groupos de especies comparten una historia evolutiva en común sobre todo en lo que se refiere al extremo sur de sus rangos de distribución. En investigaciones llevadas a cabo en décadas recientes, se han revisado varias hipótesis relativas al origen y diversificación de la trucha del Pacífico a lo largo de su rango de distribución. Aunque se han logrado identificar adecuadamente las amenazas pasadas que enfrentó la trucha del Pacífico, las amenazas actuales y futuras que representan especies no nativas, actividades de uso de tierra y agua y el cambio climático se consideran importantes retos e incertidumbres. Al final, la conservación de la trucha del Pacífico depende de qué tan bien se comprendan y abordan estos temas, y de las soluciones que les permitan a estas especies coexistir con una gama creciente de influencias humanas.

Conservation de la diversité de la truite du Pacifique indigène dans l'ouest de l'Amérique du Nord

Les truites du Pacifique ou *Oncorhynchus* spp. dans l'ouest de l'Amérique du Nord sont fortement valorisées du point de vue écologique, socio-économique et culturel, et ont attiré l'attention en matière de recherche et d'efforts de conservation importants. En dépit de cela, la compréhension de leurs histoires évolutives, de leur diversité globale, et des défis liés à leur conservation est incomplète. Nous passons en revue l'état des connaissances sur ces questions importantes, en nous concentrant sur la truite du Pacifique du genre *Oncorhynchus*. Bien que la plupart des recherches sur les salmonidés mettent l'accent sur le saumon du Pacifique, nous nous concentrons sur la truite du Pacifique parce qu'elle partage une histoire évolutive commune et de nombreux taxons dans l'ouest de l'Amérique du Nord n'ont pas été formellement décrits, en particulier dans leur aire de répartition méridionale. Les recherches des dernières décennies ont conduit à la révision de nombreuses hypothèses concernant l'origine et la diversification de la truite du Pacifique dans toute son aire de répartition. Bien qu'on ait enregistré un succès considérable dans la lutte contre les menaces qui pesaient sur elle, les menaces contemporaines et futures que représentent les espèces non indigènes, l'utilisation de l'eau et des terres, et les changements climatiques posent des défis et induisent des incertitudes. Enfin, la conservation de la truite du Pacifique dépend de la façon dont ces questions sont comprises et traitées, et des solutions qui permettent à ces espèces de coexister en tenant compte des influences humaines croissantes.

INTRODUCTION

The history of Pacific trout *Oncorhynchus* spp. is a compelling story of persistence and evolutionary diversification in the face of dynamic environments. Spanning western North America and extending into East Asia, they have experienced advances and retreats of continental glaciers, volcanic eruptions, enormous floods, and major geotectonic events that led to formation of mountain ranges and plateaus, and determined the course of present-day rivers (Figure 1). Pacific trout are found in sub-arctic to sub-tropical freshwater catchments that generally drain into the Pacific Ocean, but some populations exist in closed basins, and others drain into the Gulf of Mexico east of the Continental Divide. Although Pacific trout share many notable life history traits with Pacific salmon and salmonids in general, they are also distinctive in that they are optionally anadromous (at least for some forms of *O. mykiss* and *O. clarkii*), iteroparous, spring spawners (varies with local conditions and the months of spawning can vary widely), and they can live up to 10 years or more (Quinn 2005). Their genetic, phenotypic, and life-history diversity (Behnke 1992) and their ability to migrate long distances across diverse habitats have allowed them to persist through major climatic fluctuations and environmental change. These characteristics of Pacific trout are the keys to their future persistence.

In western North America, Pacific trout are composed of the species Cutthroat Trout *O. clarkii* ssp., Rainbow Trout/redband/steelhead *O. mykiss* ssp., Golden Trout *O. aguabonita* ssp., 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) complex, Mexico (Figure 2, Table 1; Behnke 1992; Utter and Allendorf 1994; Hendrickson et al. 2002). However, substantial declines in abundance and contractions in distribution across species and subspecies, by at least two-thirds from historical levels, have led to elevated protection by federal, state, and provincial management agencies in some or whole portions of their range (U.S. Endangered Species Act; Canada Species at Risk Act [SARA]; Mexico SEMARNAT

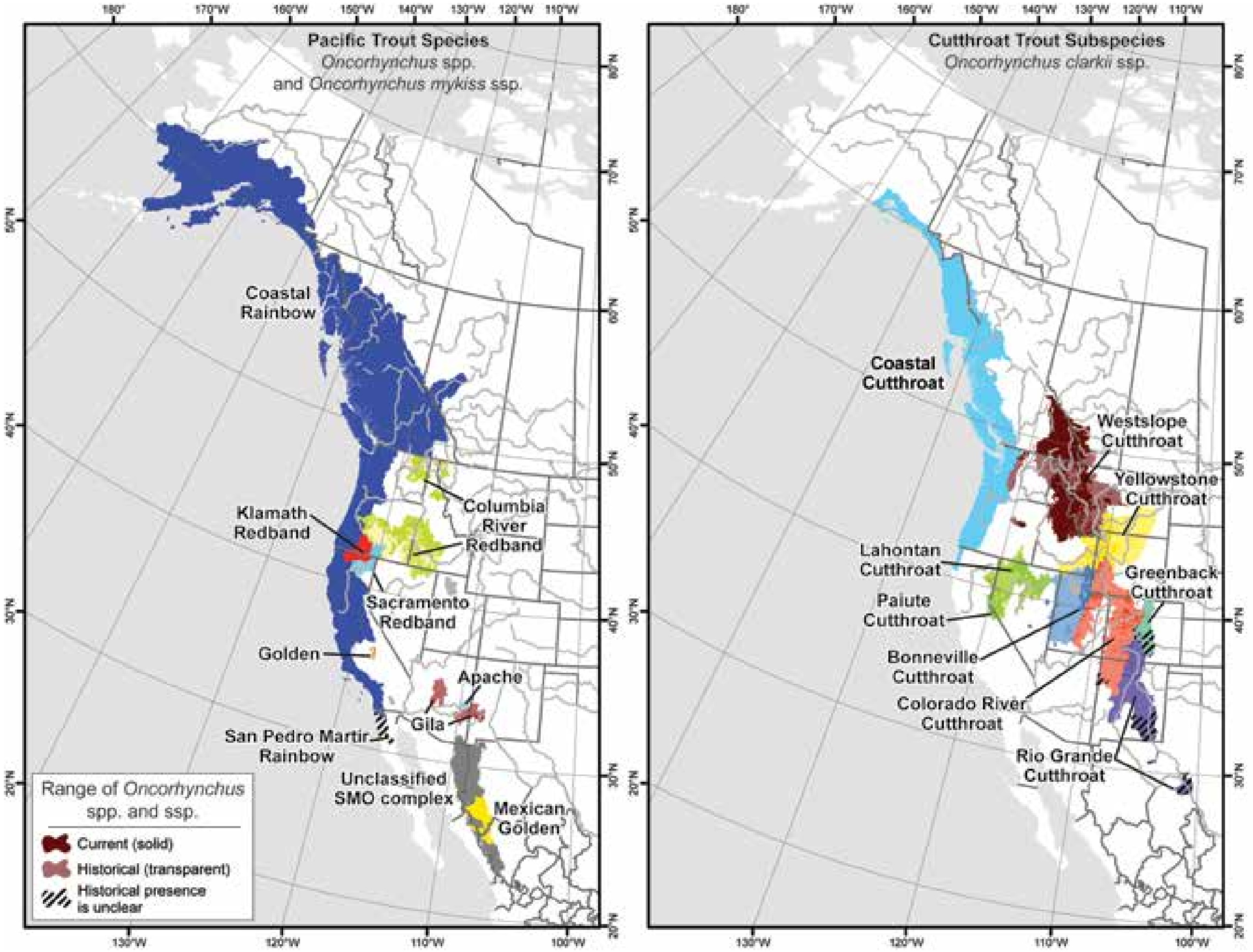

Figure 1. Historical and current distributions of Pacific trout in western North America, with distributions of *O. mykiss* ssp. and other Pacific trout (left panel), and *O. clarkii* ssp. (right panel). The distribution of Columbia River Redband Trout ends at the U.S.–Canada border because Redband Trout are not recognized taxonomically in Canada.

2000; International Union for the Conservation of Nature [IUCN] 2010). Further, two Cutthroat Trout subspecies, the Alvord Cutthroat Trout *O. clarkii alvordensis* and the Yellowfin Cutthroat Trout *O. clarkii macdonaldi*, are considered extinct (Behnke 1992, 2002). Therefore, the decline of Pacific trout over recent decades, and in some cases the last century, reflects the challenges of balancing societal values with natural resources and wild places under a changing climate.

Human influences leading to declines in Pacific trout began with Euro-American colonization of North America. As Euro-American explorers and settlers began moving westward at the turn of the 19th century, so did the destruction of riverscapes (Figure 3). Eradication of American beaver (Naiman et al. 1988), grazing of rangelands (Platts 1991), logging of forests (Northcote and Hartman 2004), diking and draining of river floodplains (Brinson and Malvárez 2002), and widespread mining (e.g., Nelson et al. 1991; Mount 1995) variably contributed to degraded conditions in riverscapes. Similar changes have occurred in northern Mexico, although somewhat later, and some are just now leading to negative consequences (Hendrickson et al. 2002; Espinosa et al. 2007). Collectively, these contemporary and historical legacies fundamentally transformed western riverscapes (McIntosh et al. 2000). Sportfishing for trout and supporting activities of hatcheries, put-and-take stocking, and a wave of introductions of nonnative trout, including Brown Trout *Salmo trutta*, Brook Trout *Salvelinus fontinalis*, and Lake Trout *S. namaycush*, have also contributed to the decline of Pacific trout (Miller 1950; Miller and Hubbs 1966; Fausch 2008). In addition, *O. mykiss* ssp. and *O. clarkii* ssp. were broadly translocated within and outside their native ranges in western North America (Miller 1950; Miller et al. 1992; Hendrickson et al. 2002). Throughout the 20th century, particularly after World War II, riverscapes became fragmented by construction of dams on major rivers (Behnke 1992) and countless smaller barriers at stream–road crossings, dikes, and diversions, isolating native Pacific trout in headwater enclaves (Rieman et al. 2003; Fausch et al. 2009).

The early 1970s heralded passage of new environmental protection laws (e.g., the Endangered Species Act and Clean Water Act in the United States) and a growing awareness among managers concerning the value of native, wild trout. After decades of neglect, conservation of Pacific trout gained momentum (e.g., Gresswell 1988) in part due to major efforts by Robert J. Behnke (Schreck et al. 2014) to communicate clearly the value of these species to the general public (Behnke 1972, 1992, 2002, 2007). Although it was evident that Pacific trout were in peril, there was a shift in perception and a new dedication to conserving and protecting these important symbols

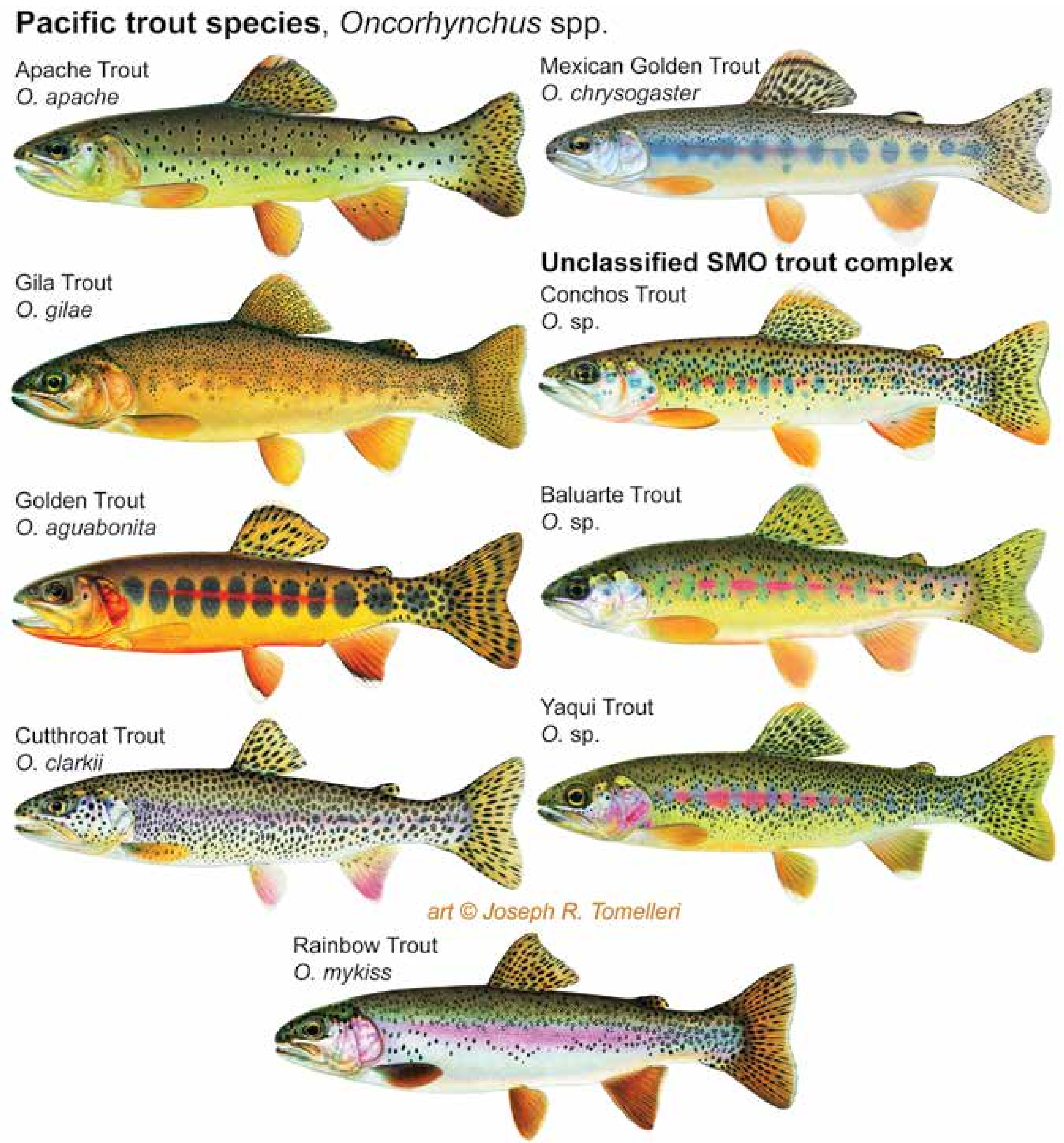

Figure 2. Pacific trout species and examples of some morphotypes from the unclassified Sierra Madre Occidental (SMO) trout complex. Illustrations by Joseph R. Tomelleri are used with permission.

of functioning coldwater ecosystems. Here, we review the recent history of the study of Pacific trout; synthesize their evolutionary diversity; describe future threats from nonnative species, climate change, and land use activities; and highlight examples that illustrate shared tradeoffs associated with native trout conservation efforts.

EVOLUTIONARY DIVERSITY

Scientific discovery and description of native Pacific trout in western North America dates to the early 19th century and has continued into the present. Early scientists described lineages collected during surveys of western North America (Cope and Yarrow 1875; Jordan 1891; Jordan and Evermann 1898), but confusion related to unknown or poorly documented localities led to misconceptions concerning the distribution of Pacific trout on the landscape and to a proliferation of named taxa. Behnke (1960, 2002) and Behnke and Zarn (1976) clarified many of these taxonomic issues. Recently, there has been a discovery of new taxa of Pacific trout in their southern extent in Mexico (Hendrickson et al. 2002; Ruiz Campos et al. 2003; Mayden et al. 2010), where multiple factors including accessibility, safety, and research support pose challenges to scientific study. Across the range of Pacific trout, however, many lineages, subspecies, and species remain to be formally described.

Table 1. Current status of Pacific trout species and subspecies in western North America.

Common name	Scientific name	Current status	Source
Alvord Cutthroat	*O. c. alvordensis*	Extinct	Behnke 2002
Yellowfin Cutthroat	*O. c. macdonaldi*	Extinct	Behnke 2002
Lahontan Cutthroat[a]	*O. c. henshawi*	Threatened, ESA	USFWS 2009a
Paiute Cutthroat	*O. c. seleneris*	Threatened, ESA	USFWS 2012b
Greenback Cutthroat	*O. c. stomias*	Threatened, ESA	USFWS 1998; Young et al. 2002; Metcalf et al. 2012; Bestgen et al. 2013
Rio Grande Cutthroat	*O. c. virginalis*	Former candidate for listing under ESA, found not warranted in October 2014	Pritchard and Cowley 2006; USFWS 2014
Yellowstone Cutthroat[b]	*O. c. bouvieri*	Former candidate for listing under ESA, found not warranted in February 2006	USFWS 2006; Gresswell 2011
Colorado River Cutthroat	*O. c. pleuriticus*	Former candidate for listing under ESA, found not warranted in June 2007	USFWS 2007; Hirsch et al. 2013
Bonneville Cutthroat	*O. c. utah*	Former candidate for listing under ESA, found not warranted in September 2008	USFWS 2008; Lentsch et al. 2000
Westslope Cutthroat	*O. c. lewisi*	Former candidate for listing under ESA, found not warranted in August 2003; Threatened in Alberta and Special Concern in British Columbia, SARA	USFWS 2003; Shepard et al. 2005; COSEWIC 2006
Coastal Cutthroat	*O. c. clarkii*	Generally healthy, some depressed populations in the United States; they have not been formally assessed at the federal level in Canada, but in British Columbia they are apparently secure but of special concern (S3S4)	Connolly et al. 2008; Costello 2008; www.coastalcutthroattrout.org; BC CDC 2015
Coastal Rainbow[c]	*O. mykiss irideus*	Many populations in the continental United States are Threatened or Endangered, ESA; at the federal level in Canada, the Athabasca River Population is a candidate for listing as Endangered, SARA; additional population assessments have not yet been completed at the federal level; in British Columbia, they are demonstrably widespread, abundant, and secure (S5) and in Alberta they are threatened	Busby et al. 1996; Good et al. 2005; NOAA 2006; SEMARNAT 2010; COSEWIC 2014
San Pedro Martír Rainbow	*O. m. nelsoni*	Special Concern and federally protected in Mexico	SEMARNAT 2010; Ruiz-Campos et al. 2014
Redband[d]	*O. m.* ssp.	Although many populations are apparently depressed in the United States, they do not have elevated status or protection	Behnke 1992; Currens et al. 2009; Muhlfeld et al. 2015
Golden[e]	*O. aguabonita*	Former candidate for listing under ESA, found not warranted in October 2011, but *O. a. whitei* is Threatened, ESA	USFWS 2011; USFWS 2012a
Gila	*O. gilae*	Threatened, ESA	Behnke and Zarn 1976; Rinne 1990; USFWS 2010
Apache	*O. apache*	Threatened, ESA	Rinne 1990; USFWS 2009b
Mexican Golden	*O. chrysogaster*	Vulnerable, IUCN; federally protected in Mexico	Contreras-Balderas and Almada-Villela 1996; SEMARNAT 2000
Unclassified SMO trout complex	*O.* spp.	Still being described, not yet evaluated	Behnke 2002; Hendrickson et al. 2002; Mayden et al. 2010

[a]Includes Humboldt Cutthroat (*O. c. humboldtensis*) and Whitehorse Basin Cutthroat (*O. c.* spp.). Source: Behnke (2002).
[b]Includes Snake River Finespotted Cutthroat (*O. c. behnkei*). Source: Behnke (1992); Montgomery (1995); Van Kirk et al. (2006).
[c]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*.
[d]In the United States, inland Rainbow Trout groups occurring east of the Cascade Range and Sierra Nevada along the Pacific Coast are classified as Redband Trout *O. m.* ssp. Three subspecies of Redband Trout occur: Columbia River Redband Trout *O. mykiss gairdneri*, which occur east of the Cascade Range in the Columbia river and Harney Basin; Klamath Redband Trout *O. mykiss newberrii* of the northern Great Basin and Klamath region; and Sacramento Redband Trout *O. mykiss stonei* of Warner Valley, Goose Lake, and Chewaucan Basin (Currens et al. 2009).
[e]Includes Little Kern Golden (*O. a. whitei*). Source: Behnke (1992); Stephens (2001).

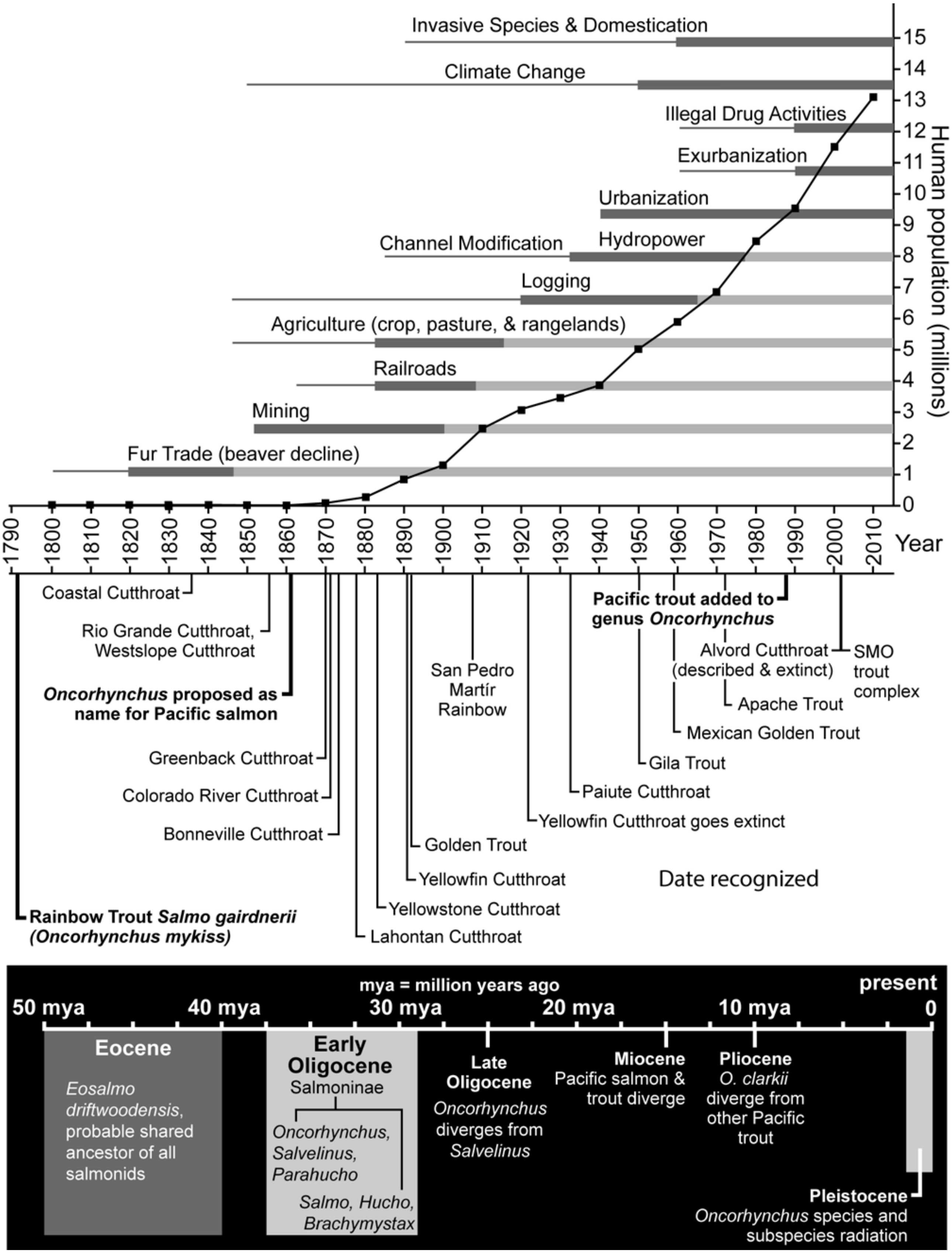

Figure 3. Timeline covering past, current, and future anthropogenic threats to Pacific trout (modified from ISAB 2011; Rieman et al. 2015); identifying dates of scientific description in recent history; and displaying dates of evolutionary significance on the geologic timescale. Although a wide range of uncertainty over divergence times for salmonids exists, we have displayed the most widely accepted chronology. For the top bar chart, wide dark bars mark the period of peak development and rapid habitat conversion. Wide light bars depict continued effects following the initial period of rapid change. Concurrent change in human population size for the Pacific Northwest of the United States is shown, but we added climate change (IPCC 2013), invasive species and domestication (Sanderson et al. 2009), and illegal drug activities (Bauer et al. 2015).

Phylogenetic understanding of native Pacific trout has evolved considerably since Behnke's influential publications (Behnke 1972, 1992, 2002). Advances in molecular genetic techniques and associated analyses over the last several decades have given rise to new hypotheses regarding taxonomic relationships and revealed increased species diversity (Allendorf and Leary 1988; Crespi and Fulton 2004; Crête-Lafrenière et al. 2012). However, the taxonomy of Pacific trout in western North American is subject to ongoing debate (Metcalf et al. 2007; Pritchard et al. 2008; Loxterman and Keeley 2012). For example, recent studies used century-old museum collections to define the native range and diversity of lineages in the southern Rocky Mountains for Greenback, Colorado River, and Yellowfin Cutthroat trouts (Metcalf et al. 2012; Bestgen et al. 2013), and this information is being used to identify extant native populations and to guide the search for remaining pockets of diversity.

The genera *Oncorhynchus* and *Salmo* are thought to have last shared a common ancestor 15–35 million years ago in the Miocene and Oligocene (Figure 3; Devlin 1993; Waples et al. 2008; Wilson and Turner 2009; but see Shedlock et al.1992; Oakley and Phillips 1999). During the Miocene–Pliocene–Pleistocene, geologic activity and climate variability in western North America likely promoted radiation of salmonid taxa (Montgomery 2000), and the fossil record shows that trout occurred as far south as Lake Chapala, Jalisco, Mexico, near 20° N, during interglacial periods (Cavender and Miller 1982). According to the most widely accepted chronology, by the end of the Miocene, about 6–15 million years ago, the genus had diverged into a distinct lineage for Pacific trout and other lineages for Pacific salmon (Stearley and Smith 1993; Wilson and Turner 2009; Crête-Lafrenière et al. 2012). By the Pliocene, about 4–6 million years ago, *O. clarkii* diverged from the other Pacific trout, including *O. chrysogaster*, then likely diverged from *O. mykiss* (Abadía-Cardoso et al. 2015). A wide range of uncertainty still exists, however, over divergence times for salmonids, with no defensible reason to favor one set of dates over another.

In the interior regions of western North America, *O. clarkii* colonized multiple basins, including several on the eastern side of the Continental Divide, and subspecies continued to evolve in isolation (Behnke 2007), giving rise to distinct lineages that generally align with major drainage basins (Figure S1; Behnke 2002; Smith et al. 2002; Bestgen et al. 2013). Exceptions to this pattern reflect historical connections among catchments over the evolutionary history of the species (Loxterman and Keeley 2012). However, researchers continue to identify native lineages and subspecies of Cutthroat Trout. Current molecular evidence suggests that there are at least nine genetically distinguishable extant lineages (Figure 1) and two extinct ones (Allendorf and Leary 1988; Loxterman and Keeley 2012; Metcalf et al. 2012). Behnke (1992, 2002), however, recognized 14 subspecies of Cutthroat Trout (based on morphological differences), including two extinct lineages. Future research is needed to reconcile these differences in the number of subspecies, based on morphological and genetic results.

In contrast, it has been hypothesized that the *O. mykiss* complex underwent various periods of isolation and convergence, leading to greater overall mixing and fewer distinct lineages, with the exception of lineages that inhabit Asia, Gulf of California tributaries, and *O. m. nelsoni* in Mexico (Figure S2; Behnke 2002, 2007). Similar to *O. clarkii*, however, taxonomic nomenclature for this species also remains unresolved across their range. In Canada, no subspecies of *O. mykiss* are recognized (Scott and Crossman 1998; McPhail 2007). Although there are no subspecies of *O. mykiss* recognized in the United States, there are genetic divisions between coastal and interior populations and among some interior groups of populations that are considered distinctly different lineages (Behnke 1992; Currens et al. 2009; Muhlfeld et al. 2015). These interior populations of native *O. mykiss* occurring east of the Cascade Range and Sierra Nevada are referred to as Redband Trout in the United States (Smith et al. 2002; Meyer et al. 2014; Muhlfeld et al. 2015) and consist of three genetically distinct lineages, comparable to those among other Pacific trout subspecies (Figure 1; Currens et al. 2009). Some of the diversity of both *O. clarkii* and *O. mykiss* has been obscured by extensive introductions of both domesticated Rainbow Trout and other lineages of Rainbow and Cutthroat trouts into locations where they were not historically present (Metcalf et al. 2012; Escalante et al. 2014; Abadía-Cardoso et al. 2015).

The southernmost trout taxa make up a diverse group of the least-known Pacific trout of western North America (Figure 2; Behnke 2002). Although there are still many unanswered questions about the evolutionary relationships and taxonomy of many southernmost trout taxa, the current hypothesis is that Gila, Apache, Golden, and Mexican Golden trouts lineages were derived from the ancestral *O. mykiss* lineage, with Mexican Golden Trout hypothesized as the basal sister lineage (Hendrickson et al. 2002). The SMO trout complex consists of potential subspecies and species that are believed to be derived from colonization of tributaries in the Gulf of California by sea-run *O. mykiss* (Behnke 1992) and by colonization of *O. clarkii* through the Rio Grande basin (Hendrickson et al. 2002). Recent work suggests, however, that the SMO trout complex is more closely related to *O. mykiss*, and contemporary trout in the Conchos River, a tributary of the Rio Grande that drains into the Gulf of Mexico, seem to be most closely related to *O. chrysogaster* (Abadía-Cardoso et al. 2015; García-De León et al., unpublished data).

Identifying appropriate conservation units and ecologically adaptive variation in Pacific trout has been complicated by significant morphological, behavioral, and life history variation found within and among species (Northcote 1997; Taylor et al. 2011; Kendall et al. 2015). Although Pacific trout populations are tied to stream habitats for spawning in spring and subsequent rearing, many exhibit a range of morphological and life - history characteristics (Behnke 1992; Keeley et al. 2007; Phillis et al. in press). Pacific trout populations with access to larger downstream water bodies often migrate from headwater spawning and rearing streams to lake and river habitats where they generally achieve larger size and fecundity than they would in headwater streams alone (Northcote 1997). Populations of *O. clarkii* and *O. mykiss* with access to the ocean move between freshwater and marine environments, but even within those populations, some individuals may become sea run, whereas others remain in freshwater (Hall et al. 1997; Kendall et al. 2015). Trophic specialization and tolerance for extreme dynamic conditions by individuals in some populations also highlight the evolutionary potential of Pacific trout populations (Behnke 1992; Gamperl et al. 2002; Gresswell 2011). For example, Redband Trout populations from Bridge Creek, Oregon, have anatomical phenotypes that support a greater swimming ability at elevated stream temperatures compared to nearby populations (Gamperl et al. 2002).

CURRENT AND FUTURE THREATS

In addition to legacies of past and continuing land use activities, including habitat degradation from forest harvest, agriculture, cattle grazing, mining, and migration barriers, newer threats of nonnative species, climate change, and other land use activities have emerged (Figure 3). Interactions among threats have become increasingly apparent in recent years; hence, it is critical to recognize cumulative effects when considering the status and persistence of Pacific trout (Bisson et al. 1992; Schindler 2001; Penaluna et al. 2015).

Nonnative Species

Extensive introductions of nonnative fishes for aquaculture and recreational fishing are among the greatest threats to the persistence of Pacific trout (Miller et al. 1989; Williams et al. 1989; Bahls 1992). Introductions of nonnative fishes, such as Brook Trout, Brown Trout, Lake Trout, Northern Pike *Esox lucius*, and Smallmouth Bass *Micropterus dolomieu,* have led to the decline and local extirpation of many native Pacific trout through ecological interactions (e.g., competition, predation, disease transfer; Rahel 2000; Dunham et al. 2004; Muhlfeld et al. 2008). Further, introductions of trout outside of their native range have resulted in introgression and homogenization between historically allopatric lineages and subspecies, and widespread introductions of strains of Rainbow Trout have been a major cause of the loss of Pacific trout throughout their range (Allendorf and Leary 1988; Yau and Taylor 2013; Escalante et al. 2014). The importance of a growing list of non-salmonid nonnative species (Sanderson et al. 2009), particularly cool- and warmwater fishes (Lawrence et al. 2014) that are invading native Pacific trout habitat, warrants increasing attention, especially for streams that are warming due to climate change or local land and water uses.

Existing approaches to managing nonnative fishes pose serious challenges. As understanding increases about the processes that drive invasion success (Shepard 2004; Muhlfeld et al. 2009; Arismendi et al. 2014) and factors that mediate species interactions at different scales (Fausch 2008; Della Croce et al. 2014; Kovach et al. 2015), managers may target prevention and eradication (Dunham et al. 2002; Al-Chokhachy et al. 2014). Preventing introduction and establishment of nonnative fishes is the most effective strategy and often is the most cost-effective means to minimize environmental and economic impacts (Fausch and García-Berthou 2013). Although attempts to eradicate nonnative fishes to benefit Pacific trout can be successful (Gresswell 1991; Buktenica et al. 2013; Shepard et al. 2014), eradication requires great effort and expense (Peterson et al. 2008; Syslo et al. 2013), and there is no guarantee of success (Rahel 2004; Meyer et al. 2006; Martinez et al. 2009). However, the maintenance of environmental conditions that are favorable to native Pacific trout but unfavorable to nonnatives can be an effective strategy to minimize effects of nonnatives (Dunham et al. 2002). Effects of climate change may further influence interactions between introduced and native trout, particularly if effects on nonnative species exceed effects on native species (Wenger et al. 2011; but see Al-Chokhachy et al. 2013). In many cases, eradication of nonnative fishes and intentional isolation of native trout above migration barriers (Peterson et al. 2008) may represent a last resort when threats from nonnative species are imminent without obvious management alternatives (Fausch et al. 2009). Ultimately, approaches that incorporate a mix of alternatives, including prevention, eradication, and coexistence management may be most successful.

Climate Change

Climate change is altering freshwater ecosystems and fish faunas throughout the world. Across the range of Pacific trout, climate model projections suggest that stream habitats will become warmer and have more variable thermal and hydrologic regimes and have more extreme events, such as wildfire, flooding, and drought (Jentsch et al. 2007). For some streams, there is increasing evidence for elevated stream temperatures (Isaak et al. 2011; Arismendi et al. 2012) and reductions in flows (Luce and Holden 2009; Safeeq et al. 2013) across western North America. Combined with other threats, these climate-induced changes will continue to have noticeable effects on Pacific trout distribution (Rahel et al. 1996; Wenger et al. 2011; Roberts et al. 2013), demography (Al-Chokhachy et al. 2013; Quiñones et al. 2014; except Penaluna et al. 2015), phenology (Kovach et al. 2013; Penaluna et al. 2015), and genetic diversity (Muhlfeld et al. 2014; Kovach et al. 2015). Pacific trout are especially vulnerable to the effects of climate change in freshwater habitats because they require cold, interconnected, and high-quality habitats, which have already been fragmented and degraded by other anthropogenic activities in many areas. Many populations inhabit waters that are near or at thermal limits (Sloat and Osterback 2013; Matthews and Nussle 2014), and such populations are likely more susceptible to climatic change (Haak and Williams 2012). Pacific trout have persisted under dynamic conditions for millennia, likely due to their broad diversity and ability to disperse, both of which may be critical if they are to persist in a warming world combined with other emerging threats (Waples et al. 2008). On the other hand, there is abundant evidence in the fossil record that small, isolated populations do not persist for long in evolutionary history (Smith et al. 2002).

Land and Water Use Activities

Past efforts to mitigate the negative consequences of a legacy of land and water use activities on Pacific trout have focused on degradation, loss, and fragmentation of habitats in areas where human population densities are relatively low (Rieman et al. 2015). It is clear, however, that rapidly increasing human populations and related urbanization of landscapes is a threat to Pacific trout (Feist et al. 2011; Hughes et al. 2014). Distributions of people and Pacific trout increasingly overlap, particularly in coastal areas. The collective effects of urbanization, referred to as urban stream syndrome (Walsh et al. 2005), include rapid runoff and flashy stream flows due to a greater extent of impervious surfaces in urbanized areas, altered stream channel morphology, increased delivery of nutrients, and the presence of a host of contaminants, including an increasingly complex mixture of highly bioactive personal care and pharmaceutical products (Backhaus 2014). In addition to these effects from urbanization, as human populations grow and their demands for water also grow, there may be less water to support Pacific trout (Vörösmarty et al. 2000). The rise of the illegal drug trade in remote areas of western North America in recent decades is also likely having a negative effect on native Pacific trout, through water withdrawals (Bauer et al. 2015) and the use of agricultural chemicals, but the specific effects are difficult to document. The likelihood of extreme water scarcity has been brought into direct focus in the wake of an exceptional regional drought that gripped much of the Pacific Region of western North America in recent years (Wise 2016).

MANAGING PACIFIC TROUT ACROSS CHANGING LANDSCAPES

Conservation of native Pacific trout and their habitats commonly involves debate over the best practices and strategies to conserve remnant populations. Great strides have been made in understanding and developing conservation planning for native Pacific trout, including the topics of habitat restoration, invasion versus isolation, translocations, recognizing uncertainty, as well as the social and institutional dimension of conservation. Among this selection of conservation measures, habitat restoration is perhaps the least controversial, although the effectiveness of different practices often comes into question. Below we touch on some of the continuing debates in adaptive management regarding invasion versus isolation, translocations, scientific uncertainties, and management priorities.

Although barriers block the invasion of nonnative species, isolating native populations of Pacific trout upstream of barriers represents a severe conservation tradeoff (Fausch et al. 2009), given that small, isolated populations are highly susceptible to genetic drift and potential inbreeding depression (Woffard et al. 2005), loss of phenotypic variation, extreme stochastic events, environmental change, and potentially negative demographic shifts and their life-history implications (Kruse et al. 2001; Peterson et al. 2008; Roberts et al. 2013). Reductions in available habitat associated with drought or isolated headwater population fragments result in reduced survival for migratory or larger-bodied individuals (Berger and Gresswell 2009). Climate change threatens isolated populations because trout have less opportunity to move to avoid adverse conditions. However, some Pacific trout populations located above barriers in cold, high-elevation stream fragments may not be as strongly affected by stream warming as those in lower elevations (Isaak et al. 2010; Al-Chokhachy et al. 2013; Roberts et al. 2013). Blocking invasion upstream with barriers can prevent movement into upper parts of catchments; however, isolation of Pacific trout in headwater streams may increase the threat of local extinction.

Although widespread introductions of nonnative trout have played a prominent role in the decline of many Pacific trout populations (Gresswell 1988; Behnke 2002), in some cases, translocation of some lineages of Pacific trout outside their natural ranges has provided a last refuge (Hickman and Behnke 1979; Behnke 2007; Metcalf et al. 2012). Translocation or managed relocation may be a management option for facilitating range shifts for species that are restricted in their ability to move in response to climate change or other threats (Lawler and Olden 2011). Preserving population structure and diversity by using wild, most-closely-related populations in translocation efforts is important (Metcalf et al. 2007, 2012), but hatchery supplementation of native species may provide a viable alternative in some cases (Andrews et al. 2013). In addition, high-quality habitat is important for successful reintroductions (Cochran-Biederman et al. 2014), although a thorough assessment is warranted to ensure success (Perez et al. 2012). Translocation may be a management option for some populations, given the realities of land use activities, climate change, and adaptive management strategies (Harig et al. 2000; Harig and Fausch 2002; Lawler and Olden 2011).

Managing for and protecting the diversity of Pacific trout entails preservation of the high genetic diversity and multiple life histories among populations across as wide a geographic range and variety of habitats as possible. Managers often make conservation decisions with incomplete information (USFWS and NMFS 1998; RGCT Conservation Team 2013) and thus it is important to remember that the first principle of "intelligent tinkering" is keeping every "cog and wheel" (Leopold 1949:190), and for Pacific trout that means maintaining diversity of populations and habitats that are broadly distributed across western North America. Conservation actions that spread risk across the riverscape and among potential strategies (e.g., isolation of headwater areas versus connection; Fausch et al. 2009) reduce the negative consequences of scientific uncertainty (Haak and Williams 2012). Riparian restoration, water leases, and formal conservation easements may be used to improve and protect critical habitats, especially in catchments that might be more resistant to climate change. In addition, conservation of Pacific trout may require collaboration among stakeholders who are nontraditional partners in conservation (e.g., agriculture, forestry) to bridge gaps between public lands in headwater streams and private landowners who often manage land and water in the low- to mid-elevation habitats of these same catchments. Indeed, some of the most effective restoration initiatives in western North America have adopted an education-based strategy including cooperation among stakeholders and long-term monitoring, with an emphasis on adaptive management (Koel et al. 2010; Pierce et al. 2013). Likewise, adaptive management allows experimentation with approaches and management to adjust in the face of future uncertainty (Folke et al. 2005; Huitema et al. 2009). Ultimately, these conservation approaches warrant an inclusion of a human dimension that enables social learning (Rieman et al. 2015) and builds collaboration and appreciation for native Pacific trout (Behnke 2002).

CONCLUSIONS

Pacific trout in western North America are iconic fishes that have high ecological, economic, social, and cultural value. They play a key ecological role in lakes, rivers, and streams as aquatic predators contributing to top-down influences on food webs (Quinn 2005). Species and populations that are sea run transport nutrients from the ocean into freshwaters when they return to spawn and die, a subsidy that that enriches the growth of local plants and animals (Quinn 2005). Pacific trout are the target of commercial and recreational fisheries, bringing substantial economic value to those industries and to local economies. In addition to their special place in the culture, nutrition, and economy of indigenous peoples across the region, society in general places high intrinsic value on sustainable trout populations.

By collectively considering aspects of Pacific trout, we highlight the need for an integrated perspective crossing ecological, social, and political boundaries to conserve them in western North America. Strengthening the relationships among science, management, and the public at large is necessary, along with increasing flexibility in management, restoring the diversity of Pacific trout, and considering social factors that increase their vulnerability (Frissell et al. 1997; Rieman et al. 2015). Advancing the understanding of the evolutionary diversity and distribution of Pacific trout in western North America, especially in northern Mexico, and for both *O. clarkii* and *O. mykiss* will be necessary to fully describe and formally designate lineages, subspecies, and species of Pacific trout, thereby elevating their importance and scientific significance. Protecting sea-run in addition to stream-resident forms of Pacific trout where they occur sympatrically will be important to enhance their persistence of the full range of biodiversity within catchments (Kendall et al. 2015). In the past, the high societal values assigned to Pacific trout led to changes in land use practices related to mining, forestry, hydroelectric production, and flood control that have promoted their conservation. Ultimately, societies in western North America may have to undergo a fundamental change in attitude to reverse the current trend of increasing habitat degradation and fragmentation in streams and rivers that support this diverse group of native fishes (Hartman et al. 2006). Pacific trout still swim in many streams and rivers in western North America and, if given a chance, they may swim on into the future.

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