The Future of Salmonids in a Rapidly Changing World

Jack E. Williams, Jeffrey L. Kershner, and John A. Zablocki

Abstract Salmonid fishes are among the most adaptable and resilient to change of any fish group but also among the most threatened. The pace of change in today's world and the ever-increasing human footprint are limiting the ability of these remarkable fish to successfully adapt. Land use modifications, the introduction of non-native salmonids, aquaculture, pollution, and diminishing water supply all threaten salmonid populations across the globe. Climate change adds significant threats to populations that may already on the brink. We ask "How do we ensure the future of salmonids in this rapidly changing world?" and provide a three-part strategy for stream conservation consisting of (1) protecting and restoring important habitats and populations, (2) building resistance and resilience to disturbance, and (3) forming alliances with diverse interests to solve common problems. Conservation in the twenty-first century is challenged by twin complications of climate change and demands of an ever-growing human population. As we look into the future of salmonid and stream conservation, novel approaches such as World Heritage Site designations and the growing Rights of Nature movement should receive more attention. Ultimately, conservation success will be driven as much or more by societal perceptions and desires than by scientific principles.

Keywords Climate change · Conservation · Protection strategy · Resilience · Restoration · Threatened species

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J. Lobon-Cervia et al. (eds.), *Advances in the Ecology of Stream-Dwelling Salmonids*, Fish & Fisheries Series 44,
https://doi.org/10.1007/978-3-031-44389-3_28

1 Introduction to a Brave New World

Early in the summer of 2021, we witnessed the highest temperatures ever recorded in a number of countries representing a large component of the remaining salmonid habitat. Record temperatures in the western USA coupled with years-long drought threatened habitat for native salmonids. The Colorado River USA reservoirs are now at their lowest point since the reservoirs filled after the dams were built in the 1930s. Temperatures exceeding 45 °C occurred in British Columbia, Canada, reaching thresholds resembling the deserts of Mexico or the USA. Numerous weather records were broken. At the same time, temperature records in Lapland, Norway, and Siberian Russia also were broken, areas that rarely if ever have seen temperatures above 40 °C in the early summer.

In 2021, large wildfires burned across many parts of North America, Europe, and Siberia. Fires greater than 200,000 ha now occur almost every year in some part of the world and future projections indicate the high likelihood of a fire-prone environment driven by increasing temperatures (Pechony and Shindell 2010). Smoke filled summers in the USA and Canada as well as in southern Europe and Russia are now a new normal. Catastrophic flooding in Germany, other parts of Europe as well as in China and the USA has devastated human communities and ecosystems alike.

Record breaking heat and drought have unfortunately become a new normal in today's world. The top ten hottest years on record have all occurred during this century with 2016 and 2020 virtually tied for the hottest years on record (NASA 2021). It is clear that our weather and climate are now changing in a dramatic and threatening fashion.

Worldwide, drought conditions and wildfires have severely impacted streams and waterways, causing conflicts between water users, municipalities, and environmentalists. As we attempt to conserve salmonids in an uncertain future, we face the harsh reality that clean water is in increasingly short supply in many regions, pitting the needs of human society against the needs of aquatic ecosystems. Ultimately, both human and natural systems will require sustainable water use, but in many parts of the world, human demands for water outpace our ability to plan for sustainable resource allocation.

While the uncertainty of climate change has brought many of these issues to the forefront, traditional threats to salmonids and freshwater ecosystems such as pollution, land use change, and the presence of non-native species continue to be significant threats worldwide. Meanwhile, the growing human population in many countries compounds both traditional and novel threats.

One might argue that salmonids have learned to live with change as a constant theme over millions of years (Montgomery 2003). They are among the most successful and adaptable of fishes and are native to a myriad of habitats across the Northern Hemisphere, including small and large freshwater lakes, streams of all shapes and sizes, large rivers, estuaries, and oceans. As a group, salmonid fishes are remarkable in their diversity of life history patterns among the species, including their long migrations between oceans and freshwaters (anadromy) and migrations within freshwaters (fluvial, adfluvial), allowing them to fully exploit available habitats and express great variation in longevity, breeding seasons, and growth rates (Quinn 2005). Salmonids also distinguish themselves from other fishes in their ability to colonize new habitats and to re-colonize habitats that have recovered from disturbances such as floods or wildfires (Rieman and Clayton 1997; Pess et al. 2014).

While their ability to adapt and change is significant, the ever-growing human footprint on their ecosystems has severely restricted their ability to react to changing environmental conditions. In this chapter, we ask "What are the most serious threats to salmonid populations worldwide and how do we design future conservation efforts to ensure the long-term persistence of this remarkable group of fishes?"

2 The Changing Landscape and Evolving Threats to Salmonids in the Anthropocene

Native salmonids face rapidly changing environments as a result of the interaction of climate change with other stressors (Kovach et al. 2017). The impacts of these stressors have resulted in significant worldwide declines in many species and caused others to be threatened with extinction or in some cases to become extinct (IUCN 2018). Muhlfeld et al. (2018) reported that approximately 54% of the 124 recognized species and subspecies of trout and char worldwide have been assessed for conservation status by the IUCN and of those, 73% are threatened with extinction and four are now extinct.

2.1 The Multiple Effects of Non-native Fishes

Climate change has emerged as a significant global factor in the decline of coldwater-dependent salmonid fishes, but most salmonids face multiple risk factors (Fig. 1). Historically, perhaps the most significant threat to native salmonids has been the introduction of non-native species. Ironically, two of the most damaging introduced species to native salmonids are salmonids themselves, Rainbow Trout *Oncorhynchus mykiss* and Brown Trout *Salmo trutta*, which are native to North America and Europe, respectively, but have been widely introduced beyond their native ranges (IUCN 2018). The introductions of these species have in many cases led to replacement of native salmonids, reduced the abundance and diversity of other native species, resulted in introduced diseases in native trout populations, and through hybridization, reduced the genetic diversity of native stocks (Muhlfeld et al. 2019; Borgwardt et al. 2020).

Fish culture and the introduction of hatchery salmonids have had significant impacts on many native salmonid populations. For example, a recent study estimates that the costs to wild salmon from ocean farming of Atlantic Salmon *S. salar*

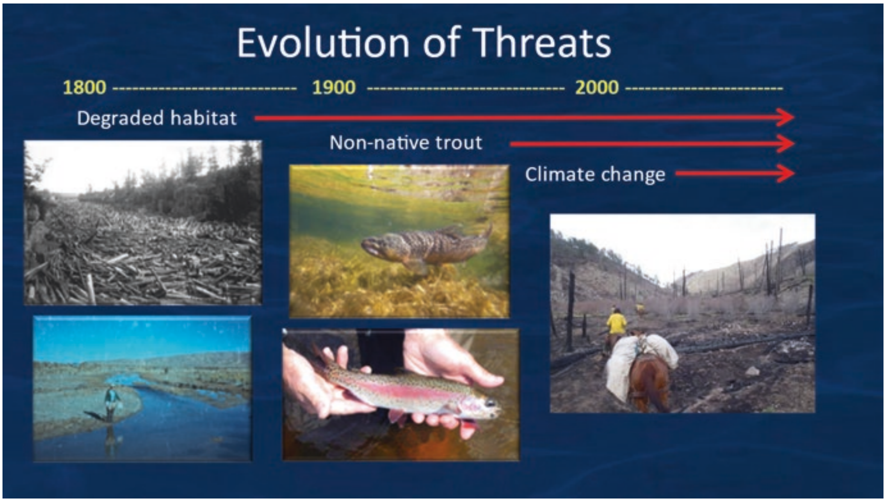

Fig. 1 Evolution of threats to stream salmonids. Starting in 1800s: overfishing and overgrazing; followed by pollution, non-native species introductions, and hatchery impacts in the 1900s; then combined with climate change in more recent decades. Figure modified from Trout Unlimited State of the Trout report; additional photo credit Jim Brooks (lower right, Gila trout habitat)

may exceed US$300 million due to introduced diseases, loss of forage fish, and introgression between farmed salmon and wild fish (Just Economics 2021). Sea lice associated with salmon farming have been shown to impact native Atlantic Salmon and sea-run Brown Trout (Thorstad and Finstad 2018) and to migrating smolts of Pacific Salmon in Canadian waters (Krkosek et al. 2007). The presence of elevated levels of disease pathogens also increased in areas around fish farms in proximity to local native salmon waters (Shea et al. 2020).

Culture of non-native Brown Trout and their introduction into waters where native Marble Trout *Salmo marmoratus* or other subspecies of Brown Trout may occur has led to hybridization with native fish and in some cases local extinctions (Schöfmann et al. 2019). Introduction of Rainbow Trout, Brown Trout, and Brook Trout *S. fontinalis* into native Cutthroat Trout *O. clarkii* waters in North America has led to widespread replacement of native fish in many waters and hybridization with native cutthroat in others (Leary et al. 1984; Henderson et al. 2000).

2.2 *Overfishing and Fisheries Management*

Overfishing of native freshwater salmonids has resulted in the decline and in some cases local extirpation of life history forms and species (Lobón Cerviá et al. 2019; Markevich and Esin 2019). Overfishing can result from both intensive commercial harvest of salmonids and/or harvest from sport anglers, or for food. Where salmonids are important food sources, non-native salmonids are often viewed as desirable fish to introduce into waters which have been over-harvested. Overfishing of freshwater forms occurs by local anglers harvesting fish for food or commercial fishing, particularly in lake fisheries where there may be large-bodied life history forms (Markevich and Esin 2019). Evolutionary consequences of overfishing may include not only the loss of larger life history forms, but also change in life history patterns such as feeding, habitat use, and spawning (Markevich and Esin 2019).

Anadromous salmonids show similar patterns of overfishing in many parts of the world. Overfishing can occur at almost any stage of their life history, but often occurs when fish stage to spawn. These fish are most vulnerable in the estuaries of rivers or in the rivers themselves as they ascend to their spawning grounds. Salmon are highly prized as food sources by many cultures and as a source of income from the sale of these fish. Angling for anadromous salmonids has become a multimillion dollar industry in many parts of the world and while angling harvest is strictly regulated in many areas, other parts of the world have less restrictive angling regulations or regulations that are poorly enforced (World Wildlife Fund 2001). Many countries have enacted strict catch and release requirements for anadromous salmonids, but there have been concerns over the long-term effects of catching, playing, and releasing a fish that still must travel long distances to spawn (Hume 2021).

2.3 Habitat Loss and Degradation

One of the most pressing threats to salmonids worldwide is loss of habitat. Habitat degradation can affect both the amount of habitat available to salmonids and the quality of remaining habitat. Loss of habitat can be linked to changes in population size as well as limiting the expression of life history attributes (migration, spawning) that may influence the persistence of a population. For example, populations of native trout in western North American deserts may be limited to headwater streams where access is precluded from larger fluvial habitats (Hendrickson and Tomelleri 2019; Propst et al. 2020). Similar issues have been noted for native Cutthroat Trout, Brook Trout, and Bull Trout *S. confluentus* in Canada and the USA, native Brown Trout in Europe, and native Char in Japan (Dunham et al. 1997; Rieman et al. 1997; Colyer et al. 2005; Hudy et al. 2008; Morita 2019). Populations of trout and char that lose access to larger river systems and lakes may no longer express the large-bodied life history forms that migrate between these habitats, but also represent founders of other populations that may have been extirpated through human or natural caused disturbances such as wildfires or severe floods (Rieman et al. 1997).

In some cases, the loss of habitat may not represent the loss of a physical connection but represent a change in water quality. In western North America, extreme summer temperatures may limit the ability of salmonids to move to downstream habitats that may provide important rearing areas (Armstrong et al. 2021). Identifying suitable temperature gradients for salmonids that exist across the landscape during these critical periods may provide one strategy for conserving remaining resident salmonids and identifying possible strongholds (Isaak et al. 2014), but habitats that may not be suitable during one part of the year may provide important connectivity to feeding habitat or migratory corridors during other times (Colyer et al. 2005, Armstrong et al. 2021).

Traditional land use practices such as logging, livestock grazing, and the increased development of human communities continue to influence ecosystems across the globe (Foley et al. 2005). While forest practices have been modified to protect salmonid habitat in parts of the world, effects from logging in riparian areas and sediment inputs from logging roads continue to be an issue in many countries. The consequences of poorly designed and implemented timber harvest may influence the types and amounts of woody debris that provide important stream habitat and increase channel complexity (Bisson et al. 1997). The results of these changes can include the amount and depth of large pools in streams (Woodsmith and Buffington 1996; McIntosh et al. 2000) and may increase the amount of fine sediment in pools (Lisle and Hilton 1992).

Livestock grazing is a dominant land use worldwide and occurs on almost one quarter of the land surface (Ramankutty et al. 2008). Riparian corridors along streams are relatively small areas of land that make up less than 1% of the landscape but provide water and enhanced forage opportunities for livestock (Armour et al. 1994). This increased livestock use can have direct effects on stream habitat where stream banks are trampled, causing increased sediment inputs and a loss of riparian cover along the stream (Platts 1981; Knapp and Matthews 1996; Belsky et al. 1999). This loss of cover may increase stream temperature during the summer and decrease the amount of terrestrial food inputs that are available to salmonids (Saunders and Fausch 2012).

2.4 Water Supply Degradation

The demand for water to supply industrial, agricultural, and domestic uses increases worldwide as the climate warms and water availability declines in many areas (UNESCO 2019). The alteration of stream habitat by the creation of dams and diversions has had a significant impact on riverine fish populations worldwide (World Wildlife Fund 2004). In combination with the alteration of spawning and rearing habitat, anadromous salmonids have exhibited significant reductions in historically available habitats. In the western USA, almost half of the formerly available habitat for anadromous salmonids is now blocked or unavailable (McClure et al. 2008). Blockages of migratory habitat may lead to a truncation of life history forms where only resident, non-migratory forms remain. Similar trends exist for almost all salmonids worldwide. In Japan, low head dams and diversions threaten Southern Asian Char populations by altering stream habitat and restricting access to migratory habitat (Morita 2019). As the demand for water increases, the potential impact on salmonid populations will increase as well.

As the climate changes, effects that were associated with current management may be amplified (Jonsson and Jonsson 2009; Smialek et al. 2021). Summer stream temperatures in many areas have been increasing and as temperatures have warmed, physiological effects such as decreased growth, cardiac stress, and an increase in the occurrence of disease outbreaks have occurred (Borgwardt et al. 2020). As stream flows decline and temperatures rise during critical summer months, the competition for scarce water may limit available water for stream-dwelling salmonids.

Sidebar—*Upper Klamath Lake and River USA*—The Klamath River was once one of the most important anadromous salmonid fisheries in the western USA. Originating in the mountains of Oregon, tributaries of the Klamath River flow into Upper Klamath Lake, an important stronghold for native fishes such as Redband Trout and Lost River *Deltistes luxatus* and Shortnose Suckers *Chasmistes brevirostris*. Downstream of Upper Klamath Lake, the river acquires flows from tributaries in California and supports populations of Chinook *O. tshawytscha* and Coho Salmon *O. kisutch* as well as Steelhead (anadromous Rainbow Trout). These fish are important to indigenous peoples who live along the Klamath River as well as in the area of Upper Klamath Lake. Four dams were built along the river near the Oregon-California border in the early twentieth century to provide hydroelectric power and irrigation water. The Bureau of Reclamation encouraged settlement of lands around the Upper Klamath Lake and river to develop irrigated agriculture. Unfortunately, the dams also blocked fish migrations and impounded water that warmed and produced toxic algal blooms. In the early 2000s, competition for water to protect endangered salmonids and native suckers and agricultural interests became intense as a changing climate was providing less water into the system over a period of a decade. In 2008, state water managers in Oregon and California found that removal of the dams would reduce energy costs by US$100 million compared to needed upgrades of the structures. Removal of the four dams began in 2023 and will restore nearly 500 km of salmonid habitat and improve water quality for people and fish.

In recent years, scientists have warned that the combination of hotter temperatures, increased wildfires, earlier snowmelt, and flooding due to rain on snow events will significantly impact salmonid habitat and increase population loss (Keleher and Rahel 1996; Haak and Williams 2012). Similar predictions for various parts of the world were made in the recent volume "Trout and Char of the World" (Kershner et al. 2019; Kovach et al. 2019). As the climate warms and conditions change for native salmonids worldwide, additional threats from hydropower, irrigation, land use, overfishing, and non-native species introductions make the future of salmonids problematic. Against this backdrop, we propose the following actions to help ensure the future of salmonids in this rapidly changing world.

3 A Blueprint for Stream Salmonid Conservation

As conservation scientists, we've operated under the basic tenant of protecting the best and restoring the rest where possible (Rieman and Allendorf 2001; Williams et al. 2011). The meaning of this is clear. Where we can, protect large interconnected landscapes to maintain the best habitat for native salmonids. Watersheds containing strong populations should be protected by regulation or special designation to the greatest extent possible. Protected landscapes with interconnected populations will be critical to the long-term success of salmonids worldwide. How to achieve these principles is less clear, especially as human populations continue to expand, exotic species proliferate, and the problems of a rapidly changing climate manifest themselves across a warming planet. Furthermore, within the current range of many salmonids, large landscapes of high-quality habitat are becoming increasingly rare. Restoration is necessary but difficult in many areas as competition for land and water is intense. So, how best to proceed with conservation in this era of competing uses and rapidly changing environment?

We describe the following three-part strategy for stream salmonid conservation that can work across the vast regions where salmonids are native.

1. Protect and restore important habitats and populations
2. Build resistance and resilience to degradation and disturbance
3. Form alliances and work with diverse interests to solve common problems

3.1 Protecting and Restoring Important Habitats and Populations

High-quality stream habitat for salmonids is characterized by natural or near natural flow regimes, rivers that are connected with and not isolated from their floodplains, vibrant and diverse riparian habitat along streams, and complex, sometimes braided stream channels with abundant structure in the form of large wood, boulders, or rock ledges. In wetter environments, high-quality stream habitat is part of an interconnected stream network where salmonid populations have access to various headwater and downstream channels. But in more arid zones, high-quality habitats may consist of single isolated streams. Such is the case in Mexico, Northern Africa, and elsewhere where remaining native trout populations occur in small streams that may themselves be subject to drying during summer months (Hendrickson and Tomelleri 2019; Lóbon-Cervía et al. 2019).

Examples of high-quality river systems in North America include the upper Flathead River (Canada, USA), upper Snake River (USA), and rivers such as the Alagnak, Kvichak, and Nushagak in Bristol Bay (Alaska). Russia's Kamchatka Peninsula and the Zhupanova River are widely known for major salmon and rainbow fisheries in near-pristine conditions. The Neretva River (Bosnia, Herzegovina) is one of the largest and most diverse rivers in the eastern part of the Adriatic Basin.

Of course, few rivers in today's world are as pristine as Alaska's Alagnak or Russia's Zhupanova. Identifying the best remaining habitat can be challenging, especially in regions where knowledge of historical conditions prior to modern human intervention is limited. In many parts of the world, the fish themselves may be among the best indicators of habitat conditions. Diverse native fish communities that include native salmonid populations are likely indicative of quality streams and healthy watersheds (Dauwalter et al. 2011, 2019).

Protecting large, diverse populations, often known as "strongholds," is a proactive approach to conservation. Most existing conservation efforts focus on threatened populations and degraded habitats, which are important to recover but are expensive and complex undertakings. As a result, some scientists and organizations encourage increasing efforts to protect remaining high-quality populations and habitats in river systems before they become degraded (Williams et al. 2011; Garrett et al. 2019). The Wild Salmon Center has mapped a network of "salmon strongholds" in countries across the Pacific Rim where salmonid diversity is highest and populations are robust, which provides good targets for protection efforts (wildsalmoncenter.org/stronghold-approach/).

While large, connected metapopulations are generally desirable, threats from land use and non-native introductions are cause for concern in many areas. How do we conserve populations and species in areas where large, high-quality landscapes no longer exist? Restoration efforts that focus on securing and expanding remaining populations may provide the best conservation option. Expanding existing habitat patches by removing barriers (dams, roads, culverts, water diversions) or rewatering stream reaches should produce larger salmonid populations with a greater chance of long-term persistence. In the arid American Southwest, conservation efforts for native trout usually focus on rebuilding large populations by reconnecting streams and improving riparian habitats in areas where increasingly large wildfires threaten remaining populations (Propst et al. 2020).

Climate change poses increasing threats to cold-water dependent fishes and freshwater stream habitats. Increasing stream temperatures may decrease habitat availability for salmonid fishes, especially in lower-elevation valley bottom habitats that were historically some of the most productive habitats available to these fishes. At the same time, higher stream temperatures increase the potential for invasion and spread of native and non-native warm-water fishes (Rahel and Olden 2008). Parasite and pathogen problems also increase with these changing conditions.

Climate change is responsible for a myriad of problems beyond temperature, including reduced late-season stream flows, drought, wildfires, and paradoxically, increasing storm severity and intense flooding. Existing stressors for stream systems often are made worse as climate change increases. For instance, elevated rates of erosion and sedimentation that are common in many developed watersheds, typically increase with more intense storms and flooding. Fortunately, there are many restorative and adaptation opportunities that can improve habitat conditions in areas where climate-driven disturbances such as drought, wildfires, and floods occur (Table 1; Isaak et al. 2012; Williams et al. 2015).

Some salmonid streams may be naturally resistant to temperature increases as ambient conditions warm because of their high elevation, heavily forested watershed, or inflow from cold-water springs (Isaak et al. 2014). Such cold-water refuge streams should be identified and protected. Most streams, however, warm as air temperatures increase. Many natural stream restoration actions can improve local habitats for cool-water and, at least in theory, reduce stream warming more broadly. These include improvements in riparian habitats and replanting native trees, developing narrower and deeper channels (rather than wide shallow channels that expose more surface water to ambient temperatures), increasing channel complexity (braided channels and sinuosity), adding structure (large wood, boulders) that can facilitate development of deeper, cool-water pools, and restoring instream flows (Williams et al. 2015). These actions, if applied broadly to headwaters, may provide cumulative cooling for downstream rivers. As with most restorative actions, project monitoring is essential to demonstrate effectiveness of actions and to encourage additional funding for future efforts.

In many areas, stream channels have been relocated or simply pushed to the edge of meadows and valleys to make way for farms or other human development. This typically results in a straighter channel, and subsequent loss of sinuosity and pool habitats. Restoring the channel to its original location reverses these problems and increases cool-water habitat as pools reform and hyporheic flows are recreated between pool habitats. In one example from Idaho (USA), stream channel restoration resulted in increased stream length (from 1007 m to 1973 m) as sinuosity increased and the number of pools increased (from 9 to 86), greatly improving cold-water habitat availability for native Yellowstone Cutthroat Trout *O. clarkii bouvieri* (Williams et al. 2015; Fig. 2).

Table 1 Comparisons of common climate impacts, corresponding adaptation strategies, and restoration response for stream and river ecosystems

Climate impacts	Strategic response	Restoration actions
Heat: Warmer summer temperatures; reduced snowpack	Increase shading and cold-water refuge habitats	Restore riparian vegetation; add instream structure to create deep pools
Drought: Earlier peak flows; reduced late season flows	Improve watershed function to improve flows	Restore headwater meadows and wetlands; restore channel meanders and complexity
Wildfires: Widespread burns of increasing intensity; debris flows; ash flows	Increase resistance to fire within stream and riparian areas by increasing their width and depth	Restore width and vigor of riparian habitats; reintroduce beavers; construct beaver analog dams
Floods: Higher peak flows; increased stream erosion and sedimentation	Increase capacity of streamside zones to absorb and dissipate flood energy; increase flow capacity at road-stream crossings	Reconnect rivers to floodplains; restore floodplain habitats; replace small culverts with large culverts or bridges

Fig. 2 Photo of Crow Creek, Idaho (USA) as the former stream channel was being restored. Water remains in the straightened channel (adjacent to the road near the bottom of the photo), and the restored, more sinuous channel (now flowing across the middle of the meadow near the top of the photo). Figure from Williams et al. (2015)

3.2 Building Resistance and Resilience to Degradation and Disturbance

Much of the success of salmonids over time can be attributed to their wide diversity of life history strategies, including short and long migrations, variation in timing of migrations, seasonal spawning variation, spawning habitat variation, differences in size and age at maturity, variation in feeding habitats, and changes in habitat preferences among juvenile and adult fish (Quinn 2005; Jonsson et al. 2019). Restoring the full expression of life histories in populations will increase their resistance to loss (resistance) and increase their ability to recover following disturbance (resilience).

Life history diversity exhibited by salmonid fishes is a product of their evolutionary history combined with habitat diversity. The diversity of lotic and lentic habitats, the complexity of these habitats, and diversity of estuarine habitats act as templates for life history strategies (Southwood 1977). Hence, many habitat restoration efforts should be aimed at increasing habitat complexity and reconnecting stream and stream-lake networks in an effort to increase life history diversity within populations.

The ability of diverse natural systems to persist over time in the face of changing environmental conditions has been attributed to the "portfolio effect" (Figge 2004) or to their "biocomplexity" (Hilborn et al. 2003). The large number of separate stocks of Sockeye Salmon supporting the Bristol Bay (Alaska, USA) fishery has been credited with the long-term success of that fishery (Hilborn et al. 2003; Schindler et al. 2010); whereas the "weak portfolio" of Fall Chinook Salmon in California's (USA) Central Valley appears to have contributed to the collapse in 2008 of that fishery, which was supported by a single run of Chinook in the Sacramento River (Carlson and Satterwaite 2011).

Haak and Williams (2012, 2013) stress the importance of developing a diverse portfolio of habitats and populations in salmonid conservation efforts. They emphasize the need to restore and protect life history diversity within stream salmonid populations because this component of diversity is among the first lost as habitats are degraded and migratory pathways become fragmented. For instance, salmonids that are isolated in a lake or stream will often display the ability to migrate once habitats are reconnected and barriers to movement are eliminated. In trout and char populations, reconnection of larger rivers with their tributary streams can result in development of fluvial and adfluvial life histories in addition to resident populations (Dunham et al. 1997; Colyer et al. 2005).

The value of developing and protecting a diverse portfolio in conservation is similar to goals of financial managers to develop a diverse investment portfolio as a hedge against future financial uncertainty (Fig. 3). If multiple populations exist in a target area or could be restored, portfolio theory can help managers understand the role of each population to future conservation and how to manage for a "strong portfolio" and long-term persistence (Haak and Williams 2012).

Salmonid populations that exist in isolated streams will be more susceptible to disturbances than will populations that occur more broadly across multiple interconnected streams where the chances of escaping lethal conditions are increased

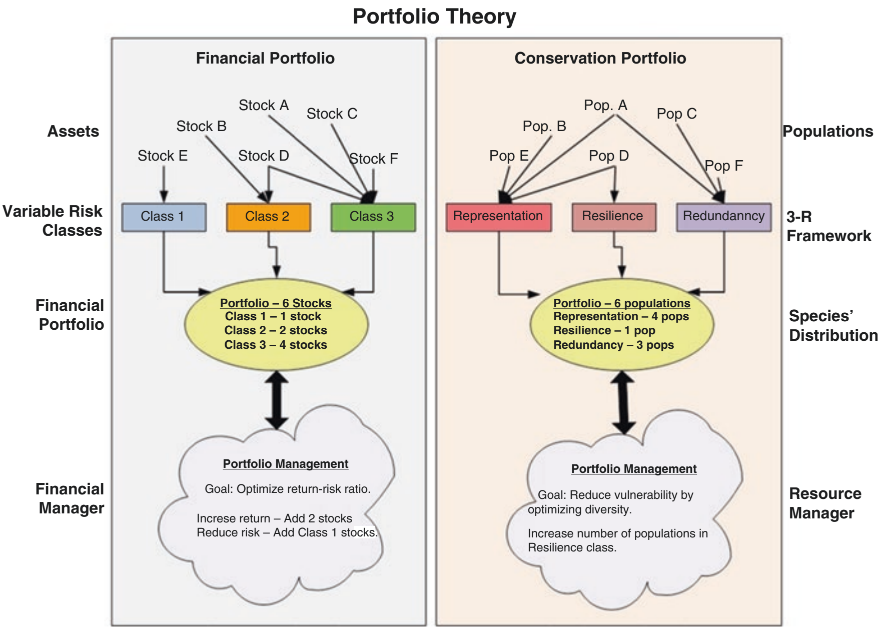

Fig. 3 Comparison of portfolio theories in the financial and ecological realms. In this hypothetical comparison, fish populations are the assets to be managed in the portfolio. The 3-R framework is a way to classify populations for their conservation value. In this example, the conservation portfolio lacks assets in the Resilience category, indicating the need to develop larger populations that can recover from major disturbances. Figure from Haak and Williams (2012)

(Haak and Williams 2012). Isaak et al. (2012) describe the value of large, interconnected trout populations in western USA as a hedge against climate change uncertainty and population loss by large-scale disturbances such as wildfires.

Despite the benefits of interconnected stream networks, stream reconnection projects also may have the inadvertent effect of facilitating invasion by warm-water fishes (Fausch et al. 2009). Such fish passage projects must proceed with caution and include adequate fisheries surveys of habitats that will be reconnected. Developing replicate populations in additional stream systems can achieve some of the same benefits of stream reconnection projects in terms of protecting scarce resources from loss from drought, wildfire, or flood (Vincenzi et al. 2012; Propst et al. 2020).

Sidebar—*Disturbance and Trout Persistence*—Wildfires are becoming an increasing cause of population declines in stream salmonids, especially as populations are progressively more isolated in small stream segments and wildfires are larger in size and intensity. In the American Southwest, isolated populations of Gila Trout *O. gilae*, Apache Trout *O. apache*, and Cutthroat Trout have been increasingly susceptible to population losses (Neville et al. 2006; Propst et al. 2020). Large and intense wildfires during 2012 and 2013 eliminated populations of the rare Gila Trout, which not only reduced the number of extant populations but also decreased remaining species-level genetic diversity and heterozygosity (Propst et al. 2020). In reaction to increased wildfire intensity, beavers have been introduced into small stream systems to improve watershed function and to create wide and deep pool habitats that are more resistant to wildfire impacts (Fig. 4). Decreased heterozygosity and allelic richness have also been observed in a population of Marble Trout in Slovenia subjected to repeated catastrophic flood events (Pujolar et al. 2016). The long-term implications of such genetic degradation cannot be good even if populations persist in the short term.

It is difficult to quantify the size of populations necessary to provide resistance or resilience to disturbance. Researchers have attempted to answer this question and have developed varied answers that are dependent on the density of the stream network, the species in question, and habitat availability, among other factors. Nonetheless, in studies of western USA trout populations, Hilderbrand and Kershner (2000) determined that occupied habitat of 27.8 km or more in length is adequate for long-term persistence. Dunham et al. (2002) found that stream salmonid populations occupying large habitat patch sizes (≥10,000 ha) have a greater likelihood of withstanding environmental change over time. Such studies help quantify the size of smaller populations that may be at risk and in need of habitat supplementation.

The science of adapting streams for climate change is relatively new and much remains to be learned not only about the effectiveness of stream restoration actions on climate change resistance and resilience, but how adaptation efforts may impact non-target ecosystem dynamics. Studies examining the results of planting riparian woodland species along upland UK streams found increased levels of coarse particulate matter and corresponding increases in the shredder components of macroinvertebrate communities (Thomas et al. 2016). In this case, resilience to climate change impacts may occur not only through desired changes in the riparian

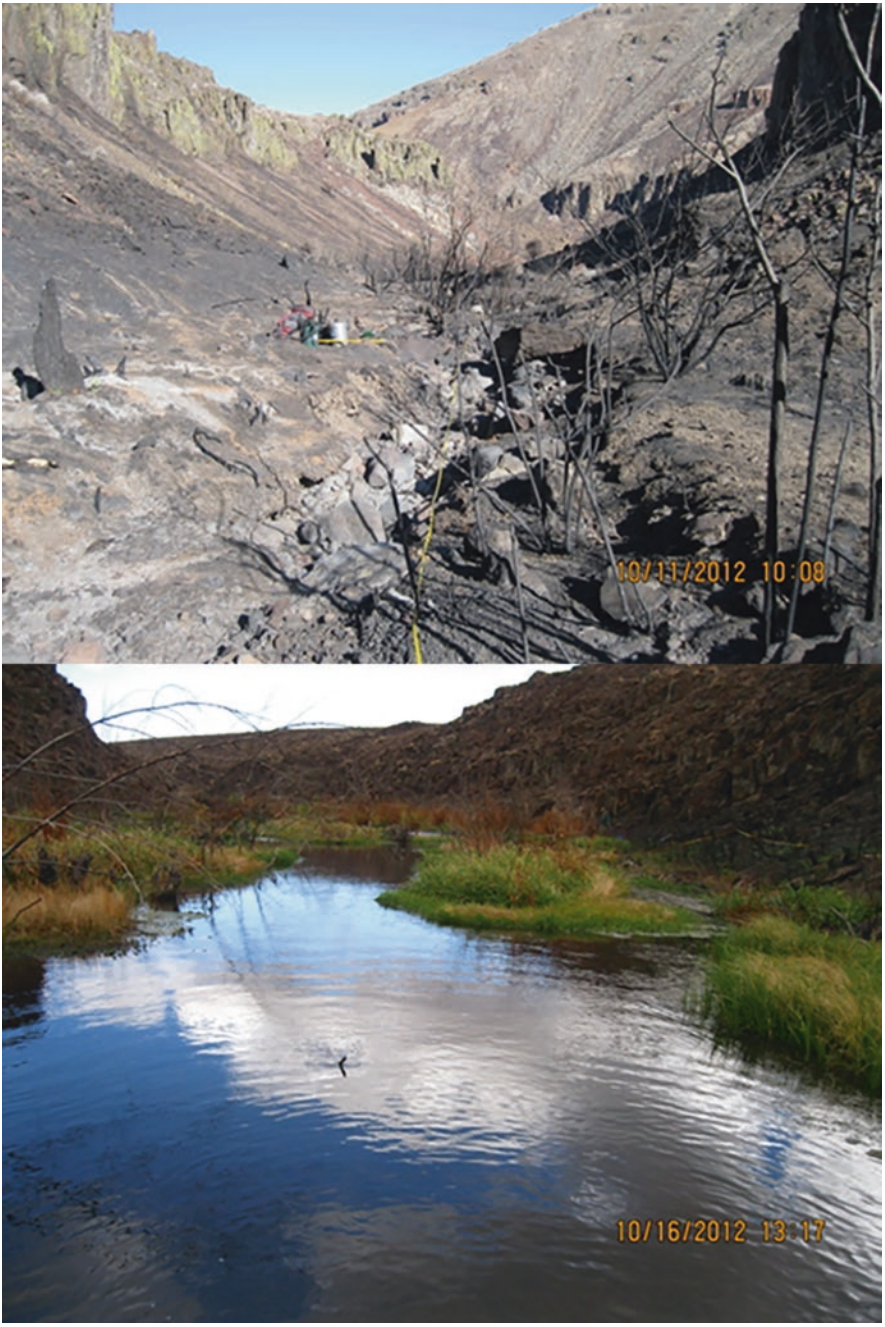

Fig. 4 Lahontan Cutthroat Trout *O. clarkii henshawi* habitat in southeastern Oregon, USA, following Halloway wildfire that burned 99,350 ha in 2012. Top: Stream segment without beavers showing thorough burn through narrow stream channel. Bottom: Stream segment with beavers showing unburned wetland area surrounding beaver pond

community but also through increased diversity in macroinvertebrate taxa. The study illustrates the complexity inherent in stream-riparian dynamics and caused Thomas et al. (2016) to advocate for additional efforts to understand ecosystem consequences of adaptation projects. We concur with that admonition and encourage project monitoring and additional studies to improve our understanding of adaptation opportunities and impacts.

3.3 Forming Alliances to Solve Common Problems

Science provides important information to society on the health of ecosystems and often describes threats and needed changes to natural resource management. Unfortunately, science alone is seldom sufficient to move society in the necessary direction of conservation and sustainability. Additional forces are needed to gain the social and political will to implement the changes described by scientists as necessary.

For conservation to succeed, especially at the time scales of decades and human generations, novel and powerful coalitions and partnerships must be formed with societal factions that, more often than not, have proved detrimental to conservation goals in the past. Finding common ground and identifying common problems is key.

Anglers and conservationists are natural allies in the pursuit of salmonid conservation. Non-governmental organizations like Trout Unlimited (USA), Wild Salmon Center (Pacific Rim Countries), Salmon and Trout Conservation (UK) Save the Blue Heart of Europe (Balkan Region), and The Nature Conservancy (worldwide) are good initial partners for scientists seeking help and increased capabilities to achieve conservation goals. These organizations and their memberships can help drive progressive policies with government managers and can greatly expand the capacity for monitoring and restoration work.

Citizen science programs and opportunities are rapidly expanding in many regions and will not only increase the capability of conservationists to achieve their goals but will help build scientific literacy among the participating public. Although anglers have been assisting in stream monitoring for decades, the recent proliferation of iPhone apps and other data recording devices has simplified stream monitoring for the interested public and facilitated the rapid expansion of angler-based monitoring programs beyond water quality and into fish distribution studies, spawner surveys, and the monitoring of threats from energy development to climate change (Williams et al. 2016).

Indigenous peoples often depend on abundant fish and wildlife populations for subsistence as well as cultural enlightenment. Although individual tribes and indigenous governments may approach fish and wildlife management from their own differing perspectives, many advocate for policies that favor robust fish populations and are natural allies in stream and river restoration projects. Similarly, partnerships between private conservation groups and indigenous people have proven critical to protect the headwaters of Bristol Bay and its Sockeye Salmon *O. nerka* fishery in Alaska from large-scale mining proposals (www.savebristolbay.org).

Dwindling water supplies are a serious problem for many stream salmonids and also are a concern to society more broadly. Cities and local governments are increasingly worried about maintaining the quality and quantity of municipal water supplies as human populations grow and droughts become more severe. Those working to restore streams in upper parts of watersheds may find allies with those dependent on water supplies further downstream. Many municipal water supplies originate in native forests and rangelands that also provide habitat for remaining stream salmonid populations.

Farmers and water irrigation districts are potential partners in conservation. As water supplies become scarce, improvements in irrigation efficiency and delivery can benefit both farmers and fish. Installing drip irrigation systems or lining canals to prevent subsurface losses may allow for more water to remain in streams. Alternate crop choices may require less water or chemical applications, which would benefit stream integrity.

As climates warm, drought and heat are driving large wildfires across many regions. Streams and rivers can provide natural fire breaks. Improving riparian habitats and expanding the width of wet zones along streams by introducing beavers, constructing beaver analog dams, or restoring riverine floodplains increase the ability of farms and forests to resist large-scale wildfires by providing a network of natural firebreaks across the land. In the western USA, the reintroduction of beavers has increased habitat quality for Cutthroat Trout in small rangeland streams and provided ponds that increase the survival of fish and amphibians during wildfires while increasing the resistance of the landscape to rapid wildfire spread (Talabere 2002; Williams et al. 2015).

Finding common ground with other organizations and working to solve common problems will create conservation opportunities that would otherwise go unrecognized. Developing conservation partnerships with anglers, non-governmental organizations, indigenous peoples, local governments, foresters, or local irrigation districts provides important weight for science to influence politicians and policymakers. When properly designed, stream and water conservation should benefit a wide audience of collaborators, be broadly supported by the public, and promote societal engagement (Higgins et al. 2021).

4 Looking Toward the Future

Conservation of streams and rivers in the twenty-first century is a complex yet urgent task. On the one hand, conservationists need to understand what has been lost, how much damage has occurred, what stressors are impacting our streams, and how they might be alleviated or mitigated. But at the same time, we must be able to envision a sustainable future. The public must be engaged and understand the commonality among risks to human systems and nature. What remains possible and how can it be achieved? Our environment and human-built systems are changing rapidly and challenge us not only to make the right decisions but to make them quickly.

As the natural world degrades, there is much at risk. Not only are native species and biodiversity threatened with extinction, but watersheds that support biodiversity also are the source of clean and abundant water for agriculture, industries, and human consumption. Streams and rivers also are part of our spirit; a source of enlightenment and a place to relax and recreate. This then is what makes the task of conservationists so urgent. Future generations risk not only a loss of diversity, but also the capacity for experience and wonder that inspire people to hold on to what they have. People are part of nature, and in the end, we all share a common fate.

In the western USA, the native Lahontan Cutthroat Trout *Oncorhynchus clarkii henshawi* has been extinguished from somewhere on the order of 90% of its historic stream habitat, and close to 99% of its historic lake habitat. Historically, native Americans witnessed runs of thousands of large Cutthroat Trout from Pyramid Lake, Nevada, into Lake Tahoe on the California border and its tributaries. These fish provided an important food source to native Americans and early white settlers who moved into that area. Within a period of decades, this fishery declined due to water diversion, land use, non-native fish introductions, and overfishing.

Today, there are some 15 million people a year that visit Lake Tahoe. This great glacial lake in the Sierra Nevada is among the 99% of lake habitat that is now gone. Probably more consequential than large Cutthroat Trout vanishing from the lake is their vanishing from memory and human experience. Imagine the imprint on the human psyche that a giant run of 10 kg trout coursing up through the Truckee River to Lake Tahoe today. Imagine the inspiration that has been lost. Oscar Wilde described a cynic as a person who knows the “price of everything and the value of nothing.” To be successful, conservationists must be the quintessential anti-cynic. It is incumbent upon us to remind the world of the value of something. Conservation is not an exercise in being right about things, it is an exercise in doing right about things.

The example of the Lahontan Cutthroat Trout is representative of the fate of many native salmonids worldwide. Today, freshwater biodiversity is declining at a rate more than twice as fast as terrestrial and marine biodiversity (Tickner et al. 2020). And yet despite being lost at a far greater rate, the proportion of freshwater protection has lagged far behind terrestrial and marine protection. To the extent that freshwater systems do still provide suitable habitat for stream-dwelling salmonids, in the vast majority of cases, the native salmonid has been supplanted by introduced species.

Across Europe, seven nations (Iceland, Finland, France, Norway, Slovenia, Spain, Sweden) have legislation aimed at preserving the remaining free-flowing rivers within their borders (Schäfer 2021). These protections are similar to those of the Wild and Scenic Rivers Act in the USA that seeks to protect the free-flowing nature of rivers with outstanding natural, cultural, or recreational value. Some of the European laws were enacted during recent decades in reaction to large-scale and controversial hydroelectric projects. The potential for a European network of protected rivers clearly exists if development of river protection laws could be enacted in remaining countries. Without specific legislation to protect rivers and their headwaters, aquatic conservation goals will be increasingly hard to achieve. River conservationists have realized that most existing schemes for habitat protection focus on terrestrial boundaries and are inadequate for large river systems that may flow in and out of protected areas and across political boundaries (Higgins et al. 2021).

Science must inform and guide efforts to restore what has been damaged and to protect what is threatened with loss. But at the same time, scientists must reach beyond technical knowledge to share with the public their values and concerns in order to achieve common goals. Efforts like "Save the Blue Heart of Europe" combine scientific expertise with citizen science to highlight the importance of restoring and protecting the critically important rivers of central Europe. Over 3000 new hydroelectric projects are planned in addition to the 100 plus plants under construction. Combining scientific expertise that highlights the important aquatic and riparian values of these rivers with public advocacy for the protection of these systems has increased public and governmental awareness of their importance, as well as highlighting the social impacts of riverine development on local communities.

In 2019, salmonid ecologists gathered in Granada, Spain, argued for adding outstanding cold-water rivers around the world to the United Nation's World Heritage List in order to gain international recognition of their values and increase the likelihood of their protection (Dauwalter et al. 2020). The Nakama River on Iriomote Island is part of a four-island chain in Japan on the World Heritage List. In the USA, several National Parks that include iconic salmonid rivers are included in the World Heritage List. While many countries include a mix of cultural and natural sites on their World Heritage Lists, there are many high-quality rivers with high biological diversity that need recognition and protection and could conceivably be added as World Heritage Sites.

In recent years, the "Rights of Nature" movement has provided a small but growing number of rivers with legal rights against harm, opening up a new opportunity for river protection. The movement claims that certain ecosystems have the right to exist, flourish, to naturally evolve without human-caused disruption, and to be represented by a guardian in a court of law (Challe 2021). Since Ecuador became the first country to formally recognize the Rights of Pachamama (Mother Earth) in 2008, notable rivers around the world have been granted legal rights. In the USA, the Yurok First Nation granted the Klamath River legal personhood in order to address habitat threats through legal action. Rights of Nature protection also has been provided to the Riviére Magpie (Canada), Río Salado (Mexico), and Yarra River (Australia), among others (http://riverresourcehub.org/resources/rights-of-rivers-global-map/). Of course, time will tell as to how effective the Rights of Nature movement becomes in actually protecting nature but the potential is intriguing.

Scientists with a strong ethical concern for the natural world often puzzle as to our seeming inability to live in harmony with nature. Aldo Leopold (1949) wrote that "*We shall never achieve harmony with land, any more than we shall achieve justice or liberty for people. In these higher aspirations, the important thing is not to achieve, but to strive*." Kurt Fausch (2015), a fisheries scientist and ethicist, argues that humans will always treat land and rivers poorly if we believe we own them, and therefore have the right to degrade them. Although perhaps difficult to explain, we think that a growing number of scientists who have studied nature over the course of their lives would agree that natural, free-flowing rivers have some innate value to humans in their natural state and should have some sort of right to protection. As others grow to understand and appreciate these same values of a natural river, our ability to provide for their protection increases accordingly.

So "What is the Future of Salmonids in a Rapidly, Changing World?" Conservation and protection of rivers and their species will depend not only on laws and regulations, but also on the will of the people. So, it becomes part of the duty of scientists and conservationists generally to inform the broader human community about what is at risk and the importance of protecting rivers and aquatic systems that support not only aquatic biodiversity but human communities as well. Our future will not only be defined by science, but also by our emotions, our collective imagination, and our collective actions or inactions.

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