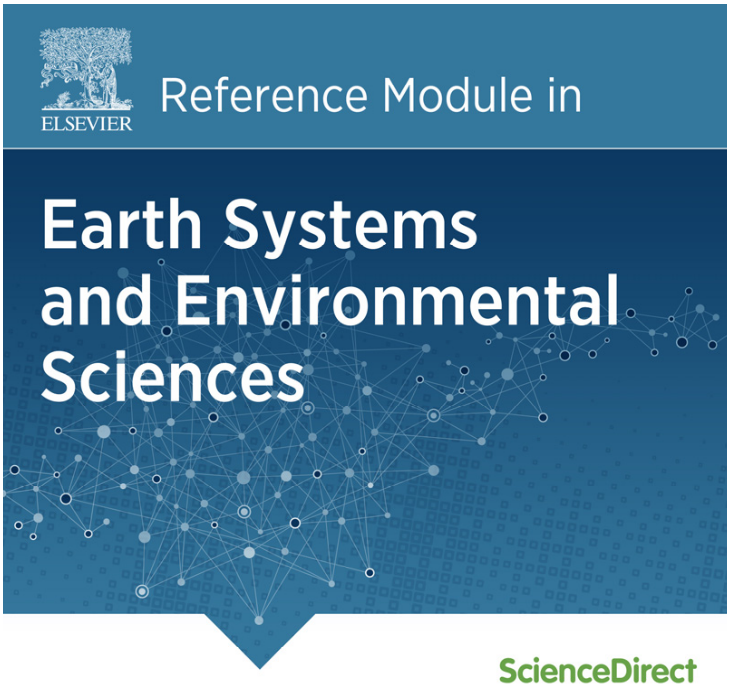

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Cold-Water Fishes and Climate Change in North America

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The Diversity and Vulnerability of Salmon, Trout, and Their Relatives

Fishes of the family Salmonidae, including trout (*Oncorhynchus*), char (*Salvelinus*), salmon (*Oncorhynchus* and *Salmo*), grayling (*Thymallus*), and whitefish (*Prosopium*), are likely to be particularly vulnerable to climate change because of their dependence on cold, clean water. Salmonids are among the most sought after fish by recreational anglers. In North America, their native range includes much of the continent from the Arctic Plains, along the Pacific and Atlantic coasts, and throughout most mountainous regions (Behnke, 2002). In Mexico, trout naturally occur in the mountainous regions of Baja California and throughout the Sierra Madre Occidental as far south as the Rio Presidio and Rio del Baluarte basins (Hendrickson et al., 2002). Brown trout (*Salmo trutta*) are native to Europe but have been broadly introduced in North America. Additionally, rainbow trout (*O. mykiss*) and brook trout (*Salvelinus fontinalis*) and other salmonids that are native to North America have been widely introduced into lakes, reservoirs, and river systems outside of their native ranges to increase angling opportunities.

Climate change is likely to continue affecting salmonids throughout their ranges. Increasing air temperatures have been warming stream and lake temperatures (Isaak et al., 2012; Schneider and Hook, 2010) with impacts ranging from increasing stress and metabolic rates to loss of lower-elevation habitats as waters warm (Eby et al., 2014; Keefer and Caudill, 2015). Warmer conditions will also impact salmonids through changes in winter precipitation and altered flow regimes (Haak et al., 2010). Disturbance events, such as wildfires, floods, and drought, are likely to increase as well (Westerling et al., 2006) with resulting stream sedimentation (Goode et al., 2012). Many existing stressors for salmonids are likely to be made worse by climate change (Williams et al., 2015). For instance, nonnative fishes, which now prey on and compete with native salmonids, are likely to increase in numbers and distributions as climate changes (Lawrence et al., 2014; Rahel and Olden, 2008). The synergies that emerge from the combined effects of these stressors will be hard to predict with accuracy but are likely to magnify the negative consequences of climate change for cold-water fishes in North America.

The range of climate change impacts will not be equally harmful across all salmonid species. Although, all salmonids tend to be dependent on cold, clean water supplies, some species, such as bull trout (*Salvelinus confluentus*), Arctic grayling (*Thymallus arcticus*), and Dolly Varden (*S. malma*), are particularly sensitive to increasing temperatures and sedimentation (Jones et al., 2013; Selong et al., 2001). Changes in winter precipitation from snow to rain may impact fall-spawning species such as brook trout or brown trout to a greater degree than spring-spawning trout because of increased scouring of their egg beds (Goode et al., 2013; Wenger et al., 2011a,b). Other species, such as California golden trout (*O. aguabonita*) and Lahontan cutthroat trout (*O. clarkii henshawi*), may occur in regions that are in the midst of sustained drought and particularly vulnerable to loss because of increasing isolation and small population size.

Despite our understanding of climate-driven impacts and known sensitivity of salmonids to warming conditions, predictions of future ecological conditions are complicated by the interactions among climate, biological, and geologic processes. None of these factors act in isolation. The degree that warming and changes in disturbances impact particular habitats and species depends on the resilience of the habitat or species in question, including the interactions of biological, geomorphic, and hydrologic systems. Impacts from climate change are likely to be more severe where stream and lake habitats are degraded or fragmented and less severe where habitats are robust and interconnected (Rieman and Isaak, 2010). Unfortunately, many habitats of native salmonids have a legacy of pollution and fragmentation caused by dams, water diversions, agricultural runoff, and roads. The majority of native trout and char species and subspecies currently occupy $<25\%$ of their historical habitat (Trout Unlimited, 2015).

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The purposes of this article are to (1) review existing and likely future climate change impacts to salmonids in North America, (2) provide a primary bibliography for these impacts, and (3) describe how restoration can help trout adapt to climate change. The reader should keep in mind that the conservation status of most native salmonids already has declined as a result of the legacy of agricultural development, hydropower development, and the introduction of nonnative species (Behnke, 2002; Trout Unlimited, 2015). Some taxa already are classified as vulnerable, threatened, or endangered by state, provincial, and federal agencies. Furthermore, as occupied habitat becomes increasingly fragmented and isolated, risks from climate-driven disturbances increase as well. Conservation efforts such as building artificial barriers to protect native trout from upstream invasions of nonnative trout and warmwater fishes may result in further vulnerability to climate change because of range restrictions. Thus, it is important to view increasing risk not only from the perspective of one or two factors but also from the full variety of impacts that may accumulate over space and time.

Climate Change and Disturbance Regimes

Climate change often acts to compound existing stressors and increase their cumulative impacts (Williams et al., 2015). Increased warming, for instance, will result in earlier snowmelt, earlier forest drying, and more frequent and intense droughts and wildfires (Westerling et al., 2006). Impacts of forest road networks, which speed runoff and erosion (Luce and Black, 1999), become even more pronounced as disturbance regimes increase in variability and intensity.

The current and likely future effects of a changing climate on trout, salmon, and their habitats are varied and dependent on the conditions of local fish populations and available habitats (**Table 1**). Disturbances such as landslides, wildfires, and floods are a historical part of the landscapes inhabited by trout and salmon. Historically, these disturbances have been infrequent and short-lived, allowing for the systems to recover between events or even improve conditions as new habitat patches were created in formerly homogeneous landscapes. But as disturbances become larger and more frequent and occupied habitats become smaller and more isolated, the long-term impacts of landslides, wildfires, and drought become detrimental to persistence of salmonid populations.

Flooding may have little long-term impact to natural river systems if streams are connected to their floodplains and riparian habitats are in good condition (Poff, 2002). Flooding may benefit stream habitats by increasing sediment transport, creating exposed gravel bars, and promoting riffle and pool formation. Repeated flooding, or peak flows that are higher than historical averages, may cause increased rates of stream erosion and sedimentation. Erosion and downcutting of stream channels are more likely if streams have been channelized or riparian vegetation has been eliminated along streamside zones. Riparian habitats can

Table 1 Existing and likely future effects of climate change on cold-water-dependent fishes

Impact from climate change	*Effects on trout and salmon and their habitats*	*References*
Increasing stream temperature	Greater physiological stress; increased metabolic demand; restrictions in available habitat (especially downstream); habitat fragmentation	Selong et al. (2001), Mantua et al. (2010), Wenger et al. (2011a,b), Isaak et al. (2010, 2012), Warren et al. (2012), Jones et al. (2013), Trumbo et al. (2014)
Increasing stream temperature	Increased invasion and spread of nonnative species; increased risk from disease and parasites	Rahel and Olden (2008), Sharma et al. (2009), Karvonen et al. (2010), Lawrence et al. (2014), Mitro et al. (2014), Muhlfeld et al. (2014)
Changing flow regimes and increasing flow variability	Changing stream phenology, including timing of insect emergences and fish spawning	Harper and Peckarsky (2006), Ward et al. (2015)
Increasing wildfire intensity	Increasing stream sedimentation; direct mortality; increased vulnerability for isolated populations	Brown et al. (2001), Goode et al. (2012)
Increasing drought	Decreased streamflow; reduction in suitable habitat; habitat fragmentation	Luce and Holden (2009), Williams and Meka Carter (2009), Zeigler et al. (2012, 2013)
Increasing flooding	Increased stream scouring and erosion, disruption of spawning redds	Poff (2002), Hamlet and Lettenmaier (2006), Wenger et al. (2011a,b)
Changes in groundwater recharge and discharge	Changes in baseflow conditions and increased groundwater temperature	Taylor et al. (2013)
Sea-level rise	Increased flooding and erosion of coastal zones	Bijma et al. (2013), Theuerkauf et al. (2014), Goddard et al. (2015)
Increasing ocean temperature	Disruption of migratory pathways for anadromous species	Bijma et al. (2013)
Increasing ocean acidification	Reduced food supplies for anadromous species	Bednarsek et al. (2014)

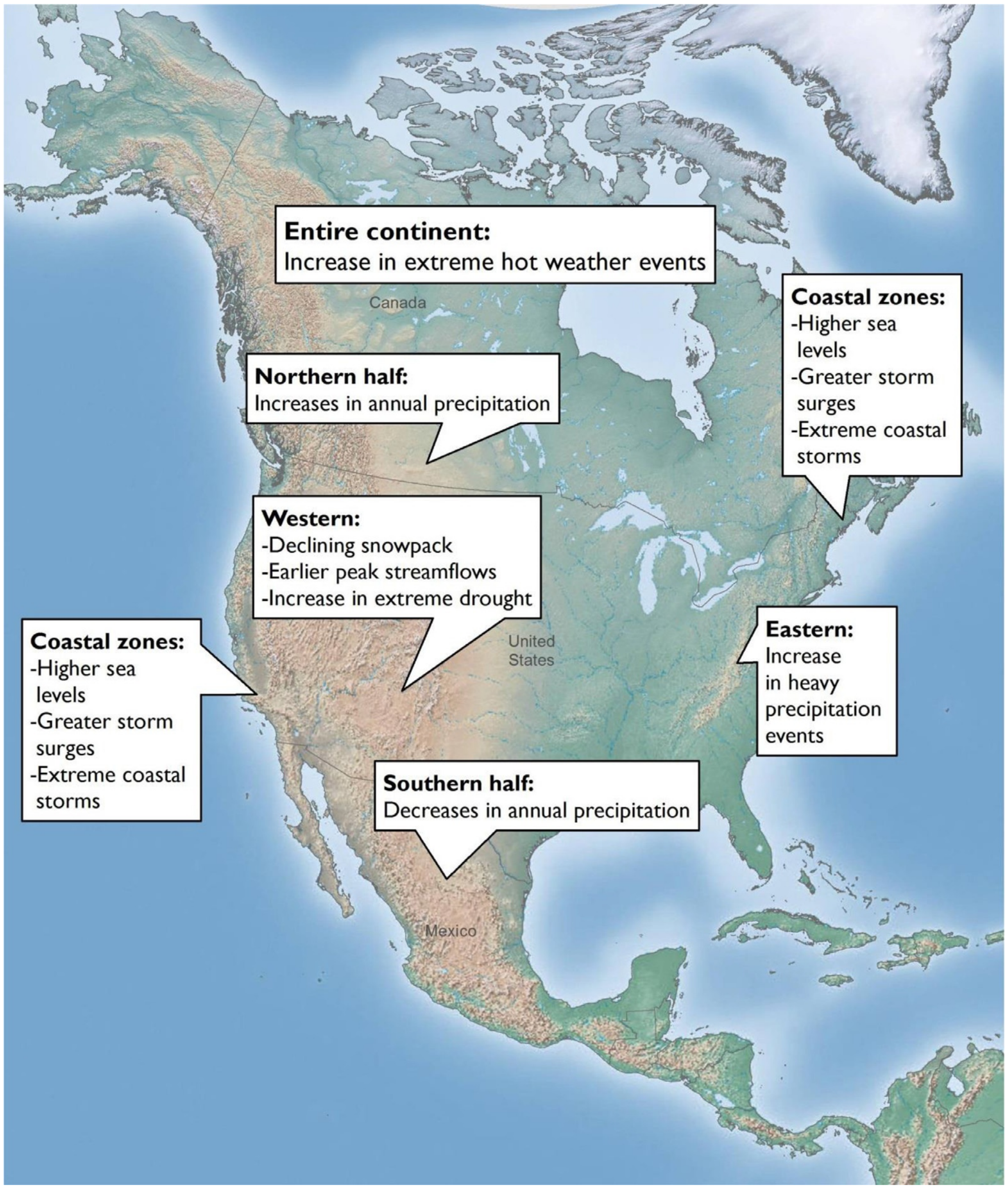

Figure 1 Critical climate trends classified as 'high' to 'very high' confidence for North America according to the Intergovernmental Panel on Climate Change. Information from Romero-Lankao P and Smith JB (2014). North America. In: *Climate change 2014: impacts, adaptation, and vulnerability. Part B: Regional aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. New York: Cambridge University Press.

protect stream banks from erosion and help dissipate the high energy of floods, but the lack of riparian vegetation can leave stream banks vulnerable to swift changes in flows.

In interconnected stream networks, trout may be able to escape wildfires or floods and find suitable habitat conditions elsewhere within the stream network. But the same disturbance event may eliminate the trout population if habitat is fragmented and they are not able to relocate to suitable conditions (Fausch et al., 2009; Rieman and Clayton, 1997).

Impacts from climate change will vary across North America although all regions of the continent will experience higher temperatures and more extreme weather events (**Figure 1**). Changes in streamflows are likely to be most pronounced where hydrology is snow-dependent and winter air temperatures are near freezing. As temperatures increase, precipitation regimes rapidly pass the threshold from snow to rain and higher winter streamflows and increased likelihood of redd scouring for fall-spawning species may occur (Hamlet and Lattenmaier, 2007; Luce et al., 2014). Ward et al. (2015) examined flow regimes in Pacific Northwest rivers and found that more than half have experienced increased flow variability during the past 60 years. Furthermore, the authors found that increasing flow variability had more negative impact on salmon and steelhead than any other climate change effect. In some regions, drought will reduce streamflows (Leppi et al., 2011; Luce and Holden, 2009), especially during summer and fall, when flows are typically at their lowest and temperatures at their highest (Arismendi et al., 2013).

Changing Ocean Conditions

Increased carbon dioxide emissions and associated warming of the atmosphere are having a profound impact on oceans. Impacts from climate change to oceans are fourfold: increasing acidification, seawater warming, deoxygenation, and increased sea level (Bijma et al., 2013). The oceans serve as a vast sink for increasing levels of atmospheric carbon dioxide. As carbon dioxide is absorbed in the ocean, seawater becomes more acidic. During the past few decades, surface layers of the ocean have decreased 0.02 pH units per decade (Bijma et al., 2013); a rate of change that is about 30–100 times faster than has occurred in the geologic past.

As surface layers of the ocean warm in response to increasing air temperatures, ocean temperature stratification increases, which increases deoxygenation. The loss of oxygen is being enhanced in some coastal areas by increased upwelling of deep, deoxygenated waters (Bijma et al., 2013).

Sea-level rise poses several risks to cold-water fishes, including inundation of shallow estuaries, increased beach erosion, and increased flooding of tidal areas. Sea-level rise may not be uniform along all coastal areas. In recent years, the sea level has risen dramatically along the northeast US coastline. An extreme sea-level rise of 128 mm was recorded in 2009–10, apparently the result of a combination of changing coastal circulation patterns (Goddard et al., 2015). Warmer air temperature speeds melting of ice sheets and increases sea level. Warmer ocean water expands and the increased heating encourages larger storm events inland.

Impacts to salmon, steelhead, and other highly migratory salmonids from changing ocean conditions are hard to predict with certainty. Bednarsek et al. (2014) recently demonstrated dissolution of pteropod shells along coastal waters of the western United States from increasing ocean acidity. Pteropods are small zooplankton that form a critical component of many oceanic food webs. Changes in ocean temperatures and currents and deoxygenation of coastal zones could change the distribution and abundance of salmon prey species. The timing or direction of migration could shift but many such impacts are poorly understood at present.

Broadscale Implications for Salmonid Distributions

Eastern United States and Canada

In eastern North America, the native Salmonidae were chars (lake trout (*S. namaycush*), brook trout, and Arctic char), the Atlantic salmon (*Salmo salar*) in the Maritimes and historically in Lake Ontario, and the whitefish and freshwater herrings and cisco in the Great Lakes and inland lakes. Other species of salmonids have been introduced widely in the region and include brown trout from Europe, rainbow trout, and Pacific salmons from the Pacific Northwest.

The distribution of native salmon and trout in eastern North America will likely be negatively affected by a changing climate in many areas of their existing range, exacerbated by the effects of historical and present land uses and human population growth. Eastern United States and Canada have a higher population density than most of the rest of the countries and a longer period of settlement by Europeans. As a result, this region has highly modified landscapes and watersheds. The trend to increasing populations will likely exacerbate the effects of climate change on affected watersheds (Moore et al., 1997). The northern portions of eastern Canada, like western Canada, are less heavily populated but are now the focus of more intensive hydroelectric development, forestry, and mining.

The predicted pattern of climate change for eastern Canada is higher variability in temperature and weather patterns, warmer, wetter winters, and drier summers. Although considered a temperate, humid climate, with modest temperature increases resulting from climate change, there will be significant increases in evapotranspiration in both winter and summer that could lead to reduced or modified average streamflows that may have impacts on groundwater recharge and groundwater temperature as well (Chu et al., 2008; Meisner, 1990; Moore et al., 1997; Taylor et al., 2013).

Increasing stream temperatures in the southeast and mid-Atlantic United States will decrease available habitat for salmonids and fragment much of what will remain of their distribution in stream networks as trout are restricted to cooler, higher-elevation islands near mountain tops (Meisner, 1990). Flebbe et al. (2006) predicted a 52.9% loss of native and wild trout habitat from northern Georgia to Virginia if air temperatures increased 2.5 °C and a 78.4% loss if temperatures increased 3.5 °C.

A number of studies predict warmer, wetter winters with more precipitation and more intense storm events in the form of rain rather than snow for eastern North America (e.g., Magnuson et al., 1997; Spierre and Wake, 2010). Already, data from 1948 to 2007 show an increased frequency of large storm events in New England (Spierre and Wake, 2010). These changes may create higher baseflow conditions in the winter with drier summers interspersed with more rainfall in the form of intense, localized storms in the summer. The incidence of more frequent intense storms will likely lead to faster channel evolution that will also affect the physical habitat of cold-water fishes and may increase sediment loadings and degrade water quality. This situation in combination with highly settled landscapes and significant fragmentation of streams, limiting free movement of trout to areas or refuge, modified by forestry, farming, and urban development, will create real challenges for the persistence of native trout that rely on cold, clean water (Schindler and Bruce, 2012).

Lake ecosystems will also change under climate change predictions. Milder winters will lead to less ice cover, which will increase evaporation and potentially winter temperatures in smaller lakes and higher rates of evaporation and reduced lake levels in larger lakes. This trend was first clearly detected in the Experimental Lakes Area of northwestern Ontario in 1990 (Schindler et al., 1990). Increased summer temperatures will change dissolved oxygen levels, especially below the hypolimnion, and this combination of diminished dissolved oxygen and higher temperatures will also shrink the habitable living space for lake trout and other salmonids (Alofs et al., 2014; Magnuson et al., 1997; Schindler and Bruce, 2012).

Evidence of northward shifts of the distributions of warm- and cold-water fish communities in Canada (Chu et al., 2005) and Ontario (Alofs et al., 2014) has already been demonstrated, with some recommendations provided to try to protect remaining cold-water fish communities as major northward shifts of warmwater and cold-water fish occur (Fang et al., 2012; Jacobson et al., 2013).

Western United States and Canada

In western North America, the native Salmonidae were salmon, steelhead, coastal and inland rainbows (redbands), cutthroat trout, char (bull trout, Dolly Varden, and lake trout), whitefishes, and grayling. Several of these species are anadromous and others are highly migratory within freshwater river systems or between lakes and rivers. Brown trout and brook trout have been widely introduced, and rainbow trout have been cultured in hatcheries and broadly introduced as well.

Native salmonids in western North America are facing mounting stressors as a result of climate change and the resulting warmer streams, higher variability in precipitation, and reduced snowpack. Earlier snowmelt and runoff lead to more extreme forest drying, and outbreaks of forest insects and the spread of invasive annual cheatgrass are creating more hazardous wildfire conditions across much of the West (Westerling et al., 2006). Stream sedimentation can increase as a result of wildfires with losses of trout populations in areas where distributions have already been fragmented by human disturbances (Brown et al., 2001).

Throughout much of the Northwest and Northern Rockies, stream temperatures are predicted to increase by about 2.4 °C by mid-century (Figure 2). This region includes habitat for salmon, steelhead, chars, whitefishes, grayling, rainbows, and cutthroat

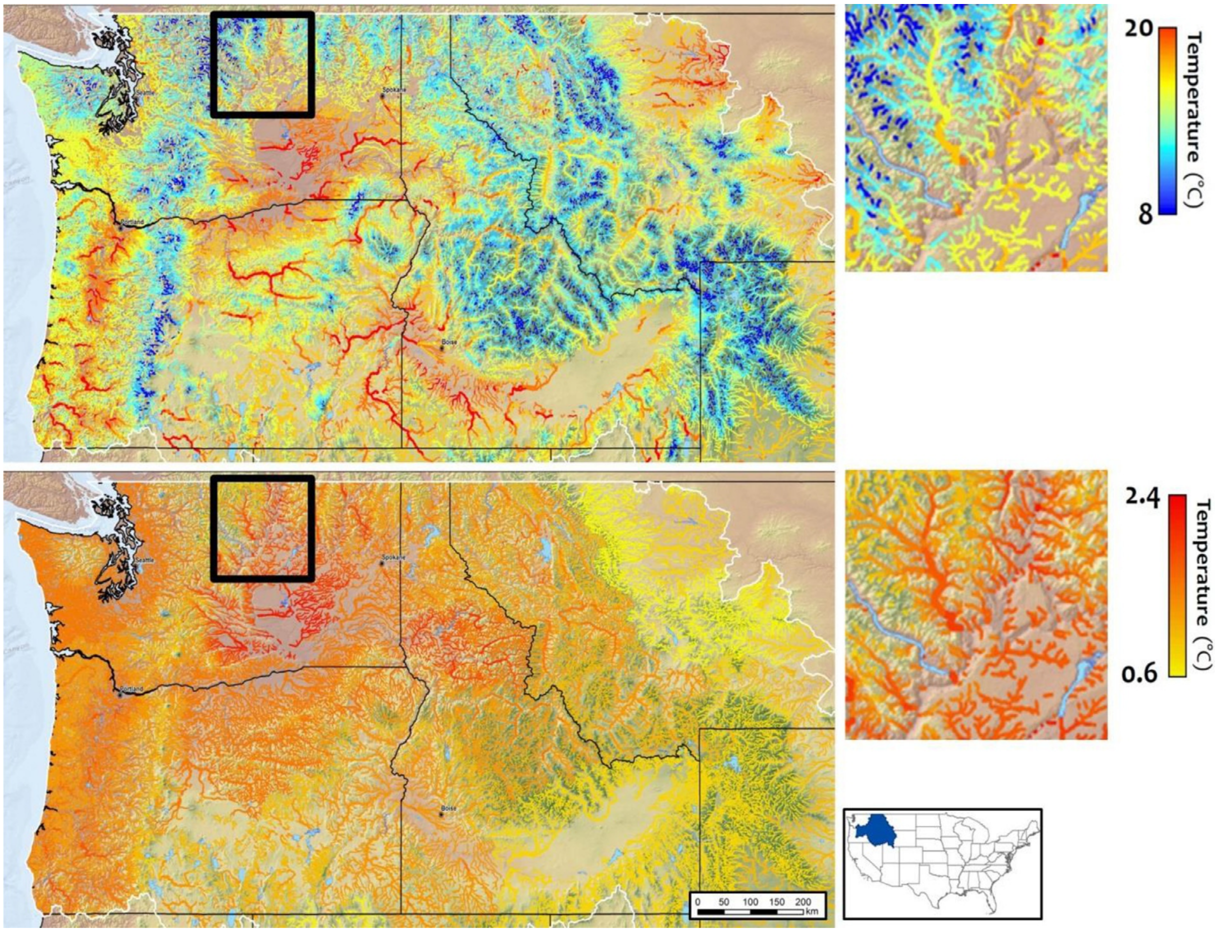

Figure 2 Summer temperature scenarios for the northwestern United States that were developed from 45 000 summers of monitoring data across this 300 000 stream kilometer network. Top panel shows mean summer temperatures for a 21-year historical period (1993–2013) and bottom panel shows temperature increases predicted for a mid-century period (2030–59). Black box outlines detail stream network map to the right.

trout. Using a middle-of-the-road scenario for the accumulation of greenhouse gases, native cutthroat trout are expected to lose an additional 58% of their habitat compared to current conditions by 2080 based on predicted changes in flows, temperatures, and nonnative species interactions (Wenger et al., 2011a,b). Bull trout and many salmon and steelhead populations in this region already are listed as endangered or threatened pursuant to the US Endangered Species Act. Additional stream warming will push the remaining distribution of nonanadromous species to higher elevations. Anadromous salmon and steelhead will find many main stem rivers uninhabitable for large portions of the year.

Unprecedented drought is forecast in the southwestern United States, where most native trout already are listed as threatened or endangered species because of range declines and invasions of nonnative species (Cook et al., 2015). This region may be particularly vulnerable to uncharacteristic wildfire as indicated by the Wallow Fire of 2011, which was the largest wildfire in Arizona history and impacted Apache trout (*O. gilae apache*) distribution, and the Whitewater–Baldy Wildfire, which swept through the core of remaining Gila trout (*O. gilae*) habitat in 2012 and became the largest wildfire in New Mexico history. Extended drought will be especially serious for southwestern trout like the Rio Grande cutthroat (*O. clarkii virginalis*), where a majority of populations in recent years have experienced baseflows of less than 1 cfs (Zeigler et al., 2013), or in California's Sierra Nevada where the Paiute cutthroat trout (*O. clarkii seleniris*) and other native trout have an extremely limited range.

It is predicted that with the higher variability in streamflows identified by various studies (e.g., Hauer et al., 1997; Morrison et al., 2002; Stewart et al., 2004), there will likely be a shift in spring runoff in both timing and volume (though volume is somewhat less uncertain) across the West. In addition, the projected changes in air temperature to warmer summers will also affect river temperatures, especially in areas where riparian and stream channel habitats already are degraded. The combination of changes in high flow timing, increased summer temperatures, and potentially more variable low flow conditions will likely affect migration timing of anadromous Pacific salmon and trout and in many cases push these populations further up their watersheds closer to the colder water melting from the remaining glaciers and snow while at the same time increasing stress on the adults moving up these warmer main stem river systems (Eby et al., 2014). Die-offs of salmon and steelhead will become increasingly common as adults move through warmer, lower-elevation river corridors during summer and fall.

On the eastern slopes of the Rocky Mountains, even higher variability in precipitation and temperatures are expected (Schindler and Bruce, 2012) with reduced snowpack, which has already occurred in many parts of the West (Pederson et al., 2011). Many western watersheds are primarily fed by a combination of snowmelt in the spring and early summer and glacial melt in the summer. Relatively little precipitation occurs through the late spring and summer months because this region has a semiarid climate influenced by weather patterns moving up the eastern slopes from the American southwest (Schindler and Bruce, 2012).

Although there has not been clear evidence of changes in mean annual precipitation on the Saskatchewan River Basin (headwaters Rocky Mountains), there are discernible changes in seasonal precipitation and air temperature in this region (Dibike et al., 2012). Reduced snowpack and earlier spring runoff have been observed across many western river systems from 1948 to 2000, and the likelihood is that these trends will become more severe in the coming decades (Stewart et al., 2004). Multiple lines of evidence have confirmed the trend towards reduced snowpack in the West. If older tree ring data are added to recent snowpack measurements, the recent decline in snowpack becomes strikingly clear in the Yellowstone region (Tercek et al., 2015).

Warmer temperatures are also leading to changes in winter and early spring precipitation from snow to rain, which can result in massive, short-duration floods, followed by extremely low summer baseflows only being maintained by glacial melt and smaller snowpacks. Shifts in winter precipitation patterns from snow to rain may pose additional problems for fall-spawning species like bull trout that face increased potential for redd scouring (Goode et al., 2013).

Substantial reductions in glacial mass have been observed across much of the western United States and Canada. There has been a 25% reduction in the Bow Glacier that feeds the Bow River over the last century, and this trend continues with the Bow Glacier and with the Athabasca and Saskatchewan Glaciers that comprise almost 75% of Alberta's current ice mass (Marshall and White, 2010). Schindler and Bruce (2012) suggested that even though glacial contribution to annual streamflow is very low, it makes up close to 7% in the summer when water temperatures are normally high and dissolved oxygen can be at its lowest. Any deterioration in this important contribution to cold, clean water will have dire impacts on fishes such as grayling, trout, and chars that require cold water. Similar problems are likely as glaciers in Montana's iconic Glacier National Park melt and disappear. The implications of changes in seasonal precipitation, reduction in glacial flows, and higher summer temperatures in combination with fragmentation due to highways, logging roads, fracking, and mining all lead to reductions or potential extirpation, of some trout and salmon populations across much of the western United States and Canada (Chu et al., 2005; Hauer et al., 1997; Schindler and Bruce, 2012).

Populations of the chars (bull trout, Dolly Varden, lake trout, and Arctic char), grayling, whitefish, and other species face perhaps the greatest challenges resulting from climate change. Most general circulation models predict the greatest increases in mean annual temperature in the far north, including northern Canada and Alaska. There are multiple implications from these higher temperatures including melting of permafrost, changes in snow pack and earlier spring runoff, and lower summer baseflows along with changes in the food webs and trophic structure of both rivers and lakes (Schindler and Bruce, 2012). The thawing of permafrost can also cause land slumpage that can alter stream patterns and groundwater movements in the summer. All of these changes will vary in intensity under specific local conditions across the arctic (Reist et al., 2006). In general though, the majority of arctic salmonids are cold-water stenotherms that cannot withstand major changes in flow patterns, timing, and temperature. These various changes can decouple fish from important environmental cues and affect their bioenergetics and ability to find habitat, food, and spawning sites under the new more variable conditions (Reist et al., 2006; Schindler and Bruce, 2012).

Mexico

It has long been known that the natural distribution of North America's native trout extends broadly across the upper elevations of much of the Sierra Madre Occidental of northwestern Mexico (Cope, 1886), but only two Mexican forms have been formally described. Both of these are considered by the Mexican Government to be of conservation concern; the Mexican golden trout (*O. chrysogaster*) (Needham and Gard, 1964) is considered threatened, and the San Pedro Martir trout (*O. mykiss nelsoni*) of Baja California is given special protection status. The Baja trout is now well studied (e.g., Ruiz-Campos and Pister, 1995) and most closely related to rainbow trout in California, but the native species of the northwestern mainland of Mexico appear to be distant relatives and remain poorly known.

An overview of Mexican native trout (Hendrickson et al., 2002) reported on fieldwork and preliminary morphometric analyses that indicated that the Sierra Madre Occidental between about 23.6 and 30.3° N harbors perhaps 10 or more unnamed species that occur mostly as small isolated populations in the highest elevations of 12 independent major drainages in Durango, Sinaloa, Chihuahua, and Sonora. A few years later, the international survey group known as 'Truchas Mexicanas' discovered the first Mexican trout from a Gulf of Mexico drainage. Immediately recognizing it as critically endangered, within a week of its discovery, the Truchas group electronically published a 'white paper' to rapidly disseminate the news. The Conchos trout (*Oncorhynchus* sp.) (named for the Río Grande tributary in which it was found) is clearly on the brink of extinction and is represented by one tiny population (likely less than 200 fish) in a tiny and very precarious isolated headwater stream reach (Camarena-Rosales et al., 2006). Though it is hopefully an extreme example of limited distribution and small population size, results of subsequent genetic studies (Abadia-Cardosa, 2014; Camarena-Rosales et al., 2008) report small population sizes for many of the Mexican trout species of the Sierra Madre Occidental.

Clearly many, if not most, of the impacts of climate change described for salmonids in the western United States are also likely to affect Mexican trout; however, given what we do know of these most southern salmonids, it seems clear that they will be extremely vulnerable to warming, drought, and increased variability in streamflow. Though all Mexican species except the Conchos trout have more than one known population, most populations are in isolated, short, and high-gradient stream fragments near drainage divides, often with barriers to upstream movements, and with very little upstream perennial water. Downstream distributions appear largely determined by higher temperatures and interactions with warmwater species. Thus, most Mexican trout would be highly susceptible to general climate warming, which would likely cause widespread extirpations and extinctions since, for most populations, the cool habitats they require will become either nonexistent or not accessible and their already fragmented and isolated small populations will surely limit their ability to adapt via genetic selection to any changing environmental condition.

The Path Forward

Climate change is rapidly altering aquatic systems as temperatures warm, precipitation and streamflow patterns change, and disturbances increase. These changes are likely to be particularly problematic for trout, char, and salmon that depend on cold and clean water among interconnected stream networks for their survival. The magnitude of challenges posed by climate change require new strategies and tactics that help salmonids adapt to climate change and increase resistance and resilience of aquatic habitats and watersheds to increasing disturbance (Rieman and Isaak, 2010). Restoration actions should address local climate-driven change but work across entire watersheds to achieve significant benefit in the face of rapidly changing environmental conditions (Williams et al., 2015). A new generation of models based on high-resolution temperature scenarios can be combined with watershed-scale restoration efforts to target areas that are less susceptible to climate change and more likely to harbor trout and salmon strongholds in the future (Isaak et al., 2015). Such an approach will be especially important to maintain future populations of particularly sensitive salmonids such as bull trout, Arctic char, and Dolly Varden.

Restoration efforts that cool stream systems (Johnson and Wilby, 2015) may help prevent invasion by downstream populations of warmwater fishes (Lawrence et al., 2014), which is an increasing problem for many trout, char, and salmon populations. The importance of management actions that address larger spatiotemporal scales, synergy among stressors, and environmental uncertainty is a clear need as agencies grapple with climate change (**Table 2**). Wade et al. (2013) argued that habitat protection alone will not be sufficient to save steelhead in the Pacific Northwest, but must be accompanied by landscape-scale actions to restore resiliency and improve watershed function. Williams et al. (2015) made similar arguments for saving western trout populations.

As described in a recent State of the Trout report (Trout Unlimited, 2015), climate change is one of the top threats to survival of cold-water fishes. According to the report's authors, we have the proper scientific understanding to adequately address many of the impacts of climate change. The problem is not one of science, but rather one of the willingness of our society to make substantive change in our consumption rates and lifestyles. Needed changes include greater conservation of water and energy resources, better controls for nonnative species, and more rigorous restoration efforts. As society grapples with the broader policy questions, proper management and restoration should be envisioned and conducted at larger scales so as to preserve as many of our salmonid populations and future options as possible. Lastly, increasing societal awareness of climate change and resulting environmental degradation through increased environmental education, citizen science, and resource stewardship programs will provide one of our best paths forward to sustain water supplies and native fish populations in the face of climate change.

Table 2 Management actions that support the adaptation of cold-water fish populations and their habitats to the impacts of climate change

Management action	*Anticipated effect and rationale*
Reduce nonclimate stressors such as hot season livestock grazing, agricultural runoff, or polluted stormwater runoff	Because climate change increases cumulative stress to natural habitats, any reductions in the total stream disturbances will help accommodate climate impacts and reduce their severity
Improve watershed function through restoration and expansion of wetlands, riparian areas, wet meadows, and floodplains	Increasing the high-elevation storage and slow release of water will mitigate for reduced snowpack and maintain late-season stream baseflows
Improve watershed resiliency to disturbances by improving culverts, bridges, and other stream/road crossings	Improving stream crossings enable the watershed to handle floods and large storms, reduce the likelihood of tributary failure and debris flows, and generally increase the connectivity of stream systems
Increase cold-water refuge habitats by adding large wood structure, increasing channel complexity, and narrowing and deepening stream channels	Increasing deep channels, pools, and shade decrease stream temperature and provide refuge habitats during summer and drought periods
Increase stream shading and reduce stream siltation by increasing riparian habitats and their native plant species	Riparian habitats that are wider and harbor more native plants, including trees, will not only provide shade but also help filter polluted runoff from upstream activities
Improve efficiency of restoration work by focusing on watershed scales and in areas that are more likely to withstand climate impacts	If restoration work is to be effective, work must proceed at larger scales, be adequately monitored, and be maintained over the long haul
Increase stream connectivity by removing instream barriers and replacing poorly designed culverts	Allow fish to move freely among stream network to find suitable areas and to express migratory life histories
Rebuild stronghold populations of salmon and trout by increasing availability of high-quality interconnected habitats	Larger populations are more resilient to disturbance and more likely to survive severe change

Source: Rieman, B. E. and Isaak, D. J. (2010). Climate change, aquatic ecosystems, and fishes in the Rocky Mountain West: implications and alternatives for management. *General Technical Report* RMRS-GTR-250 USDA Forest Service, Ft. Collins, CO; Williams, J. E., Neville, H. M., Haak, A. L., Colyer, W. T., Wenger, S. J. and Bradshaw, S. (2015). Climate change adaptation and restoration of western trout streams: opportunities and strategies. *Fisheries* **40**, 304–317.

References

Abadia-Cardoso, A. (2014). *Genetic investigation of the Pacific trout complex*: *From pedigree to phylogenies*. Ph.D. Dissertation, University of California, Santa Cruz.

Alofs KM, Jackson DA, and Lester NP (2014) Ontario freshwater fishes demonstrate differing range-boundary shifts in a warming climate. *Diversity and Distributions* 20: 123–136.

Arismendi I, Safeeq M, Johnson SL, Dunham JB, and Haggerty R (2013) Increasing synchrony of high temperature and low flow in western North American streams: Double trouble for coldwater biota? *Hydrobiologia* 712: 61–70.

Bednarsek N, Feely RA, Reum JCP, Peterson B, Menkel J, Alin SR, and Hales B (2014) *Limacina helicina* shell dissolution as an indicator of declining habitat suitability owing to ocean acidification in the California Current Ecosystem. *Proceedings of the Royal Society B* 281: 20140123.

Behnke RJ (2002) *Trout and salmon of North America*. New York: The Free Press.

Bijma J, Portner HO, Yesson C, and Rogers AD (2013) Climate change and the oceans: What does the future hold? *Marine Pollution Bulletin* 74: 495–505.

Brown DK, Echelle AA, Propst DL, Brooks JE, and Fisher WL (2001) Catastrophic wildfire and number of populations as factors influencing risk of extinction for Gila trout (*Oncorhynchus gilae*). *Western North American Naturalist* 61: 139–148.

Camarena-Rosales F, Cutter R, de Los Santos AB, Espinosa-Perez H, Garcia de Leon FJ., Hendrickson DA and Kahajda,BR (2006). *Conservation of the Conchos trout*: *A white paper on history of its discovery*, *report on its status*, *and an urgent plea for action*. University of Texas. http://hdl.handle.net/2152/22233.

Camarena-Rosales F, Ruiz-Campos G, Rosa-Velez J, Mayden RL, Hendrickson DA, Varela-Romero A, and Garcia FJ (2008) Mitochondrial haplotype variation in wild trout populations (Teleostei: Salmonidae) from Northwestern Mexico. *Reviews in Fish Biology and Fisheries* 18: 33–45.

Chu C, Mandrak NE, and Minns CK (2005) Potential impacts of climate change on the distributions of several common and rare freshwater fishes in Canada. *Diversity and Distributions* 11: 299–310.

Chu C, Jones NE, Mandrak NE, Piggott AR, and Minns CK (2008) The influence of air temperature, groundwater discharge, and climate change on the thermal diversity of stream fishes in southern Ontario watersheds. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 297–308.

Cook BJ, Ault TR, and Smerdon JE (2015) Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Science Advances* 1: e140082. http://dx.doi.org/10.1126/sciadv.1400082.

Cope ED (1886) The most southern salmon. *American Naturalist* 20: 735.

Dibike Y, Prowse T, Shrestha R, and Ahmed R (2012) Observed trends and future projections of precipitation and air temperature in the Lake Winnipeg watershed. *Journal of Great Lakes Research* 38: 72–82.

Eby LA, Helmy O, Holsinger LM, and Young MK (2014) Evidence of climate-induced range contractions in bull trout *Salvelinus confluentus* in a Rocky Mountain Watershed, USA. *PLoS One* 9(6): e98812. http://dx.doi.org/10.1371/journal.pone.0098812.

Fang X, Jiang L, Jacobson PC, Stefan HG, Alam SR, and Pereira DL (2012) Identifying cisco refuge lakes in Minnesota under future climate scenarios. *Transactions of the American Fisheries Society* 141: 1608–1621.

Fausch KD, Rieman BE, Dunham JB, Young MK, and Peterson DP (2009) Invasion versus isolation: Trade-offs in managing native salmonids with barriers to upstream movement. *Conservation Biology* 23: 859–870.

Fleebe PA, Roghair LD, and Bruggink JL (2006) Spatial modeling to project Southern Appalachian trout distribution in a warmer climate. *Transactions of the American Fisheries Society* 135: 1371–1382.

Goddard PB, Yin J, Griffies SM, and Zhang S (2015) An extreme event of sea-level rise along the Northeast coast of North America in 2009–2010. *Nature Communications* 6: 6346. http://dx.doi.org/10.1038/ncomms7346.

Goode JR, Luce CH, and Buffington JM (2012) Enhanced sediment delivery in a changing climate in semi-arid mountain basins: Implications for water resource management and aquatic habitat in the northern Rocky Mountains. *Geomorphology* 139–140: 1–15.

Goode JR, Buffington JM, Tonina D, Isaak DJ, Thurow RF, Wenger SJ, et al. (2013) Potential effects of climate change on streambed scour and risks to salmonid survival in snow-dominated mountain basins. *Hydrological Processes* 27: 750–765.

Haak AL, Williams JE, Isaak D, Kershner JK, Gresswell R, Hostetler S, and Neville HM (2010) The potential influence of changing climate on the persistence of salmonids in the Inland West. *U.S. Geological Survey Open-File Report* 2010–1236.

Hamlet AF and Lettenmaier DP (2007) Effects of 20th century warming and climate variability on flood risk in the Western U.S. *Water Resources Research* 43: W06427.

Harper MP and Peckarsky BL (2006) Emergence cues of a mayfly in a high-altitude stream ecosystem: potential response to climate change. *Ecological Applications* 16: 612–621.

Hauer FR, Baron JS, Campbell DH, Fausch KD, Hostetler SW, Leavesley GH, et al. (1997) Assessment of climate change and freshwater ecosystems of the Rocky Mountains, USA and Canada. *Hydrological Processes* 11: 903–924.

Hendrickson DA, Espinosa Perez H, Findley LT, Forbes W, Tomelleri JR, Mayden RL, et al. (2002) Mexican native trouts: A review of their history and current systematic and conservation status. *Reviews in Fish Biology and Fisheries* 12: 273–316.

Isaak DJ, Luce CH, Rieman BE, Nagel DE, Peterson EE, Horan DL, et al. (2010) Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecological Applications* 20: 1350–1371.

Isaak D, Wollrab S, Horan D, and Chandler G (2012) Climate change effects on stream and river temperatures across the northwest US from 1980–2009 and implications for salmonid fishes. *Climatic Change* 113: 499–524.

Isaak DJ, Young MK, Nagel DE, Horan DL, and Groce MC (2015) The cold-water climate shield: Delineating refugia for preserving salmonid fishes through the 21st century. *Global Change Biology* 21: 2540–2553.

Jacobson PC, Fang X, Stefan HG, and Pereira DL (2013) Protecting cisco oxythermal habitat from climate change: Building resilience in deep lakes using a landscape approach. *Advances in Limnology* 64: 323–332.

Johnson MF and Wilby RL (2015) Seeing the landscape for the trees: Metrics to guide riparian shade management in river catchments. *Water Resources Research* 51: 3754–3769. http://dx.doi.org/10.1002/2014WR016802.

Jones LA, Muhlfeld CC, Marshall LA, McGlynn BL, and Kershner JL (2013) Estimating thermal regimes of bull trout and assessing the potential effects of climate warming on critical habitats. *River Research and Applications* 30: 204–216.

Karvonen A, Rintamaki P, Jokela J, and Valtonen ET (2010) Increasing water temperature and disease risks in aquatic systems: Climate change increases the risk of some, but not all, diseases. *International Journal for Parasitology* 40: 1483–1488.

Keefer ML and Caudill CC (2015) Estimating thermal exposure of adult summer steelhead and fall Chinook salmon migrating in a warm impounded river. *Ecology of Freshwater Fish*, vol. 24. http://dx.doi.org/10.1111/eff.12238.

Lawrence DJ, Stewart-Koster B, Olden JD, Ruesch AS, Torgensen CE, Lawler JJ, et al. (2014) The interactive effects of climate change, riparian management, and a nonnative predator on stream-rearing salmon. *Ecological Applications* 24: 895–912.

Leppi JC, DeLuca TH, Harrar SW, and Running SW (2011) Impacts of climate change on August stream discharge in the Central-Rocky Mountains. *Climatic Change* 112: 997–1014.

Luce CH and Black TA (1999) Sediment production from forest roads in western Oregon. *Water Resources Research* 35: 2561–2570.

Luce CH and Holden ZA (2009) Declining annual streamflow distributions in the Pacific Northwest United States. *Geophysical Research Letters* 36: L16401. http://dx.doi.org/10.1029/2009GL039407.

Luce CH, Lopez-Burgos V, and Holden Z (2014) Sensitivity of snowpack storage to precipitation and temperature using spatial and temporal analog models. *Water Resources Research* 50: 9447–9462.

Magnuson JJ, Webster KE, Assel RA, Bowser CJ, Dillon PJ, Eaton JG, et al. (1997) Potential effects of climate changes on aquatic systems: Laurentian Great Lakes and Precambrian Shield region. *Hydrological Processes* 11: 825–871.

Mantua N, Tohver I, and Hamlet A (2010) Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. *Climatic Change* 102: 187–223.

Marshall S and White E (2010) *Alberta glacier inventory and ice volume estimation. Crowfoot Ice Research and Consulting*. Alberta: Canmore.

Meisner JD (1990) Potential loss of thermal habitat for brook trout, due to climatic warming, in two southern Ontario streams. *Transactions of the American Fisheries Society* 119: 282–291.

Mitro MG, Marcquenski S, Saltau K, and Kanehl P (2014) Gill lice as a proximate cause of brook trout loss under changing climatic conditions. In: *Proceedings Wild Trout Symposium XI*, pp. 200–206.

Moore MV, Pace ML, Mather JR, Murdoch PS, Howarth RW, Folt CL, et al. (1997) Potential effects of climate change on freshwater ecosystems of the New England/Mid Atlantic region. *Hydrological Processes* 11: 925–947.

Morrison J, Quick MC, and Foreman MGG (2002) Climate change in the Fraser river watershed: Flow and temperature projections. *Journal of Hydrology* 263: 230–244.

Muhlfeld CC, Kovach RP, Jones LA, Al-Chokhachy R, Boyer MC, Leary RF, et al. (2014) Invasive hybridization in a threatened species is accelerated by climate change. *Nature Climate Change* 4: 620–624.

Needham PR and Gard R (1964) A new trout from Central Mexico: *Salmo chrysogaster*, the Mexican golden trout. *Copeia* 1964: 169–173.

Pederson GT, Gray ST, Woodhouse CA, Betancourt JL, Fagre DB, Littell JS, et al. (2011) The unusual nature of recent snowpack declines in the North American Cordillera. *Science* 333: 332–335. http://dx.doi.org/10.1126/science.1201570.

Poff NL (2002) Ecological response to and management of increased flooding caused by climate change. *Philosophical Society of the Royal Society of London* 360: 1497–1510.

Rahel FJ and Olden JD (2008) Assessing the effects of climate change on aquatic invasive species. *Conservation Biology* 22: 521–533.

Reist JD, Wrona FJ, Prowse TD, Power M, Dempson JB, Beamish RJ, et al. (2006) General effects of climate change on Arctic fishes and fish populations. *Ambio* 35: 370–380.

Rieman B and Clayton J (1997) Wildfire and native fish: issues of forest health and conservation of sensitive species. *Fisheries* 22: 6–15.

Rieman BE and Isaak DJ (2010) Climate change, aquatic ecosystems, and fishes in the Rocky Mountain West: implications and alternatives for management. *General Technical Report* RMRS-GTR-250 USDA Forest Service, Ft. Collins, CO.

Romero-Lankao P and Smith JB (2014) North America. In: *Climate change 2014: Impacts, adaptation, and vulnerability. Part B: Regional aspects*. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, New York: Cambridge University Press.

Ruiz-Campos G and Pister EP (1995) Distribution, habitat, and current status of the San Pedro Martir rainbow trout, *Oncorhynchus mykiss nelsoni* (Evermann). *Bulletin of the Southern California Academy of Sciences* 94: 131–148.

Schindler DW and Bruce J (2012) Freshwater resources, Chapter 3. In: *Climate change adaptations: a priorities plan for Canada*. University of Waterloo Climate Change Adaptation Project, pp. 122.

Schindler DW, Beaty KG, Fee EJ, Cruikshank DR, DeBruyn ER, Findlay DL, et al. (1990) Effect of climatic warming on Lakes of the Central Boreal Forest. *Science* 250: 967–970.

Schneider P and Hook SJ (2010) Space observations of inland water bodies show rapid surface warming since 1985. *Geophysical Research Letters* 37(22): L22405.

Selong JH, McMahon TE, Zale AV, and Barrows FT (2001) Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. *Transactions of the American Fisheries Society* 130: 1026–1037.

Sharma S, Jackson DA, and Minns CK (2009) Quantifying the potential effects of climate change and the invasion of smallmouth bass on native lake trout populations across Canadian lakes. *Ecography* 32: 517–525.

Spierre SG and Wake C (2010) *Trends in extreme precipitation events for the northeastern United States 1948–2007*. Durham: Carbon Solutions New England, University of New Hampshire.

Stewart IT, Cayan DR, and Dettinger MD (2004) Changes in snowmelt runoff timing in Western North America under a 'business as usual' climate change scenario. *Climatic Change* 62: 217–232.

Taylor RG, Scanlon B, Döll P, Rodell M, van Beek R, Wada Y, et al. (2013) Ground water and climate change. *Nature Climate Change* 3: 322–329.

Tercek M, Rodman A, and Thoma D (2015) Trends in Yellowstone's snowpack. *Yellowstone Science* 23: 20–27.

Theuerkauf EJ, Rodrigue AB, Fegley SR, and Luettich RA (2014) Sea level anomalies exacerbate beach erosion. *Geophysical Research Letters* 41: 5139–5147.

Trout Unlimited (2015) *State of the trout: a report on the status and trends of native trout in the United States*. Arlington, VA: Trout Unlimited.

Trumbo BA, Nislow KH, Stallings J, Hudy M, Smith EP, Yun Kim D, et al. (2014) Ranking site vulnerability to increasing temperature in southern Appalachian brook trout streams in Virginia: an exposure-sensitivity approach. *Transactions of the American Fisheries Society* 143: 173–187.

Wade AA, Beechie TJ, Fleischman E, Mantua NJ, Wu H, Kimball JS, et al. (2013) Steelhead vulnerability to climate change in the Pacific Northwest. *Journal of Applied Ecology* 50: 1093–1104.

Ward EJ, Anderson JH, Beechie TJ, Pess GR, and Ford MJ (2015) Increasing hydrologic variability threatens depleted anadromous fish populations. *Global Change Biology* 21: 2500–2509. http://dx.doi.org/10.1111/gcb.12847.

Warren DR, Robinson JM, Josephson DC, Sheldon DR, and Kraft CE (2012) Elevated summer temperatures delay spawning and reduce redd construction for resident brook trout (*Salvelinus fontinalis*). *Global Change Biology* 18: 1804–1811.

Wenger SJ, Isaak DJ, Luce CH, Neville HM, Fausch KD, Dunham JB, et al. (2011a) Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proceedings of the National Academy of Sciences* 108: 14175–14180.

Wenger SJ, Isaak DJ, Dunham JB, Fausch KD, Luce DH, Neville HM, et al. (2011b) Role of climate and invasive species in structuring trout distributions in the interior Columbia River Basin, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 68: 988–1008.

Westerling AL, Hidalgo HG, Cayan DR, and Swetnam TW (2006) Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313: 940–943.

Williams JE and Meka Carter J (2009) Managing native trout past peak water. *Southwest Hydrology* 8: 26–27, 34.

Williams JE, Neville HM, Haak AL, Colyer WT, Wenger SJ, and Bradshaw S (2015) Climate change adaptation and restoration of western trout streams: opportunities and strategies. *Fisheries* 40: 304–317.

Zeigler MP, Todd AS, and Caldwell CA (2012) Evidence of recent climate change within the historic range of Rio Grande cutthroat trout: implications for management and future persistence. *Transactions of the American Fisheries Society* 141: 1045–1059.

Zeigler MP, Todd AS and Caldwell CA (2013) Water temperature and baseflow discharge of streams throughout the range of Rio Grande cutthroat trout in Colorado and New Mexico: 2010 and 2011. *US Geological Survey Open-File Report* 2013–1051.