The Past as Prelude to the Future for Understanding 21st-Century Climate Effects on Rocky Mountain Trout

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ABSTRACT: *Bioclimatic models predict large reductions in native trout across the Rocky Mountains in the 21st century but lack details about how changes will occur. Through five case histories across the region, we explore how a changing climate has been affecting streams and the potential consequences for trout. Monitoring records show trends in temperature and hydrographs consistent with a warming climate in recent decades. Biological implications include upstream shifts in thermal habitats, risk of egg scour, increased wildfire disturbances, and declining summer habitat volumes. The importance of these factors depends on the context, but temperature increases are most relevant where population boundaries are mediated by thermal constraints. Summer flow declines and wildfires will be important where trout populations are fragmented and constrained to small refugia. A critical information gap is evidence documenting how populations are adjusting to long-term habitat trends, so biological monitoring is a priority. Biological, temperature, and discharge data from monitoring networks could be used to develop accurate vulnerability assessments that provide information regarding where conservation actions would best improve population resilience. Even with better information, future uncertainties will remain large due to unknowns regarding Earth's ultimate warming trajectory and how effects translate across scales. Maintaining or increasing the size of habitats could provide a buffer against these uncertainties.*

El pasado como preludio del futuro para comprender los efectos del clima del siglo 21 en la trucha de las Montañas Rocallosas

RESUMEN: los modelos bioclimáticos pronostican para el siglo 21 importantes reducciones en las poblaciones de truchas oriundas de las Montañas Rocallosas, sin embargo aun falta detallar cómo se darán estos cambios. Mediante cinco casos de estudio distribuidos a lo largo de la región, se explora cómo el clima cambiante ha ido afectando los ríos y cuáles serían las potenciales consecuencias para las truchas. Registros de monitoreo indican tendencias en la temperatura y en hidrógrafos que son consistentes con el calentamiento del clima en décadas recientes. Las implicaciones biológicas incluyen cambios en los hábitats térmicos de los caudales, riesgo de lavado de huevos, incremento en perturbaciones por incendios y decremento en los volúmenes de agua durante el verano. La importancia relativa de estos factores depende del contexto, pero el incremento en la temperatura resulta se torna más relevante en aquellas poblaciones cuyos límites están determinados por esa variable. El flujo de agua durante el verano se reduce y los incendios forestales cobrarán importancia donde las poblaciones de trucha se encuentren fragmentadas y confinadas a pequeños refugios. Un importante hueco de información es la evidencia que sirva para documentar cómo las poblaciones se están ajustando a las tendencias de largo plazo en cuanto a la condición de los hábitats, de manera que el monitoreo biológico se convierta en una prioridad. Datos biológicos, de temperatura y de descarga de ríos que provengan de redes de monitoreo pudieran utilizarse para desarrollar evaluaciones precisas sobre vulnerabilidad que provean información acerca de los lugares en los que las acciones de conservación mejorasen lo más posible la resiliencia de las poblaciones. Incluso disponiendo de mejor información, la gran incertidumbre que depara el futuro seguirá presente, ya que aun existen varias incógnitas con respecto a la trayectoria de calentamiento de la tierra y de cómo los efectos se transmitirán a través de distintas escalas. El mantenimiento o incremento del tamaño de los hábitats pudiera servir como una suerte de amortiguador contra tal incertidumbre.

INTRODUCTION

Global warming is altering the characteristics of aquatic ecosystems worldwide (Reist et al. 2006; Heino et al. 2009; Rieman and Isaak 2010) and stream environments across the Rocky Mountains of the Western United States are no exception (Stewart et al. 2005; Luce and Holden 2009; Leppi et al. 2011; Isaak et al. 2012). The high elevations of these mountains have historically provided cold stream and river habitats that support trout, salmon, and char, which are iconic of the region and sustain popular fisheries. Physiological requirements of these fishes for cold temperatures, combined with historic population declines from a century of intensive land use and development, have raised concerns regarding how climate change may affect their future status across the region. Several recent reviews described a range of potential climate effects (Independent Science Advisory Board 2007; Rahel et al. 2008; Haak et al. 2010; Rieman and Isaak 2010), but the general conclusions are that stream habitats will become warmer, more variable with regards to thermal and hydrologic conditions, and prone to larger, more frequent disturbances that are significantly different from historical conditions (Jentsch et al. 2007). Fish populations, in response, are predicted to adapt in place through phenotypic or genotypic means, move to track suitable habitats, or be extirpated (Crozier et al. 2008; McCullough et al. 2009).

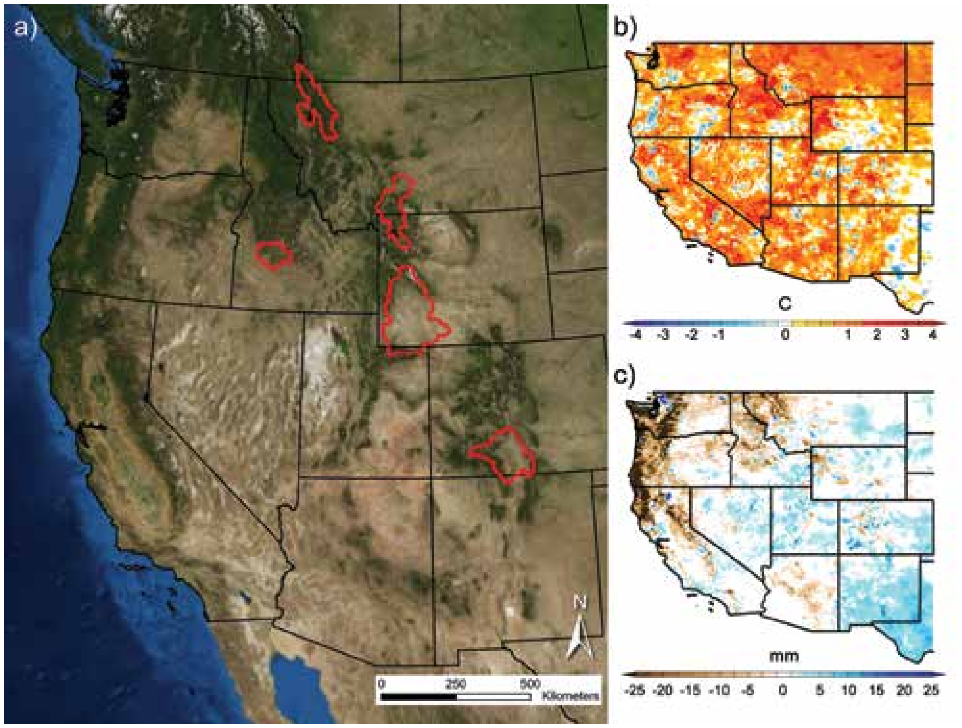

Figure 1. (a) Locations of case history areas examined to describe historical effects of climate change on trout streams across the Rocky Mountains. Change in (b) mean annual air temperature and (c) precipitation from 1950 to 2009. Mapped anomalies are the differences between averages for 1950–1959 and 2000–2009 based on PRISM data that were interpolated from climate monitoring stations (Daly et al. 1994).

Numerous bioclimatic models have been developed for trout in the Rocky Mountain region that forecast range reductions on the order of 20–90% over the next 50–100 years (Eaton and Schaller 1996; Keleher and Rahel 1996; Rahel et al. 1996; Mohseni et al. 2003; Rieman et al. 2007; Kennedy et al. 2009; Williams et al. 2009; Wenger et al. 2011a). These broad-scale assessments have been valuable for raising awareness within the scientific community and the general public about the risks posed by climate change. However, given their geographic scope and purpose (predicting changes that have yet to occur), these assessments cannot describe the mechanisms by which such large changes ultimately transpire. Predictions from current models also lack the spatial precision that managers need to make decisions about where to undertake habitat restoration within a river network and which methods would best improve population resilience against future changes. Understanding these details and improving the predictive accuracy of fish population and habitat models is essential if research is to provide the information needed to manage trout populations through a transitional century (Isaak and Rieman, 2012).

Complicating matters, environmental and biological changes will not be uniform across the ranges of species. Subregional differences in climate, diverse mountain topographies, variation in stream sensitivity to climate forcing (Hari et al. 2006; Tague et al. 2008), variation in species complexes and the strength of competitive interactions (Peterson et al. 2004; Rahel et al. 2008), availability of climate refugia (typically at higher elevations), and interactions among climate stressors (Jager et al. 1999; Wenger et al. 2011b) may all be important determinants of local changes. Thus, despite relatively consistent global and regional climate forcings as warming proceeds, the specific biological and management consequences of these trends will vary among individual streams and populations.

To better understand these consequences, we explore historical trends and the current state of knowledge in a series of retrospective case histories that include the Flathead River Basin (FRB) in northwest Montana and southeast British Columbia, the Boise River Basin (BRB) in central Idaho, the Greater Yellowstone Ecosystem (GYE), the Green River Basin (GRB) in western Wyoming, and the Rio Grande Headwaters Basin (RGB) in southern Colorado (Table 1; Figure 1, panel a). The areas selected for the case histories encompass a range of physiographic settings, species complexes, and contemporary management issues (e.g., hybridization, habitat degradation/fragmentation, wildfire, drought, nonnative species invasions) that managers of trout populations across the Rocky Mountains often address. Because climate change has been ongoing for multiple decades, it is already possible in many instances to

TABLE 1. Characteristics of river basin areas across the Rocky Mountains used in climate case histories.

Study area and land ownership	Mean air temperature trend (1950–2009)[a]	Focal species	Habitat fragmentation	Primary climate stressors	Management concerns exacerbated by climate change
Flathead River (primarily federal)	0.16°C/decade	Bull trout, westslope cutthroat trout	Moderate	Stream temperature increases, winter flow increases	Upstream movement of rainbow trout/cutthroat trout hybridization. Reduction in bull trout recruitment from higher winter flows
Boise River (primarily federal)	0.17°C/decade	Bull trout, rainbow trout	Moderate	Stream temperature increases, wildfire disturbances	Greater bull trout habitat fragmentation and loss as temperature increases and wildfires occur
Greater Yellowstone Ecosystem (federal, state, and private)	0.14°C/decade	Yellowstone cutthroat trout, brown trout, rainbow trout	Moderate for cutthroat trout, minor for brown trout and rainbow trout	Stream temperature increases	Temperature increases facilitate expansion of nonnative trout into native cutthroat trout habitat and may increasingly force closures of significant river trout fisheries
Green River (primarily federal)	0.28°C/decade	Colorado River cutthroat trout	Significant	Summer flow declines and drought, wildfire disturbances	Extirpations of local populations as summer flow decreases reduce habitat volume and increase susceptibility to drought. Wildfires cause disturbances and may excessively warm streams. Ongoing temperature increases facilitate expansion of nonnative trout into cutthroat trout habitat
Rio Grande (federal and private)	0.04°C/decade	Rio Grande cutthroat trout	Significant	Summer flow declines and drought, wildfire disturbances	Extirpations of local populations as summer flow decreases reduce habitat volume and cause some streams to become intermittent. Wildfires cause disturbances and may excessively warm streams. Ongoing temperature increases could facilitate expansion of nonnative trout into cutthroat trout habitat and reduce thermal suitability of mainstem habitats necessary to connect populations

[a]Air temperature trends were averages based on the monitoring records at the three nearest weather stations in the U.S. Historical Climate Network (Menne et al. 2009).

see the early indications of stream ecosystem responses and to think more clearly about the future. At the end of these case histories, we discuss their emergent generalities and potential management responses, put forth a brief research agenda, discuss strategies for hedging risk and dealing with uncertainty, and offer concluding thoughts on what the remainder of this century may bring.

HISTORICAL CLIMATE TRENDS

Long-term monitoring records from weather stations across the Western United States show a heterogeneous but systemic warming pattern from 1950 to 2009 (Figure 1, panel b). It is estimated that mean annual air temperatures across the West warmed by 0.8°C during the 20th century, which is significantly more than the 0.6°C global average temperature increase (Intergovernmental Panel on Climate Change 2007; Saunders et al. 2008). Westwide trends in annual precipitation were less obvious during this same time period, which is consistent with the projection uncertainties in global climate models for this factor (Figure 1, panel c). However, subregional differences in precipitation showed increases across much of the Southwest and decreases across the Northwest.

Trends within the five case history areas were also apparent. Mean annual air temperatures increased at local weather stations, although rates of warming varied among areas, as was the case at the regional scale (Table 1). Increasing air temperatures interacted with precipitation trends to affect hydrologic regimes in several ways. The most consistent response was earlier spring snowmelt runoff and lower summer flows (Figure 2). This pattern is typical in hydrologic regions dominated by snow because warmer temperatures melt accumulated snowpacks earlier each decade (Stewart et al. 2005; Luce and Holden 2009; Fritze et al. 2011; Leppi et al. 2011). An exception occurred in the RGB, where increasing annual precipitation resulted in less consistent runoff trends. Also noteworthy in the FRB and at one of the GRB gages was a second spike of increasing flows that has developed in the early winter. This pattern often occurs where winter precipitation consists of mixed snow and rain because warming temperatures cause more precipitation to fall as rain, which translates rapidly to streamflow rather than accumulating as snowpack (Knowles et al. 2006; Hamlet and Lettenmaier 2007).

PRIMARY CLIMATE STRESSORS WITHIN CASE HISTORY AREAS

Flathead River Basin, Northwest Montana

The upper FRB (14,300 km^2) is in the headwaters of the Columbia River and drains the west flank of the Rocky Mountains in southeast British Columbia and northwest Montana (elevation range: 1,000–2,800 m). The FRB is one of the most pristine and diverse landscapes in the United States and significant portions of the basin form Waterton-Glacier International Peace Park, a World Heritage Site and biosphere reserve. Streams here are recognized as range-wide strongholds for native salmonids of regional concern, including westslope cutthroat trout (*Oncorhynchus clarkii lewisi*; Muhlfeld et al. 2009a) and bull trout (*Salvelinus confluentus*; Rieman et al. 1997b, 2007).

Despite the quality of stream habitats in the FRB, climate change promises to exacerbate current threats and may create new risks for these species. In the case of cutthroat trout, for example, hybridization and introgression with introduced rain-

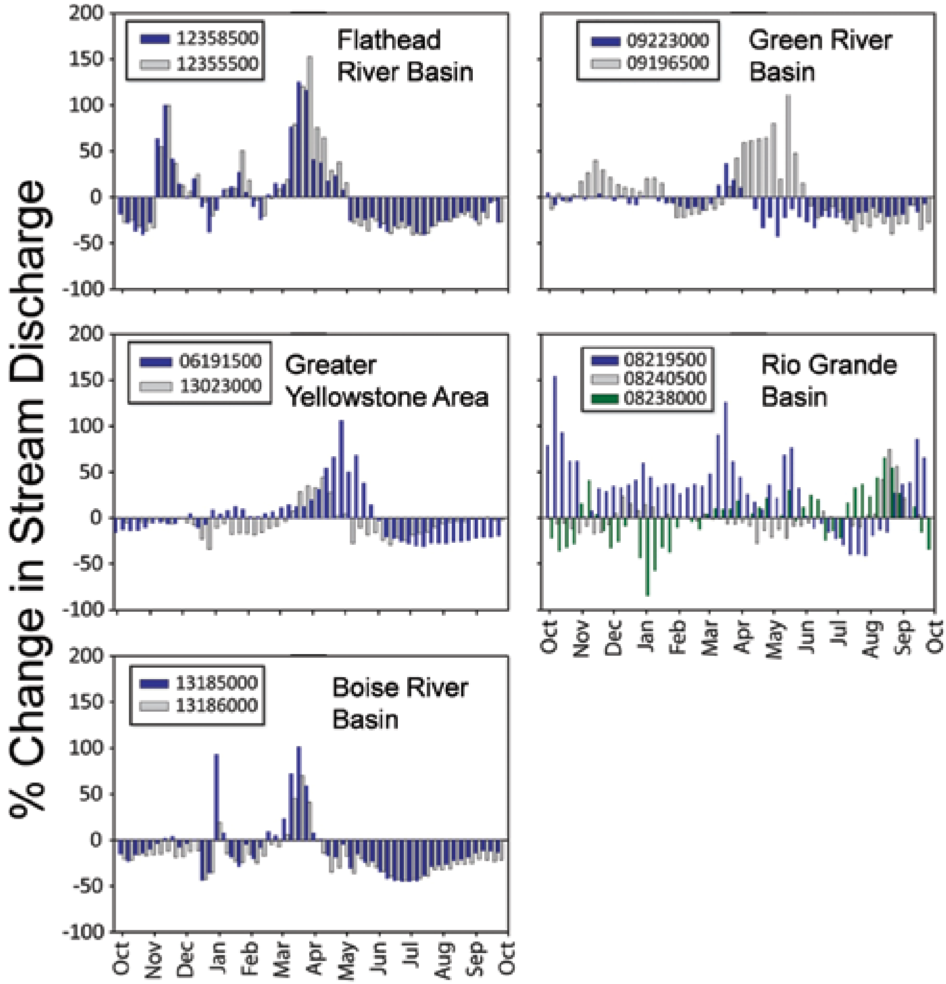

Figure 2. Changes in stream discharge as a percentage of the 1950 average determined from weekly regressions for the period 1950–2009. Streamflows were measured at U.S. Geological Survey gages within each study area and gage numbers are provided in figure legends.

bow trout (*O. mykiss*) is a significant threat (Leary et al. 1987; Muhlfeld et al. 2009b, 2009c) because pure cutthroat trout populations currently persist in only 10–20% of their historical range (Shepard et al. 2005). Zones of hybridization occur more commonly where mean summer stream temperatures exceed 9°C (Muhlfeld et al. 2009b, 2009c) and the warmer thermal niche of rainbow trout begins to overlap with cutthroat trout (Wenger et al. 2011a).

To examine how climate warming trends and recent wildfires may have affected the potential for hybridization, a multiple regression model was developed to predict summer stream temperatures in 1978 and 2008 for the North Fork FRB (Jones et al., in press). Changes between these years suggest that temperatures increased by 0.87°C, which increased the percentage of the stream network with summer temperatures ≥9°C from 15% in 1978 to 33% in 2008 (Figure 3). Over the same time period, extensive genetic surveys tracked the spread of hybridization through the North Fork FRB. Surveys in the late 1970s and early 1980s showed that most cutthroat trout populations were genetically pure, except for a few hybrids in one stream (Marnell 1988). More recent surveys suggest that hybridization has spread upstream from hybrid source populations in warmer tributaries through the mainstem of the Flathead River (Boyer et al. 2008; Muhlfeld et al. 2009c). Although factors such as habitat degradation and connectivity have important effects on hybridization, temperature increases and wildfire disturbances may be allowing rainbow trout distributions to expand upstream and enhancing the spread of hybridization. Of the estimated 1,300 km of fish-bearing streams in the North Fork FRB, approximately 350 km now contain hybridized populations, which represents a 27% increase in recent decades (Figure 3, panel d).

Bull trout are less susceptible to introgressive hybridization with introduced brook trout (*S. fontinalis*) because most hybrids are infertile (Spruell et al. 2001). However, bull trout are more sensitive to the direct effects of climate warming than cutthroat trout (Rieman et al. 2007; Wenger et al. 2011b). Bull trout have thermal niches that are several degrees colder than those of other trout and char species in the Western United States (Selong et al. 2001), so natal spawning and rearing habitats are often fragmented and constrained to the coldest headwater streams (see BRB case history below; Rieman and McIntyre 1995; Dunham and Rieman 1999). Bull trout are also fall spawners, which means that eggs and alevins are vulnerable to high winter flows that may mobilize stream substrates and crush eggs or displace newly emerged fry (Shellberg et al. 2010). This vulnerability may explain why bull trout populations often fare poorly in streams with frequent high winter flows (Wenger et al. 2011b) and suggests that recent increases in winter flood risks across portions of the FRB are a cause for concern (Figure 2; Hamlet and Lettenmaier 2007). These shifts in hydrologic regimes may have played a role in declining populations over the last 20 years, although most declines are probably due to expanding population of nonnative lake trout (Ellis et al. 2011).

Boise River Basin, Central Idaho

The upper BRB in central Idaho encompasses 6,900 km^2 of steep terrain (elevation range: 1,000–3,000 m) and is drained by approximately 2,500 km of fish-bearing streams. In contrast to the hydrologic trend of increasing winter flows observed in the FRB, there is little evidence of a similar pattern emerging in the BRB that could pose a threat to bull trout populations (Figure 2). Of greater relevance is a trend toward warmer stream temperatures, given that both the native rainbow trout and bull trout are constrained by the distribution of thermally suitable

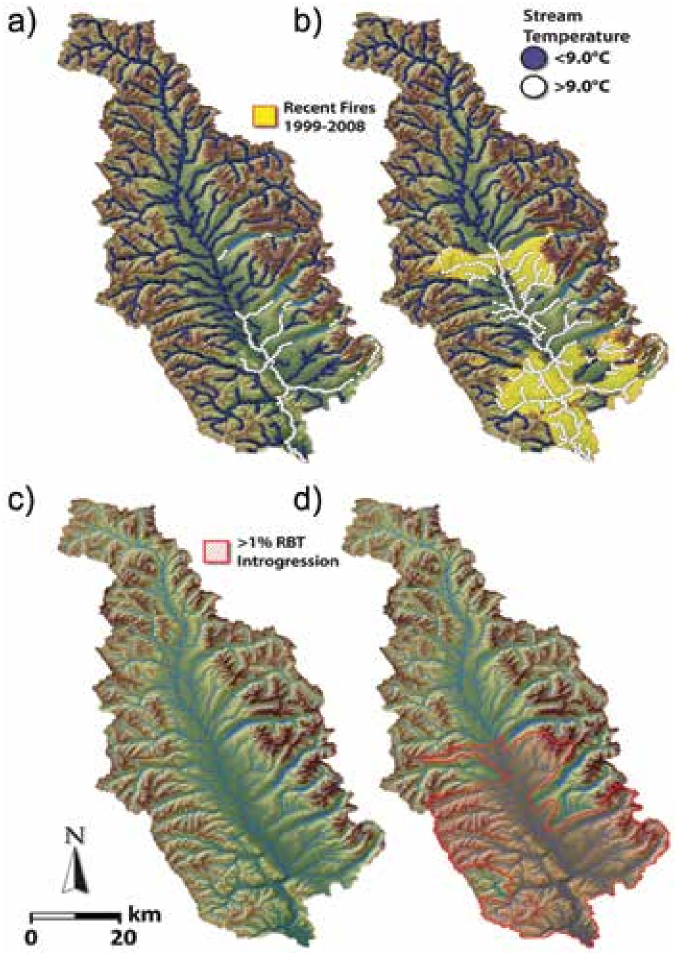

Figure 3. Changes in habitat thermally suitable for hybridization between native westslope cutthroat trout and nonnative rainbow trout in the North Fork Flathead River basin between (a) 1978 and (b) 2007. Changes in distribution of rainbow trout introgression between (c) 1978 and (d) 2007.

habitats within the basin (Rieman et al. 1997a; Dunham and Rieman 1999).

Similar to the FRB, a temperature model was developed using a database of local, empirical measurements (780 summers of data measured from 1993 to 2006), and historical stream warming trends were reconstructed using the model (Figure 4; Isaak et al. 2010). Reconstructed trends indicate that mean summer stream temperatures have been increasing at the rate of 0.27°C/decade in recent decades and that most of the increase was associated with long-term (i.e., 30 year) trends in summer air temperatures. Declining trends in summer flows and wildfires that burned 14% of the basin also played roles in stream warming but accounted for only 10–20% of the temperature increases across the basin (Isaak et al. 2010).

Stream temperature increases had different effects on thermally suitable habitats for bull trout and rainbow trout (Figure 4, panels c and d). Rainbow trout habitats, constrained to lower elevations by cold temperatures, shifted upstream as warming occurred and reductions in the total amount of habitat did not occur (Isaak et al. 2010). Bull trout distributions, in contrast, were located further upstream and constrained by stream slope and small size at the upstream extent of the network. As streams warmed, therefore, net reductions in bull trout habitat occurred, which were estimated to be 8–16% per decade (Isaak et al. 2010).

Greater Yellowstone Ecosystem

The GYE includes portions of Montana, Wyoming, and Idaho centered on Yellowstone National Park. The GYE encompasses a wide elevation range (1,038–4,189 m) and forms the headwaters of three major U.S. river drainages, the Columbia, Missouri, and Colorado rivers. The area is renowned for providing some of the world's finest trout fisheries and recreational anglers flock to the area each year (Baginski and Biermann 2010). Yellowstone National Park, for example, provided 250,000 angler days annually from 1975 to 2000 (Kerkvliet et al. 2012). As temperatures have increased in recent decades, fisheries managers have, on occasion, issued widespread angling closures during the warmest summers. Two such incidents occurred within Yellowstone National Park during the last decade and were motivated by concerns that fish growth and survival would be adversely affected by the stresses associated with catch-and-release angling (Boyd et al. 2010).

In a rarity for the GYE and Rocky Mountain streams in general, one long temperature monitoring record exists at a site on the Madison River downstream of a small lake. Temperatures at this site have been recorded throughout the year since 1977, which makes it possible to describe historical seasonal trends. Simple linear regressions suggest that river temperatures have been increasing at this site over the last several decades (Figure 5), with the smallest warming rates during the winter (December–February = 0.06°C/decade) and larger rates in the spring (March–May = 0.28°C/decade) and summer (June–August = 0.24°C/decade). During this same period, the number of thermally stressful days for trout (mean temperatures > 21°C) increased at the rate of 4.6 days/decade from 6 days/year in the 1980s to 15 days/year in the most recent decade. Although a long-term monitoring record is available for only this single site in the GYE, Madison River temperature trends were similar to those at a nearby site on the Missouri River and the general pattern of stream warming across the Northwestern United States during this same period (Isaak et al. 2012).

Green River Basin, Western Wyoming

The GRB includes the area above Flaming Gorge Dam and drains 39,194 km^2 in western Wyoming and northeastern Utah (Figure 6). Elevations range from 2,000 to 4,300 m and Colorado River cutthroat trout (CRCT; *O. c. pleuriticus*) are the native trout. This subspecies currently occupies 14% of its native range across the broader Colorado River basin (Hirsch et al. 2006). Historical declines have been attributed to interactions with nonnative trout species and habitat degradation from grazing, water withdrawal for irrigation, oil and gas development, and logging. Remaining populations of CRCT are highly fragmented and often inhabit only isolated headwater stream sections (usually < 10 km; Figure 6) above natural and anthropogenic barriers that prevent upstream invasions from nonnative brook

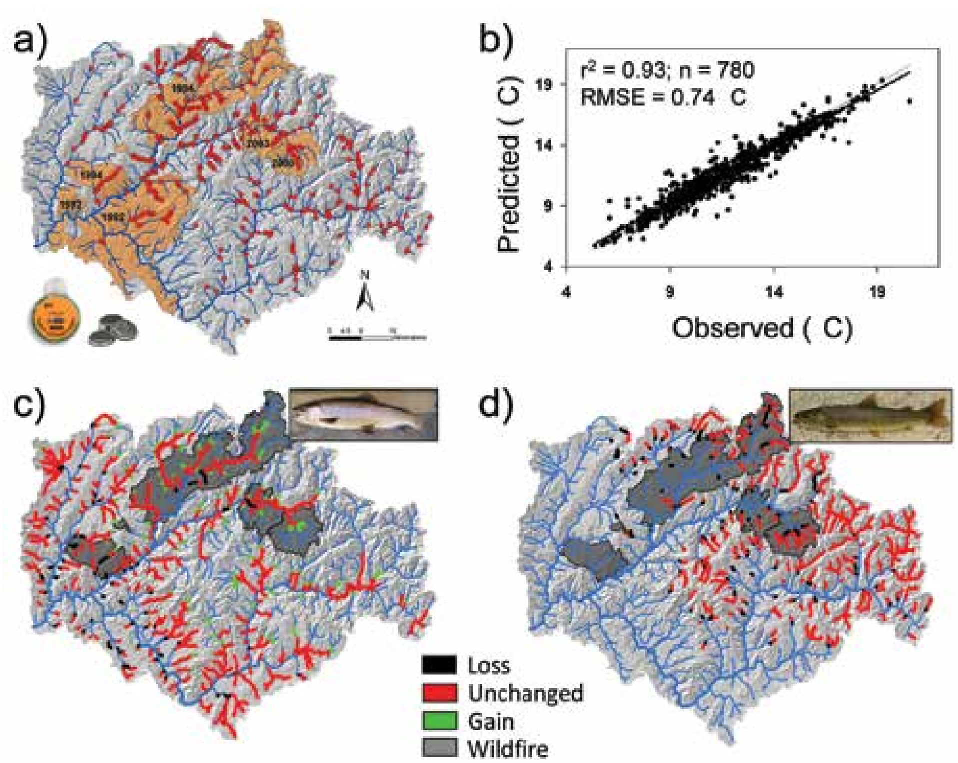

Figure 4. (a) Locations of summer stream temperature measurements in an interagency database developed for the Boise River basin in central Idaho. (b) Summer mean stream temperatures predicted from a new type of spatial statistical model for stream networks. Maps of shifts in thermally suitable habitat for (c) rainbow trout and (d) bull trout from 1993 to 2006 due to long-term trend rates (i.e., 30–50 years) in stream warming associated with climate change and wildfires (gray polygons). Figures reproduced from Isaak et al. (2010).

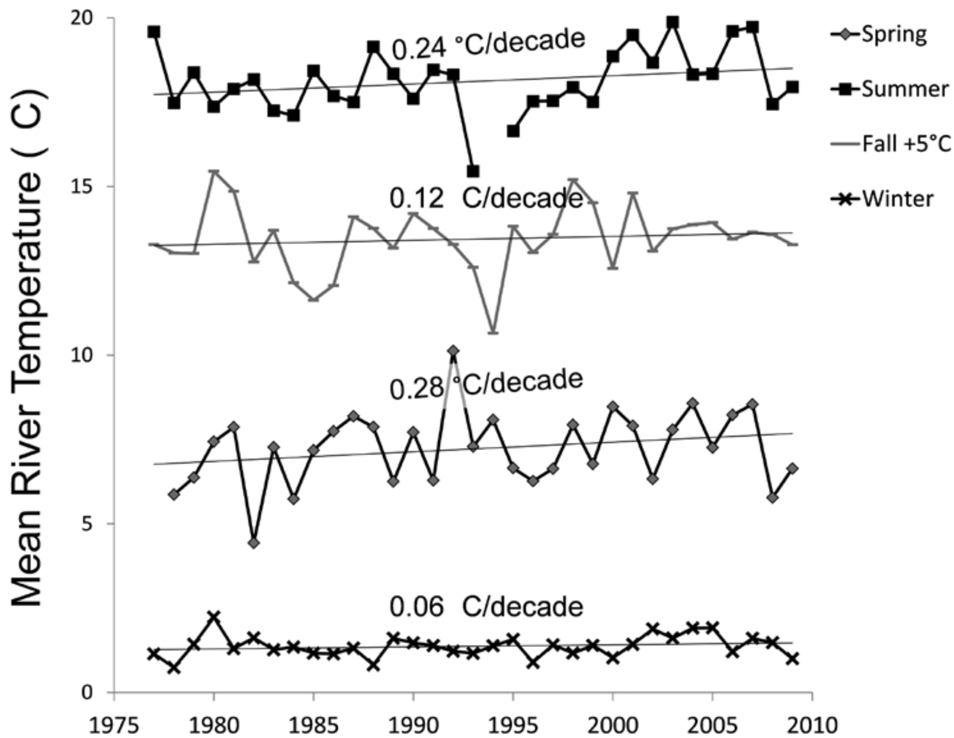

Figure 5. Trends in mean seasonal temperatures from 1977 to 2009 in the Madison River, Montana, downstream of Ennis Lake. Trend estimates are based on the slopes of simple linear regressions.

trout, brown trout (*Salmo trutta*), and rainbow trout (Fausch et al. 2006; Hirsch et al. 2006). Ironically, this fragmentation may limit the negative effects of temperature increases because the downstream boundaries of CRCT populations are often determined by other factors. Moreover, the upper extents of many streams across the GRB are currently too cold to support recruitment of juvenile fish (Coleman and Fausch 2007a, 2007b), and these areas could become more suitable with temperature increases (Harig and Fausch 2002; Cooney et al. 2005).

The limited potential for negative temperature effects on CRCT populations does not make them immune to other risks posed by climate change. In particular, the small size of the streams occupied by many populations makes them vulnerable to declines in summer discharge (Figure 2). Because discharge scales directly with habitat volume (McKean et al. 2010), there may be 20% less summer habitat in the GRB now than there was in 1950 based on historical trends (Clow 2010; Leppi et al. 2011). Where the upstream extent of populations is currently constrained by stream size rather than temperature, declining flows may shift the transition point between perennial flow and intermittency downstream or cause stream drying in places that fragment historically perennial reaches (Lake 2003). Summer flow declines could also reduce stream productivity by decreasing macroinvertebrate drift rates (Harvey et al. 2006) or interactions with riparian zones (Baxter et al. 2005; Riley et al. 2009), which could impair fish growth and survival during the brief summer season (Jenkins and Keeley 2010).

Rio Grande Headwaters Basin, Southern Colorado

The RGB encompasses 20,000 km² at elevations ranging from 2,250 to 4,400 m in southern Colorado. Approximately 50% of the area is federally managed, with most such

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lands at higher elevations surrounding the relatively arid San Luis Valley. Intensive water development in the valley has altered many streams, which are often entirely diverted into irrigation canals and ditches as they approach private lands. Rio Grande cutthroat trout (*O. c. virginalis*) are native to the RGB, and recent status assessments indicate that the remaining 120 conservation populations occupy about 12% of the historical habitat across Colorado and New Mexico (Alves et al. 2008).

Many of the climate-related threats described for Rio Grande cutthroat trout are similar to those for CRCT because both subspecies are restricted to small, isolated stream fragments (mean = 7.6 km for Rio Grande populations; Pritchard and Cowley 2006; Zeigler et al. 2012) but recent natural disturbances associated with extreme climatic conditions also highlight the extirpation risks for some of these populations. An extreme drought in 2002 reduced trout abundance in several conservation populations, and anecdotal evidence suggests that a few populations may have been extirpated (Japhet et al. 2007; Patten et al. 2007). Annual discharge measured at local stream gages in 2002 was less than 25% of the average for the previous 60-year period. Similarly, extreme low flow years occurred several times during this period, so these stresses are not unprecedented, but climate model projections of 10–20% annual precipitation declines across the Southwest (Hoerling and Eischeid 2007; Karl et al. 2009) suggest that what are currently considered extreme droughts could become the "new normal." Because Rio Grande cutthroat trout populations occur in streams with average widths < 3 m and baseflow discharges ≤ 40 L/s (Figure 7; Alves et al. 2008, A. Todd, unpublished), little capacity exists to absorb additional changes.

Warm and dry conditions associated with climate change may also be increasing the frequency and extent of wildfires across the Rocky Mountains (Westerling et al. 2006; Littell et al. 2009). Although wildfires are a natural landscape element in the West, they temporarily decrease the quality of stream habitats for fish populations through temperature increases, altered stream chemistry, and ash and sediment inputs (Rieman et al. 1997a; Dunham et al. 2003). A recent wildfire in Medano Creek illustrates the risks when interactions occur with relatively small, isolated populations. Medano Creek is one of the longest stream segments (~21 km) currently occupied by Rio Grande cutthroat trout, but in June 2010 fires burned across the lower half of this drainage (Figure 8). Post-fire surveys suggest that fish were absent from the most severely burned reaches immediately following the fire but they subsequently returned to these reaches, albeit at lower densities (Colorado Parks and Wildlife, unpublished data). Unburned portions of Medano Creek probably provided a refuge from which burned sections of stream were later recolonized. If the fire had burned across the entire drainage or a similar fire had burned across a smaller conservation area, the entire population could have been extirpated (e.g., Probst et al. 1992; Rinne 1996). Natural recolonization from another population would be unlikely given extensive habitat fragmentation, so active translocation would have been needed to refound the population.

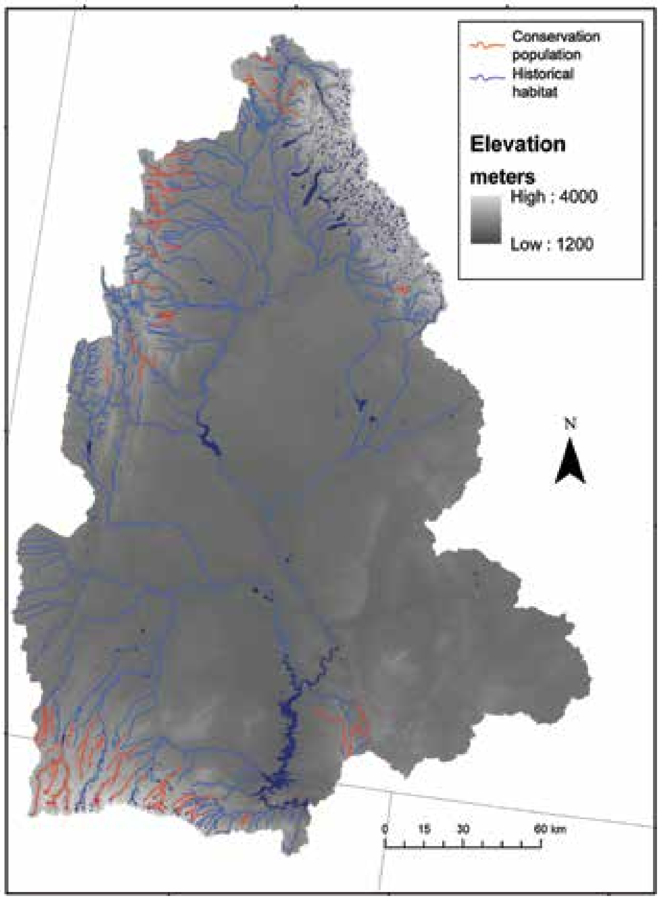

Figure 6. The Upper Green River basin showing the distribution of Colorado River cutthroat trout conservation populations and historical habitats.

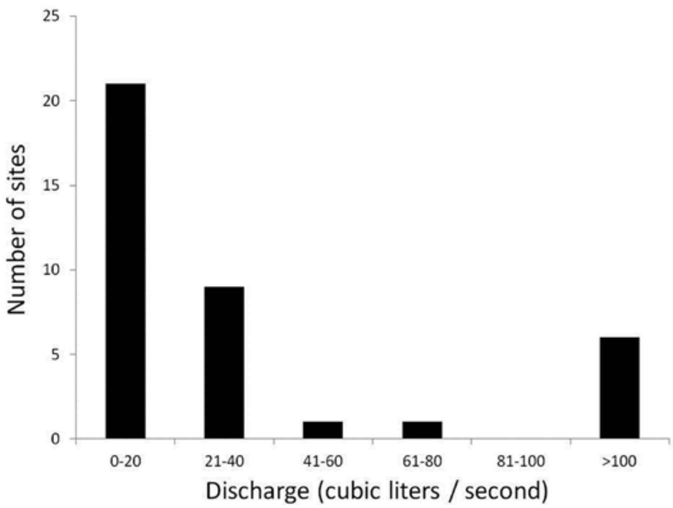

Figure 7. Frequency histogram showing the discharge in streams containing conservation populations of cutthroat trout in the Rio Grande during base flows in 2011 (n = 38). Measurement sites include mainstems near termini, important tributaries, and mainstems below the influence of important tributaries.

DISCUSSION

Climate change is often thought of as a future abstraction, but our case histories illustrate that this is not the case. Stream environments across the Rocky Mountains have been changing in ways that have important implications for trout populations.

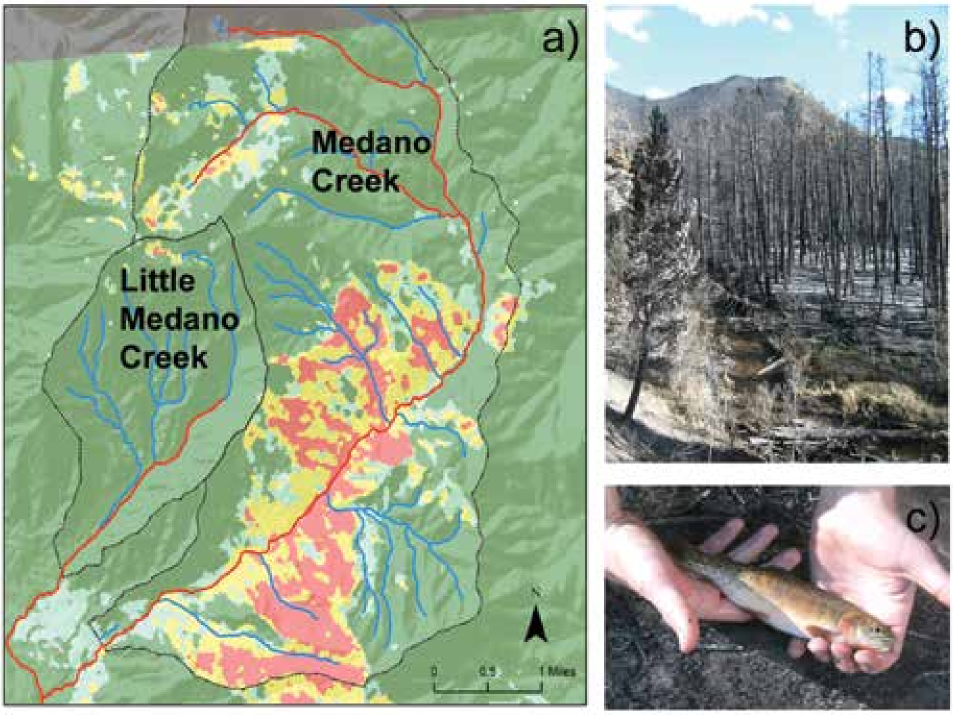

Figure 8. (a) Map showing stream kilometers occupied by Rio Grande cutthroat trout (blue lines) and wildfire extent and severity for the 2010 Medano Creek fire. Photos show (b) burn severity adjacent to the stream and (c) cutthroat trout sampled after the fire. Photo credit: Andrew Todd.

Trends in temperature and stream hydrology consistent with a warming climate are common in long-term monitoring records across the region and within case history areas. Biological implications include upstream advances in thermally suitable habitats, nonnative species and zones of hybridization, greater risk of egg scour for fall-spawning species, increased incidence of wildfires, and declining summer habitat volumes. The relative importance of these changes varies throughout the region and depends on local conditions, so context matters, even with a global phenomenon like climate change. In general, temperature increases may be more relevant in the northern Rocky Mountains where population boundaries (e.g., bull trout in the BRB), angling opportunities (e.g., some trout fisheries in the GYE), and zones of competitive overlap (e.g., cutthroat and rainbow trout in the FRB) are often mediated by temperatures. In the southern Rocky Mountains, in contrast, decreasing summer flows and disturbances indirectly related to climate change like extreme droughts and wildfires may be greater risk factors because populations are heavily fragmented and confined to small headwater streams.

Many actions may be taken to enhance the resistance and resilience of native trout populations to the effects of climate change (see Rieman and Isaak [2010] and Luce et al. [2012] for recent reviews). Briefly, these actions consist of maintaining or restoring instream flows and increasing riparian vegetation to shade streams and maximizing summer habitat volume. Where small streams are significantly degraded, these actions alone might offset significant amounts of future climate effects (Meier et al. 2003; Cristea and Burges 2009). Removal of barriers to fish movement could decrease fragmentation and allow populations to shift their distributions and track thermal habitat as needed, but removing barriers may also allow invasions of nonnative species, so assessments of the tradeoffs are needed (Peterson et al. 2008b; Fausch et al. 2009). Control or elimination of nonnative competitors is an option in some circumstances (Peterson et al. 2008a; Rahel et al. 2008), as is assisted migration to move native species into suitable but currently unoccupied habitats (Harig and Fausch 2002; Dunham et al. 2011; Lawler and Olden 2011). Where fire poses a significant threat to isolated populations, fisheries biologists and fire managers could collaborate to conduct prescribed burns and other treatments of terrestrial vegetation that reduce the risk of catastrophic wildfires (Rieman et al. 2010; Luce et al. 2012).

A 21st-Century Agenda

Perhaps more challenging than knowing which conservation actions to take is knowing where, and in some cases whether, to take them given that needs that will outstrip available resources. The changes in stream environments caused by a warming climate are complex and have location-specific implications, so precise information about the most relevant stream and biological attributes will be required. The coarse predictions output from regional bioclimatic models that rely almost exclusively on air temperature and elevation as surrogates for stream temperature and hydrology will not suffice (Wiens and Bachelet 2009). Our case histories illustrate, however, that most areas already have some information that can be used for describing local effects more precisely and providing initial threat assessments. Moving beyond this stage to develop a solid scientific foundation for assessing risk and informing decision making requires addressing key data and knowledge deficits.

Stream Data

The most relevant stream data for climate assessments consist of discharge and stream temperature measurements and, in ideal situations, would be derived from spatially representative, long-term monitoring programs. Such data rarely exist, however, and collection of new data will often be necessary. New measurements could be spread across the area of interest to cover the range of conditions and climatic variation to develop predictive models, as was the case with stream temperature in the FRB and BRB (Isaak et al. 2010; Jones et al., in press). Alternatively, new measurements could be obtained from all of the conservation populations and streams of interest, as was the case with discharge measurements in the RGB (A. Todd, unpublished) or as Trumbo et al. (2010) did with tem-

Plate 1. Climate change may exacerbate many habitat fragmentation issues like this blockage of a kokanee salmon migration by low summer flows at a poorly fit road culvert. Photo credit: Clayton Nalder.

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perature measurements in conservation populations of eastern brook trout. Regardless of the design specifics, modern digital sensors make collection of accurate stream temperature and discharge data routine and inexpensive, so expansion of these databases could occur rapidly (Stone and Hotchkiss 2007; Isaak and Horan 2011; Porter et al. 2012).

As stream databases improve, they will enable more precise assessments of climate change effects within streams, across river basins, and throughout regions. Measurements of discharge or temperature taken within all of the RGB or GRB cutthroat trout streams, for example, could be used to rank the vulnerability of all populations based on their relative sensitivities across contrasting climate years (Post et al. 2009; Trumbo et al. 2010) or by habitat size, which provides an index of population resilience (Dunham et al. 2002; Isaak et al. 2007). Across larger areas or where more data and analytical resources are available, empirical measurements could be used to parameterize models that translate climate change scenarios from global models to stream environments using statistical techniques for streams (Isaak et al. 2010; Ver Hoef and Peterson 2010) or process-based, mechanistic models (Webb et al. 2008; Wenger et al. 2010). Models that do this translation, often referred to as "downscaling," provide important advantages, including the ability to interpolate information between measurement locations so that stream attributes can be continuously mapped and to play "what-if" games and examine potential changes associated with different climate scenarios (Wiens and Bachelet 2009). These features are needed to put individual populations and streams within the broader spatial and temporal contexts that strategic assessments for climate change ultimately require.

Biological Data

Even as new analytical tools, monitoring techniques, and sensor technologies make it possible to develop more precise information about stream habitat responses to climate change, an important deficit exists in our understanding of the biological consequences. A rich literature links fish ecology to stream hydrology and thermal regimes (Fausch et al. 2001; McCullough et al. 2009; Poff et al. 2010), but most previous studies were typically of short duration or were conducted in laboratory settings. It is unknown how this knowledge translates to natural settings and multiple fish generations subject to small, incremental changes. It is not surprising, therefore, that none of our case histories provided conclusive evidence of biological responses to long-term climate trends but instead consisted of anecdotal accounts that describe potential population losses or model predictions of thermal habitat shifts. This scarcity of biological evidence is not uncommon, even globally, for freshwater fishes (Heino et al. 2009; Isaak and Rieman 2012) and, as a result, little proof exists that the large range shifts and contractions predicted for Rocky Mountain trout populations are actually occurring. Worth noting, however, is that evidence of range shifts is common for many other plant and animal taxa (Parmesan and Yohe 2003; Parmesan 2006), and early indications of range contractions may be emerging at the southern extent of trout distributions in Europe (Hari et al. 2006; Winfield et al. 2010; Almodovar et al. 2012).

The biological data necessary to document climate change effects on trout populations are not difficult to collect but do require persistence and a commitment to multi-decadal monitoring efforts. In particular, abundance and distribution monitoring near thermally mediated population boundaries are needed (e.g., Rieman et al. 2006; Isaak et al. 2009; Tingley and Beissinger 2009), as are data on occurrence dates for specific life history events such as migrations, spawning, or egg hatching and emergence (e.g., Elliott and Elliott 2010; Crozier et al. 2011). Resurveys of historical fish sampling locations (e.g., Adams et al. 2002; Hitt and Roberts 2012) and examination of changes in site occupancy relative to local climatic conditions (e.g., Beever et al. 2010) could be an especially powerful way to document possible biological trends in the short term. Useful information can also be extracted from existing databases of distributional surveys by referencing patterns of species occurrence against outputs from temperature or hydrologic models to define climatic niches in natural settings (Isaak et al. 2010; Wenger et al. 2011a, 2011b; Al-Chokhachy et al., in press).

Size as a Hedge Against Uncertainty

Better understanding of climate effects on stream ecosystems will reduce uncertainties but by no means eliminate them, given the complexities involved (Cox and Stephenson 2007). We should not wait years or decades, therefore, to create the "perfect model" before taking action. Short-term prioritization schemes are needed that begin to reduce long-term risks and also provide flexible frameworks that can be revised with better information as it is developed. One approach robust against uncertainties is to focus on the largest populations and habitats and treat them as fundamental conservation units in any climate-related conservation strategy (Hodgson et al. 2009). The locations of these areas are often known because population inventories have been completed in many places and default selection of the largest areas would significantly reduce an otherwise large array of initial possibilities. Populations in large habitats are less likely to be extirpated because these habitats encompass greater heterogeneity, are more likely to have internal refugia (Sedell et al. 1990), and may support a wider diversity of life history forms that use habitat in different ways to provide additional resilience (Hilborn et al. 2003). In more concrete terms, larger habitats mean that there is less chance that all areas will simultaneously experience a wildfire or become intermittent during a drought or that elevational refugia are lacking to allow populations an upstream retreat as temperatures increase.

As the largest habitats and populations are secured, conditions in peripheral populations that may interact with core populations via dispersal could be assessed and ranked for subsequent restoration in attempts to create local enclaves or metapopulations that possess additional resilience (Rieman and Dunham 2000; Williams et al. 2011). Such a "largest plus nearest" strategy could facilitate natural recolonization when individual populations are extirpated. If this strategy were replicated across the area of concern, it could also mitigate against climate risks posed by broadly synchronized events such as wildfires or regional droughts and heat waves that could extirpate several nearby populations simultaneously. An important element of designing effective conservation reserves may be accommodating these extreme events, which are predicted to increase more rapidly than changes in mean conditions (Jentsch et al. 2007; Meehl et al. 2009) and could alter historical relationships between habitat size and population persistence (e.g., Dunham et al. 2002; Morita et al. 2009).

CONCLUSION

The next decade will see significant improvement in our understanding and ability to predict climate change effects on stream ecosystems across the Rocky Mountains. The overarching threat and complexity that climate change presents are fostering collaborative relationships that span jurisdictional and disciplinary boundaries and accelerating the development and adoption of better spatial data sets and integrative modeling frameworks. Estimates of the rates at which important biophysical parameters are changing will be derived to facilitate more sober assessments of how this phenomenon is affecting trout populations, and this information will feed into better risk assessments.

A willingness to accept and manage in concert with many of these changes will require changing mindsets from last century's paradigm of dynamic equilibrium to one of dynamic disequilibrium for the 21st century (Milly et al. 2008; Pielke 2009). Under the new paradigm, stream habitats will become more variable, undergo gradual shifts through time, and sometimes decline. Many populations and species will retain enough flexibility to adapt and track their habitats, but others are likely to be overwhelmed by future changes. When climate impacts are combined with pressures from a growing human population and imposed on stream ecosystems already significantly degraded from their natural potential, conservation needs will be daunting and informed management more crucial than ever.

Despite the best intentions, we will not be able to preserve all populations of native trout in the Rocky Mountains this century. However, it should soon be possible to have the tools and information to know when and where resource commitments are best made under a given set of assumptions about future climate change. If broad coalitions of stakeholders can collaborate to effectively use this information, it will be possible to at least minimize the population losses that occur. Moreover, because we are relatively early in the trajectory of global climate change, management decisions in the next decade will have disproportionately large effects on the amount of native trout biodiversity that remains in Rocky Mountain streams a century from now.

ACKNOWLEDGMENTS

This work was supported by a grant from the U.S. Geological Survey, National Climate Change and Wildlife Science Center. R. Al-Chokhachy was supported by additional funding from the U.S. Geological Survey, Mendenhall Post-Doctoral Fellowship Program. J. Roberts and K. Fausch were supported by a grant from the Wyoming Game and Fish Department. D. Isaak was supported by the U.S. Forest Service, Rocky Mountain Research Station, and the Washington Office of Research and Development. J. Alder, M. Zeigler, J. Giersch, and D. Horan helped with figure preparations and data collection. The manuscript was improved by comments from M. Young, P. Budy, and three anonymous reviewers. Use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This research was conducted in accordance with the Animal Welfare Act and its subsequent amendments.

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From the Archives

The Black Bass is a good kited of fish to stock a large, clear, rapid river, with stony bottom, where the crawfish and helgamite are to be found. They scarcely ever cat other fish if they can get the crawiish, and I do not recommend putting them in any waters where the crawfish is not plenty, and they are rarely fouled except among the stones. I would not recommend them for small ponds. If Black Bass are put in small ponds they eat the young of' all kinds of' fish, bite the old fish, and before starving, would cat themselves if possible. They have the bull dog disposition as far as courage is concerned.

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FWS_LIT_023818