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Predicting future threats to the long-term survival of Gila trout using a high-resolution simulation of climate change

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Abstract Regional climates are a major factor in determining the distribution of many species. Anthropogenic inputs of greenhouse gases into the atmosphere have been predicted to cause rapid climatic changes in the next 50–100 years. Species such as the Gila trout (*Oncorhynchus gilae*) that have small ranges, limited dispersal capabilities, and narrow physiological tolerances will become increasingly susceptible to extinction as their climate envelope changes. This study uses a regional climate change simulation (Leung et al., Clim Change 62:75–113, 2004) to determine changes in the climate envelope for Gila trout, which is sensitive to maximum temperature, associated with a plausible scenario for greenhouse gas increases. These regional climate changes are downscaled to derive surface temperature lapse rates using regression models. This procedure indicates that suitable, warm season habitat for Gila trout will be reduced by 70% by decreasing the size of their climate envelope. Warmer temperatures coupled with a decrease in summer precipitation would also tend to increase the intensity and frequency of forest fires that are a major threat to their survival. The climate envelope approach utilized here could be used to assess climate change threats to other rare species with limited ranges and dispersal capabilities.

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1 Introduction

Drastic changes in climate have had profound consequences on the biota that inhabit the planet (Rees 2002). The most recent such large-scale climatic change was approximately 10,000 years ago at the end of the Pleistocene, marking the end of the last major glaciation and the beginning of the current period known as the Holocene. Earth may now be undergoing another major climatic change, toward warmer conditions, as a result of anthropogenic input of greenhouse gases (GHG) into the atmosphere from the burning of fossil fuels (IPCC 2007).

Global warming has already been detected (IPCC 2007), but major controversy remains concerning the local magnitudes and rates of change that may occur over the next century as a result of increased atmospheric GHG (Shackley et al. 1998; Khandekar et al. 2005). The evolution of 21st Century GHG forcing is not known, and climate models produce varying results from similar GHG forcing due to uncertainties associated with complex physical processes and feedback effects. Regional and local scale climate changes, and associated hydrologic changes at the watershed scale, are particularly difficult to predict. High resolution models, embedded within coarser global atmospheric models, provide the principal means for assessing the effects of future climate changes at the watershed scale.

Ecologists often use climate model simulations to make predictions about the effect of climate change on Earth's biota (Carpenter et al. 1992; Hogg and Williams 1996; Davis et al. 1998; Hill et al. 1999; Peterson et al. 2002; Mohseni et al. 2003; Schmitz et al. 2003). One common method used to predict the change in distribution of a single species is the 'climate envelope' approach. This method maps the current distribution of a species according to its climate envelope, defined as the region where a species can occur based on its observed physiological tolerances. Then, as that envelope shifts as climate changes, the species distribution is shifted to match the new envelope (Scott and Poynter 1991; Davis et al. 1998). Previous studies (Keleher and Rahel 1996; Rahel and Nibbenlink 1999; Jager et al. 1999; Cooney et al. 2005; Goosef et al. 2005; Preston 2006) have used the climate envelope approach to predict changes in distributions of Salmonids and other cold-water fish to warming scenarios.

The utility of the climate envelope approach for a single species may be limited. For example, Davis et al. (1998) demonstrated that species distribution can be affected by numerous direct and indirect interactions existing among the biota in a community. Furthermore, the range of many species may be fragmented into separate, smaller populations across a heterogeneous landscape (Levins 1969; Hanski and Gilpin 1997). Ideally, dispersal capabilities and complex interactions within a community should be considered when modeling the shifts in ranges (Davis et al. 1998; Lawton 2000).

Despite these limitations, the climate envelope approach has been successfully applied to range shifts of organisms such as higher plants and birds (Bakkenes et al. 2002; Erasmus et al. 2002). The climate envelope method is best suited to predicting changes in the distribution of species with limited ranges and dispersal capabilities. For example, Wilson et al. (2005) demonstrated that 16 species of butterflies have shifted their elevational distribution as a result of warmer temperatures, resulting in a 33% loss of habitat for those species.

For this study, we use a high resolution simulation of climate change to assess future threats to the long-term survival of the Gila trout (*Oncorhynchus gilae*, Family

Salmonidae), a federally threatened species with very limited range, physiological tolerances, and dispersal capabilities. Their extremely limited range requires a greater degree of downscaling than even the regional model provides. We therefore introduce a regression model within the climate model's computational domain in order to quantify the reduction in Gila trout habitat associated with the simulated climate change.

2 Materials and methods

2.1 Natural history of Gila trout

Cold-water trout species (Salmonids) are well suited for modeling range shifts using the climate envelope approach. Salmonids as a group are in decline worldwide (Young and Harig 2001). Many species of trout have specialized habitat requirements and narrow physiological tolerances, requiring clear, cold, pristine waters where they feed on aquatic invertebrates (Meisner 1990; Keleher and Rahel 1996). Temperature is also very important to fish, affecting their feeding and growth rates. Near the upper and lower limits of their physiological tolerances, growth rates are reduced and they become physiologically stressed near the upper limits (Meeuwig et al. 2004; Sloat et al. 2005).

Gila trout, like many other trout species, are cold water fish requiring high levels of dissolved oxygen and habitat heterogeneity to complete their life cycle (Behnke 1992). In laboratory experiments, Gila trout become stressed as temperatures approach 21°C and often stop feeding at temperatures above 22°C. They begin to die after 8 h at temperatures above 25°C, and as the temperature approaches 29°C they begin to experience mortality within 2 h (Behnke 1992) which is consistent with other laboratory studies of coldwater Salmonids (Rahel and Nibbenlink 1999; Dickerson and Vinyard 1999; Johnstone and Rahel 2003).

The current distribution of Gila trout is limited to ten small populations in the Gila and San Francisco River headwaters, between 1,660 m and 2,810 m in elevation (Propst and Stefferud 1997, Fig. 1). Their thermal tolerances, natural and man-made barriers, and the presence of non-native trout determine seasonal shifts in the distribution and movement of Gila trout. Historically, Gila trout move upstream in summer as water temperature rises, then migrate back downstream in winter to avoid freezing conditions that occur at higher elevations (Behnke 1992). Natural and man-made barriers prevent the upstream movement of non-native fishes and prevent the Gila trout from returning upstream if they pass the barriers. Most of their habitat is located in the Gila Wilderness Area, covering approximately 200,000 ha in the southwestern portion of New Mexico. It is the largest wilderness area in the contiguous United States.

Identified threats to the survival of Gila trout include limited population size, hybridization with non-native trout species, forest fire and loss of suitable habitat (Propst et al. 1992; Brown et al. 2001; Wares et al. 2004). Catastrophic forest fires greatly reduce ground and canopy cover. Fires caused the extirpation of six populations of Gila trout in the late 1980s and the 1990s (Brown et al. 2001). Heat from fire can directly cause mortality. Ash, debris, and siltation from post-fire runoff also increase mortality of Gila trout (Brown et al. 2001).

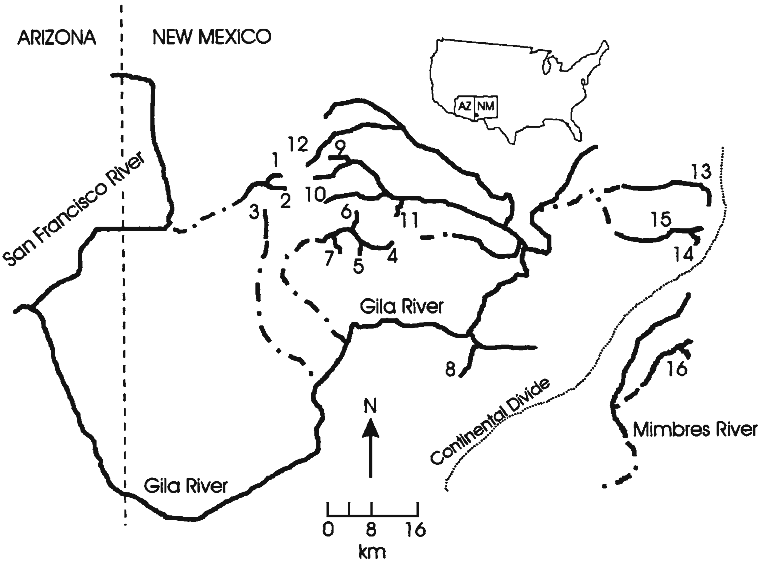

Fig. 1 The current distribution of the Gila trout in New Mexico. The *numbers on the map* indicate individual remaining populations of the Gila Trout that are confined to the upper head waters of the San Francisco and Gila Rivers. The *dashed lines* represent where the streams become intermittent, typically drying during the summer

2.2 The climate change simulation

For this study, potential impacts of climate change on the distribution of Gila trout were assessed using simulations from a regional model nested within a coarse resolution global model (Leung et al. 2004). The global model (the U.S. Dept. of Energy/National Center for Atmospheric Research Parallel Climate Model) was forced by increasing GHG for the entire 21st Century. Future GHG and atmospheric aerosol changes were derived from a “Business As Usual” scenario in which atmospheric CO_2 reaches a concentration of about 710 ppm by the end of the 21st Century (Dai et al. 2004). Two subperiods were selected for high resolution simulations by Leung et al. (2004) using the Penn State/NCAR MM5 regional model over a domain that covered the western United States. The first simulation uses GHG concentrations for the period 1996–2014. This simulation is designed to reproduce current and near-term climate conditions. The second simulation differs from the first only in its changed concentrations of GHGs and aerosols, representing projected climatic conditions for the period 2040–2059.

The focus of this study is warm season conditions in the restricted habitat region of the Gila trout. For this purpose, temperature and precipitation time series from four 40-km^2 MM5 grid cells closest to the trout’s current habitat were selected for study. Daily precipitation values during the summer season (defined here as the 3 month period July 1–September 30) were examined. The four grid cells were also used to determine differences in mean July air temperatures. Adjacent grid cells and elevations were used to build a regression model to predict changes in temperature with elevation. Assuming that the Gila trout has physiological characteristics similar to other Salmonids, the lower limit of their distribution in the summer will be determined by mean July air temperature of approximately 22°C, and 25°C (Keleher and Rahel 1996). During this time, their populations will be the most spatially restricted and susceptible to stochastic events. Winter precipitation and temperature were also examined because the base flow of many mountain streams is determined by cold season precipitation.

The 22°C and 25°C temperature thresholds were selected because they exceed the physiological tolerances of Salmonids in laboratory conditions and distributional limits in the wild (Keleher and Rahel 1996; Dickerson and Vinyard 1999; Sloat et al. 2005). Air temperature is often cited as a major factor in determining surface water temperatures and distributions of cold water species (Shuter and Post 1990; Dunham et al. 2003; Morrill et al. 2005). Keleher and Rahel (1996) used mean average July air temperature less than 22°C to successfully predict current geographical ranges of Salmonids in the Rocky Mountains. The average lower elevation for Gila trout determined by Propst and Stefferud (1997) was 2,125 m (±239), corresponding to a mean average July air temperature of 21.9°C (±1.6), very similar to the temperature threshold established by Keleher and Rahel (1996).

The relationship between surface water and air temperatures is nonlinear, best described with an S-shaped curve, so that the temperature of surface water increases less than air temperature in hot conditions (Mohseni et al. 2003; Morrill et al. 2005). Previous studies by Morrill et al. (2005) indicate an approximate linear increase of 0.6–0.8°C in temperature is observed with a 1°C change in weekly averages in air temperature until approximately 25°C, which also corresponds to the upper physiological limit of Gila trout. At temperatures above 25°C, the relationship flattens out as a result of increased evaporative cooling (Mohseni et al. 2003). Although the studies relating air temperature to surface water temperature do not indicate a linear relationship, empirical observations of mean air temperature during the warmest months have successfully predicted the lower elevation of several species and races of coldwater Salmonids (Keleher and Rahel 1996; Rahel and Nibbenlink 1999). Therefore, for this study we also assume that a direct relationship between mean July air temperature and the distribution will also apply to Gila trout.

Some potentially important indirect effects of temperature and precipitation change are not simulated by the climate model, and can only be inferred. Higher temperatures are associated with lower humidity and increased drought conditions that are conducive to increased fire intensity. Flow reduction associated with lower precipitation, especially in the higher altitudes, could limit the trout's ability to migrate to cooler temperatures to avoid thermal stress during the summer.

2.3 Determining habitat loss

To determine the habitat loss based on predicted changes in mean July surface air temperature, the United States Geological Survey (USGS) National Map and 7.5 min quadrangle maps were used to calculate changes in stream length based on changes in elevation. Changes for each stream were calculated based on the elevation for the mean July air temperature for 22°C (denoted Z_{22}) and 25°C (denoted Z_{25}).

3 Results

3.1 Changes in precipitation

The model simulates average Jul–Sep monsoonal precipitation of 51 mm (±30) for years 1995–2015 (Fig. 2). The corresponding 3-month average precipitation (for years 1982–2005) at the Silver Creek Divide snotel site (2,740 m) is 32.8 mm, somewhat less than the area-averaged model result. (Silver Creek Divide is the only instrumented high-elevation site in this region.) For the period 2040–2059, the model predicts summer average rainfall of 40 mm (±20), approximately 20% less than the 1996–2014 simulation. Using a one-tailed, paired *t*-test, the precipitation difference between the two summer time periods is marginally significant ($P = 0.06$).

For winter (Nov–Mar) precipitation, the model simulates 276 mm (±48) for years 1996–2015. For the period 2040–2060, the model predicts, 257 mm (±32), which is approximately 7% less than the 1995–2015 simulation. The model predicts somewhat less interannual variability in mid-century than is currently observed, although the statistical significance of the difference in interannual variance is questionable.

3.2 Changes in surface air temperature

Average, 24-h surface air temperatures in July (Fig. 3) are predicted to increase from 23.8°C (±1.6) to 25.7°C (±1.6) which is significantly different ($P = 0.0049$). Daytime maximum temperatures are predicted to increase from 32.6°C (±5.43) to

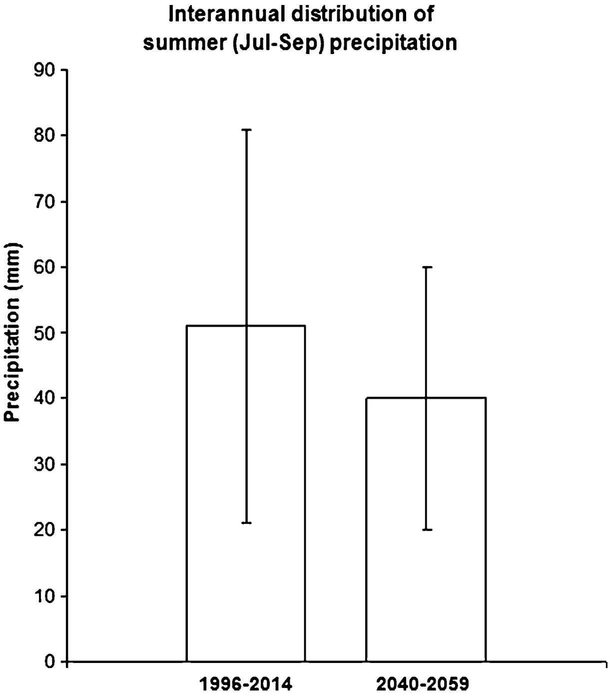

Fig. 2 The predicted, Jul–Sep average warm season precipitation (mm) for the current time period (1996–2014) and mid century (2040–2059). *Error bars* represent one standard deviation. There is a marginally significant ($P = 0.06$) decrease in total summer precipitation for the two time periods. Predicted precipitation was extracted from four 40 km^2 grid cells in the Gila Wilderness

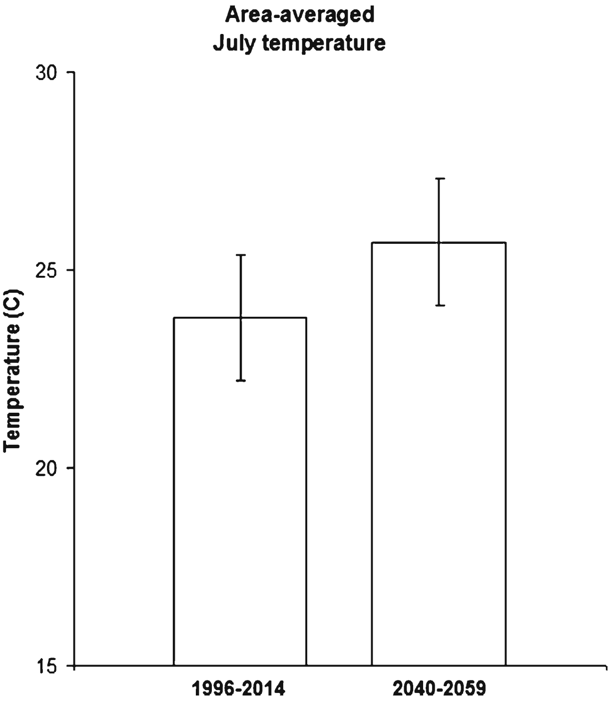

Fig. 3 The predicted change in mean daily air temperature for July, the warmest month of the year. Predicted temperatures were extracted from four 40 km^2 grid cells in the Gila Wilderness. There is an approximate 1.9°C increase in the future simulation which is a significant increase from the control simulation ($P = 0.0049$)

35.1°C (±5.28) and nighttime minima are predicted to increase from 11.8°C (±2.93) to 12.9°C (±2.93). The number of days predicted to be above 37°C more than doubles from 23 days (±11.7) in the current climate to 47 days (±13.5) by mid century. In order to interpret these temperature changes in terms of reduction in Gila trout habitat, the surrounding 12 grid cells were used to determine the relationship between elevation and temperature in these simulations. Average elevations for the grid cells ranged from 1,594 m to 2,145 m. The average surface air temperature lapse rate based on yearly averages was 7.1°C/km ($R^2 = 0.969$, $T = -0.0071z + 24.8$). The slope of this regression line is very similar to the environmental lapse rate of 7.2°C/km in Wyoming based on empirical observations (Keleher and Rahel 1996).

A regression using mean July air temperatures was used to further refine the model to predict Z_{22} and Z_{25} respectively (Fig. 4). Based on the control simulation for 1995–2015, $T = -0.0071z + 36.8$ ($R^2 = 0.93$). The elevation corresponding to mean July temperature of 22°C is 2,114 m, which is within 16 m of the average lower elevation reported for Gila Trout (Propst and Stefferud 1997). The corresponding elevation associated with 25°C is 1,686 m. This value of Z_{25} is within 30 m of the lowest reported elevation of Gila trout. Using the simulations for 2040–2059, the regression model was $T = -0.0072z + 39.0$, $R^2 = 0.927$. The lapse rate does not change appreciably in the simulated future climate, but Z_{22} and Z_{25} are raised to 2,394 m and 1,972 m respectively. Between the control and future simulations, a change in elevation of 269 and 286 m is predicted for Z_{22} and Z_{25} respectively.

To determine habitat loss, the shift in elevation based on Z_{22} and Z_{25} were both used. A change in 286 m represents a 25% loss in elevational habitat available to Gila trout based on the lowest recorded elevation. Actual stream loss for Z_{25} is

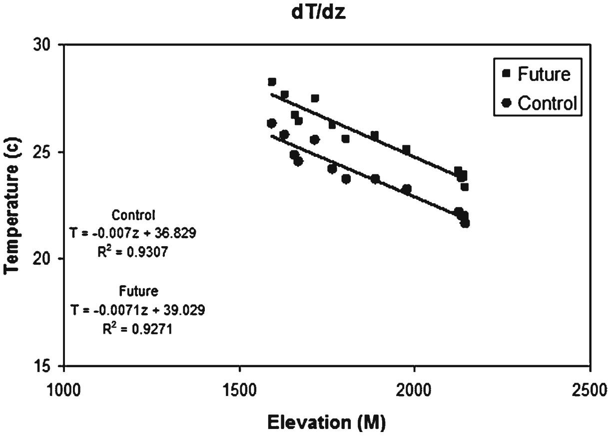

Fig. 4 Regression models used to predict the environmental lapse rate in July. Lower elevational limits of Gila trout are predicted for control, 1995–2014 and future simulations 2040–2059 using the mean air temperature of 22°C and 25°C

approximately 7.3 km or 6% of the total stream habitat available. However, this would mean a complete loss of two trout streams (Table 1). A 61% loss in elevational habitat was predicted for Z_{22}. The actual stream loss for Z_{22} was approximately 82.9 km of a total of 118.7 km of inhabited stream reaches reported by Propst and Stefferud (1997), which includes five streams in addition to the streams listed in the 2003 US Fish and Wildlife Recovery Plan (Table 1). This is a 70% loss in habitable stream length and a total loss of three streams which are in listed in the

Table 1 Current occupied stream length with elevational distributions for Gila trout

Stream	Drainage	Length (km)	Elevation upper/lower	Current Temp °C	Predicted loss (km)	
					Z_{22}	Z_{25}
Spruce Creek	San Francisco	3.7	2,500/2,055	22.4	2.9	0
Big Dry Creek	San Francisco	1.9	2,555/2,365	20.74	0.34	0
Sacaton Creek[b]	Gila River	1.6	2,279/2,084	22.2	1.6[a]	0
Mogollon	Gila River	28.8	2,255/2,036	22.6	28.8[a]	0
Trail Creek[b]	Gila River	1.8	2,121/2,036	22.6	1.8[a]	0
Sheep Corral	Gila	1.3	1,740/1,660	25.2	1.3[a]	1.3[a]
White Creek[b]	Gila River	14.2	2,255/2,036	22.6	14.2[a]	0
McKenna Creek[b]	Gila River	1.2	2,110/2,015	22.7	1.2[a]	0
Iron Creek[b]	Gila River	4.3	2,810/2,675	18.1	4.3[a]	0
Main Diamond	East Fork	6.1	2,675/2,320	20.6	0.8	0
South Diamond	East Fork	6.7	2,560/2,365	20.3	1.2	0
McKnight	Mimbres	8.5	2,510/2,100	22.1	6.2	0
Black Canyon	East Fork	18.2	2,734/2,058	22.4	14.3	0
Lower Little Creek	West Fork	6.0	1,960/1,850	23.9	6.0[a]	6.0[a]
Upper White Creek	West Fork	8.8	2,805/2,250	21.2	2.6	0

The column for current temperature was calculated using the predicted environmental lapse rate for mean July air temperature for the control simulation (1995–2014). Predicted loss of habitat was based on the changes in elevation corresponding to the predicted temperature increases of 1.9°C ($Z_{22} =$ 2,398 m, $Z_{25} = 1{,}976$ m for the future simulation)

[a] Total loss of stream habitat

[b] Gila trout streams not in the US Fish and Wildlife recovery plan

USFWS recovery plan (2003) and all five additional streams listed by Propst and Stefferud (1997).

4 Discussion

The regional climate model predicts a 20% decrease summer precipitation, a nearly 2°C increase in summertime average air temperature, and a pronounced increase in the number of days above 32°C and 37°C, by mid century (years 2040–2059) in the region inhabited by Gila trout. The combination of precipitation and temperature change in this simulation would have a profound long-term impact on the Gila trout. Assuming the strong relationship between weekly air temperature and surface water temperature, the increase in average summertime temperatures and the number of days above 37°C will increase thermal loading in the water, limiting the movement of the Gila Trout to lower altitudes during the summer season. Gila trout populations are currently limited to 1,660 m and 2,810 m in elevation depending on the drainage they inhabit (Propst and Stefferud 1997). Our calculations indicate that a 2°C change in average seasonal air temperatures may cause an elevational range shift of approximately 269 m to 286 m. This could represent a 70% loss in suitable habitat for existing trout streams in July based on changes in elevation.

The control simulation for the current climate accurately predicted that the lowest elevation for Gila trout would be 1,686 m based on a thermal tolerance of 25°C, and predicted the average low elevation based on mean July surface air temperature of 22°C. This corresponds well with other published reports for cold water Salmonids and laboratory studies (Behnke 1992; Keleher and Rahel 1996; Rahel and Nibbenlink 1999). Gila trout habitat is located at a lower latitude than many other trout species so Gila trout may be better acclimated to slightly warmer temperatures, as shown by laboratory studies on races of cutthroat trout that inhabit wide geographic regions (Wagner et al. 2001). Our results are qualitatively similar to other predictions that global warming will reduce suitable habitat for cold water species (Keleher and Rahel 1996; Jager et al. 1999; Mohseni et al. 2003).

We have extended previous modeling studies predicting change at the regional scale by deriving a regression model for the lapse rate of surface air temperature to quantify changes at the catchment scale. We do not empirically demonstrate changes in stream flow based on air temperatures, but the close agreement between our regression results and the current elevational limit of Gila trout based on reported thermal limits helps validate the approach.

Gila trout are capable of long-distance dispersal to many habitats, especially during the cooler months. However, in some streams, dispersal is limited and the lower elevational limit is not realized due to natural and man-made barriers that prevent the upstream movement of non-native trout species. During the summer, they most likely move to colder waters at higher elevations. At this time, the amount of suitable habitat for Gila trout will be at its smallest extent and the populations will be most susceptible to extirpations due to stochastic events (Lande 1993).

Decreases in summer precipitation, which are less pronounced and less certain than the temperature changes, would reduce stream flow. In addition, base flow could decrease as a result of diminished snow pack and earlier snowmelt runoff associated with warmer winter temperatures (as described by Hurd and Coonrod 2007, in a recent study of the nearby Rio Grande). If the headwater streams that currently act as warm season refugia for the trout become greatly reduced or ephemeral, then the Gila trout would become stressed or suffer higher mortality as they are limited to sub-optimal habitat in warmer waters downstream. More detailed examination of the effects of climate change on snow pack and stream flows in the Gila Wilderness is beyond the scope of this study but deserves additional analysis.

A decrease in suitable Gila trout habitat as a result of the predicted scenario would lead to further declines in populations and increased risk to environmental and demographic stochastic events (Lande 1993). For example, decreased precipitation and a longer warmer season would increase the fire potential, both in frequency or severity. Thus, even if local climate change does not directly cause of the demise of Gila trout, indirect effects and stochastic events could be equally important.

Quantitative climate change predictions are dependent on the particular model and forcing scenario chosen, and do not account for climate forcings other than GHG and aerosols, so any prediction is subject to very high levels of uncertainty. However the changes described here are qualitatively similar to many other large-scale simulations of climate change at high elevation in the interior of North America (IPCC 2007; NAST 2001). For example, similar to the climate scenarios we used, the most recent IPCC report (Christensen et al. 2007) summarized that the southwest will likely experience larger warming during summer, especially for maximum summer temperatures, and annual precipitation will likely decrease. With regard to temperature changes, moreover, a strong scientific consensus now exists suggesting that the principal uncertainty in the predictions described here is simply timing: different scenarios and models would yield similar warming either somewhat sooner or somewhat later than the 2040–2059 period simulated here (IPCC 2007).

A more sophisticated assessment of future trends in Gila trout habitat would require a coupled watershed-scale hydrologic model that explicitly simulates stream flow, water temperature, and perhaps even water quality, in association with climate change. For example, Leung et al. (1996), Leung and Wigmosta (1999) used a one-way coupled regional climate and watershed model to study climate change effects on snow pack and stream flow. Their watershed model has been extended to simulate stream temperature as well. Such an assessment is well beyond the scope of the present study, but we advocate the further development and use of coupled atmosphere-land-hydrology models that are capable of carrying out simulations of such scope and scale.

There are also many non-climatic factors that affect a species range within its climate envelope. However, the combination of small population size, restricted range, limited dispersal capabilities, and narrow physiological tolerances, greatly increases the susceptibility of the Gila trout to extinction through environmental and demographic stochasticity. The use of climate models to predict changes in the climate envelope of these sensitive species will aid in predicting future threats such as loss of suitable habitat to species with limited dispersal capabilities and narrow physiological tolerances. To foster the long-term survival of the Gila trout and other, similar aquatic species, long term monitoring projects should be developed and implemented, especially at high elevations. The need to determine temperature changes and thermal loading in headwater streams is crucial, but these changes occur on spatial scales that are smaller than the resolution of most global climate change simulations. Better estimation of base flow rates, based on seasonally varying precipitation rates (and other variables not considered here) are also important. Long-term data collection and climate monitoring efforts will be valuable assets for validating current models and promoting the development of long-term species management plans.

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