2005

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Western North American Naturalist 65(3), © 2005, pp. 371–381

MODELING GLOBAL WARMING SCENARIOS IN GREENBACK CUTTHROAT TROUT (*ONCORHYNCHUS CLARKI STOMIAS*) STREAMS: IMPLICATIONS FOR SPECIES RECOVERY

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ABSTRACT.—Changes in global climate may exacerbate other anthropogenic stressors, accelerating the decline in distribution and abundance of rare species throughout the world. We examined the potential effects of a warming climate on the greenback cutthroat trout (*Oncorhynchus clarki stomias*), a resident salmonid that inhabits headwater streams of the central Rocky Mountains. Greenbacks are outcompeted at lower elevations by nonnative species of trout and currently are restricted to upper-elevation habitats where barriers to upstream migration by nonnatives are or have been established. We used likelihood-based techniques and information theoretics to select models predicting stream temperature changes for 10 streams where greenback cutthroat trout have been translocated. These models showed high variability among responses by different streams, indicating the usefulness of a stream-specific approach. We used these models to project changes in stream temperatures based on 2°C and 4°C warming of average air temperatures. In these warming scenarios, spawning is predicted to begin from 2 to 3.3 weeks earlier than would be expected under baseline conditions. Of the 10 streams used in this assessment, 5 currently have less than a 50% chance of translocation success. Warming increased the probability of translocation success in these 5 streams by 11.2% and 21.8% in the 2 scenarios, respectively. Assuming barriers to upstream migration by nonnative competitors maintain their integrity, we conclude that an overall habitat improvement results because greenbacks have been restricted through competition with nonnatives to suboptimal habitats, which are generally too cold to be highly productive.

Key words: global warming, greenback cutthroat trout, Oncorhynchus clarki stomias, *stream temperature modeling, endangered species, resident salmonid.*

Global climate change may exert profound effects on human and natural systems (Scavia et al. 2002, Walther et al. 2002). There is widespread concern that these effects may harm efforts to conserve rare and threatened species (e.g., Houghton 2001, Wlodarska-Kowalczuk and Weslawski 2001). Coldwater fishes are thought to be particularly vulnerable (e.g., Jager et al. 1999, Clark et al. 2001). Warmwater fishes replace coldwater and coolwater guilds as water temperatures rise in a downstream gradient (Taniguchi et al. 1998). For salmonids in river drainages, increased upstream migration in summer and loss of downstream habitat area are widely recognized potential consequences of global warming (Meisner 1990, Eaton and Scheller 1996, Rahel et al. 1996, Jager et al. 1999). Moreover, warming water temperatures appear to dramatically retard protein synthesis (a measure of fish health) in the liver and gill of juvenile rainbow trout (Reid et al. 1997). The combination of rapid global climate change combined with existing anthropogenic stressors will likely present a tangible threat to the biodiversity of freshwater fauna (Peterson and Kwak 1999).

The greenback cutthroat trout (*Oncorhynchus clarki stomias;* hereafter GCT) is a good candidate for understanding potential effects of climate change on a rare, coldwater species with high conservation values. Most populations are protected from further encroachment by nonnatives because of barriers to upstream migration (e.g., dams, waterfalls, etc.). As a result, these populations are also geographically isolated from other populations of GCT. Furthermore, some GCT populations have relatively small geographic ranges (e.g., a 2-km reach of stream) and may therefore be highly susceptible to shifts in abiotic factors such as

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TABLE 1. Translocation success of greenback cutthroat trout sites by location and type of translocation site. Success (as defined in USFWS 1998) has been better in predominantly lake sites (>1 ha) and within Rocky Mountain National Park (RMNP). Data presented here are results of translocation attempts in the South Platte River drainage, Colorado.

Area of translocation	Potentially stable populations	Stable populations	Unstable populations	Totals
Inside RMNP				
Lakes	9	5	2	16
Streams	2	2	0	4
Outside RMNP				
Lakes	0	1	1	2
Streams	2	1	6	9
TOTALS	13	9	9	

temperature (Kruse et al. 2001). The current ranges of most populations are well known, and range expansion or migration below barriers to avoid stressors is not likely as GCT are displaced by nonnative salmonids (Behnke 1992, Wang and White 1994).

The GCT is 1 of 2 native trout in the Arkansas and South Platte River systems and was once considered extinct (Behnke 1992). The GCT was listed as endangered in 1973 and upgraded to threatened in 1978. Six stable, historic populations were discovered above natural barriers (e.g., steep cascades) that limited upstream migration of nonnative salmonids. The recovery program has consisted primarily of translocation attempts in streams and lakes above such barriers. Locations and results of these translocation projects are described in the GCT recovery plan (USFWS 1998) and in Harig et al. (2000). Success is defined as a population that maintains a minimum of 22 kilograms of GCT per hectare, a minimum of 500 adults (>120 mm total length), and a minimum of 2 year classes within a 5-year period that are established through natural reproduction (USFWS 1998). In the South Platte drainage, 11 of 13 projects that have resulted in stable populations are in Rocky Mountain National Park (RMNP), Colorado, including 9 predominantly lake sites (>1 ha lake area; USFWS 1998). The percentage of translocation populations in the South Platte drainage considered stable was not as high for areas outside of RMNP or for sites that were predominantly stream sites (Table 1). Failure of predominantly stream sites to support stable populations is thought to be partially due to the limited number of degree-days available for young-of-the-year (YOY) trout to grow and attain sufficient lipid reserves to survive winter conditions (Harig and Fausch 2002).

Here, we examine the potential effects of climate warming on conservation of the GCT by assessing the potential effects of stream warming on GCT populations in 10 translocation streams. Given the characteristically cold nature of these headwater streams, we hypothesized that some of these sites may improve as potential habitat if water warms. Global warming may result in an increase in growth rate and consequently higher overwinter survival of YOY GCT.

METHODS

Study Sites

Water temperatures of 10 GCT translocation streams were measured (±0.2°C) a minimum of once every 96 minutes using either an Optic StowAway® or TidbiT® thermograph (8 K and 32 K models, Onset Computer Corporation, Pocasset, MA) placed in the deepest pool along the stream segment during a 3-year period (data from Harig and Fausch 2002). We chose these 10 streams based on similarities of habitat types, including no substantial lake habitat. In high-elevation Rocky Mountain streams of this type, hydrology is dominated by snowmelt. The resulting hydrograph is characterized by a peak discharge in the spring and low base flows during the summer (Hauer et al. 1997). These sites have water temperature regimes typical of high-elevation headwater streams (Fig. 1). Most remain at 0°C for 5–7 months, and summer temperatures in some streams do not reach 10°C. Perennially persistent snowpacks and headwater glaciers as well as rain-on-snow events can have a

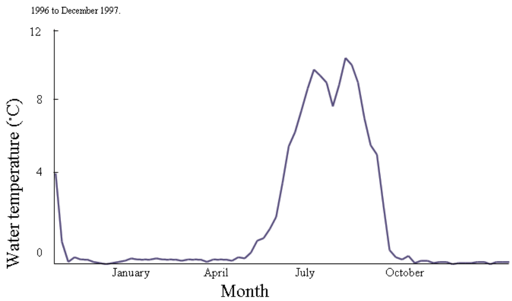

Fig. 1. Water temperature in Cony Creek, CO. Water temperature regime typical of subalpine streams where greenback cutthroat trout were translocated. Stream temperatures remain at or near freezing for 6 months or more and typically have a maximum temperature of about 10°C. These data represent October 1996 to December 1997.

large influence on water temperatures and discharge in these systems. As a result of these factors, these streams are likely to have higher interstream temperature variability than streams in less complex topography.

Modeling

Our modeling proceeded in 3 steps. First, we used a global model of mean summer water temperatures in high-elevation streams to determine whether water temperatures could accurately be modeled with regional air temperatures alone, or whether they were more dependent on site-specific physical habitat variables. This analysis was intended to determine whether stream temperatures could be more accurately predicted using site-specific models as opposed to models applied to a region or a set of streams. After establishing that need, we developed models based on air temperature alone, but specific to each stream. These site-specific models are developed using existing water and air temperature data for several years at most sites. Site-specific models reflect the way water temperature responds to air temperature changes at a particular site, thus incorporating exposure to the sun, gradient, and other site-specific habitat variables that are otherwise impractical to model in global climate change projections. We then used these site-specific models to investigate effects of stream warming on translocation success, onset of spawning period, and length of the growing season for GCT.

GLOBAL STREAM MODEL.—We developed models for predicting mean July water temperatures in 27 high-elevation streams (17 of these were translocation sites of Rio Grande cutthroat trout, *O. c. virginalis,* a native species with physiological requirements similar to those of GCT, while 10 were GCT streams) in the central Rockies using the data collected by Harig and Fausch (2002) and air temperature data gathered from National Oceanographic and Atmospheric Administration (NOAA) climate stations. Harig and Fausch (2002) collected some habitat data directly and some using data from a geographic information system analysis (see Harig and Fausch 2002 for details). The model is a multiple linear regression that gives mean July water temperature as a function of mean July air temperature, latitude, average pool width, total number of pools, total number of deep pools (>30 cm residual depth), drainage area, watershed gradient, basin relief, aspect, main channel length, elevation, average pool depth, and mean sun arc.

Harig and Fausch (2002) used mean July water temperature as representative of the summer growing season for cutthroat trout. Therefore, we chose a set of a priori candidate models derived from the global model to represent multiple working hypotheses (Burnham and Anderson 1998) portraying influences on mean July water temperature in high-elevation sites. These linear regression models were chosen to determine which of these variables or combinations of variables most affected water temperature in July at each site.

We selected best approximating models from the candidate set using likelihood techniques and information theoretics (Akaike's Information Criterion for small samples, AICc; Burnham and Anderson 1998) to evaluate the influence of habitat variables on water temperature. This analysis is solely intended to elucidate the importance of some habitat variables and to determine the relative value of individual stream models. If air temperatures were found to be the most important determinant of stream temperatures, it could be concluded that regional air temperatures could be applied to numerous streams. If, on the other hand, habitat variables (e.g., aspect) were more important, it would indicate that these variables, which change from stream to stream within a region or basin, are important to include in a predictive model of stream temperatures. One way to do that is to use individual stream models.

INDIVIDUAL STREAM MODELS.—We gathered regional air temperature data for the period from NOAA weather stations close to the stream site. Given the topographic complexity of the region, proximity (elevation and linear distance) of air temperature source to stream site was considered very important. Thus, we generated models for individual streams rather than applying a regional model. Climate stations (n = 10) averaged 183.6 m (s = 168.8, median = 133.0) difference in elevation and 24.3 km (s = 30.3, median = 12.4) linear distance from streams. These parameters are well within the limits of previous studies of this type (Stefan and Preud'homme 1993, Webb and Walling 1993, Mohseni et al. 1998, Clark et al. 2001).

For each stream in the study area, we developed nonlinear models predicting weekly average stream temperatures from weekly air temperatures. Weekly mean temperature values are used preferentially (though subjectively) in studies of this type due to practicality and for inference to fish physiological health (Eaton et al. 1995, Mohseni et al. 1998, but see Caissie et al. 2001 for support of the use of daily maximum stream temperatures). We used Akaike's Information Criterion (AIC; Akaike 1973) for model selection from the following candidate models:

$$Tw = \mu + (\alpha - \mu)*[1 + e^{(\gamma*(\beta - Ta))}]^{-1}$$
(Mohseni et al. 1998)

$$Tw = \alpha*[1 + e^{(\beta - (Ta*\gamma))}]^{-1}$$
(Ratkowsky 1990)

$$Tw = {}_{e}\,(\alpha - \gamma*(\beta^{Ta}))$$
(Ratkowsky 1990)

where Tw = water temperature, Ta = air temperature, α = stream temperature maximum, e = mathematical constant, and β and γ = variables determined by the data.

The nonlinear shape of these models results from freezing water temperatures at low air temperatures and a vapor pressure deficit (causing evaporative cooling) at high air temperatures (Mohseni and Stefan 1999). Therefore, the candidate models employed in this analysis have upper asymptotes that limit the potential rise of summer water temperatures in global warming scenarios. To account for this potential limitation in model projections, we employed a method in which we arbitrarily fixed the upper limit at the maximum observed water temperature, 2°C above this maximum value, and 4°C above this maximum value. These models were then objectively tested using AIC to determine the strength of evidence for each model. This method allows extrapolation based on strengths of evidence using weighted models. Thus, if an asymptote is suggested by the existing data, the modeled stream maximum will be near that of the observed stream maximum. If there is no asymptote suggested by the data, higher maxima models will have more strength of evidence. In the latter case, global warming projections will have more of a warming effect on stream temperature maxima than in the former case. This method allows extrapolations of global warming scenarios that do not rise linearly (and potentially limitlessly) with air temperature, as in many other studies of this type (e.g., Clark et al. 2001) and take into account the nonlinear heat storage capacity of water (Mohseni and Stefan 1999). Thus, site-specific models used in this study are actually an average of 9 different models, weighted based on their relevance to existing data. The more accurate a candidate model is based on its AICc score, the more influence it has on the subsequent site-specific model. Other models, which may be only marginally less fit, are represented based on their strength of evidence as well. The resulting site-specific models, therefore, though based solely on air temperature, can be thought of as representative of the other factors (e.g., stream length, stream width, mean pool depth) that are highly specific to the individual stream.

EFFECTS OF STREAM WARMING.—We projected water temperature changes for the 10 GCT translocation streams using the weighted model averages of individual stream models and based on global warming scenarios of 2° and 4°C. These scenarios were based on outputs of global warming climate models for the central Rocky Mountains (Hauer et al. 1997). We used the model averages to estimate the response of several variables to global warming. These included number of degree-days (average temperature in Celsius multiplied by the number of days in the growing period, as defined by Harig and Fausch 2002) for growth and survival of GCT YOY cohorts, probability of translocation success (based on a model in Harig and Fausch 2002), and expected 1st

TABLE 2. AIC analysis of candidate models to determine relevance of certain parameters for inclusion in stream-specific models for Rocky Mountain streams (n = 10). Akaike weights for candidate models indicate strengths of evidence. Higher weights indicate higher strength of evidence for a particular model. Indications are that predictive models used for stream temperatures based solely on air temperature might be misleading, as other parameters appear to carry more relevance in determining stream temperatures at a particular site. RSS = residual sum of squares (error).

A priori model (water temperature as a function of . . .)	Akaike weight	r^2	RSS
Elevation	0.18	0.22	82.5
Length, depth	0.14	0.37	67.5
Length, latitude	0.11	0.34	70.7
Air temperature	0.10	0.13	93.1
Total # of pools, mean sun arc	0.07	0.28	77.0
Total # pools, width	0.07	0.28	77.1
Latitude	0.07	0.05	100.2
Air temperature, elevation	0.05	0.24	80.6
Air temperature, mean sun arc	0.03	0.17	88.7
Length, gradient, watershed area	0.03	0.35	68.7
Mean sun arc, latitude	0.03	0.14	91.6
Width, depth	0.03	0.13	93.1
Length, elevation, latitude	0.03	0.33	70.7
Width, gradient	0.02	0.09	97.2
Air temperature, drainage relief, # deep pools	0.02	0.30	74.5
Depth, aspect, mean sun arc	0.02	0.30	74.7
Air temperature, elevation, latitude	0.01	0.24	80.6
Aspect, elevation	0.01	0.21	125.3
Aspect, air temperature	<0.01	0.28	77.1
Latitude, aspect	<0.01	0.07	148.5

spawning period. Criteria exist for some of these variables, and we estimated others based on data available. We used the number of degree-days in July and August as a surrogate for the growing season, selecting 470 degree-days in those months based on existing data that show most successful translocations (determined by high population status) above this range, and unsuccessful (determined by low or no population status) translocations below this level (data from Harig et al. 2000). Spawning was assumed to begin when weekly mean water temperatures first reached 5°C after spring runoff (USFWS 1998). Probability of translocation success was determined using a logistic regression model developed by Harig and Fausch (2002). The model gives the probability of either a high population, low population, or no population based on water temperature, mean pool width, and total number of deep pools (>30 cm). These variables were determined to be the best predictors of translocation success (Harig and Fausch 2002). We calculated the probability of success (high population status) of the streams under the global warming scenarios, using the assumption that mean pool width and total number of deep pools would remain constant over time.

RESULTS

The distribution of Akaike weights suggests considerable uncertainty in selecting a best approximating model portraying general influences of physical variables on stream temperature (Table 2). The best model included elevation alone (Akaike weight = 0.18). The model including only air temperature had an Akaike weight of 0.10. Relative to this single-variable temperature model, 3 models (all without air temperature as a parameter) had stronger support in the data. All other a priori models with air temperature as a parameter carried small (≤0.05) Akaike weights (Table 2).

Global warming scenarios of 2°C and 4°C produced different warming in mean July water temperatures between streams (0.70°C ± 0.28, median = 0.89°C, and 1.29°C ± 0.36, median = 1.50°C, in the 2 scenarios, respectively, n = 10; Fig. 2). The range of mean July water temperature stream warming was 0.42°C–1.09°C and 0.85°C–1.77°C, respectively, in the 2 scenarios. Table 3 summarizes the stream warming produced by the 2 scenarios, model variances, and 95% confidence intervals for the projections of 10 streams.

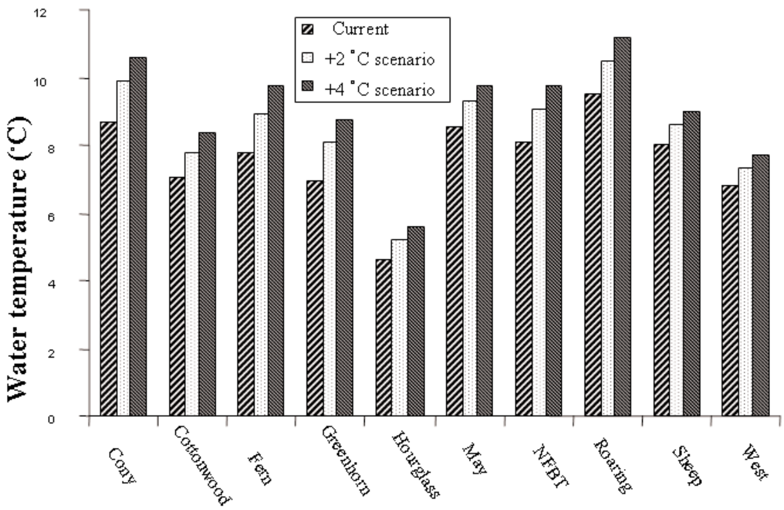

Fig. 2. Projections of mean July water temperatures for 10 translocation streams under global warming scenarios. Global warming scenarios of +2°C and +4°C yield heterogeneous warming trends between streams due to the application of individual stream models. NFBT = North Fork of the Big Thompson River.

The average number of degree-days in July and August (the parameter we used as a surrogate for growing season) increased by 58.2 (s = 17.1) for the 2°C scenario and 99.2 (s = 28.2) for the 4°C scenario (Fig. 3). Several streams exceeded the criterion of 470 degree-days for suitable growth and survivorship of YOY GCT in the 2°C scenario, and others reached it in the 4°C scenario (Fig. 3). Only 1 stream (Hourglass Creek) remained below 470 degree-days in both scenarios.

Growing seasons were extended for GCT in these streams in both global warming scenarios. Spawning activity was predicted to begin from 2.0 (s = 1.6) to 3.3 (s = 1.7) weeks earlier in the 2°C and 4°C scenarios, respectively. Figure 4 gives an example of the scenarios and onset of spawning times for Cony Creek (1 of 10 GCT translocation streams).

Warmer water temperatures in global warming scenarios resulted in higher probabilities of translocation success (Fig. 5). Five streams would currently have <50% chance of translocation success, and 7 of the 10 would have <75% chance. The average increase for these streams was 11.2% for the +2°C warming scenario, and 21.8% for the +4°C scenario, for the 5 streams with <50% probability of translocation success. In the 7 streams with <75% current chance of translocation success, the percentage increase was 12.6% for the +2°C scenario and 22.7% for the +4°C scenario.

DISCUSSION

Results of the analysis on the global model indicate the value of individual stream modeling because of the importance of variables that differ significantly from site to site. An example of the need for a stream-specific approach can be seen in Hourglass Creek, which is similar to several of the other streams in terms of mean air temperature, location, elevation, gradient, aspect, and shading (mean sun arc). Hourglass Creek has historically been very cold compared with neighboring streams. It is likely that Hourglass Creek is heavily influenced by meltwater from persistent snowpack (stream length = 2.0 km). Without a specific model for Hourglass Creek, this critical difference would likely go undetected, and, consequently, global warming projections would be exaggerated in this stream (unless interannually persistent snowpack were to disappear). Therefore, a predictive model of stream temperatures as a result of global warming for Hourglass Creek should be more conservative than models for some other nearby streams that may not be as influenced by snowpack. In this analysis global warming projections for

TABLE 3. Mean July water temperatures (Tw), as estimated by stream-specific models, summarized by stream. Also given are recorded mean July air temperatures (Ta), model variances (S^2), and 95% confidence intervals for stream-specific model averages (n = number of weekly water temperature averages used to generate model).

		+2°C scenario					+4°C scenario				
					95% CI					95% CI	
Stream	n	Ta	Tw	S^2	Low	High	Ta	Tw	S^2	Low	High
Cony	154	14.0	9.4	0.4	8.2	10.7	16.0	9.8	0.6	8.3	11.3
Cottonwood	164	20.7	7.9	0.0	7.5	8.2	22.7	8.6	0.1	7.9	9.2
Fern	155	14.5	9.0	0.7	7.3	10.7	16.5	9.5	1.0	7.5	11.5
Greenhorn	113	14.7	7.9	0.2	7.0	8.9	16.7	8.4	0.4	7.2	9.7
Hourglass	125	17.0	4.8	0.0	4.4	5.1	19.0	4.9	0.0	4.4	5.3
May	55	17.6	8.9	0.3	7.9	9.9	19.6	9.2	0.5	7.8	10.5
NFBT	56	15.1	9.4	1.1	7.3	11.5	17.1	10.3	3.0	6.8	13.8
Roaring	109	15.1	10.3	0.5	8.9	11.8	17.1	10.9	1.1	8.8	13.0
Sheep	49	18.0	8.4	0.2	7.6	9.2	20.0	9.7	0.3	7.6	9.7
West	115	15.1	7.9	0.1	7.5	8.4	17.1	8.3	0.1	7.5	9.0

Hourglass Creek remained on the lower range of the projections for all streams, indicating the efficacy of the approach.

Individual stream models may help eliminate many complexities associated with projections of global warming. Regional climatic changes are expected to be highly spatially heterogeneous (Walther et al. 2002). Therefore, accurate projections of climate change in topographically complex regions (such as the current habitat range of the GCT) are more difficult than generalized global scenarios (Hauer et al. 1997). Hauer et al. (1997) conclude, "It is unclear whether projected climate change would result in a generalized warming trend throughout the Rocky Mountain region, or whether change would be strongly regionalized." Extrapolating warming scenarios from atmospheric models to aquatic systems adds a further layer of complexity. Limits on extrapolation are due in part to the nonlinear heat storage capacity of water (Mohseni and Stefan 1999) and the complex surface and subsurface flow paths of water sources prior to entering stream channels. The water temperature of a stream may be influenced by groundwater inflows, riparian or topographic shading (slope and aspect), weather forcing (air temperature, relative humidity, solar radiation, and wind), snowmelt, and anthropogenic effects (Larson and Larson 2001). Thus, single models applied across regions may have little merit for any particular site in that region. As GCT are relegated to high-elevation streams and lakes, projections of climatic change from global circulation models require specific attention to regional and site specific factors.

Global warming will likely have mixed effects on GCT. The species has been extirpated from much of its previous range due to overharvest, habitat degradation, and the presence of nonnative salmonids (Behnke 1992). As a result, most GCT populations currently exist in headwater streams or high-elevation lakes, where water temperatures are likely colder than optimal for GCT growth and reproduction. Harig and Fausch (2002) found cold water temperatures to be among the factors most closely related to limitation of the success of translocation sites, likely due to winterkill of juveniles with insufficient lipid reserves (e.g., Hutchings et al. 1999). After spawning in the spring, more than a month of incubation, and emergence, juveniles have only a limited time in which to feed, grow, and produce lipid reserves before water temperatures drop to near 0°C for the winter. If insufficient reserves are stored to meet the metabolic needs of the juveniles during winter, they may not survive and the population may not persist over time. Therefore, a warming trend may improve habitat conditions in many GCT restoration sites, as spring activities are generally expected to begin earlier (Walther et al. 2002).

Given that GCT are currently restricted to cold, unproductive systems, global warming may potentially aid these populations and make more headwater habitat suitable for GCT reintroduction. Before the introduction

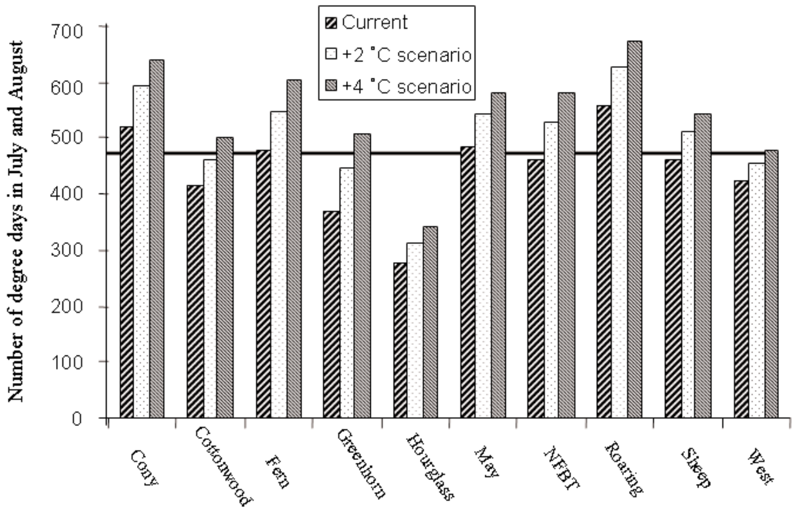

Fig. 3. Growing seasons of cutthroat trout translocation sites. The number of degree-days in July and August (dd) is used as a surrogate parameter for the growing season. It is estimated from results of translocation attempts that 472 dd (indicated by thick line) are required for adequate growth of cutthroat trout young-of-the-year to persist through the winter.

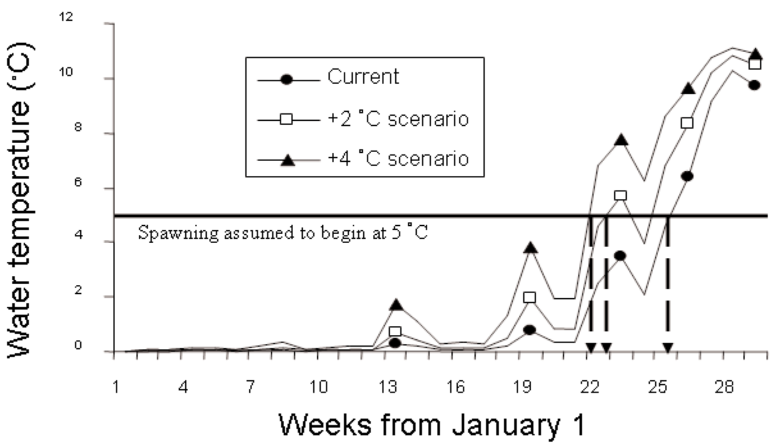

Fig. 4. Effects of global warming on the projected earliest greenback cutthroat trout spawning events. GCT are assumed to begin spawning when water temperatures first reach 5°C (USFWS 1998). These models represent global warming scenarios based on actual data from January to July 1999 in Cony Creek, CO. Arrows indicate when spawning would be predicted to first occur based on the models.

of nonnative trout (ca. 1880s), the historic range of the GCT extended north into Wyoming and east into the Great Plains (Harig 2000). Thus, the range of the GCT would likely extend far downstream from most headwater segments it currently occupies, if not for the presence of nonnative salmonids that outcompete GCT. Several measures of habitat suitability improved for GCT restoration sites in global warming projections. As water temperatures increase, the number of degree-days in July and August increases (Fig. 3), spawning generally begins earlier (Fig. 4), and shorter periods are required for incubation (Hubert et al. 1994). As a result, the duration of the growing season increases and chances of overwinter survival may

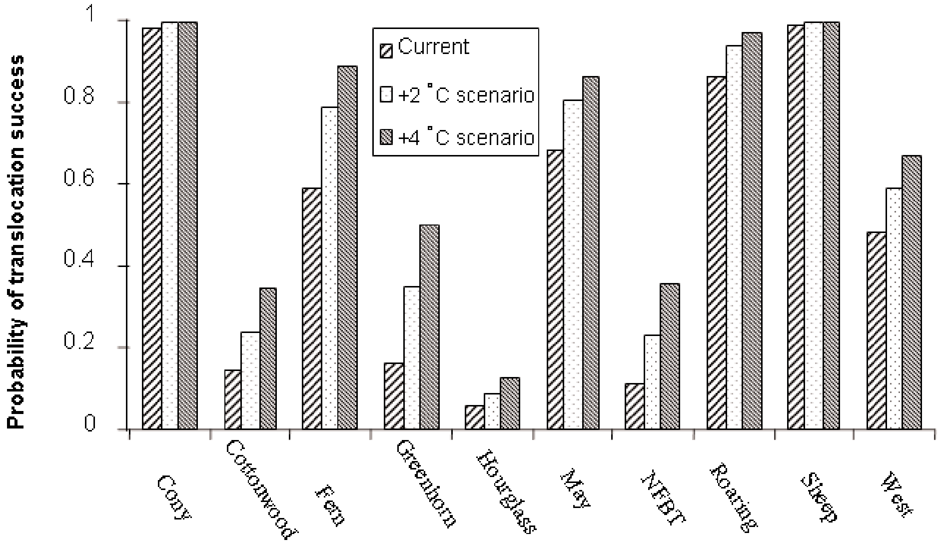

Fig. 5. Projected probability of translocation success of 10 greenback cutthroat trout populations. Differences exist in projected probability of translocation success under the current thermal regime of 10 translocation sites compared with the regime expected from global warming scenarios.

increase as well (Hauer et al. 1997). These factors make long-term viability of populations in warmed streams more likely (all else being equal), assuming nonnative species can continue to be excluded from these habitats. Whirling disease, however, may be expected to increase in virulence under these warming scenarios (Cooney 2002).

Concerns over the effects of global climate change on biota are not limited to temperature. A comprehensive species-specific review of the potential effects of climate change should include several other aspects. For the GCT, important aspects of climate change are likely to be temperature, flow regimes, and climatic extremes. Although this paper deals solely with temperature, flow regimes may be important for the GCT, as many of their habitats have very low flows during extended parts of the year. Possible hydrologic responses to climate change are extremely variable (Carpenter et al. 1992, Fagre et al. 1997), though earlier spring runoff and lower summer base flows seem most probable in headwater systems (Hauer et al. 1997). Rain-on-snow events are expected to increase in frequency and intensity as global warming occurs (Hauer et al. 1997). These events can result in flash floods that may extirpate or dramatically reduce populations and scour potential spawning habitat (Seegrist and Gard 1972, Pearsons et al. 1992, Latterell et al. 1998, Jager et al. 1999, Clark et al. 2001). A significant limitation of the modeling method presented in this paper is that it does not account for how changes might affect groundwater or persistent snowpacks and hence flow regimes. Our analyses are intended for use only with air temperature changes, all else being equal.

Increased air temperature and seasonal changes in precipitation may lead to increased intermittency of Rocky Mountain streams in the summer (Hauer et al. 1997). Increased intermittency, in turn, may lead to water temperature increases and deoxygenation in remaining pools (Gu et al. 1999), which may be detrimental to headwater cutthroat trout populations. Populations of cutthroat trout isolated in headwater reaches are likely to be highly susceptible to stochastic perturbations (Kruse et al. 2001). This effect may be exacerbated in the case of the GCT, as recolonization from downstream is not effectively possible for this species.

The definition of stability given in the GCT recovery plan does not include an account of how these sites may change over time (Young and Harig 2001). Climate change can play a major role in the structural and functional dynamics of an ecosystem (Meyer et al. 1999), leading to extinctions, range changes, and species invasions (Lodge 1993) for resident stream salmonids (Eaton and Scheller 1996, Keleher and Rahel 1996, Rahel et al. 1996). Other abiotic factors associated with global change, such as hydrologic regimes, acid precipitation, and seasonality and intensity of precipitation events, droughts, and floods, may similarly influence biotic systems (Grimm 1993). Climate change may therefore influence the continued success of GCT populations.

Managers of the GCT have established populations in diverse habitats that may help reduce future uncertainties regarding external threats such as climate change. Populations have been established in many lakes, which may provide refugia from persistent low flows associated with drought, stochastic events such as flash floods, and thermal extremes (Beeton 2002). Lakes also provide cover from avian or mammalian predators (depth) regardless of what effects climate change has on riparian vegetation, a significant factor in cutthroat trout survival (Boss and Richardson 2002). Alternatively, populations established in fast-moving, high-gradient streams may have a refuge from whirling disease, a malfeasance common in more stagnant waters. Populations of GCT have been established in Rocky Mountain National Park, as well as on U.S. Forest Service and private land. Most of these sites are open to catch-and-release angling only, while several are no-fishing areas. Thus, GCT have a potential refuge from fishing-related stresses, as well as intentional restocking of nonnative trout (see Harig et al. 2000 for examples). This variety of habitat conditions may help GCT adapt to persistent stressors such as global climate change. As managers continue to establish new populations, diversity of habitat selection should remain a priority for these reasons.

ACKNOWLEDGMENTS

This project was funded in part by a Science To Achieve Results (STAR) grant from the U.S. Environmental Protection Agency (Agreement R-827449-01-0) and was additionally funded by the Colorado Water Resources Research Institute and the College of Natural Resources at Colorado State University. We extend special thanks to Jessica Higgins for volunteering on the project. We also thank Bruce Rosenlund (U.S. Fish and Wildlife Service), Tom Nesler (Colorado Division of Wildlife), Jill Baron, LeRoy Poff, Brett Johnson, David Anderson, Bob Behnke, Andy Holland, Nolan Doesken, Ken Burnham, Tom Hobbs (Colorado State University), Mike Hartman, and Mark Losleben (Niwot Ridge C1 weather station) for suggestions, advice, information, and revisions of this manuscript.

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Received 10 June 2003
Accepted 28 September 2004