

# Thermal controls of Yellowstone cutthroat trout and invasive fishes under climate change

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## Abstract

We combine large observed data sets and dynamically downscaled climate data to explore historic and future (2050–2069) stream temperature changes over the topographically diverse Greater Yellowstone Ecosystem (elevation range = 824–4017 m). We link future stream temperatures with fish growth models to investigate how changing thermal regimes could influence the future distribution and persistence of native Yellowstone cutthroat trout (YCT) and competing invasive species. We find that stream temperatures during the recent decade (2000–2009) surpass the anomalously warm period of the 1930s. Climate simulations indicate air temperatures will warm by 1 °C to >3 °C over the Greater Yellowstone by mid-21st century, resulting in concomitant increases in 2050–2069 peak stream temperatures and protracted periods of warming from May to September (MJJAS). Projected changes in thermal regimes during the MJJAS growing season modify the trajectories of daily growth rates at all elevations with pronounced growth during early and late summer. For high-elevation populations, we find considerable increases in fish body mass attributable both to warming of cold-water temperatures and to extended growing seasons. During peak July to August warming, mid-21st century temperatures will cause periods of increased thermal stress, rendering some low-elevation streams less suitable for YCT. The majority (80%) of sites currently inhabited by YCT, however, display minimal loss (<10%) or positive changes in total body mass by midcentury; we attribute this response to the fact that many low-elevation populations of YCT have already been extirpated by historical changes in land use and invasions of non-native species. Our results further suggest that benefits to YCT populations due to warmer stream temperatures at currently cold sites could be offset by the interspecific effects of corresponding growth of sympatric, non-native species, underscoring the importance of developing climate adaptation strategies that reduce limiting factors such as non-native species and habitat degradation.

**Keywords:** climate change, Greater Yellowstone, growth, non-natives, trout

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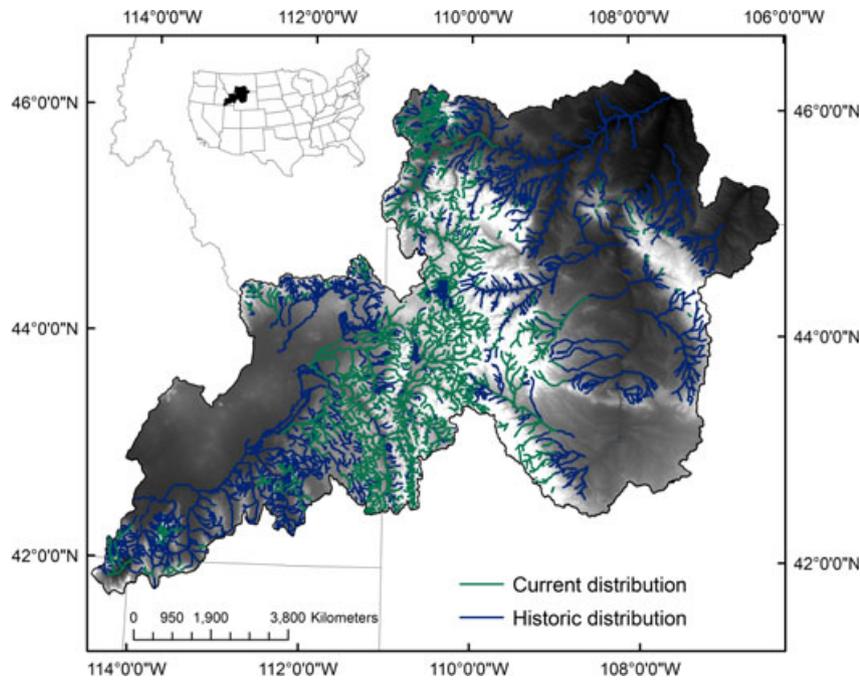
## Introduction

Regional expression of changes in global climate is expected to result in substantial shifts in species distributions and migratory behavior (Parmesan & Yohe, 2003), which are likely to vary considerably across taxa (Walther *et al.*, 2002). Some groups, (e.g., avifauna; Charmantier *et al.*, 2008) distributional shifts in latitude, elevation, or both are possible as means of adaptation to escape unsuitable conditions. For species restricted to islands, either in the classic sense or disconnected montane systems (*sensu* Brown, 1971), the ability to follow climate-induced habitat shifts is limited.

As a group, native inland salmonids of North America are particularly vulnerable to climate-induced changes in stream temperatures directly (Bear *et al.*, 2007; McMahon *et al.*, 2007) and through interrelated

impacts of altered hydrologic regimes (Meyer *et al.*, 2003; Xu *et al.*, 2010; Wenger *et al.*, 2011b) and disturbance such as wildfire (Rahel *et al.*, 2008). Current distributions of most salmonids in the Rocky Mountains present a typical pattern wherein native species occupy limited, upstream portions of stream networks with progressively increasing populations of non-native species downstream (Franco & Budy, 2005; Rieman *et al.*, 2006). Salmonids are poikilothermic as ambient stream temperatures strongly influence metabolic rates and growth (Brett, 1971; Mangel, 1994), and interspecific differences in thermal constraints influence both realized and fundamental niches (Rieman *et al.*, 2006). Where possible, salmonids are mobile and can mediate periods of thermal stress within streams through proximate or larger scale movements to optimize ambient conditions (Kaeding, 1996; Torgersen *et al.*, 1999; Ruff *et al.*, 2011); however, given their current distributions, salmonids have limited potential for large-scale

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**Fig. 1** The range of Yellowstone cutthroat trout. Stream segments currently inhabited are indicated by green and segments where historical populations have been extirpated are indicated by blue.

shifts in distribution to adapt to climate-induced changes in ambient stream conditions (*sensu* Parmesan & Yohe, 2003).

Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*, YCT) is an endemic salmonid in the Greater Yellowstone Ecosystem (GYE), one of the largest, intact ecosystems in the midlatitudes of North America (Fig. 1) (Noss *et al.*, 2002). As a native species, YCT has high societal value (Gresswell & Liss, 1995) and is a key food resource for over 40 species throughout its range (e.g., grizzly bear *Ursus horribilis* and bald eagles *Haliaeetus leucocephalus*) (Stapp & Hayward, 2002; Wengeler *et al.*, 2010). Local populations of YCT have been lost over a broad range of elevations (820–3126 m) as a result of historical land use, fragmentation of stream habitat, and the ingress of non-native species (Kruse *et al.*, 2000; Gresswell, 2011). The largest range contractions have occurred in lower elevation streams (Fig. 1) and existing populations of YCT currently occupy thermally suitable streams (range of average daily temperatures May 1st to September 30th = 5.9–16.8 °C) at elevations ranging from 1168 to 3317 m. Extant populations of YCT continue to be vulnerable to the adverse effects of non-native species (Gresswell, 2011). Populations of non-native brook trout (*Salvelinus fontinalis*) and rainbow trout (*O. mykiss*) represent significant threats to YCT through competition (Destaso & Rahel, 1994; Seiler & Keeley, 2007; Buys *et al.*, 2009), higher

survival via life-history differences (Peterson *et al.*, 2004; McGrath & Lewis, 2007), and hybridization (Allendorf *et al.*, 2001; Gunnell *et al.*, 2008; Muhlfeld *et al.*, 2009; Kovach *et al.*, 2011).

Stream temperature records within the mountainous Western United States exhibit warming trends consistent with observed trends in air temperature (Kaushal *et al.*, 2010; Isaak *et al.*, 2012a,b), yet there is considerable uncertainty as to how future climate changes might influence both native YCT and non-native populations given the relatively cold climate and wide elevation range of the GYE. Previous assessments of the effects of climate change on native salmonids of North America characterize potential shifts in thermally suitable habitat based on changes in average summer or peak monthly (e.g., August) stream temperature (Isaak *et al.*, 2010; Wenger *et al.*, 2011b). Here, we follow a different strategy to quantify changes in fish growth potential based on daily stream temperatures for the typical May 1st to September 30th growing season (hereafter MJJAS) in our study area. The objectives of our study are to (i) develop a distributed model to associate air and stream temperatures for MJJAS across the range of YCT; (ii) integrate the stream temperature model with thermally driven growth models for native and non-native species' to quantify seasonal growth at a daily time step (e.g., Sloat *et al.*, 2005); and (iii) use dynamically downscaled climate data to project future

stream temperatures for the growth models to investigate how changes in climate during the mid-21st century are likely to influence periods of thermal suitability and species-specific growth rates. We anticipate that future climate changes are likely to increase periods of thermal stress during the summer months. However, given recent trends of longer growing seasons for terrestrial species of North America (e.g., Zhu *et al.*, 2012), we hypothesize that overall YCT growth during MJJAS would not be compromised, particularly at mid-to upper elevations. We also anticipate that future changes in temperature are likely to favor non-native brook trout and rainbow, resulting in additional stress on native YCT.

## Materials and methods

### Study area

Our study area is the historical range of YCT that extends over approximately 4° of latitude and 7° of longitude (166 450 km<sup>2</sup>) and includes portions of Montana, Wyoming, Idaho, Nevada, Utah, and much of the GYE (Fig. 1). Vegetation types in the study area vary from low elevation, arid grassland, and shrub communities to high-elevation, alpine tundra. The range of elevations and the seasonal interplay of different air masses within the GYE result in considerable variability in climate throughout the year (Whitlock & Bartlein, 1993), but the climate of the area is generally characterized by cold, winter months and warm to hot summer months.

### Stream and air temperature data

We assembled stream temperature data within the study area from all available records collected at 291 sites by local, state, and federal agencies, academic institutions, and non-governmental organizations. To expand the spatial and temporal coverage of observations in key watersheds, we supplemented the existing data by deploying temperature loggers ( $n = 47$ ; Tidbit and Pendant models; [www.onsetcomp.com](http://www.onsetcomp.com)). The combined temperature data set represents 338 sites that span a range of elevation from 924 to 2787 m (median = 1871 m). We manually screened the raw stream temperature data sets for erroneous data, such as abrupt changes in stream temperature, which are indicative of the sensor being out of the water (Dunham *et al.*, 2005), and use the remaining data to compute the daily average temperatures at each site for the MJJAS period.

We also assembled a corresponding air temperature data set from 76 sites distributed across the study area that covered the months of interest of this study (i.e., May to September). Air temperature records were obtained from Remote Automated Weather Stations (RAWS; [www.raws.dri.edu](http://www.raws.dri.edu)), NOAA National Climate Data Center (NCDC; [www.ncdc.noaa.gov](http://www.ncdc.noaa.gov)), and Natural Resource Conservation Service SNOTEL sites ([www.wcc.nrcs.usda.gov/snow](http://www.wcc.nrcs.usda.gov/snow)). The air temperature

stations span a similar range of elevations (1112–2919 m; median = 1896 m). The screened data sets included a total of 524 291 daily air temperature values and 137 566 daily stream temperature values.

### Stream temperature modeling

Stream temperature is the result of the interplay of the components of the heat budget including solar radiation, heat advection by groundwater, and evaporation (Mohseni & Stefan, 1999; Webb *et al.*, 2008; Wu *et al.*, 2012). Aquatic biologists have long relied on the fact that stream temperatures are correlated with air temperature (Mohseni *et al.*, 1998; Mohseni & Stefan, 1999; Johnson, 2003). Logistic functions can be fitted to temperature data through non-linear regression to achieve realistic representations of the annual stream-air temperature relationship (Mohseni *et al.*, 1998; Webb *et al.*, 2008). Such functions capture the asymptotic behavior of the annual cycle that is characterized by minima (freezing) during winter and maxima during summer when evaporative and radiative cooling of the water surface can limit maximum temperatures (Mohseni *et al.*, 1998; Bogan *et al.*, 2003; Webb *et al.*, 2008).

For high-elevation field studies such as ours, stream temperature data are typically collected from spring or summer into fall, when sites are accessible and both air and stream temperatures are above freezing (Isaak *et al.*, 2010). In our study area, maximum stream temperatures do not in general exceed 25 °C where temperatures exhibit asymptotic behavior attributed to evaporative and radiative cooling (Mohseni *et al.*, 2002). Moreover, the data collected during MJJAS span the linear portion of logistic curves where linear regression between air and stream temperature are a viable option (Mohseni *et al.*, 1998). We confirmed the applicability of the linear relationship by inspecting plots of all our 338 stream temperature records (not shown), which did not reveal any substantial asymptotic behavior of maximum stream temperatures.

Our fish growth models require daily water temperatures as input; however, daily time series of air temperature and stream temperature are autocorrelated, which potentially violates the underlying assumptions of linear regression. Moreover, previous studies have shown that weekly to monthly time intervals provide optimal results when using linear regression (Mohseni & Stefan, 1999) because the thermal inertia of the water attenuates high frequency day-to-day variability in air temperature. To address these issues, we derive weekly average temperatures from daily data and use the weekly data to develop regression equations. Weekly time series also reduce, but do not eliminate, autocorrelation in the data (Sinokrot & Gulliver, 2000).

We derived paired weekly air and stream temperatures for each site by spatial interpolation of the daily air temperature records, constrained by the condition that at least 4 days are present in a given week. The interpolation is based on inverse distance weighting (IDW) that uses a third-order weighting function centered on our study area. We adjusted the air temperature records to sea level using a nominal moist adiabatic lapse rate of  $-6.5$  °C km<sup>-1</sup> to reference the temperatures to a common datum prior to interpolation; after interpolation, we

adjusted the temperatures from sea level up to elevations of the stream sites to establish lapse-rate corrected pairs of air-stream temperature data for each site for MJJAS.

The air temperature data sets have missing values and changing spatial coverage through time. Between 1984 and 1994, 20 stations are available, after 1994, there are >60 stations. The majority of the stream sites lie within 50 km of an air temperature station. Missing data and the addition or loss of stations alter the balance of weights used in IDW, specifically the distance to the nearest station, and thereby lead to inconsistent interpolations of air temperature. To eliminate inconsistencies from our analysis, we inspected each of the 338 interpolated time series and exclude stream-air temperature pairs where the distance from the stream site to the nearest air temperature site changed by >10 km as a result of missing data. We also removed sites with fewer than 8 weeks of record, resulting in a total of 272 remaining sites for our analysis.

We fit linear regressions of water temperature as a function of air temperature at each of the sites using the weekly average data. We inspected each of the 272 regressions to assess air- and stream-temperature slope parameters, model fit, and potential violations of normality. We removed sites with Pearson's  $R^2$  coefficient < 0.6 ( $n = 46$ ) to maximize spatial coverage while eliminating weak relationships and spurious regressions from further analyses (higher  $R^2$  cutoffs could be specified, but would sharply reduce the number of sites remaining for analysis). The 46 removed sites may be groundwater dominated, downstream from a reservoir, influenced by water withdrawals for irrigation or there may have been problems with the temperature sensors.

The average slope coefficient for the 226 retained regressions is  $0.56\text{ }^{\circ}\text{C }^{\circ}\text{C}^{-1}$  with a standard deviation of  $\pm 0.20\text{ }^{\circ}\text{C }^{\circ}\text{C}^{-1}$ , indicating a ca.  $0.6\text{ }^{\circ}\text{C}$  change in stream temperature with every  $1\text{ }^{\circ}\text{C}$  change in air temperature, which is consistent with previous site-specific studies in the region (Sloat *et al.*, 2005). We found no discernible spatial pattern of model fit among retained and removed sites; however, higher elevation sites on the Yellowstone Plateau tended to have marginally lower  $R^2$  values. The regressions explain an average of 83% of the variance ( $R^2 = 0.83$ ) in stream temperature over all sites. In addition, 60% of the sites have mean squared error associated with the regressions of  $<1\text{ }^{\circ}\text{C}$ .

### Application of the stream temperature model

We employ the stream temperature regression models to calculate past (20th century), present (our base period; 1980–1999), and future (2050–2069) stream temperatures. For the historical perspective, we used monthly air temperatures from the PRISM data set (Daly *et al.*, 1994) to calculate anomalies of decadal average stream temperature for the 20th century. To calculate future stream temperatures we used air temperatures from the regional climate simulations of Hostetler *et al.* (2011).

The climate simulations were performed with the RegCM3 regional climate model (Pal *et al.*, 2007) on 15-km horizontal grids. The simulations provide present and future dynamically downscaled climate data from four general circulation

models: the US National Oceanic and Atmospheric Administration National Center for Environmental Prediction Reanalysis (NOAA NCEP; Kalnay *et al.*, 1996; Kanamitsu *et al.*, 2002), the Max Plank Institute (ECHAM5; Roeckner *et al.*, 2003), the Geophysical Fluid Dynamics Laboratory (GFDL CM2.0 Anderson *et al.*, 2004), and GENMOM (Alder *et al.*, 2011). The simulations of the 1980–1999 period are based on the Climate of the 20th Century emissions scenario and the simulations of the 2050–2069 period are based on the A2 emission scenario (Nakicenovic *et al.*, 2000; IPCC, 2007). Further details about the models, techniques, and data are provided by Hostetler *et al.* (2011) and at <http://regclim.coas.oregonstate.edu>.

Similar to all climate models, the temperatures in the RegCM3 simulations are to some degree biased relative to observations (Jacob *et al.*, 2007). We therefore used the PRISM temperature data to adjust for bias (i.e., shift the mean) in the 1980–1999 MJJAS temperature data for each model. To be consistent with our derivation of observed data, we applied a lapse rate correction ( $-6.5\text{ }^{\circ}\text{C km}^{-1}$ ) to adjust the temperature from the elevation of the RegCM3 grid to the elevation of the stream site. The same bias and lapse rate corrections were applied to the 2050–2069 time series. To provide input for the regression models, we smoothed the raw daily data with a 7-day window to reduce day-to-day variability in the projected stream temperatures for the growth models. We evaluated the effect of smoothing by comparing computed stream temperature and growth rates for the smoothed time series with results from the raw daily data and from interpolating daily values from weekly averages, and found insignificant differences among the methods (Fig. S1).

### Salmonid growth modeling

We use the daily stream temperatures as input to growth models to estimate MJJAS daily growth rates for YCT and non-native brook trout (BKT) and rainbow trout (RBT) (Bear *et al.*, 2007; McMahon *et al.*, 2007). Juvenile cutthroat trout, BKT, and RBT exhibit similar feeding behavior with considerable overlap in diets (Angradi & Griffith, 1990; Hilderbrand & Kershner, 2004). Growth models for YCT have not been developed so we relied on the model of Bear *et al.* (2007) for closely related westslope cutthroat trout (*O. c. lewisi*), a subspecies with a similar thermal niche (Isaak & Hubert, 2004). The species-specific, empirical growth models are derived from laboratory experiments with juvenile fishes (ages 1–2). Juvenile-based models are appropriate for our analysis given the relative importance of fitness in the juvenile stages to overall population growth (Van Kirk & Hill, 2007). The temperature based growth models for each species are given in the following:

$$G_{YCT} = -4.1727 + 0.946T_W - 0.0348T_W^2$$

$$G_{RBT} = -0.7691 + 0.4514T_W - 0.0173T_W^2$$

$$G_{BKT} = -1.2653 + 0.5213T_W - 0.0196T_W^2$$

where  $T_w$  is daily stream temperature in degrees Celsius and  $G_{YCT}$ ,  $G_{RBT}$ , and  $G_{BKT}$  is the daily growth potential in percent of initial body mass for YCT, RBT, and BKT, respectively.

We note that these equations can result in negative growth during periods where water temperatures are high and metabolic demands (e.g., respiration) exceed energy inputs (Brett, 1979).

We categorize the sites where YCT occurred in allopatry, in sympatry with RBT, and in sympatry with BKT, based on current fish distribution data for the study area (May *et al.*, 2006). We assume a constant forage base for the growth models in our analyses as there is no clear understanding of how future increases in temperature will alter secondary production in streams (Domisch *et al.*, 2011) and hence the energy potential of salmonid forage. At each site, we use daily temperatures averaged across the three climate simulations (see above) to calculate species-specific measures of daily growth potential and MJJAS growth for the present and future. To relate the growth potential to fish size, we specified an April 30th body mass of 13 g, which is typical for juveniles at early life stages for each species within our study area, and iteratively calculated the daily growth in mass during MJJAS. Finally, we select three basins with sites in upper and lower reaches to illustrate growth trajectories across elevations and in differing physiographic settings: the Greys River, Wyoming (elevation 2403 and 1889 m); the Yellowstone River, Wyoming, and Montana, respectively (elevation 2388 and 1221 m); and the Raft River/Goose Creek, Idaho and Utah (elevation 2510 and 1496 m).

## Results

### *Historic, current, and future stream temperature*

Our models indicate that stream temperatures over much of the YCT range warmed by at least 1 °C during the 20th century, (Fig. 2a). Warming during the decade of the 2000s exceeded that of the Great Dustbowl of the 1930s in our study area (Fig. 2a) and represents the greatest rate of change over the past century, consistent with documented trends in the Northern Hemisphere (Fig. S2; Baringer *et al.*, 2010).

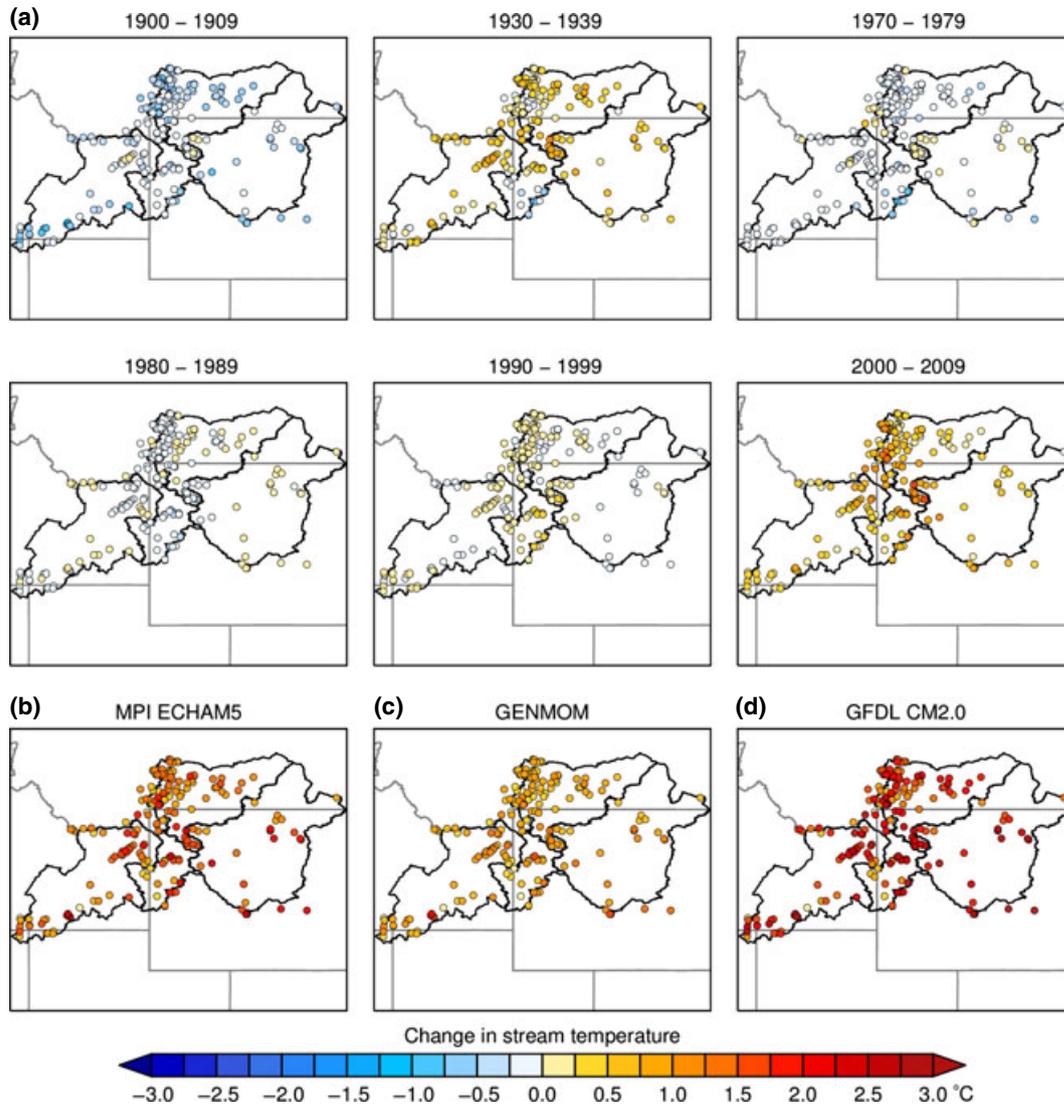
All three climate simulations indicate warming in the study area by midcentury, where changes for the 2050–2069 period range from 1 °C to over 3 °C (Fig. S3). In response to warmer air temperatures, future stream temperatures increase by  $1.2 \pm 0.5$  °C for MPI ECHAM5 ( $\pm$ denotes SD),  $0.8 \pm 0.3$  °C for GENMOM and  $1.8 \pm 0.7$  °C for GFDL CM2.0 (Fig. 2b–d), exceeding the warming of the 2000s. The GFDL CM2.0 air temperatures produce a few sites (5/226 or 2.2%), where stream temperatures exceed 25 °C. As previously discussed, at temperatures > 25 °C evaporative and radiative cooling would likely become increasingly significant; therefore, the linear regression models may over estimate maximum summer stream temperature at these 5 sites. The three models display similar, heterogeneous patterns of increased stream temperature to a large extent due to the spatial variability

in warmer air temperature, but also due to variability in fitted slope coefficients from the linear regressions that implicitly reflects the influence on stream temperature of physical controls such as elevation, groundwater, flow volume, and shading at the site locations.

In addition to changes in seasonal means, the 2050–2069 stream temperature simulations exhibit variability in the distribution of the warming over MJJAS. During the warmest part of the summer (between July and early August), GFDL CM2.0 simulated the highest amplitude warming (Fig. S4). The MPI ECHAM5- and GENMOM-based simulations do not display as much change in peak stream temperatures, but rather distribute the warming over May, June, and September. While differences in the magnitude of warming in the peak summer temperature are evident, the three simulations are consistent in projecting warmer water temperatures throughout the growing season and the onset of earlier warming in May and the persistence of warming through September.

### *Salmonid growth*

Changes in average growth rates for YCT between 1980 and 1999 and 2050–2069 periods vary considerably throughout the growing season and across the study area (Fig. 3). High-elevation sites tend to have increased growth rates in the future, whereas lower elevation sites display a reduction in growth rates between June and August. For sites currently occupied by YCT, we find 100% of the sites in May, 97% of the sites in June, and 82% of the sites in September demonstrated minimal (–10% to 10%) or positive (>10%) changes in YCT growth rate by midcentury (Table 1). During the summer months, we find a decrease in YCT growth rate (<–10%) at 23% and 22% of the occupied sites during July and August, respectively. Sites where YCT have been extirpated have higher proportions that are negatively impacted, particularly during July (36%), August (42%), and September (36%). Accordingly, the extirpated sites have a smaller proportion of sites exhibiting increased growth rates when compared to occupied sites, indicating that many of the sites that are currently unoccupied by YCT will become increasing less suitable in the future. However, none of the sites has a decrease in the number of days with positive growth rates during May and September (Table S1), and 47% of the sites occupied by YCT have an increase in the number days with positive growth rates during May and 15% of the sites increase during September. Combined, these increases represent a lengthening of the growth season. Furthermore, only 1% of the occupied sites in June and 3% of the occupied sites in July and August

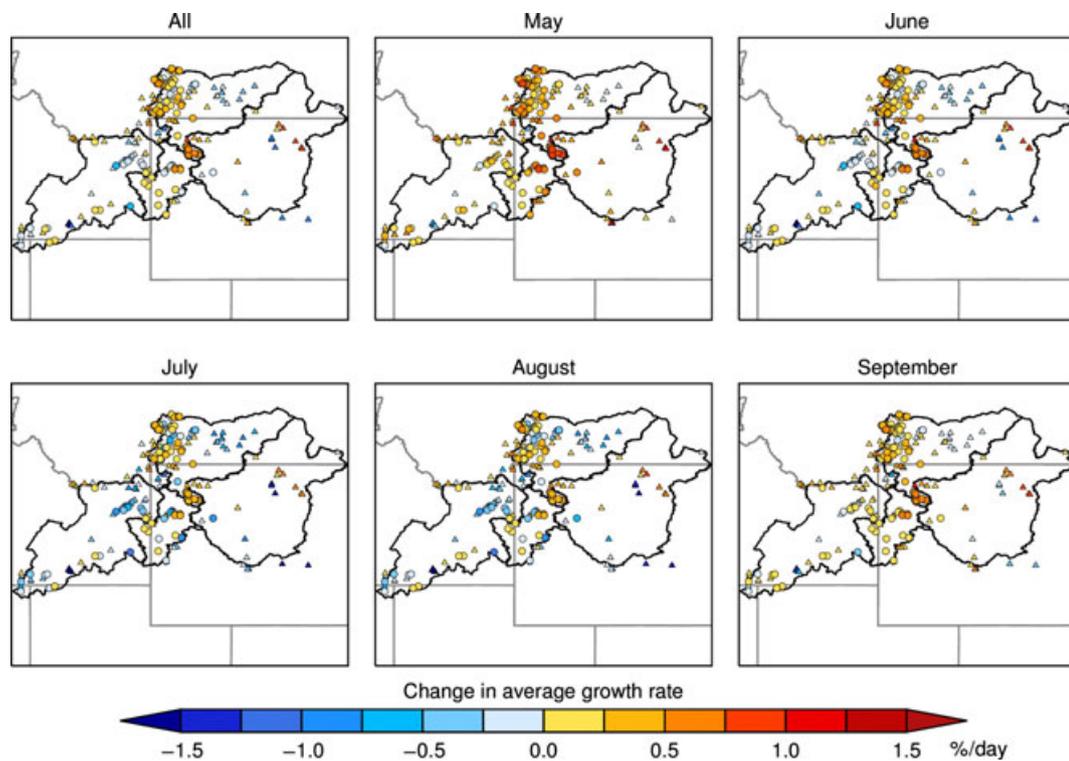


**Fig. 2** Decadal anomalies of average stream temperatures from May 1st to September 30th relative to the based period (1980–1999) using PRISM air temperature data for a historic periods (a) and future (2050–2069) changes in stream temperature as simulated using air temperature data from three dynamically downscaled climate simulations: (b) MPI ECHAM5, (c) GENMOM, and (d) Geophysical Fluid Dynamics Laboratory (GFDL CM2.0). The mapped sites are the 226 locations retained in the regression analyses.

had an increase in the number of days with negative growth rates. For sites where YCT have been extirpated, we note patterns consistent with those for occupied sites, but with considerably higher number of sites demonstrating  $< -10\%$  growth during JJAS (22–36%; Table 1). For these unoccupied sites, greater proportions demonstrate an increase in the number of days with negative growth during MJJAS (Table S1).

We project substantially different seasonal and total MJJAS growth for the upper sites of the Yellowstone River, Greys River, and Raft River/Goose Creek, despite the similar elevations of the sites (Fig. 4a–c). For the 1980–1999 base period, the Greys River site

displays a broad, constant and relatively high rate of growth throughout the growing season. In contrast, the Yellowstone River and the Raft River/Goose Creek sites are characterized by narrower growth curves associated with attendant high-elevation climate. During the base period, the three lower elevation sites have higher end-of-season (September 30th) body mass predictions than their high-elevation counterparts; however, the daily growth predictions reflect the varying influence of high water temperatures during the middle of the growing season where growth rate is reduced. Daily growth at the lower elevation site on the Greys River is similar to that of the upper site, but the lower



**Fig. 3** Changes in average (May to September) and monthly average Yellowstone cutthroat trout growth rates (percentage of body mass per day) at extant (circles) and extirpated (triangles) populations sites.

**Table 1** Summary of future (2050–2069) changes in average monthly growth rates at the 110 sites within the extant (i.e., occupied) range of Yellowstone cutthroat trout (YCT) and 116 sites where YCT have been extirpated. Growth is divided into sites with negative (<−10%), minimal (−10% to 10%), and positive (>10%) changes in growth rate relative to 1980–1999. Table values are the number of sites and the percent of total sites are given in parentheses

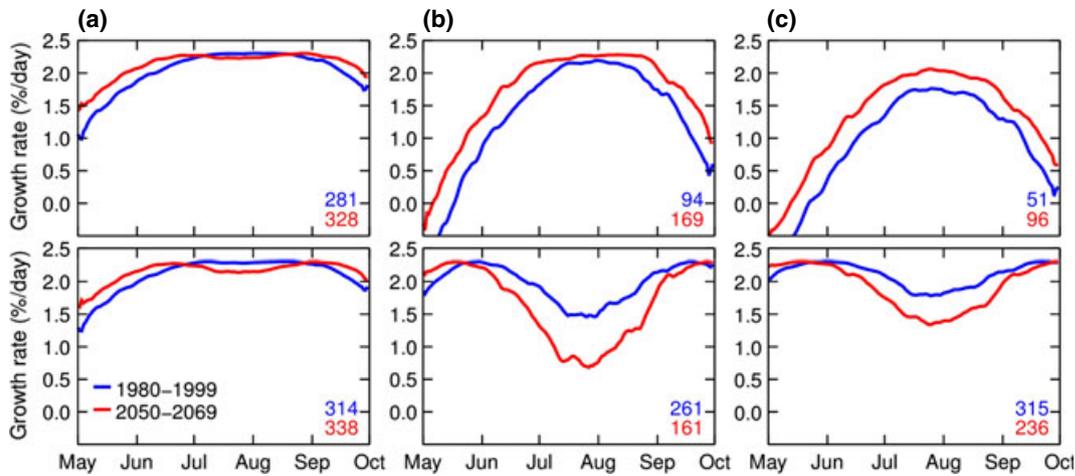
		May	June	July	August	September
Extant	<−10%	0	3 (3%)	25 (23%)	24 (22%)	20 (18%)
	−10% to 10%	36 (33%)	20 (18%)	14 (13%)	16 (15%)	11 (10%)
	>10%	74 (67%)	87 (79%)	71 (65%)	70 (64%)	79 (72%)
Extirpated	<−10%	8 (7%)	26 (22%)	42 (36%)	48 (42%)	42 (36%)
	−10% to 10%	54 (46%)	36 (31%)	25 (22%)	19 (16%)	25 (22%)
	>10%	54 (46%)	54 (47%)	49 (42%)	49 (42%)	49 (42%)

sites on the Yellowstone and Upper Raft River/Goose Creek both display marked bimodal growth with higher daily growth rates occurring during early and late summer and suppressed growth rates during the period of peak water temperatures.

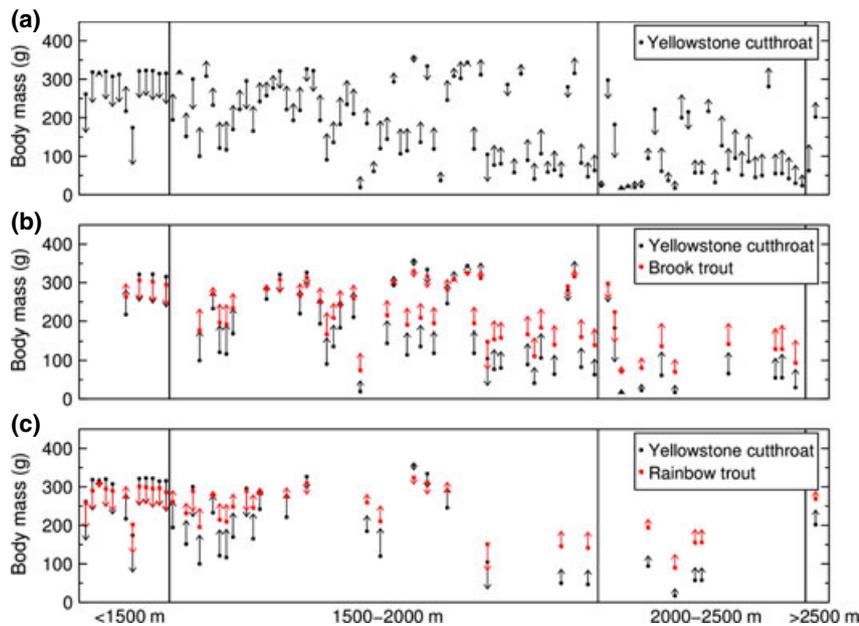
Midcentury warming substantially alters seasonal growth at all sites (Fig. 4a–c). End-of-season (September 30th) body mass increases at all high-elevation sites and decreases at two of the three low-elevation sites. There is little within-stream difference at the upper and lower sites on the Greys River, whereas the upper and lower sites on Yellowstone River and Raft River/Goose Creek are increasingly divergent. In response to

predicted warmer water temperatures in the future, the onset of growth at the upper sites is nearly a half month earlier, persists for nearly a half a month later, and is enhanced throughout the growing season. At lower elevation sites, the shape of the MJJAS growth curve transitions from unimodal to slightly bimodal for the Greys River site and more pronounced bimodal growth emerges at the other two sites, suggesting stronger physiological stress on YCT during peak summer temperatures.

By the end of MJJAS, the majority (80%) of sites that are currently inhabited by YCT ( $n = 110$ ) display minimal or positive changes in future body mass (Table S2;



**Fig. 4** Daily predictions of Yellowstone cutthroat trout growth rates from May 1st to September 30th for upper and lower elevation sites for (a) the Greys River basin, Wyoming, (b) the Yellowstone River, Wyoming, and Montana, and (c) the Raft River/Goose Creek Region, Utah, and Idaho. Inset values in the bottom right of each figure are the end-of-season (September 30th) body mass in grams for the 1980–2000 (blue) and 2050–2069 (red) periods.



**Fig. 5** Changes in 2050–2069 end-of-season (September 30th) body mass relative to the 1980–1999 base period stratified by elevation bands at sites where Yellowstone cutthroat trout (YCT) are in (a) allopatry, (b) in sympatry with non-native brook trout, and (c) in sympatry with non-native rainbow trout. The dots indicate present body mass, the arrowheads indicate future body mass, the arrows indicate the direction of future change, and elevation bands are indicated by the vertical lines.

Fig. 5a). However, for sites where YCT has already been extirpated, body mass would decrease by more than 10% at 39% of these sites, a considerably higher proportion than for sites still occupied by YCT. Decreases in body mass occurs primarily at lower elevations for occupied sites (average elevation = 1640 m; SD = 298 m).

For extant populations, however, any benefits to YCT from climate are likely to be limited due to concomitant

growth of sympatric populations of non-native BKT and RBT (Fig. 5b and c). For these sympatric sites, we find minimal or positive changes in future growth rates for both species at more than 90% of the sites during May, June, and September (Table 2). During July and August sympatric BKT populations display minimal or positive changes in future growth rate at more than 80% of the sites. Although BKT on average have a

**Table 2** Summary of future (2050–2069) changes in average monthly growth rates at sites where non-native brook trout (BKT) and rainbow trout (RBT) are sympatric with native Yellowstone cutthroat trout. Growth is divided into sites with negative (<–10%), minimal (–10% to 10%), and positive (>10%) changes in growth rate relative to 1980–1999. Table values are the number of sites and the percent of total sites are given in parentheses

Species		May	June	July	August	September
BKT	<–10%	0	2 (4%)	9 (17%)	7 (13%)	1 (2%)
	–10% to 10%	16 (31%)	32 (61%)	40 (77%)	40 (77%)	36 (69%)
	>10%	36 (69%)	18 (35%)	3 (6%)	5 (10%)	15 (29%)
RBT	<–10%	0	2(5%)	13 (34%)	13 (34%)	1 (3%)
	–10% to 10%	25 (66%)	34 (90%)	25 (66%)	25 (66%)	35 (92%)
	>10%	13 (34%)	2 (5%)	0	0	2 (5%)

smaller increase in body mass in the future than YCT where they are sympatric, the BKT have an end-of-season body mass exceeding that of YCT at 83% of the sites during the base period (Fig. 5b). We find negative changes in growth rate for RBT during July and August at 34% of the sites where currently sympatric with YCT, which is considerably higher than observed for BKT. We find RBT to have a slightly larger average decrease in body mass than do YCT, yet still have a larger body mass relative to YCT at 86% of sympatric sites (Fig. 5c).

## Discussion

Both the timing and amplitude of seasonal climate change will affect the life cycle of aquatic species in ways that are known and, as yet, unknown (Isaak *et al.*, 2010). By extending beyond studies based solely on the period of peak summer stream temperature (e.g., Wenger *et al.*, 2011b) our results indicate prolonged periods of warmer stream temperatures are likely to considerably alter salmonid growing seasons and potentially shift the structure of aquatic communities. Considering a longer within-year growth period, our results demonstrate a measure of optimism in the foreseeable future in the adaptive potential of cold-water species such as YCT that inhabit broad latitudinal and elevation ranges (Hoffmann & Sgro, 2011).

### Changing stream temperatures

From a historical perspective, it is apparent that the streams within the range of YCT have already undergone considerable changes in thermal conditions over the past century (e.g., Isaak *et al.*, 2012b). The observed patterns are consistent with findings for the Rocky Mountains (Isaak *et al.*, 2012a), illustrating regional differences in climate patterns across western North America. Our simulations indicated mid-21st century changes in climate are likely to influence not only the magnitude of change during the peak summer months (Mohseni *et al.*, 2003; e.g., Isaak *et al.*, 2010) but also the

duration of the warm period with an earlier onset of warming in May and the persistence of warming through September, consistent with Wu *et al.* (2012).

### Implications for native Yellowstone cutthroat trout

Our climate simulations consistently indicate warming across the entire growing season resulting in considerable shifts in the MJJAS growth trajectories. Predicted increases in early and late growth rates during May and September (Fig. 3) are evident range wide, a shift that is similar to observations for North American vegetation over recent decades (Zhu *et al.*, 2012). During the warmer summer months, future increases in temperatures at some locations (e.g., low-elevation sites) would increase metabolic costs resulting in periods of decreased growth potentials; a pattern consistent with results for distribution modeling analyses using summer only climate data in the Rocky Mountains (Isaak *et al.*, 2010; Wenger *et al.*, 2011a). Even with limited ability to migrate, however, our results suggest net growth in such streams is likely to change little as enhanced growth during May and September will mostly compensate for negative or decreased growth during JJA.

We note considerable variability in the effects of increasing stream temperatures on YCT growth rates, but overall, found positive or relatively little change in future growth potential for extant populations. The spatial variability in growth is likely due to the local controls of stream temperature and influence of elevation on air and stream temperatures (Caissie, 2006) in the topographically diverse GYE. At high elevations cold water temperatures and short growing seasons can limit salmonid growth and recruitment, thus dictating life-history expressions (Downs *et al.*, 1997). For these high-elevation sites, future warming would both extend the length of the growing season and augment growth during the summer, thereby leading to greater over-winter survival and population biomass (Isaak & Hubert, 2004). While future increases in peak summer temperatures are likely to reduce the thermal suitability

of low-elevation streams, our results suggest the impacts to native YCT are likely to be minimal as the majority of populations at lower elevations have already been extirpated due to land use, habitat fragmentation, and non-native species (Gresswell, 2011).

#### *Native species conservation in a changing climate*

The Greater Yellowstone Ecosystem (GYE) is ideally suited for conservation under predicted changes in climate given the extent of public land holdings, two national parks, and topographic diversity (McClanahan *et al.*, 2008; Lawrence *et al.*, 2011). A key component in designing climate adaptation strategies is to remove factors that restrict the ability of species to ameliorate the effects of changing climatic conditions (Noss, 2001; Lawler, 2009). Our results illustrate the importance of developing management strategies to combat the effects of non-native species on YCT (e.g., Peterson *et al.*, 2008). Across the Greater Yellowstone BKT and RBT were introduced during the early 1900s to enhance recreational angling opportunities. The unintended consequences of the introductions has led to extirpation and range contractions of YCT which remain as the largest threats to the persistence of YCT (Kruse *et al.*, 2000). Here, we found any biological advantages of increased growth potential for YCT from changing thermal regimes are likely to be challenged by similar advantages afforded to non-native populations of BKT and RBT (Rahel *et al.*, 2008).

Because YCT have a narrower range of thermal tolerance than do either BKT or RBT (Bear *et al.*, 2007; McMahon *et al.*, 2007), future changes in growth potential will vary as a result of shifts and changes in MJJAS daily stream temperatures. Future growth of YCT is likely to exceed that of non-natives in many locations which may continue to be or emerge as strongholds; however, the climate-driven pattern of strongholds is not uniform across elevations (Fig. 3). Sympatric populations of BKT and RBT that have growth rates similar to, or higher than, YCT are likely to be particularly problematic as any advantage associated with increased growth potential for YCT could be offset by temperature-mediated competition (Fausch *et al.*, 1994; McMahon *et al.*, 2007). Moreover, higher growth rates for BKT and RBT, taken together with the strong relationship between growth and fecundity for salmonids (Downs *et al.*, 1997), suggest that warmer stream temperatures may indirectly increase the abundance and propagule pressure of BKT and RBT and thus support further colonization of non-native species within the range of YCT. Larger populations of RBT pose an additional threat given their propensity to hybridize with YCT (Gresswell, 2011) and the detrimental effects of

hybridization on native cutthroat trout populations (Allendorf & Leary, 1988; Muhlfeld *et al.*, 2009).

Periods of thermal stress during the growing season underscore the importance of habitat restoration and connectivity (Lawler, 2009). With warming temperatures, it will become increasingly important to maintain adequate connectivity to enable individuals to mediate periods of thermal stress by seeking cold-water refugia, either locally (e.g., groundwater inputs) or in tributaries or both (Torgersen *et al.*, 1999) and maximize energy assimilation (Levy, 1990; Nowak & Quinn, 2002; Ruff *et al.*, 2011).

#### *Study limitations*

Our projections of stream temperature are derived from air temperature projections from our regional climate model. We acknowledge the effects of warming could be amplified or attenuated by changes in seasonal streamflow (Luce & Holden, 2009), particularly during the summer months (Isaak *et al.*, 2012a; Wu *et al.*, 2012). The response of stream temperature to streamflow in mountainous catchments is complex, and considerable uncertainty remains with regard to estimates of future streamflow within the GYE. Much of the uncertainty surrounds the limited continuous streamflow data that are available for higher elevation, remote basins that are the strongholds for YCT. The paucity of existing data lends to inaccurate summer baseflow predictions from hydrologic models for the Rocky Mountains (Wenger *et al.*, 2010). However, based on proximal estimates from our climate models, altered streamflows are unlikely to differentially affect the growth of YCT and non-native species (Fig. S5). We also recognize there is uncertainty in site-specific growth predictions as a result of individual variation in factors influencing growth (*sensu* Alvarez *et al.*, 2006), downscaled climate projections (Hostetler *et al.*, 2011), and stream-temperature models developed herein. Incorporating this variability may result in changes in site-specific growth totals, but is unlikely to alter the general trends of our results.

Furthermore, our growth modeling is constrained to the period of MJJAS by the availability of data. While the overall patterns are likely to be parallel, extending the period of focus to the months preceding and subsequent to MJJAS may provide more accurate measures of changes in growth under warming climates in the future (*sensu* Zhu *et al.*, 2012). Finally, our analyses focus only on one metric of fish health, yet the intra and interspecific effects due to climate warming are likely to be complex as a result of changing phenologies (Warren *et al.*, 2012), fish densities (Clews *et al.*, 2010), competitive interactions (Taniguchi & Nakano, 2000),

which individually or in synergy may be affected by the time at which individual species adapt to changing climatic conditions (Westley *et al.*, 2012). Despite our focused effort, our novel assessment of the effects of a warming climate on within-season growth provides alternative means for considering species' response to changing climatic conditions.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Comparisons of stream temperature and YCT growth potential computed from daily temperature (blue), 7-day smoothed daily temperatures (red), and daily interpolated data interpolated from weekly averages (green) for May 1st to September 30th at Tom Miner Creek (a and b) and the Shields River (c and d).

**Figure S2.** Decadal anomalies of average stream temperatures from May 1st to September 30th relative to the based period (1980–1999) using PRISM air temperature data for a historic period of 1900–2009.

**Figure S3.** Changes in mean May 1st to September 30th surface air temperature from 2050 to 2069 relative to 1980–1999 from the MPI ECHAM5 (a), GENMOM (b), and GFDL CM2.0 (c) climate simulations (Hostetler *et al.*, 2011).