Contributed Paper

Projected Climate-Induced Habitat Loss for Salmonids in the John Day River Network, Oregon, U.S.A.

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Abstract: *Climate change will likely have profound effects on cold-water species of freshwater fishes. As temperatures rise, cold-water fish distributions may shift and contract in response. Predicting the effects of projected stream warming in stream networks is complicated by the generally poor correlation between water temperature and air temperature. Spatial dependencies in stream networks are complex because the geography of stream processes is governed by dimensions of flow direction and network structure. Therefore, forecasting climate-driven range shifts of stream biota has lagged behind similar terrestrial modeling efforts. We predicted climate-induced changes in summer thermal habitat for 3 cold-water fish species—juvenile Chinook salmon, rainbow trout, and bull trout (Oncorhynchus tshawytscha, O. mykiss, and Salvelinus confluentus, respectively)—in the John Day River basin, northwestern United States. We used a spatially explicit statistical model designed to predict water temperature in stream networks on the basis of flow and spatial connectivity. The spatial distribution of stream temperature extremes during summers from 1993 through 2009 was largely governed by solar radiation and interannual extremes of air temperature. For a moderate climate change scenario, estimated declines by 2100 in the volume of habitat for Chinook salmon, rainbow trout, and bull trout were 69–95%, 51–87%, and 86–100%, respectively. Although some restoration strategies may be able to offset these projected effects, such forecasts point to how and where restoration and management efforts might focus.*

Keywords: climate change, river network, spatial model, summer extreme, thermal habitat

Proyección de la Pérdida de Hábitat de Salmónidos Inducida por el Clima con Base en un Red de Modelos de la Temperatura de Arroyos

Resumen: *Es probable que el cambio climático tenga profundo efectos sobre especies de peces dulceacuícolas de agua fría. A medida que incrementa la temperatura, la distribución de peces de agua fría puede cambiar y contraerse en respuesta. La predicción de efectos del calentamiento proyectado en redes de arroyos es complicada debido a la baja correlación entre la temperatura del agua y la temperatura del aire. Las dependencias espaciales en las redes de arroyos son complejas porque la geografía de los procesos en los arroyos esta determinada por las dimensiones en la dirección del flujo y por la estructura de la red. Por lo tanto, la predicción de cambios dirigidos por el clima en la biota de arroyos está rezagada en comparación con*

lo esfuerzos de modelado terrestre. Pronosticamos cambios inducidos por el clima en el hábitat térmico de 3 especies de peces de agua fría – Oncorhynchus tshawytscha, O. mykiss y Salvelinus confluentus – en la Cuenca del Río John Day, en el noroeste de Estados Unidos. Utilizamos un modelo estadístico espacialmente explícito diseñado para pronosticar la temperatura del agua en redes de arroyos con base en el flujo y la conectividad espacial. La distribución espacial de los extremos de temperatura en los arroyos durante los veranos de 1993 a 2009 estuvo determinada principalmente por la radiación solar y los extremos interanuales de la temperatura del aire. En un escenario de cambio climático moderado, estimamos que las declinaciones en 2100 en el volumen de hábitat de Oncorhynchus tshawytscha, O. mykiss y Salvelinus confluentus fueron de 39–95%, 51–87% y 86–100%, respectivamente. Aunque algunas estrategias de restauración pueden ser capaces de compensar estos efectos proyectados, tales predicciones apuntan hacia como y donde se pueden enfocar los esfuerzos de restauración y manejo.

Palabras Clave: cambio climático, extremo de verano, hábitat térmico, modelo espacial, red hidrológica

Introduction

Changing climate has caused systemic reorganization of many ecosystems globally (Parmesan 2006), and both recent and projected changes have promoted heightened interest in the vulnerability of freshwater organisms (Poff et al. 2002; Heino et al. 2009). Trout, char, and salmon (Salmonidae), as cold-water stenotherms, represent some of the freshwater species most sensitive to increases in temperature. This sensitivity, combined with their current status, has drawn attention to climate-related research on salmonids (Ruckelshaus et al. 2002; Schindler et al. 2003). Results of previous studies show that measuring and forecasting climate-driven changes in stream environments is difficult because the spatial structure of river networks is complex (Heino et al. 2009). Research investigating the effects of climate change on freshwater salmonid habitat generally focuses on coarse spatial resolutions at which network structure may be irrelevant (Eaton & Scheller 1996; Keleher & Rahel 1996), and on migration within downstream reaches, where temperature variability is often limited (e.g., Quinn & Adams 1996). However, flow and water temperatures in headwater reaches (where juvenile and oversummering salmonids often occur) tend to be more susceptible to weather extremes during summer months. Therefore, potentially intensified weather events due to climate change may compromise the probability of persistence during these life stages (Mantua et al. 2010).

Increases in summer stream temperature may reduce thermal habitat to only the coolest pools, tributary junctions, and headwater reaches (Crozier et al. 2008). In the southern extents of salmonids' ranges, thermal habitat for juveniles is reduced substantially in summer (Ebersole et al. 2001). Several researchers have empirically documented thermal tolerances of rainbow trout (*Oncorhynchus mykiss*), Chinook salmon (*O. tshawytscha*), and bull trout (*Salvelinus confluentus*) (Eaton et al. 1995; Dunham et al. 2003; Wenger et al. 2011). The primary challenge for forecasting the effects of climate change on the distribution of thermal habi-

tat is to model spatial and temporal variability of stream temperature.

Many attempts have been made to quantify the complexity of stream temperature with mechanistic models that compute stream temperature from energy-budget equations (e.g., Chen et al. 1998) and correlative models that incorporate a set of covariates that either directly or indirectly influence stream temperature (reviewed by Webb et al. 2008). In general, correlative models of stream temperature fail to address the spatial connectivity between locations in the stream network. The physical characteristics of any stream location (including stream temperature) may be highly autocorrelated, particularly when locations are connected by flow (Cooper et al. 1997). Recently, geostatistical network models have been developed, which incorporate flow-dependent, network-based theory and have resulted in more accurate predictions when data are spatially correlated (Webb et al. 2008; Isaak et al. 2010; Peterson & Ver Hoef 2010). Because many abiotic and biotic processes depend on annual, seasonal, and diel fluctuations in stream temperature (Caissie 2006) and stream temperature is often dependent on landscape and climate characteristics that can be remotely sensed, network-based geostatistical methods allow one to assess climate-induced changes in thermal habitat both more efficiently and with greater precision than with ordinary least-squares regression.

We built and applied a geostatistical network model of stream temperature to forecast potential climate-induced changes in the availability of thermal habitat for 3 salmonid species of conservation concern throughout a river network. We sought to quantify potential loss of summer habitat for juvenile spring-migrating Chinook salmon, juvenile summer-migrating rainbow trout (although resident rainbow trout occur sympatrically), and all life stages of bull trout. Using predictions of stream temperature, we inferred where thermal habitat exists on the basis of empirically derived thermal tolerances (Eaton et al. 1995; Rieman & Chandler 1999) and forecasted changes in the spatial distribution of that habitat in the future. We aimed to advance understanding of how

threatened cold-water fish species will be affected by a warming climate. To do so, we increased the resolution of predictions of stream temperature on the basis of a new modeling framework and investigated differential responses of 3 salmonid species at the margin of their thermal range.

Methods

Study Area and Focal Species

The John Day River is an unimpounded tributary of the Columbia River in north-central Oregon (U.S.A.) (Supporting Information). The John Day basin encompasses a large drainage area (21,000 km^2) and supports warm-water fish species in the lower reaches and cold-water species in the headwaters (Torgersen et al. 2006). The lower reaches are dominated by cyprinids, catostomids, and nonnative centrarchids, whereas the upper reaches are dominated by salmonids. Juvenile Chinook salmon and rainbow trout occupy thermally marginal reaches during the summer months when temperatures peak. Therefore, our modeled results are only applicable to that life stage. Bull trout require cold water, which is limited to the upper reaches of the basin, and we included all life stages of this species in our model.

Wild anadromous rainbow trout (i.e., steelhead) of the John Day River are listed under the U.S. Endangered Species Act (ESA) as a threatened evolutionarily significant unit of the middle Columbia River basin in the Pacific Northwest (U.S.A.). The upper John Day River contains critical habitat for steelhead. Chinook salmon in the lower Columbia River are listed as a threatened evolutionarily significant unit under the ESA. The John Day River supports one of the last remaining robust populations of wild Chinook salmon in the Columbia River basin (Carmichael et al. 2001), and it may be a source population for those populations that are threatened with extirpation in downstream main-stem reaches. Under the ESA, bull trout are listed as threatened within the conterminous United States, but throughout most of the John Day watershed they are at risk of extirpation due to climate change (Rieman et al. 2007).

Stream Temperature Modeling

Our approach to modeling the potential change in thermal habitat for salmonids had 3 components: modeling stream temperature as a function of landscape and climate (Supporting Information), modeling and subsequently forecasting stream temperature as a function of landscape and climate with specific emphasis on changing air temperature, and calculating lost habitat on the basis of whether thermal-tolerance temperatures were exceeded. To identify thermal habitat, we used empirically derived (Eaton et al. 1995; Pacific Northwest U.S.

database, Dunham et al. 2003) thermal tolerances of each of the 3 salmonid species. We based these tolerances on the maximum weekly mean stream temperature (MWMST) (yearly maxima of a 7-day moving average) for each species. To this end, we built a statistical model to predict MWMST:

$$\text{MWMST}_Y = \max_{t,Y} \left\{ \left(\overline{T}_{t-3} + \overline{T}_{t-2} + \cdots + \overline{T}_{t+3} \right) / 7 \right\}, \quad (1)$$

where $\overline{T}$ is the mean temperature observation at day t and year Y. We collected stream temperature data with digital temperature loggers accurate to within 0.53 °C (Tidbit, Water Temp Pro, and Hobo Pendant, Onset, Cape Cod, MA, U.S.A.). In collaboration with the Northwest Fisheries Science Center (National Oceanic Atmospheric Administration), we compiled data from 298 independent data-collection events from 1993 to 2007 (Supporting Information). All data-collection events represented continuous sampling from 21 June through 21 September within a single year from 1993 to 2009. Sampling intervals were ≤60 minutes, and MWMST was ≤30 °C (Dunham et al. 2005). We assumed that recorded temperatures above 30 °C were air temperatures.

We compiled a set of candidate covariates (Supporting Information) of stream temperature previously identified in the literature (Caissie 2006; Webb et al. 2008) and appended them to the NHDPlus data set (Environmental Protection Agency and Horizon Systems 2008). We retrieved most covariates from NHDPlus value-added attribute tables. To compute covariates that were not included in NHDPlus, we used a combination of ArcGIS Desktop (version 9.3.1) (ESRI 2009), NHDPlus CA3T (Horizon Systems 2008), and R statistical software (R Development Core Team 2010). We undertook exploratory analyses of potential covariates of MWMST by visually analyzing bivariate scatterplots and log-transforming skewed distributions. We used the covariates that exhibited the closest relation to MWMST to develop a set of a priori candidate models (Burnham & Anderson 2002) (Supporting Information). In each candidate model, only one metric of air temperature (or any variable closely correlated with air temperature) was included. We used nonspatial linear models for candidate model selection because they are more computationally efficient to fit than geostatistical models. Also, nonspatial model selection tends to include additional covariates that may not be significant within a geostatistical model, rather than omitting potentially significant covariates (Ver Hoef et al. 2001).

Variables that fit the above criteria (i.e., cumulative riparian solar exposure [CRSE] and maximum weekly maximum air temperature [MWMAT]) are described below (see Results section and Table 1 for the functional form of the final model). We computed CRSE from 3 data sets: mean annual solar radiation (modeled with ArcGIS Solar Analyst), percent canopy cover derived from LANDFIRE (Rollins et al. 2006), and potential riparian land cover

Table 1. Summary statistics of the covariates of the geostatistical model for predicting maximum weekly mean stream temperature (MWMST) in the John Day River network.*

Parameters	n	Units	Minimum	Maximum	Mean	Estimate (SE)
Intercept						−13.2 (3.5)
Log(CRSE)	165	log(GW/year)	1.8	13.9	9.2	1.4 (0.1)
MWMAT	13	°C	31.5	35.5	33.7	0.6 (0.1)

Predictions were based on log-transformed cumulative riparian solar exposure (CRSE) and maximum weekly maximum air temperature (MWMAT).
Abbreviation: GW, gigawatts.

extracted from the LANDFIRE biophysical settings data set. We computed CRSE as follows:

$$\text{CRSE} = \sum_p R_p S_p (1 - C_p), \qquad (2)$$

where R is the riparian land cover (1, riparian; 0, non-riparian), S is the solar radiation, and C is the percent canopy cover at every pth pixel. We then summed the product of $R_p S_p (1 - C_p)$ by accumulating values downstream with CA3T. The final CRSE data product was a model of the accumulated solar radiation that penetrates through canopy cover and reaches the stream.

To calculate MWMAT, we gathered daily records from 4 Western Regional Climate Center Remote Automatic Weather Stations (WRCC 2010): Case, Board Creek, Fall Mountain, and North Pole Ridge. For each year, $Y (Y = 1993–2009)$, we calculated MWMAT as

$$\text{MWMAT}_Y$$
$$= \frac{\sum_{W=1}^{4} \left[\max_t \left\{ \left(T_{W,t-3} + T_{W,t-2} + \cdots + T_{W,t+3} \right) /7 \right\} \right]}{4}, \qquad (3)$$

where $T_{w,t}$ is the maximum air temperature observed at a weather station, W (station 1, 2, 3, or 4), on day t.

Geostatistical Network Model of MWMST

Our data were spatially autocorrelated due to the relatively large number of observations collected within a single catchment. Analyses of spatially autocorrelated data require spatial statistical methods because the assumption of independence is violated, and thus many conventional statistical methods are inappropriate (Legendre 1993). Therefore, we built the stream–temperature model with a geostatistical method designed to represent the spatial configuration, longitudinal connectivity, and flow volume and direction in stream networks (Peterson & Ver Hoef 2010; Ver Hoef & Peterson 2010). These models are based on moving averages, which permit valid autocovariances to be generated on the basis of a variety of hydrologic, or watercourse (Olden et al. 2001; Ganio et al. 2005), relations. For example, when water flows from an upstream location to a downstream location, the locations are considered flow-connected, whereas 2 locations that are in the same network (i.e., they share a com-

mon outlet somewhere downstream) but do not share flow are considered flow unconnected. The form of the equation is similar to a standard linear model, $\mathbf{y} = \mathbf{X}\beta + \varepsilon$, where the matrix $\mathbf{X}$ explains vector $\mathbf{y}$ on the basis of parameters β. In the standard linear model, random errors are contained in the vector ε. In the geostatistical network model (Supporting Information), the error term can be expanded, $\mathbf{y} = \mathbf{X}\beta + \mathbf{z} + \varepsilon$, where $\mathbf{z}$ is spatially autocorrelated random variables (Ver Hoef & Peterson 2010).

We implemented the geostatistical model selection process in 2 steps. First, we selected the fixed effects for the final model by comparing candidate model performance with conventional spatial autocovariance models (on the basis of weight of evidence measured with Akaike's information criterion [AIC]) (Buckland et al. 1997; Burnham & Anderson 2002) with a geostatistical network model. Second, we used root mean square prediction error (RMSPE) to compare spatial autocovariance models (Ver Hoef & Peterson 2010). In total, we fit 7 geostatistical models in the SSN package (Ver Hoef et al. 2012) in R statistical software (R Development Core Team 2010). We fit spatial autocovariance models to pairwise watercourse distances and spatial weights that we calculated with 2 ArcGIS toolsets: functional linkage of water basins and streams (FLoWS) (Theobald et al. 2006) and spatial tools for the analysis of river systems (STARS) (Peterson & Ver Hoef 2012). We based the spatial weights on modeled annual average flow (Jobson 1996). To select the most accurate spatial autocovariance models, we generated leave-one-out cross-validation predictions for each model and calculated RMSPE and the squared Pearson correlation (r^2) between the observations and the predictions. The model with the most accurate predictions, represented by the lowest RMSPE, was selected as the final model.

Future Projections

We used the final model and projected future air temperature (MWMAT$_{\text{GCM}}$, where GCM is a general circulation model used to predict future air temperature) to generate 3 sets of MWMST predictions. We computed future air temperatures from 3 different GCM estimates. We used a midrange greenhouse gas emissions scenario (A1B) (Solomon & Intergovernmental Panel on Climate
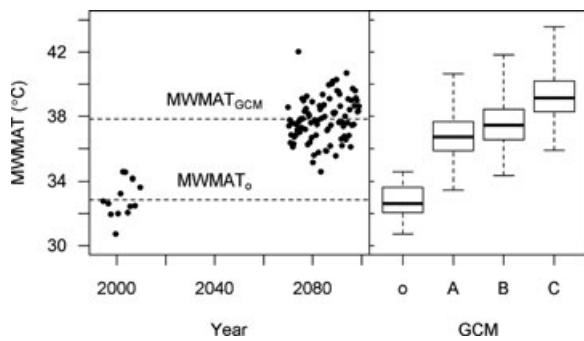
Figure 1. Historical (o) and projected future (GCMs [general circulation models] A, B, and C) variability of maximum weekly maximum air temperature (MWMAT). Boxplots indicate the median, minimum, maximum, and interquartile range of historical and future MWMAT (A, low [ECHAM5/MPI-O]; B, medium [CNRM-CM3]; C, high [UKMO-HadCM3]). The MWMAT$_{GCM}$ appears to vary more frequently than annually because the hybrid delta method (Hamlet et al. 2010) extracts the historical pattern of variability from the period 1915–2006 (i.e., 91 years of variability over the period 2070–2099).

Change 2007) that predicts a decline in energy production from fossil fuels and an asymptotic concentration (approximately 600 ppm) of atmospheric CO_2 by the year 2100. We chose the following GCMs on the basis of their forecasting performance in the Pacific Northwest (Hamlet et al. 2010): ECHAM5/MPI-O, CNRM-CM3, and UKMO-HadCM3. We also wanted to compare future MWMST with present conditions. Thus, we calculated a baseline MWMAT over the full observation period, MWMAT$_o$ (average of all MWMAT observations from 1993 to 2009), and used that estimate to predict MWMST under typical MWMAT conditions (Fig. 1). To calculate MWMAT$_{GCM}$, we used climate projections that were downscaled in dimensions of space and time (Mote & Salathe 2010). These data were downscaled from the typical GCM cell resolution of 1–3° (roughly 100–300 km at ±45° latitude) to a 1/16th° resolution (6 km at ±45° latitude) and temporally downscaled from 1 month to daily temporal resolution with a hybrid delta approach (Hamlet et al. 2010). For each of the 4 1/16th° cells closest to the 4 weather stations in the John Day basin (Supporting Information), we calculated a mean value of MWMAT across all years within the anticipated range of future variability. We then averaged the 4 mean values to describe the MWMAT in the entire basin for an average year expected for 2070–2099.

For each of the 3 values of MWMAT$_{GCM}$ that corresponded to the 3 GCM estimates for 2070–2099, we calculated the loss of habitat for each of the 3 species on the basis of estimated thermal tolerances. We used a thermal tolerance of 24.0 °C MWMST for Chinook salmon and

rainbow trout (Eaton et al. 1995). This temperature is the 95th percentile for a Gaussian probability density function that corresponds to the mean, standard deviation, and sample size of MWMST for the sample set of observations for the species. We used methods from Eaton et al. (1995) and a sample set of 237 bull trout observations corresponding to values of MWMST collected across the Columbia River Basin (Rieman & Chandler 1999) to estimate a thermal tolerance of 14.4 °C for bull trout. To ensure that we did not overestimate thermal habitat loss, we subtracted the length of intermittent stream (Environmental Protection Agency and Horizon Systems 2008; Oregon Department of Forestry 2011) and unoccupied habitat that overlapped with the predicted habitat that was lost due to climate change. Unoccupied habitat was delineated by excluding streams above physical barriers (Hein et al. 2011) and referring to existing fish distribution maps (Oregon Department of Fish and Wildlife 2010). We reported these estimates as both length and volume of stream habitat. We calculated volume by multiplying length of habitat by modeled annual average flow (Jobson 1996) and then dividing by modeled annual average velocity (Jobson 1996).

Results

Geostatistical Network Model

The network model that was most strongly supported by the data included log-transformed CRSE and MWMAT, which were both positively related to MWMST (Table 1):

$$MWMST = -13.2 + 1.4 * \log(CRSE)$$
$$+ 0.6 * MWMAT + \mathbf{z} + \varepsilon, \quad (4)$$

where $\mathbf{z}$ contains spatially autocorrelated random variables and ε contains random error. Model results and comparisons are provided in Supporting Information. Both explanatory variables were statistically significant ($p < 0.001$). Of the total variance explained by the model ($r^2 = 0.84$), the fixed effects (i.e., CRSE and MWMAT) explained 71% and the spatial autocovariance model explained 13%. The model that produced the most accurate predictions on the basis of the lowest RMSPE (1.46 for the final model) included the linear-with-sill tail-down, spherical tail-up, and spherical Euclidean autocovariance models. Of the total variance explained by the spatial autocovariance model, the Euclidean spatial component explained 5.0%, tail-up explained 2.9%, tail-down explained 2.2%, and the "nugget effect" (autocorrelation present at zero distance) explained 2.9% (Ver Hoef & Peterson 2010).

The MWMST was coolest (modeled 8.2 °C, recorded 9.2 °C) in high-elevation tributaries of the John Day River and warmest (modeled 28.4 °C, recorded 28.5 °C) in the lower reaches of the north and middle forks
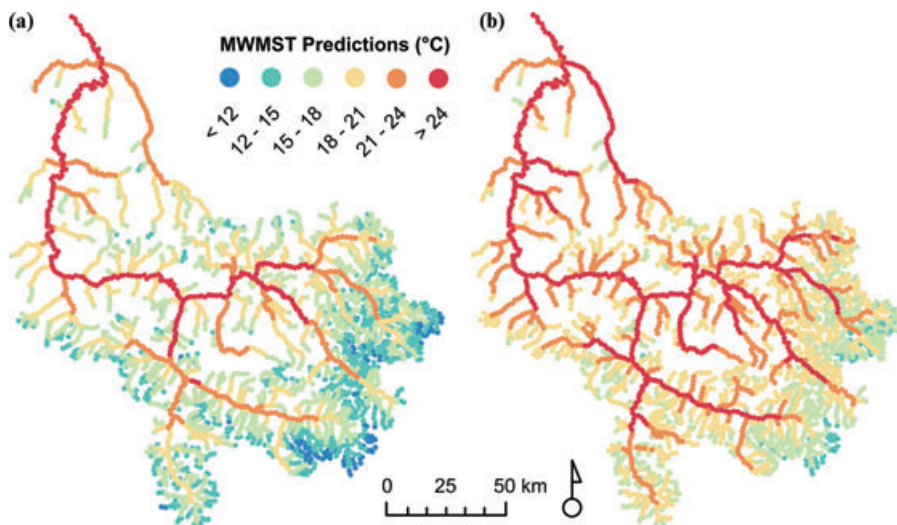
and throughout the lower main stem (Fig. 2a). Between warm and cool summers, MWMST shifted a maximum of 2.3 °C for 1993–2009 at any given location (shift of 3.8 °C MWMAT). The warmest class of modeled stream temperature (>24 °C MWMST) (Fig. 2a) was in stream reaches above the thermal tolerance for rainbow trout and Chinook salmon for an average year between 1993 and 2009.

Projecting Climate-Driven Changes in Thermal Habitat

The $MWMAT_{GCM}$ increased by an estimated 5.0 °C (on the basis of a 3-GCM ensemble average) by 2070–2099. The geostatistical network model predicted this change in air temperature would result in a change in stream temperature of 3.0 °C MWMST (Fig. 2b). The main-stem reaches of the John Day River lost the most thermal habitat because their thermal gradients were gradual (i.e., small changes in stream temperature can cause dramatic losses of thermal habitat as shown by the shift of the warmest MWMST class along the main stem and north and middle forks in Fig. 2). By comparison, headwater reaches were projected to lose less thermal habitat (i.e., MWMST analogues were closer in headwater streams).

The length of thermal habitat for rainbow trout was estimated to decline the most (332–1430 km) for anadromous rainbow trout. Resident rainbow trout habitat was more extensive, but results specific to these fish are not reported here. The length of thermal habitat for bull trout was estimated to decline the least (102–154 km). However, as a percentage of the length of current thermal habitat, rainbow trout habitat was estimated to decline the least (10–43%) compared with bull trout (66–100%) because the present-day range of bull trout is restricted. A similar pattern resulted from calculating change in the volume of thermal habitat. However, the percent loss of thermal habitat by volume for all GCMs and salmonid species was markedly higher than the percent loss of thermal habitat by length. Thus, the proportion of pre-

dicted habitat loss in high-volume reaches was greater than low-volume headwater reaches.

The volume of thermal habitat in upstream reaches was small compared with that which would be lost due to unsuitable temperatures in high-volume downstream reaches (Fig. 3). Calculations of relative volume lost were 34%, 50%, and 7% higher than calculations of length lost for Chinook salmon, rainbow trout, and bull trout, respectively (Fig. 4). This pattern was more apparent when we disaggregated projected habitat losses into main-stem and tributary reaches (Fig. 4). On the upper main stem, the loss of habitat by volume for rainbow trout increased by a factor of 0.5 relative to the loss of habitat by length and increased by a factor of 4.0 in tributaries (Table 2). Results for north fork rainbow trout were similarly sensitive to unit of measure; loss of thermal habitat increased by a factor of 0.6 in main-stem reaches and by 2.4 in tributaries (Table 2).

Discussion

Climate change will likely have large negative effects on cold-water fish species in many parts of the world (Poff et al. 2002; Heino et al. 2009). Our stream-temperature model projected losses of thermal habitat from 10% to 100%, depending on the species, climate change projection, and unit of measure. Eaton and Scheller (1996) used the same thermal-tolerance measure we used and a climate change scenario in which atmospheric CO_2 concentrations double, and estimated that thermal habitat declined approximately 50% for cool and cold-water fish species across the conterminous United States. Steen et al. (2010) modeled land-use and climate change effects on fish assemblages in the Muskegon River, Michigan (U.S.A.), and estimated large range expansions of warm-water species (up to 276%) and large range contractions of cold-water species (likely extirpation of brook trout
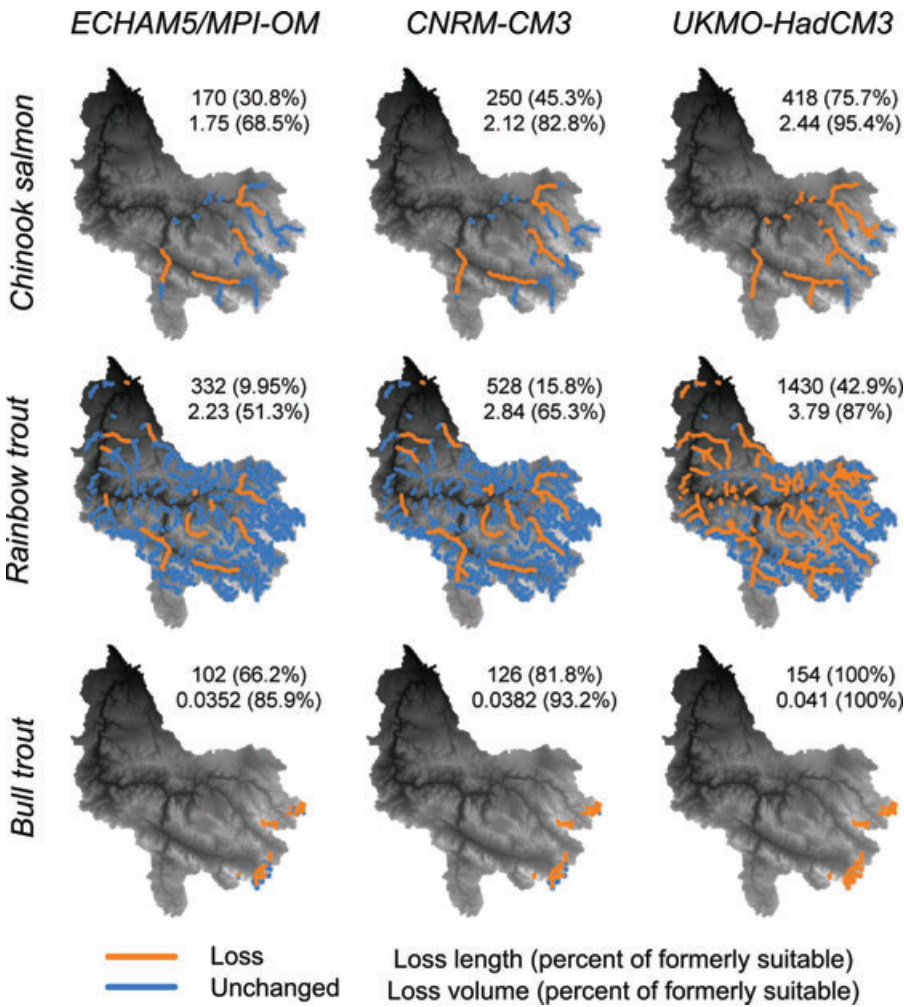
Figure 3. Projected loss of thermal habitat in the John Day River network by 2070–2099 under the A1B greenhouse gas emissions scenario by general circulation model (ECHAM5/MPI-O, CNRM-CM3, and UKMO-HadCM3) and species. Length of habitat loss (top number set) is reported in kilometers and volume of habitat loss (bottom number set) is in millions of cubic meters.

and 80% decline in rainbow trout) over the next century. Similarly, Battin et al. (2007) linked climate, land use, and population models for the salmon in the Snohomish River basin, Washington, and predicted up to 91% of salmon returns falling below a low-abundance threshold (identi-fied by the Snohomish River Basin Salmon Conservation Plan) by 2050.

Results of previous research on losses of salmonid habi-tat due to present-day warming are consistent with our results. For example, catch rates for brown trout (*Salmo*
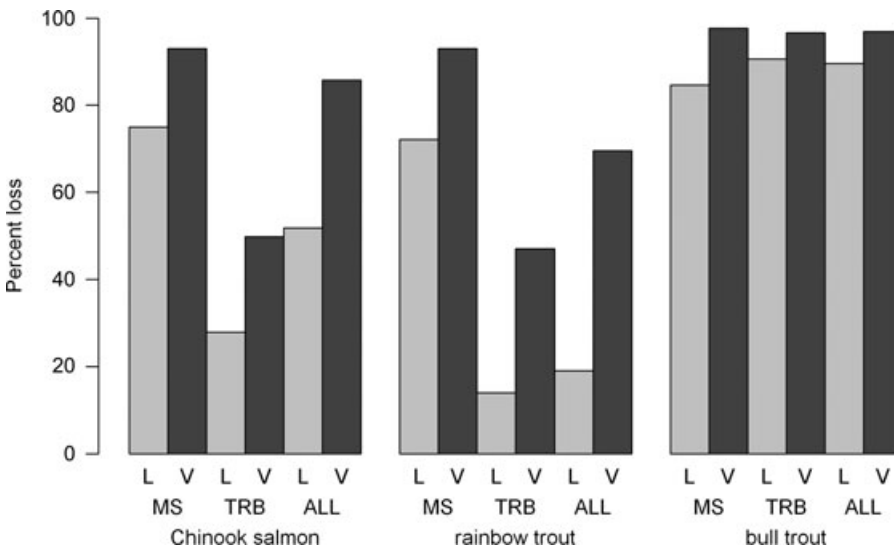

Figure 4. Percent historical thermal habitat projected to be lost for 3 species by length (L) and volume (V) within main-stem reaches (MS), tributaries (TRB), and MS and TRB combined (ALL) throughout the John Day basin for an average year (on the basis of maximum weekly maximum air temperature across all years between 2070 and 2099). The general circulation models (GCM) on which the estimates are based are an average of the 3 GCMs in this study (ECHAM5/MPI-O, CNRM-CM3, and UKMO-HadCM3).

Table 2. Percent loss of thermal habitat in the John Day River by species, channel size, subbasin, and unit of measure (i.e., length and volume) projected by 2100 (an average year during the period 2070–2099).

| Species | Channel size[a] | Lower main stem | | Middle fork | | North fork | | South fork | | Upper main stem | |
		% loss (length)	% loss (volume)	% loss (length)	% loss (volume)	% loss (length)	% loss (volume)	% loss (length)	% loss (volume)	% loss (length)	% loss (volume)
Chinook salmon											
	MS	–	–	90	97	60	88	100	100	67	92
	TRB	–	–	13	24	44	62	–	–	5	8
	ALL	–	–	45	88	50	78	100	100	47	86
Rainbow trout											
	MS	–	–	91	97	56	87	100	100	63	92
	TRB	26	57	13	41	14	48	7	33	7	34
	ALL	26	57	22	76	17	65	26	88	13	72
Bull trout											
	MS	–	–	–	–	80	96	–	–	88	98
	TRB	–	–	100	100	100	100	–	–	80	93
	ALL	–	–	100	100	97	99	–	–	82	95

[a]*Abbreviations: MS, main stem; TRB, tributary; ALL, aggregated.*
[b]*Projections are based on averaged temperature projections from 3 general circulation models run for a midrange greenhouse gas emissions scenario. When no data exist (e.g., most of the lower main stem for most species), no thermal habitat exists during the summer.*

trutta) decreased by 67% from 1978 to 2002 in low-elevation streams in the Swiss Alps due to an increase in the incidence of temperature-dependent proliferative kidney disease (Hari et al. 2006). In a Welsh river, abundances of brown trout and Atlantic salmon (*Salmo salar*) declined by 50% and 67%, respectively, between 1985 and 2004, and the decline was likely due to hotter, drier summers (Clews et al. 2010). The authors of these studies did not account for spatial autocorrelation in stream networks. Isaak et al. (2010) used a network geostatistical model to predict present-day rates of warming of summer stream temperatures in the Boise River basin, Idaho (U.S.A.), which is hydrologically similar to the north and middle forks of the John Day River. On the basis of increases in stream temperature resulting from climate change and fire, they found an 11–22% loss of habitat length for bull trout from 1993 to 2006 (rainbow trout estimates ranged from 6% gain to 2% loss).

We acknowledge our model's potential limitations. The thermal tolerances we used described approximately the spatially extensive occurrences of each species, and there are potential incongruences between the scale at which thermal tolerances were derived and the scale at which stream temperatures were measured and modeled. Thermal tolerances for rainbow trout and Chinook salmon were derived from a national database, and the thermal tolerance for bull trout was derived from records from the Columbia River basin. Thus, each species may be more or less sensitive to finer resolution variation of thermal habitat (e.g., cold-water upwelling, thermal stratification in deep pools) than could be incorporated into our model. Finer resolution information on thermal tolerances could be obtained by applying confidence intervals reported in Eaton et al. (1995), comparing range esti-

mates to spatially continuous observations of fish (Torgersen et al. 2006), and investigating the role of thermal refugia in habitat selection (Torgersen et al. 1999).

Rainbow trout and Chinook salmon are expected to be substantially affected by increasing temperatures, but not to the same degree as bull trout, which require colder temperatures (Rieman & Chandler 1999). Although our results show the likely persistence of rainbow trout and Chinook salmon, their habitat will likely be greatly reduced within the John Day basin. Conservation and restoration-based management, including stream and riparian restoration, may help minimize the loss of thermal habitat for salmonids in the John Day River. For instance, throughout the Pacific Northwest, the loss of riparian vegetation is linked to elevated water temperatures (e.g., Li et al. 1994; Chen et al. 1998), and efforts to reestablish riparian vegetation for salmon continue (e.g., Kauffman et al. 1997; Beechie & Bolton 1999). Such efforts include the reduction of cattle grazing in riparian areas in an effort to allow woody riparian vegetation to recover, thereby providing shade that reduces stream temperature. Additionally, salmonid survival increases with increased channel complexity (Quinn & Peterson 1996); thus, increasing complexity in future habitat and upstream refugia could reduce species' stress. The most effective and cost-effective management actions rely on highly precise models and the most robust climate forecasts available. Our use of a highly accurate model of stream temperature provides data and methods for assessing the relative sensitivity of different parts of a basin to climate-induced warming, the relative vulnerability of different species within the basin, and information on where management efforts may be most effective for protecting salmonids in the future.

Acknowledgments

Supporting Information

A map of the study area (Appendix S1), table of all candidate models (Appendix S2), and description of the geostatistical model (Appendix S3) are available online. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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