Transactions of the American Fisheries Society
Published 2018. This article is a U.S. Government work and is in the public domain in the USA
ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1002/tafs.10059

ARTICLE

Global Warming of Salmon and Trout Rivers in the Northwestern U.S.: Road to Ruin or Path Through Purgatory?

Daniel J. Isaak,* Charles H. Luce, Dona L. Horan, Gwynne L. Chandler, Sherry P. Wollrab, and David E. Nagel
U.S. Forest Service, Rocky Mountain Research Station, 322 East Front Street, Suite 401, Boise, Idaho 83702, USA

Abstract

Large rivers constitute small portions of drainage networks but provide important migratory habitats and fisheries for salmon and trout when and where temperatures are sufficiently cold. Management and conservation of coldwater fishes in the current era of rapid climate change require knowing how riverine thermal environments are evolving and the potential for detrimental biological impacts. Robust estimates of warming rates, however, are lacking due to limited long-term temperature monitoring, so we compiled the best available multidecadal records and estimated trends at 391 sites in the 56,500-km river network of the northwestern USA. Warming trends were prevalent during summer and early fall months in recent 20- and 40-year periods (0.18–0.35°C per decade during 1996–2015 and 0.14–0.27°C per decade during 1976–2015), paralleled air temperature trends, and were mediated by discharge trends at regional and local levels. To illustrate the biological consequences of warming later in this century, trend estimates were used to inform selection of river temperature scenarios and assess changes in thermal exposure of adult Sockeye Salmon *Oncorhynchus nerka* migrating to four population areas as well as thermal habitat shifts for resident Brown Trout *Salmo trutta* and Rainbow Trout *O. mykiss* populations throughout the region. Future warming of 1–3°C would increase Sockeye Salmon exposure by 5–16% (3–143 degree-days) and reduce thermally suitable riverine trout habitats by 8–31% while causing their upstream shift. Effects of those changes on population persistence and fisheries are likely to be context dependent, and strategic habitat restoration or adaptation strategies could ameliorate some biological impairments, but effectiveness will be tempered by the size of rivers, high costs, and pervasiveness of thermal effects. Most salmon and trout rivers will continue to provide suitable habitats for the foreseeable future, but it also appears inevitable that some river reaches will gradually become too warm to provide traditional habitats.

Salmon and trout have been cultural icons and important food resources for millennia, are the subjects of multi-billion-dollar global commercial and recreational fisheries, and are the focus of similar investments for conservation and habitat restoration efforts where populations have declined (Mills 1989; Montgomery 2003; Rieman et al. 2015). Given their requirement for cold water (Jonsson and Jonsson 2009; Isaak et al. 2017a), the specter of global warming has spawned concerns about the vulnerability of some populations, beginning with the earliest work on climate change and aquatic environments (Meisner et al. 1988; Eaton and Scheller 1996; Keleher and Rahel 1996). Those fears are not unfounded, as climate-related environmental trends are linked to shifting distributions and range contractions (Comte and Grenouillet 2013; Eby et al. 2014; Al-Chokhachy et al. 2016), adjustments in phenology (Wedekind and Kung 2010; Martins et al. 2012), and evolutionary change (Crozier et al. 2011; Kovach et al. 2012). Documented extirpations of local populations, however, remain exceedingly rare despite the frequency of this prediction in the literature and several decades of rapid, accumulated climate change. In mountain headwater environments, populations are buffered by slow climate velocities and the presence of cold refuge

---

*Corresponding author: disaak@fs.fed.us
Received December 4, 2017; accepted March 14, 2018

habitats immediately upstream (Isaak et al. 2015, 2016a). In downstream riverine environments, where popular sport fisheries and critical migratory habitats often occur, extensive coldwater areas may be absent (Torgersen et al. 1999; Fullerton et al., in press), so fish adjust during thermally stressful periods by aggregating into cool microrefugia (Ebersole et al. 2001; Keefer et al. 2009; Dugdale et al. 2016) or by altering their migration timing (Goneia et al. 2006; Crozier et al. 2011). Doing so increases the risk of pre-spawn mortality for anadromous species (Rand et al. 2006; Crozier et al. 2008) and may foreshadow locations where range contractions could occur for resident species or life stages if temperatures come to chronically exceed physiological tolerances.

The prospect of warmer coldwater fish environments has stimulated much effort to predict where and whether historical habitats will remain in the future. Forecasts of stream and river temperature increases span a range of 1–7°C (Morrison et al. 2002; Mohseni et al. 2003; Cristea and Burges 2010; Mantua et al. 2010; Wu et al. 2012; Null et al. 2013; Isaak et al. 2017b), with the specifics contingent on the warming scenario, forecast length, seasonal period, model construct, and stream sensitivity to climate forcing (Webb et al. 2008; Hannah and Garner 2015). However, climate warming is a relatively gradual process, so estimates of contemporary warming rates are also useful for gauging the plausibility of future forecasts and for calibrating bioenergetic models or species distribution models used in risk assessments. Moreover, despite frequent predictions about accelerating or decelerating climate change (Easterling and Wehner 2009), Earth's warming rate has been remarkably constant since the 1970s (Rahmstorf et al. 2017), so extrapolation of historical trends may provide some basis for forecasting, at least through midcentury, when most climate model projections are broadly similar (IPCC 2013). Despite the importance of trend estimates and emerging evidence that rivers and streams show global warming patterns (Morrison et al. 2002; Webb and Nobilis 2007; Kaushal et al. 2010; Isaak et al. 2012; Chen et al. 2016), robust descriptions of regional trends based on numerous long-term monitoring records are rare (but see Orr et al. 2014 and Arora et al. 2016) due to the inadequacies of historical monitoring networks and protocols (Orr et al. 2015).

One place in which that dearth of information is critical is the northwestern USA (hereafter, "Northwest"; Figure 1), where world-famous trout and salmon fisheries exist in parallel with broad declines for some species and stocks (Nehlsen et al. 1991). Such declines have led to federal protections under the Endangered Species Act, development of an extensive hatchery system, and habitat restoration efforts throughout hundreds of rivers and streams (Ruckelshaus et al. 2002; Rieman et al. 2015). Concerns about temperature effects on coldwater species are longstanding within the Northwest because both natural gradients and anthropogenic factors related to habitat degradation impose thermal limits on salmonid distributions (McCullough et al. 2009). Those concerns have grown in recent years as the effects of climate change increasingly manifest through warming air temperatures (ATs; Abatzoglou et al. 2014; National Climate Assessment 2014), decreasing snow accumulations (Mote et al. 2005; Knowles et al. 2006), decreasing stream runoff (Luce and Holden 2009; Kormos et al. 2016), and increasing wildfires (Littell et al. 2009). In some years, heat-induced closures of trout fisheries or salmon mass mortalities occur (Lynch and Risley 2003; Cooke et al. 2004; Bowerman et al. 2016), although no systematic analysis has been conducted to determine whether these events are increasing relative to historical averages.

The Northwest's best long-term river temperature record exists at Bonneville Dam on the Columbia River and shows warming trends (Petersen and Kitchell 2001), especially during the summer and fall, since its establishment in 1939 (Figure 2). In 2015, record-low snowpacks and summer flows coincided with warm summer ATs (Marlier et al. 2017) such that river temperatures were 2.4 SDs higher than the period average and caused catastrophic mortalities of migrating adult salmon and widespread closures of fishing seasons across the region (Columbia Basin Bulletin 2015). Despite obvious trends in the Bonneville Dam temperature record, its representativeness for regional rivers is unclear because the start date coincides with the construction of several large dams from 1938 to 1975 that transformed the Columbia River and its main tributary, the Snake River, into a series of run-of-the river reservoirs. Recent development of the NorWeST temperature database with information from dozens of agencies and thousands of stream and river sites across the region afforded the opportunity to explore river temperature trends more broadly (Isaak et al. 2017b), so in the present study, we mined the database to extract the best long-term records and describe changes during recent decades. To understand river temperature trends, we examined associations with contemporaneous trends at AT monitoring sites and river discharge (*Q*) gauges. Estimates of warming rates during the thermally stressful summer months were then used with high-resolution river temperature scenarios developed previously (Isaak et al. 2016b) to assess potential biological effects later this century. For the assessments, shifts were described in the extent of thermally suitable habitats for resident populations of Rainbow Trout *Oncorhynchus mykiss* and Brown Trout *Salmo trutta* because these species are widespread in the region and support popular fisheries. We also examined changes in the thermal exposure of adult Sockeye Salmon *O. nerka* migrating to four representative population areas because this species is of conservation concern,

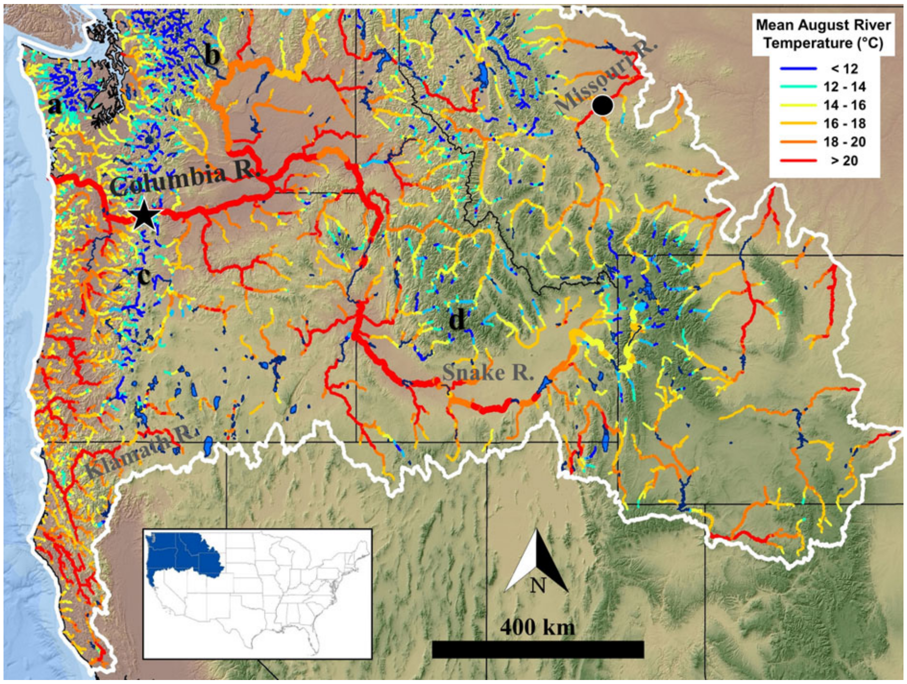

FIGURE 1. Study area extent, showing 56,500 km of rivers classified by mean August temperatures for a baseline climate period of 1993–2011. Black star denotes Bonneville Dam, black circle denotes the Great Falls of the Missouri River, and letters a–d show natal habitat locations of Sockeye Salmon populations discussed in the text (a = Lake Quinault, Washington; b = Lake Wenatchee, Washington; c = Suttle Lake, Oregon; d = Redfish Lake, Idaho).

migrates during peak summer temperatures, and shows evidence of temperature-related mortality in warm years (Cooke et al. 2004; Keefer et al. 2008). Although neither example was meant to be definitive, each illustrates with newfound precision the types of biothermal climate change effects that are frequently assessed in the aquatic ecology literature (Comte et al. 2013) and are likely to manifest later this century as coldwater fishes are forced to navigate warmer rivers.

METHODS

Study area.— The Northwest as circumscribed here encompasses 1,157,000 km^2, a broad elevation range (0–4,200 m), and is topographically complex (Figure 1). Climate is characterized by cold, wet winters with moderate to heavy snow accumulations at high elevations and by hot, dry summers. Climate cycles associated with the Pacific Decadal Oscillation (periodicity of 20–30 years; Mantua et al. 1997) and El Niño–Southern Oscillation (periodicity of 2–5 years) dampen or exacerbate seasonal patterns of precipitation and ATs (McCabe and Dettinger 1999; Mote et al. 2003). In high-elevation rivers, hydrographs are typical of snowmelt runoff systems, with high flows during spring and early summer and low flows during late summer, fall, and winter. In lower-elevation basins near the Pacific Ocean, hydrographs are rainfall dominated, with peak flows during the wet season in late fall and winter.

Northwest rivers provide habitat for salmon and trout species that include five Pacific salmon (Chinook Salmon *O. tshawytscha*, Coho Salmon *O. kisutch*, Chum Salmon *O. keta*, Pink Salmon *O. gorbuscha*, and Sockeye Salmon); Rainbow Trout and their anadromous variant, the steelhead; Bull Trout *Salvelinus confluentus*; Dolly Varden *S. malma*; and Cutthroat Trout *O. clarkii*. The native ranges of those species encompass most of the western half of the study area, but further east only nonanadromous Bull Trout and Cutthroat Trout are native. Large-bodied, riverine forms of Cutthroat Trout were once common in eastern rivers as far downstream as the Great Falls of the Missouri River (Figure 1; Lewis and Clark 1805) when the regional climate was cooler (Mann et al. 2009). During the late 19th century and much of the 20th century, however, Brown Trout and Rainbow Trout were stocked extensively throughout the Northwest and now comprise the majority of trout populations in most of the region's rivers (McIntosh et al. 2011; Young et al. 2016).

Human population densities in the Northwest are relatively low, but settlement and agricultural development focused disproportionately on river valleys to take advantage of consistent summer water supplies and fertile floodplains (Naiman et al. 2012). Anglo-American development starting in the 1800s included channelization, levy systems

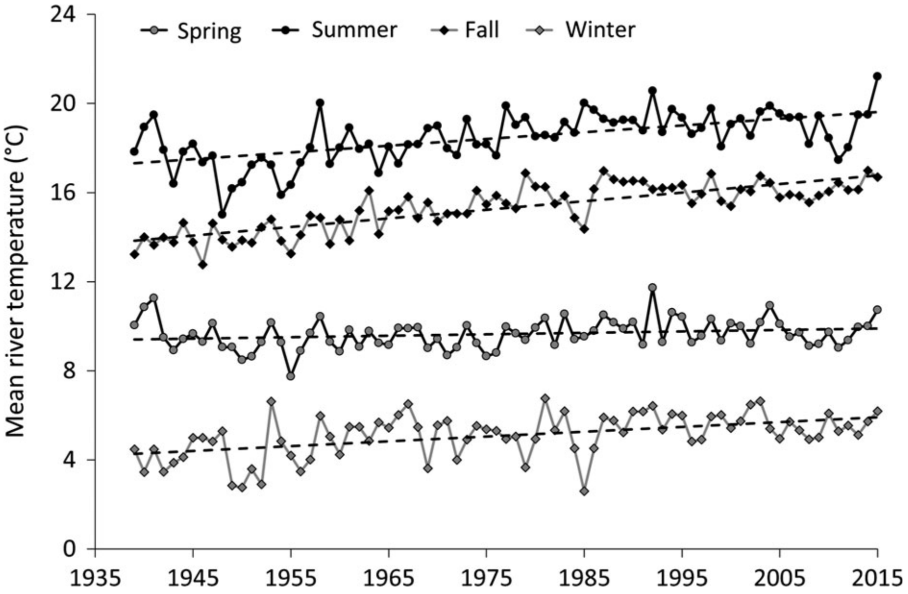

FIGURE 2. Trends in seasonal temperatures of the Columbia River upstream of Bonneville Dam at river kilometer 236 for 1939–2015. Temperatures were recorded by the U.S. Army Corps of Engineers at a powerhouse turbine intake until 1997 and in the dam forebay thereafter. The spring period was March–May, summer was June–August, fall was September–November, and winter was December–February.

that severed connections between rivers and floodplains, groundwater pumping for irrigation, removal or degradation of riparian vegetation adjacent to rivers, and dam construction for power production, flood control, and barging (Wohl et al. 2017). Anthropogenic effects on Northwest rivers are undeniable, but significant new alterations that affect temperatures probably abated several decades ago with stricter environmental regulations and the cessation of major dam projects, road building, and timber harvest adjacent to rivers. Many of the region's rivers remain free-flowing, and some drain extensive roadless wilderness areas that retain much of their natural character, especially at higher elevations where most of the land is publicly owned and federally administered by the U.S. Forest Service and the National Park Service for a variety of land use, recreational, and conservation purposes.

River network and temperature data set.— Rivers within the Northwest were delineated using the 1:100,000-scale National Hydrography Dataset (http://www.horizon-systems.com/NHDPlus/index.php), which was attributed with mean annual flow values using data downloaded from the Western U.S. Stream Flow Metrics Web site (http://www.fs.fed.us/rm/boise/AWAE/projects/modeled_stream_flow_metrics.shtml). There is no formal size threshold that distinguishes between a river and a stream, so we applied a value of 3.0-m^3/s mean annual flow (~10-m summer low-flow wetted width) based on our observation that rivers at least that large encompass most of the popular trout fisheries and salmon migratory habitats in the Northwest. Reaches with flows less than 3.0 m^3/s were removed from the network, which left 56,500 km of rivers in the study area. Fifty-five percent of that network (31,300 km) flows through private lands, whereas the remainder is publicly administered (Protected Areas Database for the United States; Gergely and McKerrow 2016). Twenty-three percent of the network (12,800 km) was flow regulated and downstream of at least one significant dam (i.e., >40 m in height) and storage reservoir. The remainder of the network was considered to be unregulated, although small dams occur somewhere in most of the larger basins. To visualize spatial heterogeneity in river temperatures, a NorWeST scenario representing a baseline historical period for the month of August (scenario 1: 1993–2011; Isaak et al. 2016b) was downloaded from the project Web site (https://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html) and linked to the National Hydrography Dataset river reaches. The scenario was developed by fitting an accurate spatial-statistical network model ($r^2 = 0.90$; root mean square prediction error = 1.0°C) to temperature observations in the NorWeST database (Isaak et al. 2017b). Thermal heterogeneity in the river network is pronounced during the warm summer months, when mean temperatures range from 10°C to 27°C, and reflects the region's climatic and topographic diversity (Figure 1). Spatial heterogeneity decreases during cooler months because many high-elevation rivers are exposed to subzero ATs for long periods and fluctuate in a narrow range at or near 0°C.

To obtain a river temperature data set for analysis, we intersected the river network with the NorWeST database of daily temperature summaries (Chandler et al. 2016) and extracted data for sites where measurements were recorded during an individual month for 10 years or more. We summarized all daily mean temperature measurements into monthly means within years. To ensure the accuracy of monthly means, data were not used if fewer than 20 d had measurements, although the average number of days representing each month in the final data set (i.e., 30 d) was much higher. Because most of the records in the NorWeST database were collected prior to 2013, we downloaded more recent data for some river sites from online databases maintained by the U.S. Geological Survey (National Water Information System; http://waterdata.usgs.gov/nwis), U.S. Bureau of Reclamation (HydroMet; http://www.usbr.gov/pn/hydromet/), and U.S. Army Corps of Engineers (Data Access in Real Time; http://www.cbr.washington.edu/dart/metadata/hourly). In most cases, however, the data sets composing the NorWeST database had been contributed by professionals from various natural resource agencies, so these individuals were contacted to obtain the most recent years of data. All temperature records were subject to standard quality assurance/quality control measures as described elsewhere (Chandler et al. 2016).

The final temperature data set consisted of 40,684 site × year × month observations from 391 river sites (Figure 3; Supplements A and B available in the online version of this manuscript). The average record length for a site × month combination was 16 years (range = 10–39 years), and observations were skewed toward the last two decades, when monitoring became more common in the region after the advent and broad adoption of inexpensive sensors. Most records were from unregulated sites (n = 239) rather than regulated sites (n = 152), and most were from the months of July, August, and September, when access to rivers in mountainous areas is most convenient and concerns about temperature effects on coldwater fish are greatest. River temperature sites in the two flow categories occurred at similar elevations, spanned almost 2,000 m, and mostly occurred in low-gradient reaches (Table 1). However, the average size of regulated river sites (mean annual flow = 385 m^3/s; median annual flow = 78 m^3/s) was larger than that of unregulated sites (mean annual flow = 18.8 m^3/s; median annual flow = 8.1 m^3/s) because the former included the region's master rivers. Annual river temperature cycles showed a seasonal pattern typical of temperate zones, with cold winters, warm summers, and intermediate spring and fall periods (Table 2). Pairwise correlations among monthly temperature values were generally strong except for correlations between winter and summer months (Table 3).

Trend estimates.— River temperature covaries with AT (Isaak et al. 2012; Arora et al. 2016), and climate-change-induced trends in AT are physically linked to river temperature trends through net increases in downwelling longwave radiation and warmer groundwater (Kurylyk et al. 2013; Caissie and Luce 2017). To obtain a data set for describing AT trends in the Northwest; therefore, we

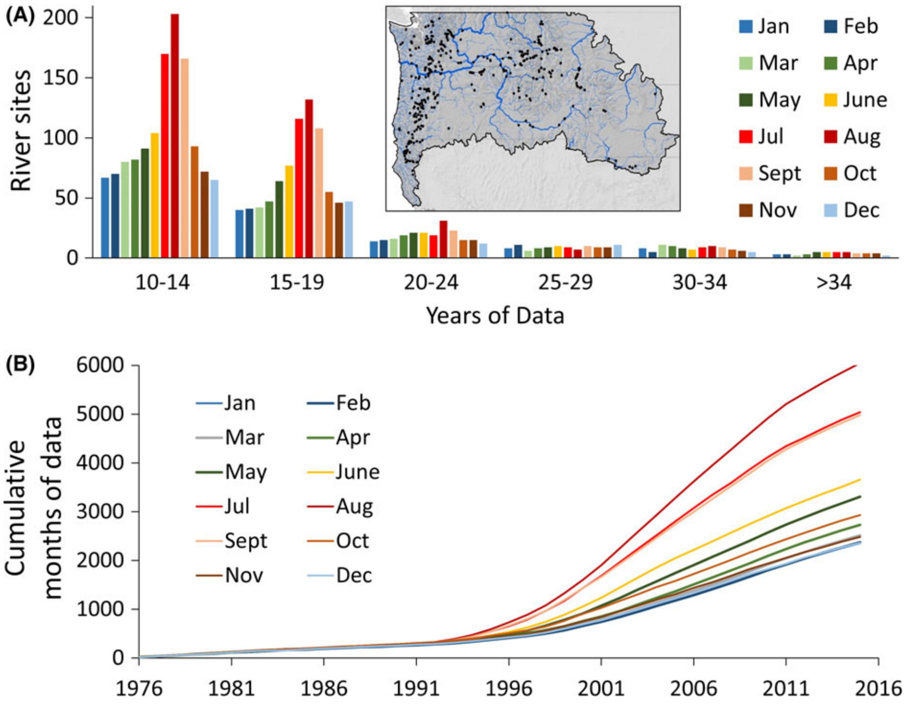

FIGURE 3. **(A)** Summary of monthly monitoring record lengths and locations of 391 river temperature sites in the northwestern USA; and **(B)** cumulative distributions of monthly monitoring data since 1976.

TABLE 1. Descriptive statistics for 391 river temperature monitoring sites in the northwestern USA.

Variable	Mean	Median	SD	Minimum	Maximum
Unregulated sites ($n = 239$)					
Elevation (m)	651	556	469	6	2,208
Drainage area (km^2)	1,194	367	2,575	56	22,706
Mean annual flow (m^3/s)	18.8	8.11	28.1	2.85	186
Reach slope (%)	1.12	0.80	1.19	0.10	7.49
Regulated sites ($n = 152$)					
Elevation (m)	608	350	590	2	1,975
Drainage area (km^2)	46,994	5,306	118,473	8	620,000
Mean annual flow (m^3/s)	385	78	1,036	3.0	7,509
Reach slope (%)	0.74	0.35	1.34	0.10	10.6

extracted records for 168 sites from the Global Historical Climate Network–Monthly online data set (http://www.ncdc.noaa.gov/ghcnm/v3.php) that spanned the 40-year period of 1976–2015. The data set is bias-corrected and homogenized to account for station relocations or changes in instrumentation and is considered to encompass the best available long-term AT records (Lawrimore et al. 2011). Months with missing values occurred for 12% of the site × year × month combinations in the extracted data set, so the records were completed using an iterative principal components analysis (PCA) imputation technique performed with the Missing Values with Multivariate Data Analysis (missMDA) package (Josse and Husson 2016) in R (R Core Team 2014). This technique uses correlations among sites and records in a data set to estimate missing values by first applying standard PCA to the incomplete data set where missing values have been replaced with column means. Data are then reconstructed from the principal components, and the initial analysis step is repeated but with missing values replaced using estimates from the reconstructed data. The process is repeated until convergence, and the missing values in the original data are ultimately replaced with estimates from the last PCA data reconstruction (Josse and Husson 2012). Covariation among the monthly AT observations at the 168 sites was strong, so the average correlation between observed AT values and those predicted by the PCA reconstructions was high ($r = 0.96$).

After imputation, decadal trends in monthly temperatures at each site were calculated as the slope parameter (multiplied by 10) from simple linear regressions of AT on year for both the 40-year period described above and a more recent 20-year period (1996–2015). Trend estimates for the longer period coincide with the globally coherent warming signal that emerged in recent decades (Rahmstorf et al. 2017) and spanned enough time to temper the effects of short-term climate cycles. Estimates for the recent 20-year period were calculated because bioclimatic linkages have been observed during this period (Copeland and Meyer 2011; Eby et al. 2014) and potential differences between short- and long-term trends are important for planning and understanding climate dynamics (Easterling and Wehner 2009).

TABLE 2. Descriptive statistics for monthly river temperatures (°C) in a data set from 391 sites used to describe climate trends in the northwestern USA.

Month	Mean	Median	SD	Minimum	Maximum
Jan	3.36	3.55	2.32	−0.78	18.8
Feb	3.76	3.73	2.33	−0.88	18.3
Mar	5.30	5.21	2.28	−0.20	17.2
Apr	7.35	7.18	2.41	0.61	20.3
May	9.82	9.76	2.97	1.96	18.9
Jun	12.8	12.5	3.49	4.00	23.4
Jul	16.4	16.3	4.00	4.62	27.3
Aug	16.5	16.4	3.68	3.89	26.9
Sep	14.0	13.7	3.22	5.18	23.2
Oct	10.3	10.1	3.20	1.97	21.4
Nov	6.31	6.51	3.04	−0.59	19.4
Dec	3.94	4.19	2.58	−0.79	17.5

Discharge mediates the relationship between river temperature and AT by dictating thermal capacity and flow velocity (Hockey et al. 1982; Gu et al. 1998). To describe regional Q trends, data were downloaded from the National Water Information System for 299 gauge sites with the most complete records from 1976 to 2015 and were summarized into monthly Q-values. Those records were missing values for 3% of site × year × month combinations, so the values were imputed using the missMDA package as described above. Of the 299 Q records, 73 were from flow-regulated sites and 226 were from sites considered to be unregulated. Flow regulation and variation in catchment hypsometry weakened the covariation among monthly Q observations, so the average correlation between observed Q-values and those predicted by the PCA reconstructions was lower ($r = 0.80$) than that for AT. Decadal trends in monthly Q

TABLE 3. Pairwise correlations (r) among monthly mean river temperatures at unregulated sites (below the diagonal) and regulated sites (above the diagonal).

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan	1.00	0.95	0.78	0.43	0.21	0.01	−0.19	−0.24	−0.08	0.34	0.72	0.88
Feb	0.98	1.00	0.89	0.55	0.33	0.13	−0.08	−0.16	−0.06	0.29	0.62	0.78
Mar	0.86	0.91	1.00	0.83	0.60	0.41	0.20	0.12	0.16	0.37	0.56	0.65
Apr	0.61	0.68	0.90	1.00	0.88	0.77	0.61	0.53	0.51	0.49	0.46	0.40
May	0.44	0.51	0.76	0.92	1.00	0.94	0.80	0.75	0.71	0.59	0.40	0.23
Jun	0.39	0.47	0.70	0.83	0.93	1.00	0.94	0.89	0.80	0.58	0.29	0.04
Jul	0.10	0.19	0.43	0.65	0.74	0.89	1.00	0.97	0.82	0.51	0.13	−0.15
Aug	0.11	0.20	0.41	0.62	0.68	0.82	0.97	1.00	0.91	0.59	0.17	−0.14
Sep	0.38	0.46	0.64	0.77	0.76	0.84	0.89	0.94	1.00	0.81	0.42	0.09
Oct	0.78	0.83	0.90	0.81	0.70	0.69	0.56	0.61	0.83	1.00	0.83	0.55
Nov	0.94	0.95	0.91	0.70	0.59	0.55	0.27	0.28	0.55	0.90	1.00	0.91
Dec	0.98	0.97	0.87	0.68	0.59	0.49	0.17	0.17	0.45	0.81	0.97	1.00

at each station were calculated from simple linear regressions of Q on year for both the 20- and 40-year periods after the records were completed.

River temperature trends were estimated in two ways: (1) directly from the original records that contained missing values and (2) after the records had been completed for the 20- and 40-year periods by imputation. Direct river temperature trend estimates were made using simple linear regressions with records that were over 75% complete such that 20-year trends were supported by a minimum of 15 years of data and 40-year trends were supported by at least 30 years of data. For the second set of estimates based on imputed river temperature records, we again used the missMDA package but only after aligning monthly river temperature records with the completed monthly AT and Q records. For example, the aligned matrices of river temperature, AT, and Q records for the month of August had a dimensionality of 40 rows (years) × 858 columns (sites). This technique enabled missing river temperature values to be predicted not just from correlations with values at other river sites but also from correlations with AT and Q-values. Correlations between observed river temperature values and those predicted by the PCA reconstructions were strong (average $r = 0.88$). Once the river temperature records were completed, decadal trends were calculated from simple linear regressions as described previously for the 20- and 40-year periods. To be conservative, trend estimates were calculated using only imputed river temperature records with r-values greater than 0.80 or records that were at least 75% complete prior to imputation. River temperature estimates derived from the imputed records were expected to be less variable than those based on the direct approach because larger numbers of sites met the completion criteria and because missing observations would not occur at the beginning or end of a record to bias trend estimates. Nonetheless, direct trend estimates were useful because they provided some validation of imputed record estimates and were based solely on observed data.

River temperature sensitivity.— The sensitivity of river temperatures (RT_{sens}) to climatic variability, often expressed as a change in river temperature divided by a change in AT (Kelleher et al. 2011; Luce et al. 2014), is an important determinant of long-term river temperature trends. To estimate monthly sensitivity values, multiple regression models were developed at an interannual time step to predict river temperatures at each site from concurrent measurements of AT and Q as in previous studies (Isaak et al. 2012; Luce et al. 2014). River temperature values in each record were matched to covariate values from the nearest AT and Q sites. The Q sites were often co-located with river temperature sites or were otherwise chosen to best represent conditions at a flow-connected downstream temperature site. Inclusion of both AT and Q in the regressions controlled for the effect of the latter to yield more precise estimates of the AT effect. Multiple regressions for RT_{sens} were developed using observed river temperature values and did not use imputed values.

Biological effects.— Northwest rivers span a broad range of thermal conditions, which act as first-order constraints to limit coldwater species to subsets of the regional network (Isaak et al. 2017a). As climate warming progresses, those constraints will shift, and we illustrate the potential biological consequences with two examples. In the first example, shifts in the distribution and extent of thermal habitat zones for Brown Trout and Rainbow Trout were examined using four NorWeST temperature scenarios for the month of August (Isaak et al. 2016b). In each scenario, river reaches were classified as suboptimally cold (<12°C mean August temperatures), optimal (12–18°C), or suboptimally warm (>18–21°C). The scenarios included a recent baseline period of 1993–2011 and three future scenarios based on simple integer additions to the baseline scenario of 1.0, 2.0, and 3.0°C. The same thermal suitability categories were used for both species and were based on thermal response curves developed previously by combining 23,000 species occurrence surveys with the NorWeST baseline scenario (Isaak et al. 2017a).

In a second example, the potential effect of warming on the thermal exposure of migrating adult Sockeye Salmon was assessed. Thermal exposure was calculated as the number of degree-days (DD) that an average fish accumulated along a river path between the ocean and a natal habitat area where spawning and juvenile rearing occur. Degree-days are commonly used for migrating salmon (Keefer and Caudill 2015; Keefer et al. 2015) to provide an index of energy expenditures and cumulative thermal stress that relates to the likelihood of migration success (Rand and Hinch 1998; Rand et al. 2006). Calculations were made using the four NorWeST scenarios described above for four population areas spread throughout the Northwest, including (1) Lake Quinault, Washington; (2) Lake Wenatchee, Washington; (3) Suttle Lake, Oregon; and (4) Redfish Lake, Idaho (Figure 1). Migration distances ranged from 54 to 1,440 km, natal areas were at elevations from 100 to 2,000 m, and routes spanned diverse thermal conditions. The cumulative DD that a Sockeye Salmon migrating back to one of the populations (i) accumulated in a river temperature scenario (j) was calculated as

$$\mathrm{DD}_{ij} = L_i \times \mathrm{RT}_{ij}/M,$$

where L_i = river length between the ocean and natal area along path i; RT_{ij} = mean daily August river temperature along path i in one of the temperature scenarios j (described above); and M = migration rate (km/d). For M, we used 50 km/d through reservoir reaches in portions of the Snake and Columbia rivers and 25 km/d in free-flowing reaches based on biotelemetry estimates (Quinn et al. 1997; Naughton et al. 2005).

RESULTS

Regional Climate Trends

Mean annual ATs at the 168 stations across the Northwest increased at the rate of 0.23°C per decade during the 20-year period of 1996–2015 and 0.27°C per decade during the 40-year period of 1976–2015 (Table 4). Variation occurred among months in trend rates (range = −0.28°C to +0.72°C per decade), although 20 of the 24 AT trends were positive and months during the summer and fall generally showed the largest warming trends. Spatial patterns in AT trends showed a range of conditions that included regional homogeneity (e.g., all sites showed warming trends), coherent divergences (e.g., eastern sites showed cooling trends, while western sites showed warming trends), and heterogeneity with no dominant patterns (Supplement C). Trend estimates for river Q at the 299 gauges indicated that mean annual flows decreased 9.3% per decade during the 20-year period and decreased 0.83% per decade in the 40-year period (Table 4). All months showed declining trends during the 20-year period, whereas declines were limited to summer and fall months during the 40-year period. Spatial patterns in Q trends sometimes showed regional coherence but were often heterogeneous (Supplement D).

River Temperature Trends and Sensitivity

Mean annual river temperatures in the Northwest increased at 0.18°C per decade for the 20-year period based on imputed records, and warming trends occurred in most months except for November, December, and January (Figure 4A). Trends estimated directly from observed records with missing values mirrored those based on imputed records but were less precise (Figure 4B). Trends based on imputed records for the 40-year period were usually smaller (average annual trend = 0.084°C per decade) than 20-year trends (Figure 4C). However, monthly warming rates during the summer and early fall for the 40-year period were two to three times higher than the annual trend (July: 0.27°C per decade; August: 0.14°C per decade; September: 0.15°C per decade). Also notable during those months was the decreased precision of trend estimates at regulated sites compared to unregulated sites, despite their similarity during other months. Local water management policies probably accounted for much of the divergence. Trend estimates obtained directly from unimputed records for the 40-year period provided negligible information due to small sample sizes and imprecision (Figure 4D). Only one or two site records were available each month for unregulated river sites, and fewer than 15 were available from regulated sites.

River temperature trends based on the imputed 40-year records are mapped for six representative months in Figure 5 (Supplement E contains maps for all months during both 20- and 40-year periods). January showed a split pattern wherein low-elevation sites near the Pacific Ocean warmed at 0.2–0.3°C per decade, while high-elevation inland sites showed few trends (Figure 5A). April and June were characteristic of the remaining months during the first half of the year, with no broadly discernable trends (Figure 5B, C). Beginning in July, however, warming trends were prevalent throughout the region and persisted into the early fall. Pronounced cooling trends appeared in July and August at approximately 20 sites downstream of large dams with deep water releases (Figure 5D, E). Regional warming trends abated later in the fall, as typified by the November map (Figure 5F).

Alignment of the monthly river temperature trends averaged across all sites with the average AT and Q trends from

TABLE 4. Trends in mean monthly air temperature and discharge (Q) for 20- and 40-year periods in the northwestern USA. Values in parentheses are SDs calculated from trends at 168 air temperature sites and 299 discharge gauges. Maps showing spatial patterns in trends among sites are provided in Supplements C and D.

	1996–2015		1976–2015	
Month	°C per decade	%Q per decade	°C per decade	%Q per decade
Jan	0.05 (0.88)	−23.1 (31.0)	0.61 (0.30)	2.6 (8.0)
Feb	0.07 (0.70)	−25.9 (30.7)	0.12 (0.20)	−4.2 (7.5)
Mar	0.62 (0.55)	−3.0 (28.6)	0.27 (0.23)	2.7 (8.5)
Apr	−0.05 (0.25)	−1.8 (19.3)	−0.09 (0.15)	2.1 (6.9)
May	0.17 (0.40)	−8.8 (16.3)	0.15 (0.19)	2.3 (7.2)
Jun	0.50 (0.24)	−5.3 (17.9)	0.13 (0.16)	3.1 (6.3)
Jul	0.42 (0.30)	−7.6 (14.7)	0.56 (0.21)	−0.9 (7.4)
Aug	0.17 (0.26)	−10.7 (14.4)	0.38 (0.15)	−4.4 (9.3)
Sep	0.55 (0.28)	−5.9 (18.3)	0.41 (0.16)	−8.5 (10.6)
Oct	0.72 (0.22)	−5.0 (19.2)	0.17 (0.15)	−0.5 (9.7)
Nov	−0.28 (0.36)	−7.9 (24.9)	0.31 (0.18)	−2.9 (13.4)
Dec	−0.21 (0.31)	−6.6 (24.5)	0.23 (0.21)	−1.4 (7.5)
Annual mean	0.23	−9.3	0.27	−0.83

Table 4 suggested that river temperatures largely paralleled AT trends (Figure 6). However, the consistency of the relationship was affected by three factors, including (1) whether the monthly Q trend was increasing or decreasing, (2) poor spatial balance and representativeness of river temperature sites across the region compared to AT and Q sites (see differences among sites in Supplements C, D, and E), and (3) changes in RT_{sens} throughout the course of a year. In the latter case, for example, the ratio of river temperature trends to AT trends for January in the 40-year period was 0.20 ([0.12°C per decade]/[0.61°C per decade]) but increased to 0.48 ([0.27°C per decade]/[0.56°C per decade]) during July (Figure 6B). Results from the RT_{sens} multiple regression models further illustrated that dynamic, showing that average sensitivities increased in the spring, remained consistent from late spring through early fall, and decreased in the fall as regional ATs and river temperatures decreased (Figure 7). Maps showing the spatial variation in RT_{sens} among sites for each month are provided in Supplement F.

Biological Effects

Of the 56,500 km of rivers in the Northwest, 50,207 km provided some level of thermal suitability for Brown Trout and Rainbow Trout in the baseline summer temperature scenario (Table 5; Figure 8; Supplement G). About 4,734 km of those rivers were suboptimally cold, with mean August temperatures less than 12°C; 30,257 km had optimal temperatures; and 15,216 km were suboptimally warm. A future river temperature increase of 1.0°C, which would occur by midcentury given historical warming rates, was predicted to cause an 8% decrease in the total length of thermally suitable river reaches to 46,230 km and declines of 18–31% under more extreme warming scenarios. The 30,257-km length of rivers with optimal temperatures where trout densities are likely to be highest decreased more rapidly—by 16% for a 1.0°C increase, by 33% for a 2.0°C increase, and by 50% for a 3.0°C increase. Not all areas were predicted to decline at similar rates, however. At the statewide scale, relatively small decreases in thermally suitable habitat were predicted for Washington's rivers, whereas the largest decreases were predicted for Oregon and northern California (Table 5). Disparities arose from interactions between the baseline river temperature conditions and their proximity to suitability thresholds. Many rivers in the northern Cascade Range of western Washington, for example, were suboptimally cold for Brown Trout and Rainbow Trout initially but were predicted to move into the suitable range in the future, which would partially offset losses in warmer reaches elsewhere in the state. Similar mitigation of future warming was rare or absent in other states where suboptimally cold rivers were less common. Nonetheless, even under the more extreme warming scenarios of 2–3°C, some rivers in small, isolated enclaves and larger subregional areas (e.g., the Greater Yellowstone Ecosystem, central Idaho, northern Cascade Range, and northwestern Montana) appeared likely to retain suitably cold temperatures for trout populations Brown Trout and Rainbow Trout (Figure 8D).

Thermal exposure among the four Sockeye Salmon populations under baseline summer temperature conditions varied considerably, from 34 DD along the short migration path in a relatively cool river for Lake Quinault fish to 920 DD along the long migration path to Redfish Lake (Figure 9). For the two most inland populations (Figure 9B, D), the DD accumulation rate decreased at

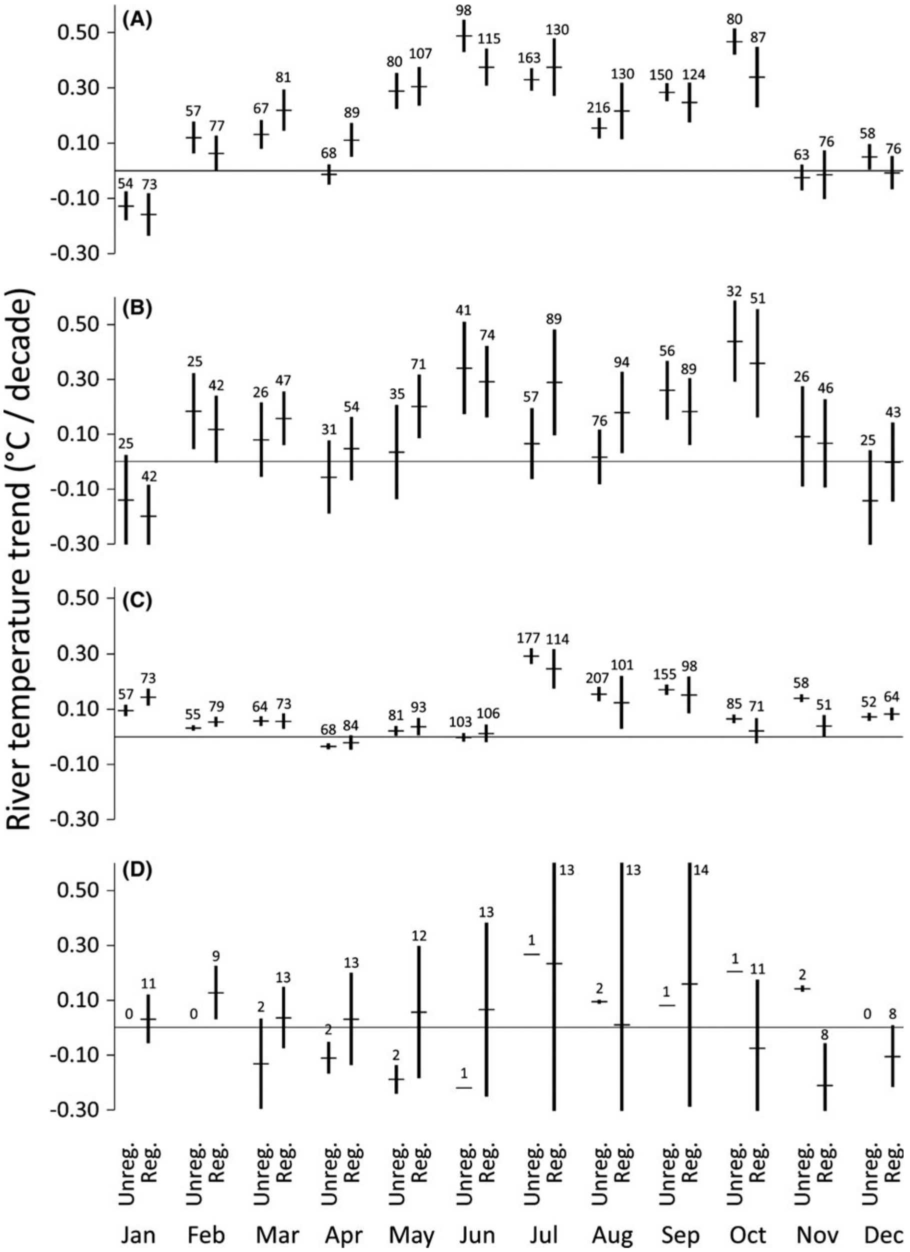

FIGURE 4. Decadal trends in mean monthly river temperatures **(A)** for the 20-year period of 1996–2015, as estimated from imputed records; **(B)** for the 20-year period, as estimated from records with at least 15 years of data; **(C)** for the 40-year period of 1976–2015, as estimated from imputed records; and **(D)** for the 40-year period, as estimated from records with at least 30 years of data (Reg = flow-regulated sites; Unreg = unregulated sites). Error bars are 95% confidence intervals; numbers above error bars are the numbers of river sites used to calculate the estimates.

river kilometer 236 after fish passed Bonneville Dam and entered the series of Columbia–Snake River reservoirs where average migration rates were assumed to be higher. Degree-day accumulation rates increased again once fish emerged from the reservoirs and migration rates slowed in free-flowing upstream river reaches. Future temperature increases of 1–3°C were predicted to increase the cumulative thermal exposure along the four population river paths by 5–16%, which equated to 3–47 DD for the 1.0°C scenario and 7–143 DD for the 3.0°C scenario. Exposure increases were proportional to the length of the river path, so populations with longer migrations incurred larger absolute DD increases.

DISCUSSION

Our results indicate that a broad pattern of seasonal warming occurred in Northwest rivers over the last two to

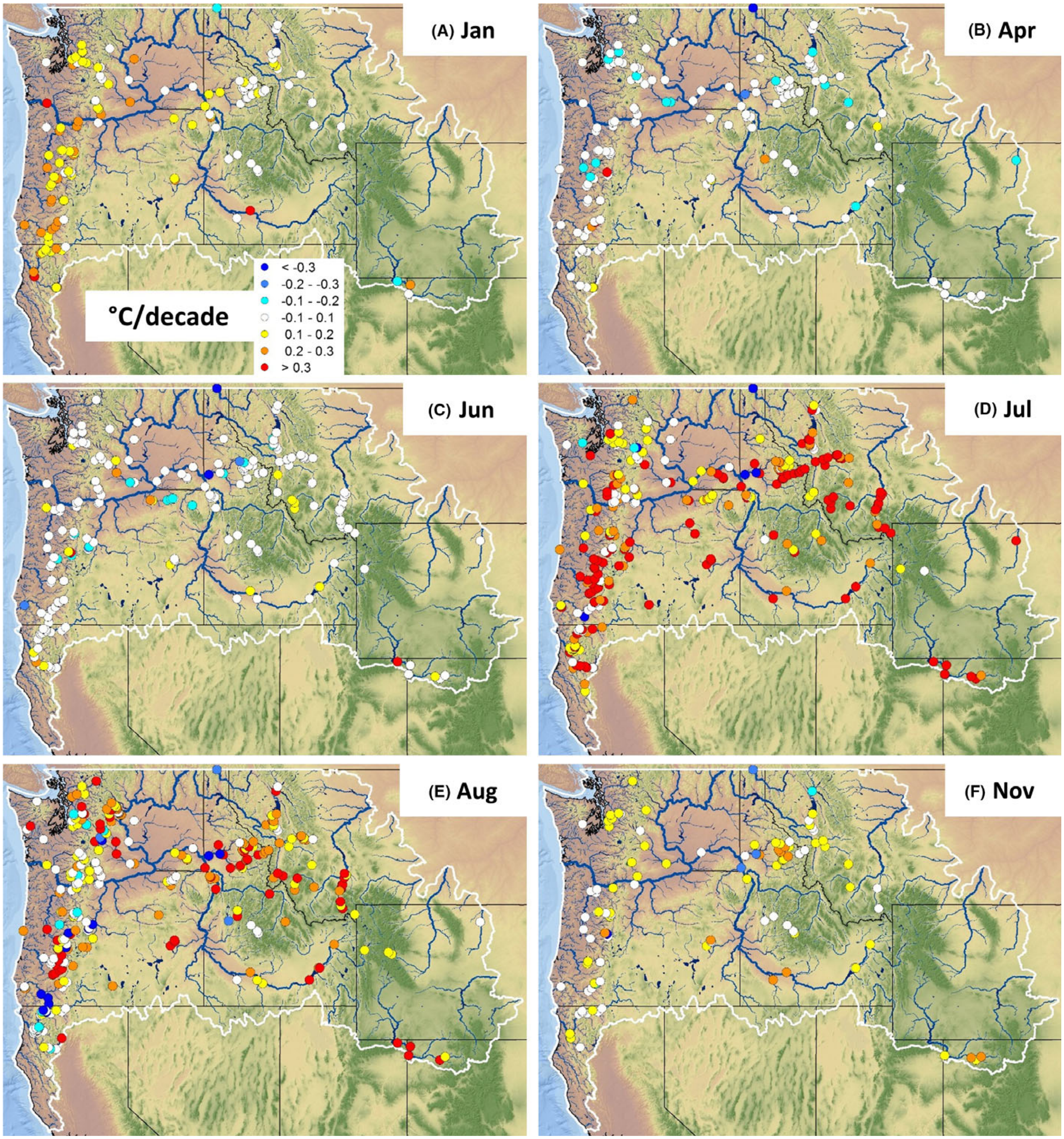

FIGURE 5. Decadal trends in river temperatures based on imputed records for the 40-year period of 1976–2015 for six representative months: **(A)** January, **(B)** April, **(C)** June, **(D)** July, **(E)** August, and **(F)** November. Detailed maps showing trends for all months during 20- and 40-year periods are provided in Supplement E.

four decades and lend generality to the Bonneville Dam temperature record. Development of run-of-the-river reservoirs probably affected that record but apparently so have regional factors associated with climate-change-induced trends of increasing AT and decreasing Q (Luce and Holden 2009; Abatzoglou et al. 2014; Kormos et al. 2016).

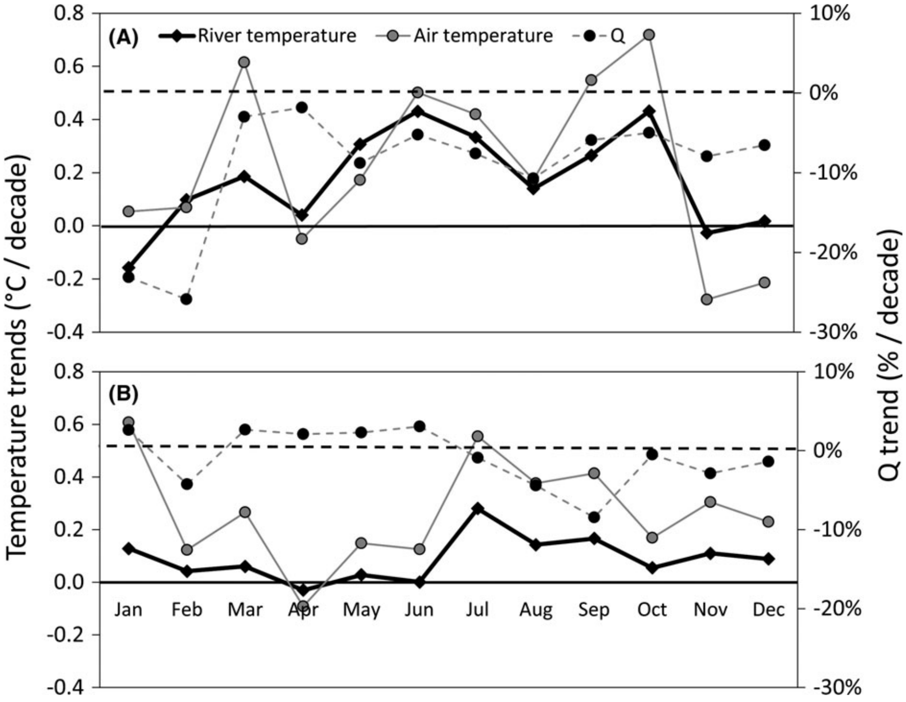

FIGURE 6. Regional average trends in mean monthly river temperature, air temperature, and discharge (*Q*) for **(A)** 20-year and **(B)** 40-year periods that ended in 2015.

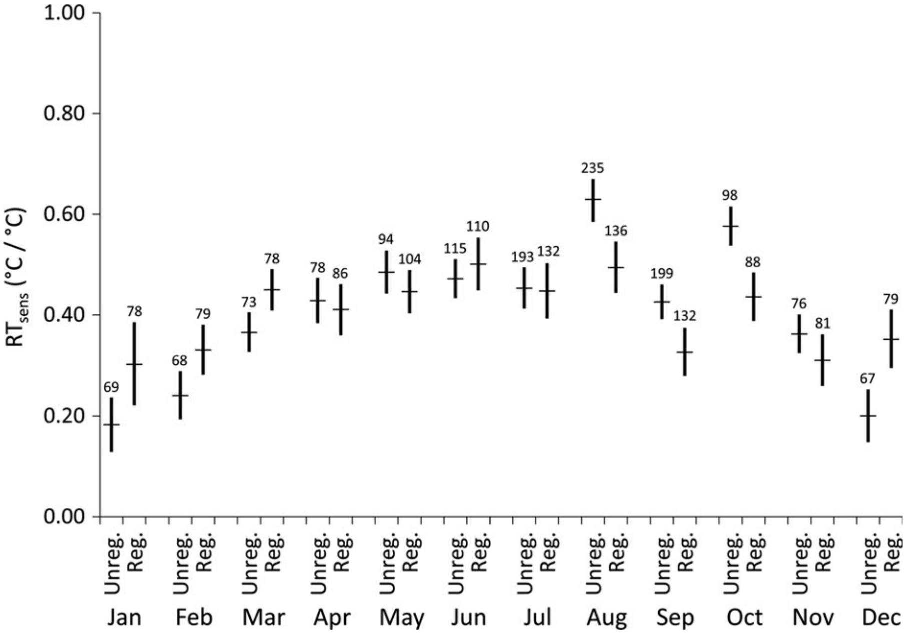

FIGURE 7. Monthly river temperature sensitivity values (RT_{sens}) estimated from multiple regression models (Reg = flow-regulated sites; Unreg = unregulated sites). Error bars are 95% confidence intervals; numbers above error bars are the number of river sites used to calculate the estimates.

Not surprisingly, river warming rates were greatest during the summer and early fall, when rivers were at baseflow and most sensitive to relatively large AT warming trends. Unfortunately, warming during that period is also most problematic for the region's salmon and trout populations due to thermal stresses associated with annual maximum

TABLE 5. Kilometers of river habitat for Brown Trout and Rainbow Trout in the northwestern USA, classified by thermal suitability in four scenarios. Values in parentheses are the percent change between the baseline and future scenario.

Scenario	Suboptimal cold (<12°C)	Optimal (12–18°C)	Suboptimal warm (18–21°C)	Total
		Northern California		
Baseline	11	1,608	1,397	3,016
1°C	2 (−78)	1,123 (−31)	1,507 (7)	2,632 (−13)
2°C	0 (−100)	590 (−64)	1,557 (11)	2,147 (−29)
3°C	0 (−100)	252 (−85)	1,367 (−3)	1,619 (−47)
		Idaho		
Baseline	439	5,622	2,695	8,756
1°C	175 (−60)	4,815 (−15)	3,109 (15)	8,099 (−8)
2°C	39 (−91)	3,837 (−32)	3,337 (23)	7,213 (−18)
3°C	12 (−98)	2,812 (−50)	3,237 (20)	6,061 (−31)
		Montana		
Baseline	867	5,295	1,714	7,876
1°C	476 (−46)	4,737 (−11)	2,359 (37)	7,572 (−4)
2°C	196 (−78)	3,878 (−27)	2,848 (66)	6,922 (−13)
3°C	86 (−91)	2,767 (−48)	3,308 (−92)	6,161 (−22)
		Oregon		
Baseline	777	6,569	4,791	12,137
1°C	461 (−41)	4,874 (−26)	5,404 (12)	10,739 (−12)
2°C	241 (−69)	3,420 (−48)	5,513 (15)	9,174 (−25)
3°C	100 (−88)	2,431 (−63)	4,814 (0)	7,345 (−40)
		Washington		
Baseline	2,267	6,689	1,895	10,851
1°C	1,393 (−39)	6,668 (−1)	2,237 (18)	10,298 (−6)
2°C	717 (−69)	6,382 (−5)	2,654 (40)	9,753 (−11)
3°C	335 (−86)	5,576 (−17)	3,014 (59)	8,925 (−18)
		Wyoming		
Baseline	315	3,607	1,956	5,878
1°C	127 (−60)	2,700 (−26)	2,649 (35)	5,476 (−7)
2°C	34 (−89)	1,911 (−47)	3,032 (54)	4,977 (−16)
3°C	12 (−97)	1,340 (−63)	2,569 (31)	8,925 (−18)
		Study area		
Baseline	4,734	30,257	15,216	50,207
1°C	2,656 (−44)	25,515 (−16)	18,058 (18)	46,230 (−8)
2°C	1,233 (−74)	20,361 (−33)	19,744 (29)	41,340 (−18)
3°C	547 (−89)	15,368 (−50)	19,045 (25)	34,960 (−31)

temperatures. Cooling trends downstream of many deep-water reservoirs indicate that water managers may already be responding to warming by releasing larger amounts of cold water to reduce maximum temperatures. Locations with the most prominent cooling trends—the Klamath River in northern California, the Yakima River in south-central Washington, and the Clearwater River in northern Idaho—are associated with critical salmon migratory corridors and are recognized within the region for their thermal management challenges (Berman and Quinn 1991; Bartholow 2005; Keefer et al. 2008). In contrast to the summer months, river temperature trends were more subtle or nonexistent during the late fall and much of the spring, when RT_{sens} and AT trends were usually smaller. An interesting exception to those monthly patterns occurred during the winter months, when low-elevation, usually coastal, river sites showed warming trends but higher-elevation sites did not. That disparity probably resulted from the insensitivity of high-elevation rivers that are exposed to subzero ATs for prolonged periods, a phenomenon that may abate at some sites in the future where local ATs begin to increase past the freezing threshold in winter.

In comparison to the long-term trends observed in other regions with extensive river temperature monitoring, the mean annual warming rate of Northwest rivers was

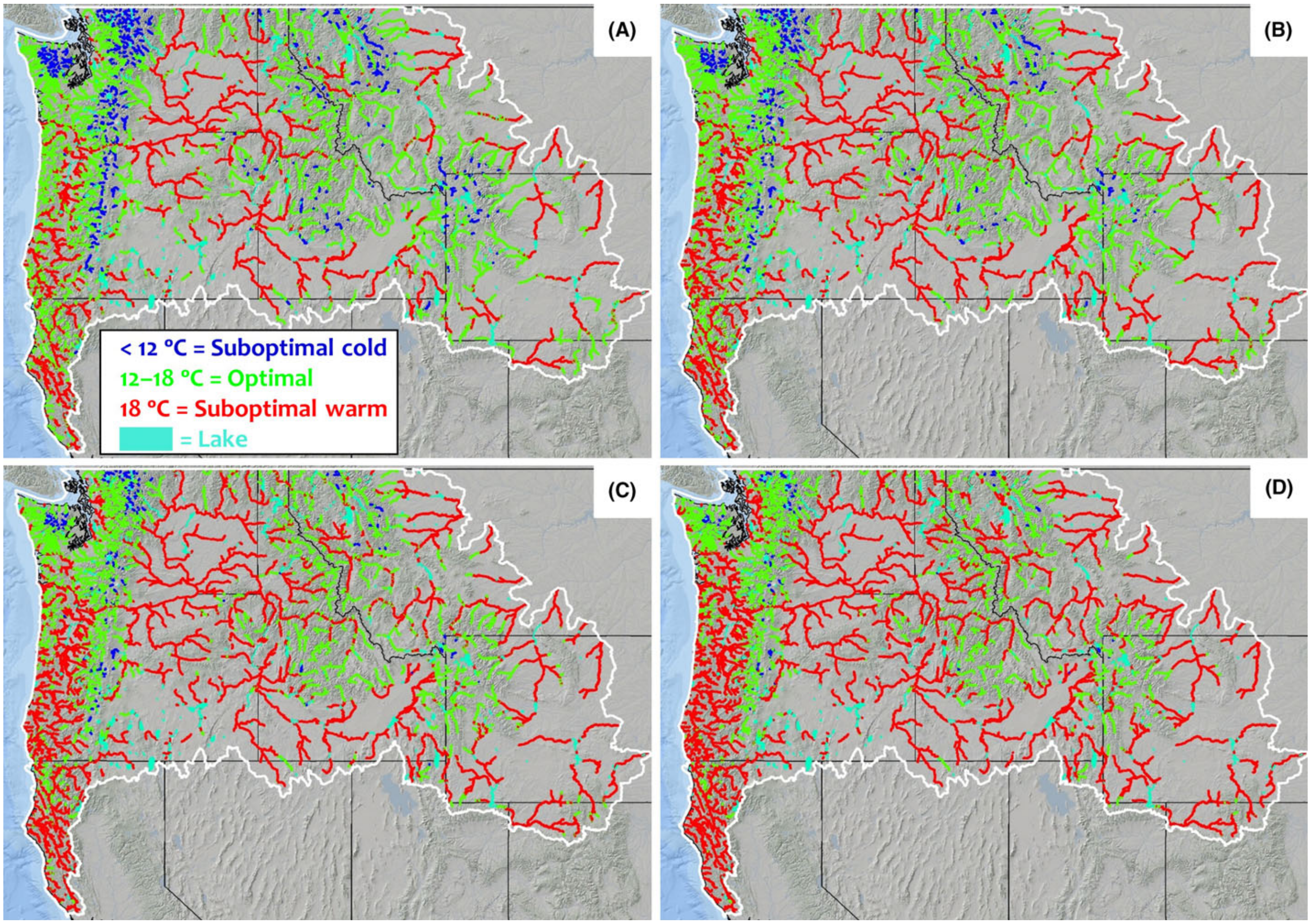

FIGURE 8. Rivers classified by thermal suitability for Brown Trout and Rainbow Trout under scenarios of mean August temperatures that represent **(A)** baseline conditions for 1993–2011, **(B)** +1.0°C, **(C)** +2.0°C, and **(D)** +3.0°C. Supplement G contains high-resolution images of the figure panels, including versions based on different color palettes.

relatively low at 0.08–0.18°C per decade. Although much variability exists among sites and seasons within all regions, annual warming rates of about 0.3°C per decade have been reported for similar historical periods from the UK (Orr et al. 2014), Germany (Arora et al. 2016), and the eastern USA (Rice and Jastram 2015). Sensitivity to climate forcing is probably higher in those regions due to rainfall-dominated hydrologic regimes and less-frequent winter periods when ATs are subzero. Common to all regions, however, is that trends in AT and the associated physical processes appear to be the dominant factors driving river temperature trends (Orr et al. 2014; Arora et al. 2016; Chen et al. 2016). Effects of Q trends are much smaller or serve primarily to cause short-term variability (Isaak et al. 2012; Arora et al. 2016). Also common among regions, except where urbanization plays a complicating role (e.g., Kaushal et al. 2010), is that river temperatures are usually increasing more slowly than AT trends —perhaps 40–80% as fast on an annual basis.

That river warming will continue this century is highly probable because virtually all global climate models project AT increases in the Northwest (NCA 2014; Rupp et al. 2017a) and globally under the current range of plausible emissions scenarios (IPCC 2013). However, uncertainties exist regarding whether AT trends will match those of historical periods, increase, or shift in magnitude among different months of the year (Abatzoglou and Redmond 2007). Trend acceleration is often discussed despite consistency in recent global average AT warming trends once records are detrended for short-term forcing factors (Rahmstorf et al. 2017). During the relatively short historical periods we examined, there was little change in mean annual AT trends (0.23°C per decade for the 20-year period versus 0.27°C per decade for the 40-year period), but future warming rates will ultimately depend on greenhouse gas emissions and evolution of global energy systems that are difficult to predict (Cox and Stephenson 2007).

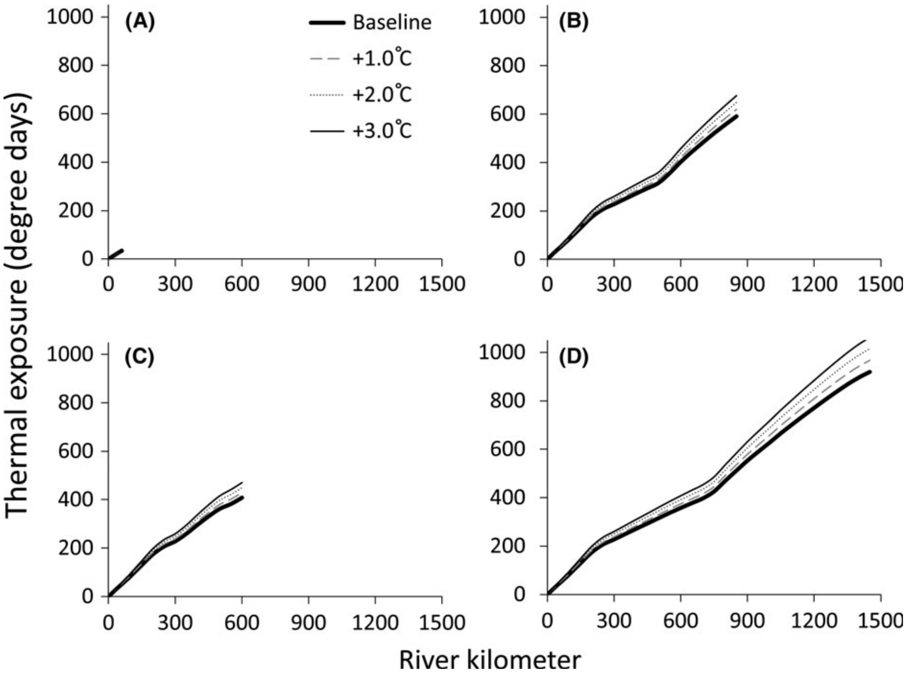

FIGURE 9. Cumulative thermal exposure along the migratory paths of adult Sockeye Salmon returning to four headwater natal areas under baseline and future climate scenarios: **(A)** Lake Quinault, Washington; **(B)** Lake Wenatchee, Washington; **(C)** Suttle Lake, Oregon; and **(D)** Redfish Lake, Idaho.

In contrast to AT trends, Q trends in the Northwest during the 20- and 40-year periods differed substantially and highlighted the role of Q in mediating the effect of AT increases on river temperatures. The large runoff declines observed during the short period of 1996–2015 were probably enhanced by regional climate cycle oscillations, so it may be unlikely that the high river warming rates experienced during this period will persist. However, the decreasing Q trend was also observed to a smaller degree during the 40-year period and is consistent with studies documenting historical runoff declines in the Northwest since the late 1940s (Luce and Holden 2009; Kormos et al. 2016). Declining annual Q trends run counter to most global-scale climate model projections of small increases in total precipitation (NCA 2014; Rupp et al. 2017a), but these projections are also subject to considerable uncertainty and are based on coarse climate models that poorly resolve mountains and orographic precipitation effects that are linked to historical Q declines in the Northwest (Luce et al. 2013). Higher-resolution regional climate models often show different precipitation projections than the global models, with increases in rain-shadow areas and smaller future precipitation increases and sometimes decreases in mountainous areas (Ashfaq et al. 2016; Rupp et al. 2017b). Uncertainties regarding future precipitation and annual river runoff will remain high, although it is likely that historical Q declines will continue at some level, as would their enhancement of river warming. That is especially true in river basins with the greatest snowpack contributions where trends toward earlier melt and runoff are very likely to continue reducing summer flows (e.g., Hamlet and Lettenmaier 1999).

Biological Effects

Our biological examples were simplistic in their focus on temperature and exclusion of other environmental covariates that sometimes mediate biothermal relationships (e.g., Wenger et al. 2011; Verberk et al. 2016). Nonetheless, thermal considerations are fundamentally important for ectotherms and coldwater fishes (Magnuson et al. 1979; McCullough et al. 2009) and have been central in previous regional climate change assessments (Keleher and Rahel 1996; Rieman et al. 2007; Isaak et al. 2016a), so a direct accounting of warming effects was useful. For resident trout species, our results suggest that river warming in recent decades is shifting thermally suitable habitats, which may account for the upstream distribution shifts observed in some of the Northwest's trout populations (Eby et al. 2014; Al-Chokhachy et al. 2016). Shifts are expected at warm downstream population boundaries because increasing temperatures will make growth, disease resistance, and survival more difficult during one or more life stages (Hari et al. 2006; Ayllón et al. 2013). Low densities of individuals may persist near warm boundaries if cold microrefugia are available (Hillyard and Keeley 2012), but refugia will become increasingly isolated in future years as the surrounding matrix of warmer waters continues to grow. Range contractions may also be exacerbated by upstream dispersal of predator species with warmer thermal preferences, as is occurring in some northwestern rivers with the expansion of Smallmouth Bass *Micropterus dolomieu* populations (Lawrence et al. 2014; Rubenson and Olden 2017).

Although infrequently considered in the climate–aquatic literature, headwater portions of especially cold rivers may present suboptimal thermal conditions for trout, especially species like the Brown Trout and Rainbow Trout that have relatively warm thermal niches compared to other trout species (Al-Chokhachy et al. 2016; Isaak et al. 2017a). As temperatures increase in cold river reaches, constraints on juvenile growth and recruitment may be relaxed (Coleman and Fausch 2007), multiple cohorts may be established, and densities likely to increase as long as other habitat factors are not limiting (Gibson-Reinemer et al. 2017). Gains in cold river reaches may partially offset losses in warmer downstream reaches but would often occur in smaller and more remote habitats, so from the perspective of anglers and fisheries managers, they may not be especially desirable. Most often, however, it appears that reductions in the overall extent of thermally suitable riverine habitat are likely with warming and upstream shifts, which could lead to losses of place-based fishing traditions, concentrate angling pressure into smaller areas, and decrease revenues associated with the recreational trout fishing economy. Despite anticipated declines, our results also suggest that the wholesale loss of thermal habitat for Rainbow Trout and Brown Trout is unlikely in the Northwest, even under relatively extreme 2–3°C warming scenarios, and that many rivers will continue to support these species.

For salmon species, warmer temperatures and shifts in thermal habitat will have similar effects on nonmigratory life stages (i.e., eggs, alevins, and parr) as those for resident trout populations, but annual migrations provide additional complexities. Several species and stocks in the Northwest show evidence of temperature sensitivity during adult migrations (Berman and Quinn 1991; Keefer et al. 2009, 2015), although Sockeye Salmon appear to be particularly vulnerable and served here as a useful example species. Our results indicate that Sockeye Salmon exhibit at least 30-fold variation in thermal exposure among populations depending on the location of their natal habitat and attendant riverine thermal conditions. Future warming and exposure increases should be relatively small for populations with short migrations but larger and potentially problematic for populations further inland. Not surprisingly, it is those inland Sockeye Salmon populations returning to Redfish Lake in Idaho or upper portions of the Fraser River in Canada for which the effects of chronic thermal stress are commonly documented (Keefer et al. 2008; Martins et al. 2012). Moreover, late-migrating salmon in those populations experience the warmest temperatures and greatest thermal exposure and often return to natal areas at lower rates than earlier-migrating fish (Keefer et al. 2008). As a result, increasing river temperatures may be acting as a selective force, and median migration dates of Sockeye Salmon in the Columbia River are now 1–2 weeks earlier than in the 1940s (Crozier et al. 2011). Earlier migrations, however, necessitate tradeoffs with other life stages, which could be deleterious to overall fitness. In the Fraser River, for example, earlier migrants spend less time in the ocean, have fewer energetic reserves, and return less successfully to the spawning grounds during years with warm river temperatures (Cooke et al. 2004). Ongoing warming of the Fraser River (Morrison et al. 2002), combined with trends in sea surface temperatures and productivity, has led to predictions that some Sockeye Salmon stocks could collapse later this century if successful migrations become bioenergetically impossible (Rand et al. 2006; Hague et al. 2011).

Compounding the chronic effects of long-term warming for summer-migrating salmon species will be increases in the frequency and duration of acutely stressful and perhaps lethal temperatures during short-term heat waves. During the 2015 mass-mortality events in the Columbia River that occurred upstream from Bonneville Dam, river temperatures exceeded a critical 21°C threshold beginning 4 weeks earlier than normal in June and persisted at levels 2–4°C above monthly averages for 3–4 consecutive weeks (NOAA 2016). Extreme events are, by definition, rare but are also predicted to increase rapidly in the future if gradual trends in average conditions are accompanied by greater climatic variability (Jentsch et al. 2007). That dynamic could unfold for northwestern rivers if the long-term warming trends we document begin to interact with climatically enhanced variability in the North Pacific Ocean (Mantua 2015; Di Lorenzo and Mantua 2016). In some late-century scenarios for the Snake and Columbia rivers, for example, it has been predicted that the number of weeks with average temperatures exceeding 21°C could increase 10-fold relative to historical baselines (Mantua et al. 2010). If that occurs, the extreme thermal conditions observed in 2015 might become "average" in the future, and the tempo of what migrating salmon experience as extreme events could threaten the persistence of some stocks.

Adaptive Responses

Options exist to ameliorate thermal stresses on salmon and trout populations, but appropriate remedies are context dependent and will require strategic prioritization (Beechie et al. 2013; Orr et al. 2015). Restoration efforts to cool rivers might include minimization of flow diversions (Elmore et al. 2015), increasing shade provided by riparian vegetation (Cristea and Burges 2010; Johnson and Wilby 2015), reconnecting rivers to floodplains to enhance habitat diversity (Beechie et al. 2013), and increasing channel roughness to encourage more water exchange between the channel and cooler hyporheic flows (Arrigoni et al. 2008; Nichols and Ketcheson 2013). More aggressive measures have also been discussed, such as excavating deep pools adjacent to warm rivers to access cool groundwater or the construction of wingwalls upstream of cold tributary inflows to limit mixing and create microrefugia (Kurylyk et al. 2015). In flow-regulated reaches, water managers may time releases of cold water during warm summer periods or coordinate their actions among multiple hydropower projects to maximize effects. Where salmon populations are a primary concern, dam breeching or installation of fish passage systems could provide access to significant lengths of cold rivers in portions of historical ranges that have been blocked (East et al. 2015; O'Connor et al. 2015). Where fish passage structures already exist, designs might be optimized to minimize migration delays that increase thermal exposure (Keefer et al. 2008, 2009). Biological adaptive responses could involve revision of hatchery policies to favor species or variants with higher thermal tolerances or that migrate during times with decreased exposure to peak temperatures. Relative to interspecific differences in thermal tolerance, however, intraspecific differences appear to be relatively small (Chen et al. 2018) and less malleable over short time spans, so more plastic phenotypic traits may offer better opportunities for manipulation (Crozier et al. 2008). Protection and maintenance of biodiversity will remain essential cornerstones to help provide future resilience (Schindler et al. 2010; Webster et al. 2017) but may need to be strategically interpreted given the difficulty of saving everything in a world with limited conservation resources and pervasive thermal effects.

As the warming process unfolds, managers and conservationists will sometimes face dilemmas. Key habitat bottlenecks and optimal locations for habitat restoration and protection may occur where rivers are too large to be effectual or where they flow through private lands and are inaccessible, or efforts may simply be trumped by society's other uses of rivers. Where investments are possible, high costs will often limit their geographic extent and draw conservation resources away from other investment opportunities. If recognition is gained that some populations are lost causes, the legal framework associated with the Endangered Species Act and intense lobbying by conservation and fisheries interests may make it difficult to redirect resources where benefits are greater. In many instances, a fog of uncertainty will exist because the information to guide strategic investments is simply lacking. Silver bullets do not exist, but discussions concerning these complex and difficult issues may be aided by better information, especially if it is developed through collaborative partnerships among relevant stakeholders and derived from robust databases and models of key biophysical factors. In this regard, development of the NorWeST temperature database from dozens of resource agencies served as an important step and salient example (Isaak et al. 2017b). The comprehensive online temperature data repository has helped highlight the relative rarity of long-term, annual records while simultaneously facilitating more efficient and comprehensive monitoring efforts that are now coordinated among multiple partners (Williams et al. 2016). Scenarios developed from the database provide spatially comprehensive thermal information that has contributed to an improved understanding of salmon migrations (Westley et al. 2015; Palmer 2017), locations susceptible to nonnative species invasions (Al-Chokhachy et al. 2016; Isaak et al. 2016a, 2016b; Howell, in press), and parameterization of distribution models that predict locations of climate refuge streams (Isaak et al. 2015; Young et al. 2016). As the NorWeST database and scenarios are periodically updated and improved, they could be used in development of spatially explicit, high-resolution behavioral and bioenergetic models that encompass the full suite of freshwater salmon habitats and life stages (Honea et al. 2016; Crozier et al. 2017) or next-generation species distribution models (Filipe et al. 2017; Ver Hoef et al. 2018) to further reduce remaining uncertainties and provide decision makers with ever more precise information.

CONCLUSION

Global warming will create increasingly challenging thermal environments for salmon and trout in the Northwest this century. That basic conclusion remains unchanged from the earliest studies on this topic (Eaton and Scheller 1996; Keleher and Rahel 1996; Hauer et al. 1997). Here, however, the use of long-term river temperature records and spatially explicit scenarios rather than earlier proxies like AT and elevation provided additional resolution and much-needed estimates of warming rates. Although warming of the region's rivers is evident and temperatures during some months are now about 1°C warmer than 20–40 years ago, it is encouraging to note that salmon and trout populations remain widespread in the Northwest. Less encouraging is that the Earth is probably in the initial decades of a long-term warming period, and temperature increases will act synergistically with regional trends in hydrology (Luce and Holden 2009; Kormos et al. 2016), nonnative species invasions (Sanderson et al. 2009), human population growth and water use (Vörösmarty et al. 2010; Feist et al. 2017), and less-favorable ocean conditions (Mantua 2015; Di Lorenzo and Mantua 2016) to negatively affect coldwater fishes. For some populations or fisheries that are heavily exposed and vulnerable, an additional 1–3°C of warming accompanied by those changes may well prove to be the road to ruin. However, for the majority of salmon and trout populations and species, we believe a more apt metaphor is a path through purgatory, as these fish continue attempting to adapt by tapping their remarkable stores of diversity and resilience. Current greenhouse gas emission rates may make their purgatory last for much of the 21st century, so concerted, ongoing, and strategic efforts by the conservation and management communities will be needed to assist in that adaptation.

ACKNOWLEDGMENTS

We thank the aquatics community in the Northwest for the temperature data used to constitute the NorWeST database that enabled this research. More recent years of data were graciously provided by professionals with the Idaho Department of Fish and Game; Montana Department of Fish, Wildlife, and Parks; Oregon Department of Fish and Wildlife; Washington Department of Fish and Wildlife; Washington Department of Ecology; King County; Burns Paiute Tribe; Confederated Salish and Kootenai Tribes; Confederated Tribes of the Umatilla Indian Reservation; Nez Perce Tribe; Yakama Nation; Idaho Power; U.S. Forest Service; U.S. Geological Survey; U.S. Bureau of Reclamation; U.S. Army Corps of Engineers; Bureau of Land Management; and the National Oceanic and Atmospheric Administration. All river temperature data used in this analysis are archived and available at the NorWeST project Web site. Earlier versions of the manuscript were improved by comments from Mike Young, Bruce Rieman, and three anonymous reviewers. This research was supported by the U.S. Forest Service Rocky Mountain Research Station, Regions 1 and 6, and grants from the U.S. Fish and Wildlife Service's Great Northern and North Pacific Landscape Conservation Cooperatives. There is no conflict of interest declared in this article.

REFERENCES

Abatzoglou, J. T., and K. T. Redmond. 2007. Asymmetry between trends in spring and autumn temperature and circulation regimes over western North America. Geophysical Research Letters 34:L18808.

Abatzoglou, J. T., D. E. Rupp, and P. W. Mote. 2014. Seasonal climate variability and change in the Pacific Northwest of the United States. Journal of Climate 27:2125–2142.

Al-Chokhachy, R., D. Schmetterling, C. Clancy, P. Saffel, R. Kovach, L. Nyce, B. Liermann, W. Fredenberg, and R. Pierce. 2016. Are Brown Trout replacing or displacing Bull Trout populations in a changing climate? Canadian Journal of Fisheries and Aquatic Sciences 73:1395–1404.

Arora, R., K. Tockner, and M. Venohr. 2016. Changing river temperatures in northern Germany: trends and drivers of change. Journal of Hydrology 30:3084–3096.

Arrigoni, A. S., G. C. Poole, L. A. Mertes, S. J. O'Daniel, W. W. Woessner, and S. A. Thomas. 2008. Buffered, lagged, or cooled? Disentangling hyporheic influences on temperature cycles in stream channels. Water Resources Research [online serial] 44(9):W09418.

Ashfaq, M., D. Rastogi, R. Mei, C. Kao, S. Gangrade, B. S. Naz, and D. Touma. 2016. High-resolution ensemble projections of near-term regional climate over the continental United States. Journal of Geophysical Research: Atmosphere 121:9943–9963.

Ayllón, D., G. G. Nicola, B. Elvira, I. Parra, and A. Almodóvar. 2013. Thermal carrying capacity for a thermally-sensitive species at the warmest edge of its range. PLoS ONE [online serial] 8(11):e81354.

Bartholow, J. M. 2005. Recent water temperature trends in the Lower Klamath River, California. North American Journal of Fisheries Management 25:152–162.

Beechie, T., H. Imaki, J. Greene, A. Wade, H. Wu, G. Pess, P. Roni, J. Kimball, J. Stanford, P. Kiffney, and N. Mantua. 2013. Restoring salmon habitat for a changing climate. River Research and Applications 29:939–960.

Berman, C. H., and T. P. Quinn. 1991. Behavioural thermoregulation and homing by spring Chinook Salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. Journal of Fish Biology 39:301–312.

Bowerman, T., M. L. Keefer, and C. C. Caudill. 2016. Pacific salmon prespawn mortality: patterns, methods, and study design considerations. Fisheries 41:738–749.

Caissie, D., and C. H. Luce. 2017. Quantifying streambed advection and conduction heat fluxes. Water Resources Research 53:1595–1624.

Chandler, G. L., S. Wollrab, D. Horan, D. Nagel, S. Parkes, D. J. Isaak, S. J. Wenger, E. E. Peterson, J. M. Ver Hoef, S. Hostetler, C. H. Luce, J. B. Dunham, J. Kershner, and B. B. Roper. 2016. NorWeST stream temperature data summaries for the western U.S. U.S. Forest Service, Rocky Mountain Research Station, Research Data Archive, Fort Collins, Colorado. Available: https://doi.org/10.2737/rds-2016-0032. (April 2018).

Chen, D., M. Hu, Y. Guo, and R. A. Dahlgren. 2016. Changes in river water temperature between 1980–2012 in Yongan watershed, eastern China: magnitude, drivers and models. Journal of Hydrology 533:191–199.

Chen, Z., A. P. Farrell, A. Matala, and S. R. Narum. 2018. Mechanisms of thermal adaptation and evolutionary potential of conspecific populations to changing environments. Molecular Ecology 27:659–674.

Coleman, M. A., and K. D. Fausch. 2007. Cold summer temperature limits recruitment of age-0 Cutthroat Trout in high-elevation Colorado streams. Transactions of the American Fisheries Society 136:1231–1244.

Columbia Basin Bulletin. 2015. Post-mortem 2015 Snake River Sockeye run: 90 percent of fish dead before reaching Ice Harbor Dam. Available: http://www.cbbulletin.com/435642.aspx. (April 2018).

Comte, L., L. Buisson, M. Daufresne, and G. Grenouillet. 2013. Climate-induced changes in the distribution of freshwater fish: observed and predicted trends. Freshwater Biology 58:625–639.

Comte, L., and G. Grenouillet. 2013. Do stream fish track climate change? Assessing distribution shifts in recent decades. Ecography 36:1236–1246.

Cooke, S. J., S. G. Hinch, A. P. Farrell, M. F. Lapointe, S. M. R. Jones, J. S. Macdonald, D. A. Patterson, M. C. Healey, and G. Van Der Kraak. 2004. Abnormal migration timing and high en route mortality of Sockeye Salmon in the Fraser River, British Columbia. Fisheries 29(2):22–33.

Copeland, T., and K. A. Meyer. 2011. Interspecies synchrony in salmonid densities associated with large-scale bioclimatic conditions in central Idaho. Transactions of the American Fisheries Society 140:928–942.

Cox, P., and D. Stephenson. 2007. A changing climate for prediction. Science 317:207–208.

Cristea, N. C., and S. J. Burges. 2010. An assessment of the current and future thermal regimes of three streams located in the Wenatchee River basin, Washington State: some implications for regional river basin systems. Climatic Change 102:493–520.

Crozier, L. G., T. E. Bowerman, B. J. Burke, M. L. Keefer, and C. C. Caudill. 2017. High-stakes steeplechase: a behavior-based model to predict individual travel times through diverse migration segments. Ecosphere [online serial] 8:e01965.

Crozier, L. G., A. P. Hendry, P. W. Lawson, T. P. Quinn, N. J. Mantua, J. Battin, R. G. Shaw, and R. B. Huey. 2008. Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. Evolutionary Applications 1:252–270.

Crozier, L. G., M. D. Scheuerell, and R. W. Zabel. 2011. Using time series analysis to characterize evolutionary and plastic responses to environmental change: a case study of a shift toward earlier migration date in Sockeye Salmon. American Naturalist 178:755–773.

Di Lorenzo, E., and N. Mantua. 2016. Multi-year persistence of the 2014/15 North Pacific marine heatwave. Nature Climate Change 6:1042–1047.

Dugdale, S., J. Franssen, E. Corey, N. E. Bergeron, M. Lapointe, and R. A. Cunjak. 2016. Main stem movement of Atlantic Salmon parr in response to high river temperature. Ecology of Freshwater Fish 25:429–445.

East, A. E., G. R. Pess, J. A. Bountry, C. S. Magirl, A. C. Ritchie, J. B. Logan, T. J. Randle, M. C. Mastin, J. T. Minear, J. J. Duda, and M. C. Liermann. 2015. Large-scale dam removal on the Elwha River, Washington, USA: river channel and floodplain geomorphic change. Geomorphology 228:765–786.

Easterling, D. R., and M. F. Wehner. 2009. Is the climate warming or cooling? Geophysical Research Letters 36:L08706.

Eaton, J. G., and R. M. Scheller. 1996. Effects of climate warming on fish thermal habitat in streams of the United States. Limnology and Oceanography 41:1109–1115.

Ebersole, J. L., W. J. Liss, and C. A. Frissell. 2001. Relationship between stream temperature, thermal refugia and Rainbow Trout *Oncorhynchus mykiss* abundance in arid-land streams in the northwestern United States. Ecology of Freshwater Fish 10:1–10.

Eby, L. A., O. Helmy, L. M. Holsinger, and M. K. Young. 2014. Evidence of climate-induced range contractions in Bull Trout *Salvelinus confluentus* in a Rocky Mountain watershed, U.S.A. PLoS ONE [online serial] 9:e98812.

Elmore, L. R., S. E. Null, and N. R. Mouzon. 2015. Effects of environmental water transfers on stream temperatures. River Research and Applications 32:1415–1427.

Feist, B. E., E. R. Buhle, D. H. Baldwin, J. A. Spromberg, S. E. Damm, J. W. Davis, and N. L. Scholz. 2017. Roads to ruin: conservation threats to a sentinel species across an urban gradient. Ecological Applications 27:2382–2396.

Filipe, A., L. Quaglietta, M. Ferreira, M. Magalhaes, and P. Beja. 2017. Geostatistical distribution modelling of two invasive crayfish across dendritic stream networks. Biological Invasions 19:2899–2912.

Fullerton, A. H., C. E. Torgersen, J. J. Lawler, E. A. Steel, J. L. Ebersole, and S. Y. Lee. In press. Longitudinal thermal heterogeneity in rivers and refugia for coldwater species: effects of scale and climate change. Aquatic Sciences. DOI: 10.1007/s00027-017-0557-9.

Gergely, K. J., and A. McKerrow. 2016. PAD-US—National inventory of protected areas, version 1.1, August 2016. U.S. Geological Survey, Fact Sheet 2013-3086, Reston, Virginia.

Gibson-Reinemer, D. K., F. J. Rahel, S. E. Albeke, and R. M. Fitzpatrick. 2017. Natural and anthropogenic barriers to climate tracking in river fishes along a mountain–plains transition zone. Diversity and Distributions 23:761–770.

Goneia, T. M., M. L. Keefer, T. C. Bjornn, C. A. Peery, D. H. Bennett, and L. C. Stuehrenberg. 2006. Behavioral thermoregulation and slowed migration by adult fall Chinook Salmon in response to high Columbia River water temperatures. Transactions of the American Fisheries Society 135:408–419.

Gu, R., S. Montgomery, and T. A. Austin. 1998. Quantifying the effects of stream discharge on summer river temperature. Hydrological Sciences Journal 43:885–904.

Hague, M. J., M. R. Ferrari, J. R. Miller, D. A. Patterson, G. L. Russell, A. P. Farrell, and S. G. Hinch. 2011. Modelling the future hydroclimatology of the lower Fraser River and its impacts on the spawning migration survival of Sockeye Salmon. Global Change Biology 17:87–98.

Hamlet, A. F., and D. P. Lettenmaier. 1999. Effects of climate change on hydrology and water resources in the Columbia River basin. Journal of the American Water Resources Association 35:1597–1623.

Hannah, D., and G. Garner. 2015. River water temperature in the United Kingdom: changes over the 20th century and possible changes over the 21st century. Progress in Physical Geography 39:68–92.

Hari, R. E., D. M. Livingstone, R. Siber, P. Burkhardt-Holm, and H. Guttinger. 2006. Consequences of climatic change for water temperature and Brown Trout populations in alpine rivers and streams. Global Change Biology 12:10–26.

Hauer, F. R., J. S. Baron, D. H. Campbell, K. D. Fausch, S. W. Hostetler, G. H. Leavesley, P. R. Leavitt, D. M. McKnight, and J. A. Stanford. 1997. Assessment of climate change and freshwater ecosystems of the Rocky Mountains, USA and Canada. Hydrological Processes 11:903–924.

Hillyard, R. W., and E. R. Keeley. 2012. Temperature-related changes in habitat quality and use by Bonneville Cutthroat Trout in regulated and unregulated river segments. Transactions of the American Fisheries Society 141:1649–1663.

Hockey, J. B., I. F. Owens, and N. J. Tapper. 1982. Empirical and theoretical models to isolate the effect of discharge on summer water temperatures in the Hurunui River. Journal of Hydrology (New Zealand) 21:1–12.

Honea, J. M., M. M. McClure, J. C. Jorgensen, and M. D. Scheuerell. 2016. Assessing freshwater life-stage vulnerability of an endangered Chinook Salmon population to climate change influences on stream habitat. Climate Research 71:127–137.

Howell, P. J. In press. Changes in native Bull Trout and non-native Brook Trout distributions in the upper Powder River basin after 20 years, relationships to water temperature and implications of climate change. Ecology of Freshwater Fish. DOI: 10.1111/eff.12386. (April 2018).

IPCC (Intergovernmental Panel on Climate Change). 2013. Climate change: the physical science basis. IPCC, Bern, Switzerland.

Isaak, D. J., S. J. Wenger, E. E. Peterson, J. M. Ver Hoef, S. Hostetler, C. H. Luce, J. B. Dunham, J. Kershner, B. B. Roper, D. E. Nagel, G. L. Chandler, S. Wollrab, S. Parkes, and D. L. Horan. 2016b. NorWeST modeled summer stream temperature scenarios for the western U.S. U.S. Forest Service, Rocky Mountain Research Station, Research Data Archive, Fort Collins, Colorado. Available: https://doi.org/10.2737/rds-2016-0033. (April 2018).

Isaak, D. J., S. J. Wenger, E. E. Peterson, J. M. Ver Hoef, D. E. Nagel, C. H. Luce, S. W. Hostetler, J. B. Dunham, B. B. Roper, S. P. Wollrab, G. L. Chandler, D. L. Horan, and S. Parkes-Payne. 2017b. NorWeST summer temperature model and scenarios for the western U.S.: a crowd-sourced database and new geospatial tools foster a user-community and predict broad climate warming of rivers and streams. Water Resources Research 53:9181–9205.

Isaak, D. J., S. Wenger, and M. K. Young. 2017a. Big biology meets microclimatology: defining thermal niches of aquatic ectotherms at landscape scales for conservation planning. Ecological Applications 27:977–990.

Isaak, D. J., S. Wollrab, D. Horan, and G. Chandler. 2012. Climate change effects on stream and river temperatures across the northwest

U.S. from 1980–2009 and implications for salmonid fishes. Climatic Change 113:499–524.

Isaak, D. J., M. K. Young, C. H. Luce, S. Hostetler, S. Wenger, E. E. Peterson, J. M. Ver Hoef, M. Groce, D. L. Horan, and D. Nagel. 2016a. Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. Proceedings of the National Academy of Sciences of the United States of America 113:4374–4379.

Isaak, D. J., M. K. Young, D. E. Nagel, D. L. Horan, and M. C. Groce. 2015. The cold-water climate shield: delineating refugia for preserving salmonid fishes through the 21st century. Global Change Biology 21:2540–2553.

Jentsch, A., J. Kreyling, and C. Beierkuhnlein. 2007. A new generation of climate-change experiments: events, not trends. Frontiers in Ecology and the Environment 5:365–374.

Johnson, M. F., and R. L. Wilby. 2015. Seeing the landscape for the trees: metrics to guide riparian shade management in river catchments. Water Resources Research 51:3754–3769.

Jonsson, B., and N. Jonsson. 2009. A review of the likely effects of climate change on anadromous Atlantic Salmon *Salmo salar* and Brown Trout *Salmo trutta*, with particular reference to water temperature and flow. Journal of Fish Biology 75:2381–2447.

Josse, J., and F. Husson. 2012. Handling missing values in exploratory multivariate data analysis methods. Journal of the Société Française de Statistique 153:79–99.

Josse, J., and F. Husson. 2016. missMDA: a package for handling missing values in multivariate data analysis. Journal of Statistical Software 70:1–31.

Kaushal, S. S., G. E. Likens, N. A. Jaworski, M. L. Pace, A. M. Sides, D. Seekell, K. T. Belt, D. H. Secor, and R. L. Wingate. 2010. Rising stream and river temperatures in the United States. Frontiers in Ecology and the Environment 8:461–466.

Keefer, M. L., and C. C. Caudill. 2015. Estimating thermal exposure of adult summer steelhead and fall Chinook Salmon migrating in a warm impounded river. Ecology of Freshwater Fish 25:599–611.

Keefer, M. L., T. S. Clabough, M. A. Jepson, G. P. Naughton, T. J. Blubaugh, D. C. Joosten, and C. C. Caudill. 2015. Thermal exposure of adult Chinook Salmon in the Willamette River basin. Journal of Thermal Biology 48:11–20.

Keefer, M. L., C. A. Peery, and M. J. Heinrich. 2008. Temperature mediated en route migration mortality and travel rates of endangered Snake River Sockeye Salmon. Ecology of Freshwater Fish 17:136–145.

Keefer, M. L., C. A. Peery, and B. High. 2009. Behavioral thermoregulation and associated mortality trade-offs in migrating adult steelhead (*Oncorhynchus mykiss*): variability among sympatric populations. Canadian Journal of Fisheries and Aquatic Sciences 66:1734–1747.

Keleher, C. J., and F. J. Rahel. 1996. Thermal limits to salmonid distributions in the Rocky Mountain region and potential habitat loss due to global warming: a geographic information system (GIS) approach. Transactions of the American Fisheries Society 125:1–13.

Kelleher, C., T. Wagener, M. Gooseff, B. McGlynn, K. McGuire, and L. Marshall. 2011. Investigating controls on the thermal sensitivity of Pennsylvania streams. Hydrological Processes 26:771–785.

Knowles, N., M. D. Dettinger, and D. R. Cayan. 2006. Trends in snowfall versus rainfall in the western United States. Journal of Climate 19:4545–4559.

Kormos, P., C. Luce, S. J. Wenger, and W. R. Berghuijs. 2016. Trends and sensitivities of low streamflow extremes to discharge timing and magnitude in Pacific Northwest mountain streams. Water Resources Research 52:4990–5007.

Kovach, R. P., A. J. Gharrett, and D. A. Tallmon. 2012. Genetic change for earlier migration timing in a Pink Salmon population. Proceedings of the Royal Society B: Biological Sciences 279:3870–3878.

Kurylyk, B., C. A. Bourque, and K. MacQuarrie. 2013. Potential surface temperature and shallow groundwater temperature response to climate change: an example from a small forested catchment in east-central New Brunswick (Canada). Hydrology and Earth System Sciences 17:2701–2716.

Kurylyk, B. L., T. B. MacQuarrie, T. Linnansaari, R. A. Cunjak, and R. A. Curry. 2015. Preserving, augmenting, and creating cold-water thermal refugia in rivers: concepts derived from research on the Miramichi River, New Brunswick (Canada). Ecohydrology 8:1095–1108.

Lawrence, D. J., B. Stewart-Koster, J. D. Olden, A. S. Ruesch, C. E. Torgersen, J. J. Lawler, D. P. Butcher, and J. K. Crown. 2014. The interactive effects of climate change, riparian management, and a nonnative predator on stream-rearing salmon. Ecological Applications 24:895–912.

Lawrimore, J. H., M. J. Menne, B. E. Gleason, C. N. Williams, D. B. Wuertz, R. S. Vose, and J. Rennie. 2011. An overview of the Global Historical Climatology Network monthly mean temperature data set, version 3. Journal of Geophysical Research 116:D19121.

Lewis, M., and W. Clark. 1805. June 13 entry in the journals of the Lewis and Clark expedition. University of Nebraska Press, Lincoln. Available: https://lewisandclarkjournals.unl.edu/item/lc.jrn.1805-06-13. (April 2018).

Littell, J. S., D. McKenzie, D. L. Peterson, and A. L. Westerling. 2009. Climate and wildfire area burned in western US ecoprovinces, 1916–2003. Ecological Applications 19:1003–1021.

Luce, C. H., J. T. Abatzoglou, and Z. A. Holden. 2013. The missing mountain water: slower westerlies decrease orographic enhancement in the Pacific Northwest USA. Science 342:1360–1364.

Luce, C. H., and Z. A. Holden. 2009. Declining annual streamflow distributions in the Pacific Northwest United States, 1948–2006. Geophysical Research Letters 36:L16401.

Luce, C. H., B. Staab, M. Kramer, S. J. Wenger, D. J. Isaak, and C. McConnell. 2014. Sensitivity of summer stream temperatures to climate variability in the Pacific Northwest. Water Resources Research 50:3428–3443.

Lynch, D. D., and J. C. Risley. 2003. Klamath River basin hydrologic conditions prior to the September 2002 die-off of salmon and steelhead. U.S. Geological Survey, Water-Resources Investigations Report 03-4099, Portland, Oregon.

Magnuson, J. J., L. B. Crowder, and P. A. Medvick. 1979. Temperature as an ecological resource. American Zoologist 19:331–343.

Mann, M. E., Z. Zhang, S. Rutherford, R. S. Bradley, M. K. Hughes, D. Shindell, C. Ammann, G. Faluvegi, and F. Ni. 2009. Global signatures and dynamical origins of the Little Ice Age and Medieval Climate Anomaly. Science 326:1256–1260.

Mantua, N., I. Tohver, and A. Hamlet. 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. Climatic Change 102:187–223.

Mantua, N. J. 2015. Shifting patterns in Pacific climate, West Coast salmon survival rates, and increased volatility in ecosystem services. Proceedings of the National Academy of Sciences of the United States of America 112:10823–10824.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069–1079.

Marlier, M. E., M. Xiao, R. Engel, B. Livneh, J. T. Abatzoglou, and D. P. Lettenmaier. 2017. The 2015 drought in Washington State: a harbinger of things to come? Environmental Research Letters 12(11): 114008.

Martins, E. G., S. G. Hinch, D. A. Patterson, M. J. Hague, S. J. Cooke, K. M. Miller, D. Robichaud, K. K. English, and A. P. Farrell. 2012. High river temperature reduces survival of Sockeye Salmon (*Oncorhynchus* *nerka*) approaching spawning grounds and exacerbates female mortality. Canadian Journal of Fisheries and Aquatic Sciences 69:330–342.

McCabe, G. J., and M. D. Dettinger. 1999. Decadal variations in the strength of ENSO teleconnections with precipitation in the western United States. International Journal of Climatology 19:1399–1410.

McCullough, D. A., J. M. Bartholow, H. I. Jager, R. L. Beschta, E. F. Cheslak, M. L. Deas, J. L. Ebersole, J. Foott, S. L. Johnson, K. R. Marine, M. G. Mesa, J. H. Petersen, Y. Souchon, K. F. Tiffan, and W. A. Wurtsbaugh. 2009. Research in thermal biology: burning questions for coldwater stream fishes. Reviews in Fisheries Science 17:90–115.

McIntosh, A. R., P. A. McHugh, and P. Budy. 2011. Brown Trout (*Salmo trutta*). Pages 285–296 *in* R. A. Francis, editor. A handbook of global freshwater invasive species. Earthscan, London.

Meisner, J. D., J. S. Rosenfeld, and H. A. Regier. 1988. The role of groundwater in the impact of climate warming on stream salmonines. Fisheries 13(3):2–8.

Mills, D. 1989. Ecology and management of Atlantic Salmon. Chapman and Hall, New York.

Mohseni, O., H. G. Stefan, and J. G. Eaton. 2003. Global warming and potential changes in fish habitat in U.S. streams. Climatic Change 59:389–409.

Montgomery, D. R. 2003. King of fish: the thousand-year run of salmon. Westview Press, Boulder, Colorado.

Morrison, J., M. C. Quick, and M. G. Foreman. 2002. Climate change in the Fraser River watershed: flow and temperature projections. Journal of Hydrology 263:230–244.

Mote, P. W., A. F. Hamlet, M. P. Clark, and D. P. Lettenmaier. 2005. Declining mountain snowpack in western North America. Bulletin of the American Meteorological Society 86:39–49.

Mote, P. W., E. A. Parson, A. F. Hamlet, W. S. Keeton, D. Lettenmaier, N. Mantua, E. L. Miles, D. W. Peterson, D. L. Peterson, R. Slaughter, and A. K. Snover. 2003. Preparing for climatic change: the water, salmon, and forests of the Pacific Northwest. Climatic Change 61:45–88.

Naiman, R. J., J. R. Alldredge, D. A. Beauchamp, P. A. Bisson, J. Congleton, C. J. Henny, N. Huntly, R. Lamberson, C. Levings, E. N. Merrill, W. G. Pearcy, B. E. Rieman, G. T. Ruggerone, D. Scarnecchia, P. E. Smouse, and C. C. Wood. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. Proceedings of the National Academy of Sciences of the United States of America 109:21201–21207.

Naughton, G. P., C. C. Caudill, M. L. Keefer, T. C. Bjornn, L. C. Stuehrenberg, and C. A. Peery. 2005. Late-season mortality during migration of radio-tagged Sockeye Salmon (*Oncorhynchus nerka*) in the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 62:30–47.

NCA (National Climate Assessment). 2014. Climate change impacts in the United States: the third national climate assessment. U.S. Global Change Research Program, Washington, D.C.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4–20.

Nichols, R. A., and G. L. Ketcheson. 2013. A two-decade watershed approach to stream restoration log jam design and stream recovery monitoring: Finney Creek, Washington. Journal of the American Water Resources Association 49:1367–1384.

NOAA (National Oceanic and Atmospheric Administration). 2016. 2015 adult Sockeye Salmon passage report. NOAA Fisheries, West Coast Region, Seattle.

Null, S. E., J. H. Viers, M. L. Deas, S. K. Tanaka, and J. F. Mount. 2013. Stream temperature sensitivity to climate warming in California's Sierra Nevada: impacts to coldwater habitat. Climatic Change 116:149–170.

O'Connor, J. E., J. J. Duda, and G. E. Grant. 2015. 1,000 dams down and counting. Science 348:496–497.

Orr, H. G., M. F. Johnson, R. L. Wilby, T. Hatton-Ellis, and S. Broadmeadow. 2015. What else do managers need to know about warming rivers? A United Kingdom perspective. Wiley Interdisciplinary Reviews-Water 2:55–64.

Orr, H. G., G. L. Simpson, S. des Clers, G. Watts, M. Hughes, J. Hannaford, M. J. Dunbar, C. Laize, R. L. Wilby, R. W. Battarbee, and R. Evans. 2014. Detecting changing river temperatures in England and Wales. Hydrological Processes 29:752–766.

Palmer, J. 2017. Cold water fish refuges: EPA's Columbia River cold water refuges project. Water Report Newsletter 164:1–8.

Petersen, J. H., and J. F. Kitchell. 2001. Climate regimes and water temperature changes in the Columbia River: bioenergetic implications for predators of juvenile salmon. Canadian Journal of Fisheries and Aquatic Sciences 58:1831–1841.

Quinn, T. P., S. Hodgson, and C. Peven. 1997. Temperature, flow, and the migration of adult Sockeye Salmon (*Oncorhynchus nerka*) in the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 54:1349–1360.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rahmstorf, S., G. Foster, and N. Cahill. 2017. Global temperature evolution: recent trends and some pitfalls. Environmental Research Letters 12:054001.

Rand, P. S., and S. G. Hinch. 1998. Swim speeds and energy use of upriver-migrating Sockeye Salmon (*Oncorhynchus nerka*): simulating metabolic power and assessing risk of energy depletion. Canadian Journal of Fisheries and Aquatic Sciences 55:1832–1841.

Rand, P. S., S. G. Hinch, J. Morrison, M. G. G. Foreman, M. J. MacNutt, J. S. Macdonald, M. C. Healey, A. P. Farrell, and D. A. Higgs. 2006. Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River Sockeye Salmon. Transactions of the American Fisheries Society 135:655–667.

Rice, K. C., and J. D. Jastram. 2015. Rising air and stream-water temperatures in Chesapeake Bay region, USA. Climatic Change 128:127–138.

Rieman, B. E., D. J. Isaak, S. Adams, D. Horan, D. Nagel, C. Luce, and D. Myers. 2007. Anticipated climate warming effects on Bull Trout habitats and populations across the interior Columbia River basin. Transactions of the American Fisheries Society 136:1552–1565.

Rieman, B. E., C. L. Smith, R. J. Naiman, G. T. Ruggerone, C. C. Wood, N. Huntly, E. N. Merrill, J. R. Alldredge, P. A. Bisson, J. Congleton, K. D. Fausch, C. Levings, W. Pearcy, D. Scarnecchia, and P. Smouse. 2015. A comprehensive approach for habitat restoration in the Columbia Basin. Fisheries 40:124–135.

Rubenson, E. S., and J. D. Olden. 2017. Dynamism in the upstream invasion edge of a freshwater fish exposes range boundary constraints. Oecologia 184:453–467.

Ruckelshaus, M. H., P. Levin, J. B. Johnson, and P. M. Kareiva. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. Annual Review of Ecology and Systematics 33:665–706.

Rupp, D. E., J. T. Abatzoglou, and P. W. Mote. 2017a. Projections of 21st century climate of the Columbia River basin. Climate Dynamics 49:1783–1799.

Rupp, D. E., S. Li, P. W. Mote, K. M. Shell, N. Massey, S. N. Sparrow, D. C. Wallom, and M. R. Allen. 2017b. Seasonal spatial patterns of projected anthropogenic warming in complex terrain: a modeling study of the western US. Climate Dynamics 48:2191–2213.

Sanderson, B. L., K. A. Barnas, and A. M. Wargo Rub. 2009. Nonindigenous species of the Pacific Northwest: an overlooked risk to endangered salmon? BioScience 59:245–256.

Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465:609–612.

Torgersen, C. E., D. M. Price, H. W. Li, and B. A. McIntosh. 1999. Multiscale thermal refugia and stream habitat associations of Chinook Salmon in northeastern Oregon. Ecological Applications 9:301–319.

Ver Hoef, J. M., E. E. Peterson, M. B. Hooten, E. M. Hanks, and M. Fortin. 2018. Spatial autoregressive models for statistical inference from ecological data. Ecological Monographs 88:36–59.

Verberk, W. C., I. Durance, I. P. Vaughan, and S. J. Ormerod. 2016. Field and laboratory studies reveal interacting effects of stream oxygenation and warming on aquatic ectotherms. Global Change Biology 22:1769–1778.

Vörösmarty, C. J., P. B. McIntyre, M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. A. Sullivan, C. Reidy Liermann, and P. M. Davies. 2010. Global threats to human water security and river biodiversity. Nature 467:555–561.

Webb, B. W., D. M. Hannah, R. D. Moore, L. E. Brown, and F. Nobilis. 2008. Recent advances in stream and river temperature research. Hydrological Processes 22:902–918.

Webb, B. W., and F. Nobilis. 2007. Long-term changes in river temperature and the influence of climatic and hydrological factors. Hydrological Sciences Journal 52:74–85.

Webster, M. S., M. A. Colton, E. S. Darling, J. Armstrong, M. L. Pinsky, N. Knowlton, and D. E. Schindler. 2017. Who should pick the winners of climate change? Trends in Ecology and Evolution 32:167–173.

Wedekind, C., and C. Kung. 2010. Shift of spawning season and effects of climate warming on developmental stages of a grayling (Salmonidae). Conservation Biology 24:1418–1423.

Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Neville, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, and A. F. Hamlet. 2011. Flow regime, temperature, and biotic interactions drive differential declines of Rocky Mountain trout species under climate change. Proceedings of the National Academy of Sciences of the USA 108:14175–14180.

Westley, P., A. Dittman, E. Ward, and T. Quinn. 2015. Signals of climate, conspecific density, and watershed features in patterns of homing and dispersal by Pacific salmon. Ecology 96:2823–2833.

Williams, J. E., S. Rummel, J. Lemon, M. Barney, K. Smith, K. Fesenmyer, and J. Schoen. 2016. Engaging a community of interest in water quality protection: anglers monitoring wadeable streams. Journal of Soil and Water Conservation 71:114A–119A.

Wohl, E., K. B. Lininger, and J. Baron. 2017. Land before water: the relative temporal sequence of human alteration of freshwater ecosystems in the conterminous United States. Anthropocene 18:27–46.

Wu, H., J. S. Kimball, M. M. Elsner, N. Mantua, R. F. Adler, and J. Stanford. 2012. Projected climate change impacts on the hydrology and temperature of Pacific Northwest rivers. Water Resources Research 48(11):W11530.

Young, M. K., D. J. Isaak, K. S. McKelvey, T. M. Wilcox, D. M. Bingham, K. L. Pilgrim, K. J. Carim, M. R. Campbell, M. P. Corsi, D. L. Horan, D. E. Nagel, and M. K. Schwartz. 2016. Climate, demography, and zoogeography predict introgression thresholds in salmonid hybrid zones in Rocky Mountain streams. PLoS ONE [online serial] 11:e0163563.

SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.