Thermal landscapes in a changing climate: biological implications of water temperature patterns in an extreme year

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Abstract: Record-breaking droughts and high temperatures in 2015 across the Pacific Northwest, USA, provide an opportunistic glimpse into potential future thermal regimes of rivers and their implications for freshwater fishes. We applied spatial stream network models to data collected every 30 min for 4 years at 42 sites on the Snoqualmie River (Washington, United States) to compare water temperature patterns, summarized with relevance to particular life stages of native and nonnative fishes, in 2015 with more typical conditions (2012–2014). Although 2015 conditions were drier and warmer than what had been observed since 1960, patterns were neither consistent over the year nor on the network. Some locations showed dramatic increases in air and water temperature, whereas others had temperatures that differed little from typical years; these results contrasted with existing forecasts of future thermal landscapes. If we will observe years like 2015 more frequently in the future, we can expect conditions to be less favorable to native, cool-water fishes such as Chinook salmon (Oncorhynchus tshawytscha) and bull trout (Salvelinus confluentus) but beneficial to warm-water nonnative species such as largemouth bass (Micropterus salmoides).

Résumé : Des sécheresses et des températures record en 2015 à la grandeur de la région du Pacific Northwest (États-Unis) offrent un aperçu opportuniste des régimes thermiques futurs potentiels des rivières et de leurs répercussions sur les poissons d’eau douce. Nous avons appliqué des modèles spatiaux de réseaux hydrographiques à des données recueillies toutes les 30 minutes pendant 4 ans à 42 sites le long de la rivière Snoqualmie (Washington, États-Unis) afin de comparer les motifs de température de l’eau en 2015, résumés en fonction de différentes étapes des cycles de vie de poissons indigènes et non indigènes, à des conditions plus typiques (2012–2014). Si les conditions de 2015 étaient plus sèches et chaudes que ce qui avait été observé depuis 1960, les motifs n’étaient pas cohérents au fil de l’année ni à l’échelle du réseau. Certains endroits présentaient des augmentations fulgurantes des températures de l’air et de l’eau, alors qu’en d’autres endroits, les températures différaient peu de celles d’années typiques ; ces résultats diffèrent des prévisions actuelles concernant les paysages thermiques futurs. Si des années comme 2015 deviennent plus fréquentes à l’avenir, les conditions devraient être moins favorables aux poissons d’eau froide indigènes comme le saumon chinook (Oncorhynchus tshawytscha) ou l’omble à tête plate (Salvelinus confluentus), mais plus favorables aux espèces d’eau chaude non indigènes comme l’achigan à grande bouche (Micropterus salmoides). [Traduit par la Rédaction]

Introduction

Record-breaking droughts and high temperatures observed across the northwestern United States in 2015 provided an opportunistic glimpse for future conditions that can provide additional information beyond modeled forecasts. Future climate can be predicted on a variety of temporal and spatial scales with varying degrees of confidence. Broadly, climate change is expected to raise temperatures and increase the likelihood of extreme events, e.g., unusually low streamflows, unusually high temperatures, in many areas (IPCC 2014). Streamflow trends across the western United States demonstrate earlier spring peak flows for the past half-century, at least in part caused by warming spring air temperatures (Regonda et al. 2005). Regional forecasts are similar. Based on numerous global climate models and emissions scenarios developed by the Intergovernmental Panel on Climate Change (Mote and Salathé 2010), mean air temperatures in the Pacific Northwest are expected to rise in the future. Most models show drier summers in the Pacific Northwest, including the occurrence of large-scale droughts (Mote and Salathé 2010). In general, global climate models systemically underpredict the occurrence of moderate to extreme drought (Palmer Drought Severity Index ≤ –3) (Wehner et al. 2011). Additionally, the quality of...
data from climate models for generating flows and defining driving forces at the extremes of their distributions is a major source of uncertainty in water quality model outputs (Hutchins et al. 2016). Although predicting future temperatures remains fraught with difficulties, insights gained from empirical data in an extreme year such as 2015 can suggest potential spatial and temporal conditions we might experience as the climate continues to change (Jackson et al. 2015; Picollozzi et al. 2018). For example, these insights can be used to explore how mesoscale climate forecasts (i.e., 1/16 degree, or ~5 km x 6 km resolution) may differ from observed fine-scale patterns in water temperature and how fish communities may react to future thermal landscapes.

Warmer and drier conditions in the Pacific Northwest are likely to have a range of ecological consequences for fish due to the complex interactions with critical physiological processes and functions. Range contractions have been predicted for many species as stream isotherms shift upwards and northwards (Isaak and Rieman 2013). Warmer mean water temperature during winter and spring would likely accelerate emergence of salmon fry from the gravel (e.g., Steel et al. 2012). Because both metabolic and growth rates in fishes increase with increasing temperature (Brett 1977; Beauchamp et al. 2007; Whitney et al. 2016), early exposure to warmer temperatures could cause mismatches in the timing at which food resources are needed and when they are available (Kennedy and Crozier 2010; Reed et al. 2010). For species migrating during this period, warmer temperatures and lower flows may also impede progress due to higher rates of metabolic stress (Whitney et al. 2016), increased susceptibility to pathogens or other stressors such as predation or angling (Goniea et al. 2006), inducing potential fitness consequences (Minke-Martin et al. 2018).

Changes in flow and temperature likely lead to shifts in temporal variability and in observed extremes of thermal conditions. Increases in variability are understood to destabilize aquatic communities through reduced predictability (Waples et al. 2009); reductions in natural patterns in variability may also have negative consequences (Steel et al. 2017). In the Pacific Northwest, community-level consequences are likely. Fish assemblages across European rivers, for example, have been linked to mean temperature of the warmest quarter of the year and also maximum temperature of the warmest month (Pletterbauer et al. 2015). A clearer understanding of potential spatial and temporal shifts in water temperature locally can help managers predict and mitigate changes in phenology of life history transitions and areas of shrinking suitable habitat.

Climate-driven stream warming is also expected to alter the pathways, rates of spread, and impacts associated with aquatic invasive species (Rahel and Olden 2008). Recent evidence suggests that warming stream temperatures are facilitating the range expansion of nonnative warm-water predators such as smallmouth bass (Micropterus dolomieui) in the region (Lawrence et al. 2014). Smallmouth bass have both direct predation impacts on salmonids as well as indirect nonconsumptive impacts on behavior, growth, and stress (e.g., Carey et al. 2011; Kuehne et al. 2012). Smallmouth bass have recently been found in traditionally cooler headwater habitats that contain endangered subspecies of Pacific salmon (Lawrence et al. 2012), heightening concerns about its distributional potential and ecological impacts.

To enact effective conservation and management plans that are resilient to climate change, aquatic resource managers require real-world examples illustrating how thermal conditions may change in a warmer climate. We provide one such example by applying spatial stream network models (SSNMs; Peterson and Ver Hoef 2010; Ver Hoef and Peterson 2010) to data collected every 30 min at 42 locations on the Snoqualmie River network, Washington State, USA. Our objectives are to (i) compare spatiotemporal water temperature patterns in 2015 with those observed during years with more typical weather (2012–2014) as an estimate of how future thermal regimes may shift on river networks and (ii) consider implications of climate-altered thermal regimes for native and nonnative fishes as well as natural resource monitoring and management.

Methods

Study area and data collection

The Snoqualmie River drains a 1813 km² watershed on the west side of the Cascade Range, Washington State (Fig. 1). Headwaters of the three main forks of the river lie in predominantly forested public land. Just below the convergence of these three forks, the river flows over Snoqualmie Falls, a spectacular 82 m drop, and then runs through a wide floodplain dominated by agricultural, residential, and commercial land use. Much of the floodplain lies within an agricultural protection district established by King County. About 16 km below the study area, the Snoqualmie River and Skykomish River merge to become the Snohomish, which empties to Puget Sound an additional 38 km downstream. The Snoqualmie watershed supports Puget Sound Chinook salmon (Oncorhynchus tshawytscha) and steelhead trout (Oncorhynchus mykiss), which are listed as threatened under the Endangered Species Act. Bull trout (Salvelinus confluentus) have been documented in the nearby Skykomish River and are presumed but not observed in the Snoqualmie River. Large-mouth bass (Micropterus salmoides) and other nonnative species favoring warm waters have been found in off-channel habitats associated with the lower main stem from the Tolt River confluence down past our lowest monitoring station (Kollin Higgins, personal communication) and in lentic habitats above the falls (Jamie Thompson, personal communication). We did not find conclusive evidence of largemouth bass in lotic habitats above Snoqualmie Falls, although Thompson et al. (2011) do report warm-water fishes, including largemouth bass, in the outflow of a pond just above the falls after a large storm event.

Water temperature loggers (N = 42) were installed throughout the main stem, on each of the three main forks of the Snoqualmie River, on major downstream tributaries including the Tolt and Raging rivers, and on a selection of minor tributaries (Fig. 1). Practical limitations forced sites to be publicly accessible, or on private property with landowner permission, and within 1 km of a road. The Raging River, a major tributary in the lower watershed, was intentionally oversampled to enable analyses of the effects of scale on monitoring designs in other studies. For this study, water temperature was recorded using Onset Tidbit loggers every 30 min from 1 October 2011 through 30 September 2015. We hereinafter use hydrologic years (1 October – 30 September) instead of calendar years, with the year of summer data as the year of reference. As part of a separate pilot study, air and water temperature data were recorded at a subsample of 12 sites distributed on the network during June of 2015 and 2016 (Fig. 1).

Data were summarized into metrics that describe fairly standard facets of the thermal regime, e.g., summer mean temperature or winter thermal variability (Steel et al. 2017), as well as customized metrics that capture facets of the thermal regime linked to success of native and nonnative fish species at particular life stages (Table 1). A number of decisions needed to be made in calculating each facet, for example, how many missing observations to allow and whether missing data were interpolated. Decisions were based on the size of the time window under consideration, with longer time windows allowing more missing observations, and on the potential impact of interpolation on the final metric value (Table 1). Air and water temperature relationships were summarized as the correlation between daily mean air temperature and daily mean water temperature in June because it was the month that saw the greatest changes in air and water temperature in 2015. Prior to calculating summary metrics, we cleaned data to remove missing or erroneous data (Sowder and Steel 2012).
Fig. 1. Map of water temperature monitoring stations in the Snoqualmie watershed (circles) and correlations between daily mean air and water temperature in June 2015 (white bars) and 2016 (black bars) at stations where we monitored both (bar charts; y axes range from 0 to 1). The six plots along the margins show time series of air temperature monitored during 2015 (black lines) relative to the range observed historically (1970–1999; dark gray shading) and predicted for the future (2070–2099; light gray shading) at that site. The star indicates the location of the USGS gaging station used for water discharge and temperature data depicted in Fig. 2. The Snoqualmie watershed boundary and streams are from the National Hydrography Dataset version 2 (McKay et al. 2012); USA state and North American country boundaries in the inset are from Esri in Redlands, California, USA.
Table 1. Metrics describing facets of the thermal regime of biological relevance to native and nonnative species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Life stage</th>
<th>Type</th>
<th>Metric</th>
<th>Weeks</th>
<th>NA</th>
<th>I</th>
<th>Interpretation (higher =)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chinook salmon</td>
<td>Eggs</td>
<td>Phenology</td>
<td>Days until 1200 degree-days accumulated (hourly) (from 15 Sept.; defines Chinook “emergence”)</td>
<td>1</td>
<td>i</td>
<td></td>
<td>Later</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Proportion of hours 10–16 °C (“emergence” to 31 July)</td>
<td>2</td>
<td>i</td>
<td></td>
<td>Increased (&gt;0.33 = good)</td>
</tr>
<tr>
<td>Adult migration</td>
<td>Survival</td>
<td></td>
<td>Maximum of the 7-day maximum (1 June – 15 Oct.)</td>
<td>2</td>
<td>i</td>
<td></td>
<td>Reduced</td>
</tr>
<tr>
<td>Bull trout</td>
<td>Spawning initiation</td>
<td>Survival</td>
<td>Hours over 13 °C (15 Sept. – 15 Nov.)</td>
<td>1</td>
<td>i</td>
<td></td>
<td>Reduced (&lt;22 = good)</td>
</tr>
<tr>
<td></td>
<td>Eggs</td>
<td>Phenology</td>
<td>Days from first temperature below 9 °C until 190 degree-days accumulated (daily) (defines bull trout “emergence”)</td>
<td>1</td>
<td></td>
<td></td>
<td>Later</td>
</tr>
<tr>
<td>Juvenile</td>
<td>Survival</td>
<td></td>
<td>Proportion of hours &gt; 20.9 °C (“emergence” to 30 Sept.)</td>
<td>2</td>
<td>i</td>
<td></td>
<td>Reduced (0 = good)</td>
</tr>
<tr>
<td>Spawning initiation</td>
<td>Phenology</td>
<td></td>
<td>Days after 1 Oct. until water temperature drops below 9 °C</td>
<td>2</td>
<td>i</td>
<td></td>
<td>Later (&lt;10 = good)</td>
</tr>
<tr>
<td>Largemouth bass</td>
<td>Eggs</td>
<td>Phenology</td>
<td>Proportion of hours 13–30 °C (“emergence” to 30 Sept.)</td>
<td>1</td>
<td></td>
<td></td>
<td>Increased (&gt;0.33 = good)</td>
</tr>
<tr>
<td></td>
<td>Juvenile</td>
<td>Habitat quality</td>
<td>Proportion hours 15–32 °C (“emergence” to 30 Sept.)</td>
<td>2</td>
<td>i</td>
<td></td>
<td>Increased (&gt;0.33 = good)</td>
</tr>
<tr>
<td>Spawning initiation</td>
<td>Phenology</td>
<td></td>
<td>Julian date at which temperatures reach 15.6 °C</td>
<td>2</td>
<td>i</td>
<td></td>
<td>Later</td>
</tr>
<tr>
<td>Peak spawning</td>
<td>Phenology</td>
<td></td>
<td>Days until 7 x 24 h of temperatures &gt; 15.6 °C accumulated (hourly)</td>
<td>1</td>
<td>i</td>
<td></td>
<td>Later</td>
</tr>
</tbody>
</table>

Note: Weeks NA documents the maximum number of weeks with missing data allowable to calculate metric. Missing data were interpolated for all metrics listed as “i” in the Interpretation column (I). Interpolation was done by averaging observations every 30 min for the 3 days before and after the missing data. Information in the Interpretation column explains the meaning of a higher value for the metric for that species, with “increased” referring to increased habitat quality and “reduced” referring to reduced habitat quality; parenthetical descriptions of good habitat refer to thresholds mapped in Fig. 8. Chinook salmon metrics are based on work by Steel et al. (2012) (eggs); Poole et al. (2001) (juvenile); and Stohr et al. (2011) (adult migration and spawning initiation). Bull trout metrics are based on work by Williamson (2006) (eggs); Selong et al. (2001) (juvenile); and McPhail and Murray (1979) (spawning). All largemouth bass metrics were developed from information in the synthesis by Stuber et al. (1982).

Understanding climate patterns observed in 2015

Past and future air temperature predictions

We graphically compared past (1970–1999) and predicted future (2079–2099) trends in air temperature with our observed air temperature data (2015) at each of the 12 sites for which we collected air temperature data. The historical data are observationally based gridded maximum and minimum daily air temperatures (Livneh et al. 2015), adjusted to match monthly time series from PRISM (Daly et al. 2008). Future air temperature data are predictions from ten global circulation models from the Coupled Model Inter-Comparison Project, Phase 5 (Taylor et al. 2012) for a high “business-as-usual” greenhouse gas emissions scenario, representative concentration pathway 8.5 (RCP 8.5; van Vuuren et al. 2011). Daily maximum and minimum air temperature from global circulation models were statistically downscaled at a 1/16th degree resolution (~5 km x 6 km) using the multivariate adaptive constructed analogs method (Abatzoglou and Brown 2012) and were bias-adjusted so that monthly data matched PRISM (Mauger et al. 2016).

Past water temperature and discharge data

We obtained all available discharge (1960–2015) and water temperature (1995–2015) data from the US Geological Service (USGS) gage above the Tolt River reservoir, USGS gage 12147600, South Fork Tolt River Near Index, Washington, which has a relatively undisturbed watershed. We then graphically compared water temperature and discharge in past years with observed data in 2015. For a subset of sites, we also compared our data from 2012–2014 with that of 2015 to assess whether the extremes observed in 2015 were consistent across the watershed. To identify which facets of the thermal regime might have differed between 2015 and past years and which parts of the calendar year might have been most affected, we calculated a set of standard water temperature metrics (mean, maximum, minimum, and variance) for all available past years of USGS water temperature data (1995–2014) at this same gage for each of four months (March, June, September, and December) and compared the past distribution of these metrics with what was observed in 2015.

Air and water correlations in 2015 versus 2016

We estimated and compared the correlation between daily mean air and water temperature in June 2015 and 2016 to explore whether relationships between air and water temperature remained consistent on the network and over years.

Estimating the distribution of thermal facets in 2015 as compared with past years

To estimate the spatial distribution of facets of the thermal regimes on the network in 2015, and to compare these patterns with those from past years, we applied spatial stream network models (SSNMs). SSNMs capture the unique branching structure of the river network, connectivity between sites that are flow-connected, streamflow volume, and directionality of streamflow, as well as discontinuities that often occur in tributaries just up-stream of the river confluences (Peterson and Ver Hoef 2010; Ver Hoef and Peterson 2010). We use an exponential tail-up SSNM structure and a model that includes three well-established covariates of water temperature in this basin: elevation (m), mean annual streamflow (feet^3/s), and percentage of the drainage area in commercial land use (Steel et al. 2016; Marsha et al. 2018). We used mean annual streamflow to determine the spatial weights that split the moving average function at confluences. Models are not intended to be best-fit models, but are reasonable models that can be used for comparing the spatial distribution of various facets of the thermal regime across years.
We compared observed summer and winter mean, minimum, maximum, and variance between 2015 and the three previous years at ten representative sites. To create maps of how 2015 differed with respect to particular facets of the thermal regime, predictions of the facet, e.g., summer mean temperature, were created for 2012, 2013, 2014, and 2015 data independently at each of 1219 prediction points along the Snoqualmie River. Spatial sub-
traction was used to map differences between predictions at each point for 2015 and the observed range for 2012–2014.

Comparing spatial patterns of August mean temperature in 2015 with past years and with future forecasts
We applied SSNMs to our observed August mean temperatures in 2012–2014 and mapped the mean of these predictions; this map illustrated conditions typical during August in the recent past as a comparison for past summaries and future forecasts of August mean temperature from the NorWeST project (Isaak et al. 2017). We also applied SSNMs to August mean temperatures in 2015 and produced a map to illustrate spatial patterns during an extreme summer. Spatial subtraction was used to describe and visualize changes between these two periods. We then examined past (2002–2011) estimates and future (2080s) predictions of mean August temperature on the Snoqualmie River network from the NorWeST project (Isaak et al. 2017). We again used spatial sub-
traction to describe and visualize predicted changes between these two periods. Finally, spatial subtraction was used to compare es-
timates of past thermal patterns between our data (2012–2014) and NorWest (2002–2011), as well as to compare estimates of future conditions between our data (2015) and NorWest (2080s).

Identifying ramifications for native and nonnative fishes of potential future spatiotemporal shifts in water temperature regimes on river networks
We created and calculated a set of species-specific and life stage-
specific thermal metrics to understand how facets of the thermal regime that regulate success at various life stages for Chinook salmon, bull trout, and largemouth bass were distributed in the extreme year 2015 and might therefore be distributed in the future (Table 1). We then compared the value for 2015 with what was observed in 2012–2014 for ten representative sites on the stream network.

To explore how nuances of the thermal landscape could be used to identify areas important for fish management, we mapped sev-
eral novel combinations of thermal facets. First, we modeled areas of the network that were good or poor for multiple life stages for Chinook salmon, bull trout, and largemouth bass were distributed in the extreme year 2015 and might therefore be distributed in the future (Table 1). We then compared the value for 2015 with what was observed in 2012–2014 for ten representative sites on the stream network.

To explore how nuances of the thermal landscape could be used to identify areas important for fish management, we mapped several novel combinations of thermal facets. First, we modeled areas of the network that were good or poor for multiple life stages of each of our three target species in both 2014 and in 2015. We used the modeled thermal facets (Table 1) to identify areas that had the most hours suitable for spawning (Chinook salmon), earliest spawning (bull trout), or most hours suitable for egg incubation (largemouth bass). To these, we overlaid areas with the most suit-
able hours for juvenile rearing by species. The overlays describe those areas of the river network in which we might expect that, even in extreme years, suitable habitat for multiple life stages will be present. Next, we modeled and mapped thermal facets associ-
ated with phenology (Table 1) to identify areas of the network for increased monitoring or areas of concern. We were interested in differentiating areas in which the life history transitions of all species are likely to be earlier or later and, more interestingly, the areas in which desynchronization is likely to occur.

Results
How did 2015 compare with other years?
Compared with past years, 2015 was notably warmer and drier during some parts of the year and in some parts of the basin
When comparing stream discharge and water temperature in 2015 with data available from a long-term gage, we found that hydrologic year 2015 was both drier and warmer in winter and in early summer (Fig. 2). There were clear seasonal shifts, with warming initiating earlier in the calendar year and periods of unusually warm and dry conditions in February and June. Comparing 2015 with 2012–2014 at four example sites on the network (Fig. 2), it is clear that water temperature in 2015 was much more unusual as compared with past years on some parts of the network, e.g., the lower main stem, the South Fork, and the North Fork, than on others, e.g., the Raging River.

We found a stronger consensus between observed 2015 air tem-
peratures and projected end-century temperatures for upstream sites compared with downstream sites (Fig. 1). Even comparing across the most upstream sites, there was considerable variability. For example, air temperature near the headwaters of the South Fork, “SF Asahel”, was much more similar to future projections than to past data. Patterns of air temperature near the headwaters of the North Fork, “NF headwaters”, were similar to those of the South Fork but less extreme (Fig. 1). By contrast, air temperature in 2015 at the downstream Cherry Creek site was well within the historical range. Across all 12 air temperature stations (data not shown), we saw considerable variability in how similar observations were to past data versus future projections, but temporal patterns at all sites showed winter temperatures and early sum-
temperatures that were unusually warm (Fig. 1). Air and water correlations in June differed somewhat across the basin but were generally higher in 2015, our extreme year, than in 2016, a more moderate year (Fig. 1).

Some facets of the thermal regime were more unusual than others in 2015, and patterns shifted seasonally on the stream network
Commonly calculated facets of the thermal regime, including mean, minimum, maximum, and variability in temperature, were unusual in 2015, more so during some parts of the year than during others (Fig. 3). All facets of the thermal regime were ex-
treme in March and June. No facets were extreme in September. Maximum temperatures were extreme in December of both the 2015 water year (December 2014) and 2016 water year (December 2015). Mean temperatures were high during these same periods. Minimum temperatures and variance in temperature were not unusual in December of either year (Fig. 3).

Zooming in on observed differences in thermal regime across seasons and at particular sites, most differences were fairly large but, for a few sites, there were only minor changes. Mean temperatures warmed at all sites during both summer and winter, but the maximum difference between 2015 and previous years ob-
served across sites investigated was only 1.53 °C in winter as com-
pared with 4.38 °C in summer (Fig. 4). Minimum and maximum weekly temperatures also increased at all sites. In winter, shifts in daily range were much smaller; there were only two sites for which overall variability in temperatures in 2015 was outside the range of what was observed in previous years. In summer, daily range generally increased a small amount, whereas overall vari-
ability decreased at most sites (Fig. 4; also refer to online Supple-
mentary material, Table SM1). All thermal facet models were reasonably successful as indicated by root mean squared errors ranging from 0.39 to 1.32. A combination of covariates and spatial structure explained at least 50% of the variance in all cases other than the juvenile Chinook salmon thermal metric for which the models were only able to explain about 30% of the observed variance in some years and the bull trout juvenile metric that explained less than 20% of the observed variance in 2012 and 2013. Total variance explained for Chinook salmon eggs, bull trout spawning initiation, and large-
mouth bass egg incubation suitability was well over 90% in 2013–
2015. Over 80% of the variation was explained for all facets in 2013.
Fig. 2. Discharge and temperature data from USGS gage 12147600, South Fork Tolt River Near Index, Washington (Fig. 1), 1960–2014 (top two panels). Observed data are from 2012 to 2015 for four sites on the Snoqualmie River, Washington (bottom four panels). Observed values from 2015 are in black for both USGS and our own data, with other years shown in gray.
except bull trout juvenile habitat suitability. We note that the sample size for some metrics was smaller in 2012 due to missing data; any unusual predictions for this one year would make our estimates of differences between 2012–2014 and 2015 conservative.

By modeling multiple facets of the thermal regime on the stream network, we found that winter means were estimated to be warmer in 2015 only in the headwater regions. Interestingly, 2015 winter temperatures on the main stem were relatively similar to what had been observed during the 3 previous years (Fig. 5). In contrast, we found that mean summer conditions in 2015 were more extreme than previous years, particularly in the main stem and also in headwater areas. Differences between winter minima in 2015 and other years were distributed similarly to differences in winter means but were, overall, less dramatic. Summer maxima
were most different from previous years in the main stem and headwaters but the largest differences were patchily distributed. Winter variance in 2015 was generally within the range of values seen in previous years. Interesting patterns emerged with respect to summer variance. Summer variance in 2015 was very low compared with previous years in all upland areas as well as in the main stem, but lowland tributaries differed by only about 1 °C from previous years. Lowland streams draining into the main stem had thermal regimes that were most similar to past years with respect to all six modeled facets (Fig. 5).

**Future August mean temperatures on the network as estimated from 2015 data differed substantially from predictions of a consistent 2 °C temperature increase on the network**

The spatial distribution of August mean temperatures on the stream network was quite different in 2015 when compared with the 3 previous years. Assuming future years will resemble 2015, we would expect that upland tributaries would warm more than the main stem; that there would be some spatial disparity in warming across upland tributaries; and lowland tributaries would warm relatively less than other parts of the network (Fig. 5).

These 2015 observations provide a relatively different vision of the future than other published forecasts. NorWeST forecasts, for example, estimate a 2 °C increase in air temperature everywhere. NorWeST forecasts suggest a future in which upland tributaries remain relatively cool and main stems hit new high temperatures.

**What are the ramifications for fishes?**

**Future thermal landscapes may reduce the success of native fishes at multiple life stages and increase the success of nonnative fishes**

The thermal landscape of 2015 provides an estimate of how habitat conditions for species of interest may shift (Table 2). Examining headwater habitats, we find that optimal spawn timing is likely to occur later for bull trout at most sites and there are likely to be more days that are too warm for optimal juvenile growth and feeding for bull trout at some sites. Days required for egg incubation may increase at some sites and decrease at others (Fig. 7; Table 2; Table SM2). Further downstream, there may be higher maximum temperatures during migration, more hours over the thermal threshold for spawning, and more hours within optimal juvenile rearing temperature windows for Chinook salmon. Chinook salmon would likely emerge earlier at all sites (Fig. 7; Table 2; Table SM2). In the lowest reaches, where largemouth bass occur, we would expect to see earlier spawning at some locations with fewer hours in the optimal thermal window for juvenile growth and feeding at one site and slightly more hours in this optimal window at another (Fig. 7; Table 2; Table SM2).

**There were shifts in the availability of areas conducive to two life history stages for all three species**

In particular areas of the river network, thermal regimes were conducive to multiple life history stages of species of interest even in the recent extreme year. In other areas, thermal regimes that had been conducive to one or more life history stages from 2012 to 2014 were no longer suitable in 2015 (Fig. 8). We also identified areas on the network that are not good for two life stages of Chinook salmon or bull trout under current conditions but that may transition to good thermal habitat for both life stages in the future. Of particular interest are large downstream areas that had been poor for largemouth bass from 2012 to 2014 but for which good habitat was estimated for multiple life stages in 2015. Lastly, by combining SSNMs, the concept of thermal facets, and insights from extreme years, we did identify areas of the basin in which desynchronization of life history transitions is likely to take place, that is, areas for which spawning or emergence is likely to be earlier for some species and later for others (Fig. 9).
Discussion

Future thermal landscapes are likely to be quite different from those of the recent past. By exploring the distribution of thermal habitats in an extreme year, we provide a potential window into the future and guidance for watershed management in the face of altered precipitation regimes, rising elevation of snow-dominated hydrology, and higher temperatures. In 2015, early summer air temperatures in parts of the Snoqualmie basin were more similar to what is forecast for the 2080s than to what we have observed in the past. If the thermal landscape of 2015 is an indication of thermal landscapes of the future, we are likely to see seasonal disparity in whether water temperatures are extreme and spatial disparity in how warmer temperatures occur on the network (Kubo and leDoux 2016).

The future may look different not simply in that it is warmer. There is also likely to be rearrangement of facets of the thermal regime, e.g., increases or decreases in variability at particular time scales or shorter time intervals between periods of unsuitably warm temperatures, which yields new and potentially non-analogue thermal landscapes. We found evidence for a decrease in

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Fig. 5. Spatial distribution of changes in (a) winter average temperature (Winter AWAT); (b) summer average temperature (Summer AWAT); (c) winter minimum temperature (Winter mWAT); (d) summer maximum temperature (Summer MWAT); (e) winter variance; and (f) summer variance. Difference (°C) depicted is the distance between the 2015 value and the range of observed values from 2012 to 2014; white indicates that location was within the range of values from 2012 to 2014. Triangles and color of triangle fill denote location and difference (°C) for observed data. Values at other locations were predicted using spatial stream network models.
thermally suitable habitat for native bull trout and an increase in thermally suitable habitat for nonnative largemouth bass in 2015. Thermally suitable habitat for Chinook salmon increased for some life stages in some parts of the basin. Patterns observed in 2015 were distinctly different from those predicted via other modeling systems. In particular, temperatures were warmer in some headwater areas (Fig. 6).

We estimate that thermal landscapes such as what was observed in 2015 will lead to phenological shifts for all species. We saw spatially distinct patterns in where particular life stages are likely to occur earlier versus later, some areas with shifts as large as 2 months, and large parts of the basin where asynchronies between species are likely to occur. Such patterns are supported by Lawrence et al. (2012, 2014), who found increased sympathy between smallmouth bass and juvenile Chinook salmon during spring stream warming.

Extreme years can provide nuanced insight into heterogeneity of future thermal landscapes

Future climate models are challenged to predict variability within landscapes due to their limited ability to represent the details of terrain and processes (IPCC 2014). Although statistical downscaling can provide more detailed patterns by combining observational data and global climate models (Abatzoglou and Brown 2012; Abatzoglou et al. 2014), analog years provide specific examples of patterns or events that are additionally useful to managers (Wilke and Morton 2017). Specific years, such as 2015, can provide harbingers of the sorts of patterns we may observe.
Table 2. Observed biological implications of differences in facets of the thermal regime between 2015 and 2012–2014.

<table>
<thead>
<tr>
<th>Species</th>
<th>Life stage</th>
<th>Type</th>
<th>Mean observed difference: 2015 versus 2012–2014</th>
<th>Potential biological implication</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chinook salmon</td>
<td>Eggs</td>
<td>Phenology</td>
<td>–28.00</td>
<td>Fry emerge from gravel nearly a month early, potentially during unsuitable flow conditions and likely desynchronizing food webs</td>
</tr>
<tr>
<td></td>
<td>Juvenile</td>
<td>Habitat quality</td>
<td>0.10</td>
<td>More time conducive to growth and survival, with potentially increased growth rates and energetic demands</td>
</tr>
<tr>
<td></td>
<td>Adult migration</td>
<td>Survival</td>
<td>2.98</td>
<td>Lower survival during adult migration</td>
</tr>
<tr>
<td></td>
<td>Spawning initiation</td>
<td>Survival</td>
<td>78.57</td>
<td>Many more hours with low survival during spawning</td>
</tr>
<tr>
<td>Bull trout</td>
<td>Eggs</td>
<td>Phenology</td>
<td>1.10</td>
<td>Fry emerge from gravel a bit later, potentially desynchronizing food webs</td>
</tr>
<tr>
<td></td>
<td>Juvenile</td>
<td>Survival</td>
<td>0.01</td>
<td>Lower juvenile survival</td>
</tr>
<tr>
<td></td>
<td>Spawning initiation</td>
<td>Phenology</td>
<td>13.62</td>
<td>Spawning occurs later, which likely further delays fry emergence</td>
</tr>
<tr>
<td>Largemouth bass</td>
<td>Eggs</td>
<td>Phenology</td>
<td>0.00</td>
<td>No change in proportion of time conducive to egg survival</td>
</tr>
<tr>
<td></td>
<td>Juvenile</td>
<td>Habitat quality</td>
<td>0.06</td>
<td>More time conducive to growth and survival, with potentially increased growth rates and energetic demands</td>
</tr>
<tr>
<td></td>
<td>Spawning initiation</td>
<td>Phenology</td>
<td>–28.71</td>
<td>Spawning could begin almost a month earlier</td>
</tr>
<tr>
<td></td>
<td>Peak spawning</td>
<td>Phenology</td>
<td>–33.20</td>
<td>Peak spawning conditions were reached just over a month earlier</td>
</tr>
</tbody>
</table>

Note: Observed mean change, across all potentially occupied sites, by species is indicated. For bull trout, potentially occupied sites included the upstream sites of the three forks of the Snoqualmie; for Chinook salmon and largemouth bass, potentially occupied sites included the main stem Snoqualmie below the falls and the main stems of both major tributaries, the Raging and Tolt rivers.

Fig. 7. Relative change (how far 2015 is outside of the range of observed values for 2012–2014) across a set of sites (highest on the network at left; see Fig. 1) in metrics representing facets of the thermal regime thought to be related to the success of particular species during particular life stages (Table 1). Data are presented only at sites presumed as habitat for each species (i.e., bull trout, if present, would use headwaters, Chinook salmon are restricted to areas below Snoqualmie Falls, and largemouth bass occur only in the lowest reaches). Sizes of circles in each row indicate relative values within a row and are scaled to the maximum value for each metric (Max Change); numerical values are in Supplementary materials (Table SM2). Shade of circles indicates that the observed value in 2015 was likely to increase (white) or decrease (black) the success of that species in that life stage; hatched circles indicate an unknown biological effect, with the angle of hatch marks depicting an increase (right-leaning) or decrease (left-leaning) in the metric; absent circles indicate that 2015 was within the range observed for 2012–2014. Abbreviations for Max Change: h = hours; d = days; h/h = proportion of hours.
Fig. 8. Locations across the watershed that were good versus poor for two life stages in 2014 (top row) and 2015 (middle row) by species. Modeled life stages for bull trout and Chinook salmon are juvenile and adult and for largemouth bass are juvenile and eggs (Table 1); good values are defined in Table 1, with all else considered poor. The bottom row of maps compares years to identify patches of habitat that might be targets for restoration or mitigation (areas currently good but likely to have reduced habitat quality in extreme years), protection of habitat (areas currently poor for native fish but expected to improve in extreme years), and nonnative species control programs (areas currently poor for nonnative fish but likely to improve in future extreme years).
with increasing frequency under a changing climate (Cooper et al. 2016; Marlier et al. 2017). As such, they can provide detailed and structured examples that we are unlikely to acquire from other sources. For instance, 2003 was an anomalously warm year in Europe. Using empirical water temperature data from 2003, Jackson et al. (2018) and Piccolroaz et al. (2018) identified particular regions of Scotland and Switzerland, respectively, that may warrant extra conservation measures in the future.

Shifts in future thermal regimes are not likely to be consistent over the annual cycle, for all facets of the thermal regime (Arismendi et al. 2012), or on river networks. In 2015, we observed the biggest changes in early summer, in maximum temperatures, and in upland tributaries. These patterns were quite different from those predicted by other methods that suggest that high elevation tributaries may provide long-term refugia for native fishes (Isaak et al. 2015; Piccolroaz et al. 2018). Nuanced change in the thermal regime observed in 2015 resulted from a combination of snowpack accumulation, solar radiation, groundwater inputs, and riparian shading, among other things, and would therefore be difficult to model or predict using mechanistic or statistical methods built from average past experience.

In the Snoqualmie River, monthly water temperature patterns for the North, Middle, and South forks, where precipitation often falls as snow and where snowmelt has contributed greatly to spring and summer flows, were quite shifted in 2015 as compared with previous years. Each fork exhibited a fairly unique pattern that likely resulted at least in part from the change in accumulated snowpack in the associated watershed. Of concern was the South Fork of the Snoqualmie River, where air temperatures were much warmer than hindcasted past temperatures and where air and water temperatures were strongly correlated in 2015 (Fig. 1).

Although other researchers have found areas where headwater temperatures remain low due to strong local topographic controls (Daigle et al. 2015; Isaak et al. 2016; Piccolroaz et al. 2018), our findings suggest that there are also headwater areas where warming is occurring more rapidly than in other parts of the network.

Conversely, in major lowland tributaries like the Raging River, we observed a much less pronounced change in monthly streamflow for 2015 as compared with years 2012–2014 and only moderately increased water temperatures (Fig. 2). The headwaters of the Raging River have rarely accumulated snowpack in the past; flows are largely driven by precipitation and possibly groundwater. As a
result, unseasonably warm spring temperatures did not induce effects that lasted into late or even early summer. The influence of groundwater inputs on observed and predicted spatial patterns of stream temperature is an area of active investigation. In southeast USA, increased future streamflow was estimated to largely offset effects of increased air temperature, allowing the persistence of thermal refugia for brook trout (Salvelinus fontinalis) provided that adequate flows persist (Merriam et al. 2017).

Our results contribute to a growing body of work suggesting heterogeneous impacts of a changing climate on future thermal landscapes. Heterogeneous patterns were predicted across salmon rivers in eastern Canada (Daigle et al. 2015). Chung et al. (2016) predicted variable water temperature increases leading to differential effects of warming temperatures on thermal habitat suitability by river basin in Korea. Chen et al. (2016) also observed heterogeneity of warming rates across seasons and river reaches in China, with more pronounced climate effects for lower-flow rivers and during the dry season; and an east–west gradient of thermal change over time was observed across Poland (Marszelewski and Pius 2016). Using data from over 20 000 river segments across mainland Britain, Jonkers and Sharkey (2016) estimated heterogeneity over space, on the annual cycle, and by facet of the thermal regime in past thermal change as well as in forecasted future thermal landscapes.

Future river temperature regimes will likely be more conducive to some species and life stages than to others.

We can use thermal landscapes observed in extreme years to forecast the distribution of future thermal habitats for particular fish species at particular life stages. In our case study of the Snoqualmie River, the future does not bode well for the most cold-water-dependent fish in our study, bull trout, or for adult life stages of Chinook salmon; yet, juvenile Chinook salmon may see some areas of increased habitat suitability. The loss of bull trout habitat during a warm, low-flow year was expected. Benjamin et al. (2016) also applied a facet-based approach to identifying thermal conditions suitable to particular species at particular life stages. In that study, bull trout thermal habitat was associated with cooler and more variable thermal regimes, and bull trout were found to be more sensitive to thermal maxima when compared with other trout species. Similarly, Ruesch et al. (2012) used a spatially explicit statistical model to predict 86%–100% loss of summer thermal habitat for bull trout in the John Day River, United States, by the end of the century.

Based on our observations during 2015, largemouth bass, a warm-water nonnative species, may expand its range farther up the mainstem Snoqualmie and Raging rivers, where thermal habitat suitability was predicted to increase for the adult life stage (Fig. 8). Patterns in which future thermal landscapes are likely to be increasingly conducive to native fishes and increasingly conducive to nonnative fishes are fairly common. Native fishes tend to be adapted to current and past thermal landscapes and potentially to a fairly specialized thermal habitat niche as opposed to possibly invasive nonnative fishes, which are often generalists (Carey et al. 2011; Lawrence et al. 2014). Increasing frequency of extreme events, e.g., very warm years and droughts, puts existing native species at a competitive disadvantage (Diez et al. 2012). More generally, researchers from around the world, including Iran (Morid et al. 2016), Korea (Chung et al. 2016), Canada (Daigle et al. 2015), and central Europe (Hardenbicker et al. 2017), have estimated losses of thermally suitable habitats for endemic fishes as a result of climate change.

A hopeful possibility is that thermally suitable juvenile Chinook salmon habitat may have increased in some areas in 2015, perhaps expanding beyond areas that are likely to be thermally suitable for largemouth bass (Fig. 8). Areas of the river network with water temperatures from 10 to 16 °C, most conducive to juvenile Chinook salmon growth from the time they emerge through midsummer, expanded upstream on main stems and into some of the larger lowland tributaries. These observations suggest that in the future, thermally suitable habitat for native fishes may be found in surprising places. Temperature is, of course, not the only driver of habitat quality. We do not know which sites may be colonized in the future, how the future spatial configuration of suitable habitats may support or fail to support population-level success, or whether new bottlenecks or opportunities may develop over the life cycle of these species. Life cycle models that can link, for example, reductions in spawning area with increased growth opportunities for juveniles will be essential to manage native species in a changing climate. Using an individual-based model, Fullerton et al. (2017) observed that modeled Chinook salmon grew larger and out-migrated to sea earlier with warmer springs and summers, and effects were more dramatic than with warmer winters or increased variability. In 2015, this earlier smolt outmigration was actually observed on the nearby Columbia River (DeHart 2016).

How shifts in phenology or growth at one life stage may filter through the life cycle and lead to new biological interactions or habitat constrictions at other life stages is an open question. For salmonids, changes in the timing of migration and reproduction, age at maturity, age at smolt migration, growth, survival, and fecundity have all been associated with changes in temperature in other studies (Crozier et al. 2008). We estimated that if Chinook salmon eggs were to incubate in smaller lowland reaches, emergence could occur over a month earlier in the future than it does now. In areas where Chinook salmon and largemouth bass might co-occur, variability in water temperatures at particular life stages and heterogeneity on the river network could lead to potentially important asynchronies that increase or mitigate competition (Fig. 9). For example, the darkest red areas in the lower map of Fig. 9 that fall along the mainstem river indicate that estimated shift in Chinook salmon egg emergence timing in 2015 was more than 30 days earlier than the estimated shift in timing for largemouth bass peak spawning in 2015. It is difficult or impossible to predict how such shifts in timing might eventually influence competition across the full life cycle. The most relevant work is on aquatic insects. Examining caddisfly (Tricoptera) distributions in the Loire and Usk rivers, Europe, over time, Hildrew et al. (2017) speculated that phenological shifts could induce spatial mismatches in key habitat characteristics that limit the ability of species to migrate into thermally suitable habitats. For fishes, our analyses suggest areas for monitoring and more intensive life cycle modeling of multiple species.

Species and community responses to future thermal landscapes are difficult to predict. Barriers to migration may differentially limit the ability of species to access thermally suitable habitats (Radinger et al. 2017), and water temperature is only one aspect of suitable habitat. Whether fishes, and in particular salmonids, can adapt to warmer thermal environments is unknown. Evidence for plasticity in responses to altered temperatures has been observed in salmonids as well as in a range of other fishes (Crozier and Hutchings 2014; Comte and Olden 2017). Though evolutionary adaption is possible, it has yet to be established for salmonids as a response to a warming climate (Crozier and Hutchings 2014). Untangling the mechanisms driving observed heat tolerance in fishes may lead to more refined estimates of freshwater fish sensitivity to particular facets of water temperature regimes.

Caveats and research needs

Our modeled thermal landscapes from 2012 to 2015 are built from empirical observations but are effectively smoothed representations of the true system. Small patches of cool or warm water, such as might be influenced by groundwater inputs, cannot be estimated at this time. Without this detail, our thermal landscapes likely underrepresent available thermal habitat in some areas and overrepresent available thermal habitat in other...
areas. Admittedly, observations from 2015 are not a crystal ball into the future but rather just one example of what an altered future thermal landscape, incorporating spatial heterogeneity in air temperatures, snow pack accumulation, groundwater inputs, and human influences, might look like. It is an example rather than a forecast. We also note that our models do not describe how fish actually responded in 2015, but rather they describe our best estimate of how thermal habitats shifted.

To better manage aquatic resources, we need two types of information to improve the applicability of these types of models. First, we need more detailed research identifying associations and dependencies of each life history stage of target fish species and specific facets of the thermal regime. We were limited to the research we could locate with specific links between life stages and water temperature, eventually modeling opportunistic estimates of species preferences and tolerances at particular life stages. To make the best use of water temperature data and spatial stream network models, it will be essential for research to link physiological and behavioral responses to likely shifts in thermal regime. For example, how do juvenile bull trout react to early season warming, and what is the threshold at which such reactions begin? Given the rapidly increasing number of researchers modeling river temperatures and future thermal landscapes, both laboratory and field studies to aid in predicting fish and community response to a range of thermal conditions should be a priority.

Second, we need water temperature data for entire river networks. Despite the recent proliferation of water temperature data and monitoring arrays (Detenbeck et al. 2016; Isaak et al. 2017; Steel et al. 2017), many opportunities exist for enhanced and relatively inexpensive river temperature monitoring. A UK-wide monitoring network, for example, has been identified as an opportunity to fill a priority knowledge gap (Hannah and Garner 2015). Deploying in-stream sensors for an entire year, selecting sites that cover the range of environmental characteristics that are likely to influence facets of most interest (e.g., Jackson et al. 2016), archiving hourly or daily information in long-term data sets, installing temperature loggers in remote tributaries, and synthesis across disparate data types are some of the ways in which monitoring programs might be improved to better assess thermal landscapes (Steel et al. 2017).

We also need continuous improvement in monitoring designs for collecting data on entire river networks and analytical tools for processing these data. Guidance on designing efficient monitoring arrays has been built from our Snoqualmie River data (Marsha et al. 2018). Future studies on efficient design of monitoring systems across ecoregions and network shapes as well on monitoring systems that combine in situ with remotely sensed data are needed (Vatland et al. 2015). Although there have been impressive recent developments in statistical methods to model phenomena on river networks, statistical tools that can capture both spatial and temporal variability simultaneously are still needed (Hannah and Garner 2015; Steel et al. 2017). As more monitoring arrays are installed, spatially continuous empirical data are incorporated, and models are better able to capture the full spatiotemporal complexity of thermal landscapes, we will be better able to capture and describe the portfolio of thermal conditions that result from a range of extreme conditions and to design nuanced management responses. Ideally, future thermal work can also provide a more detailed accounting of the uncertainty in predicted thermal regimes (Hannah and Garner 2015), including uncertainty induced through measurement error, temperature models such as spatial stream network models, climate forecasts, and models that describe the sensitivity of river temperatures to future changes in incoming solar radiation, air temperature, and precipitation patterns.

Management implications

Our approach, including measuring, modeling, and mapping the thermal conditions observed on the Snoqualmie River in 2015, can highlight local management opportunities as well as suggest more general implications for managing freshwater habitats in a changing climate. Our results, in combination with those of local resource managers (Kubo and leDoux 2016), highlight the importance of understanding spatial and temporal variation in temperature regimes, quantifying tributary and groundwater influences, and including daily patterns in thermal fluctuations when estimating future temperature issues and impacts on salmonids in the basin. Our results are intended as a proof-of-concept, describing how physiological research, novel thermal metrics, SSNNs, and data from unusual years can be combined to provide insight into the potential future distribution of fish habitat. Possible management actions that might be informed by combinations of analyses like this include riparian restoration in both the headwaters and along the lower main stems and tributaries, shifts in timing of water withdrawals, and natural flow rehabilitation, including enhancements to floodplain connectivity (Kubo and leDoux 2016; Lorenz et al. 2016; Woltemade and Hawkins 2016).

Our work, along with field tests and local knowledge, can inform where such management activities might best contribute to future resiliency of native fish populations. It is, for example, especially important to protect habitats where native species are likely to be least impacted by thermal stress and competition. Areas estimated to have improved thermal quality for juvenile Chinook salmon habitat in 2015 or estimated residual areas of higher quality bull trout habitat in the headwaters might be prime candidates for such protection activities. Restoration might, for example, focus on areas of the network that are estimated to be good habitat under common current conditions (2012–2014) but that transitioned to poor for at least one life stage in 2015. Target areas for nonnative species management programs might include areas that are conducive to nonnative species invasion at the boundary of their current range.

Our models suggest locations where increased monitoring might be particularly insightful. Areas of the basin where native and nonnative species are likely to interact in the future can be identified and monitored based on extreme years. Additionally, monitoring areas of river networks where large shifts in phenology are predicted to occur in the near future or are estimated to occur in extreme years can provide local and general knowledge about how these shifts in timing may influence species success over the full life cycle and how aquatic communities may reshape or react to thermal perturbations.

Finally, we encourage managers to build their vision of the future based on multiple models or approaches and with appreciation for the uncertainties involved in predicting the future. Combining insights from observations in extreme years, downscaled climate forecasts, and locally calibrated mechanistic models is likely to yield management strategies that are robust to the caveats and errors of any one model or approach.

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