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ORIGINAL ARTICLE

WILEY Ecology of FRESHWATER FISH

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

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Abstract

Many bull trout populations have declined from non-native brook trout introductions, habitat changes (e.g. water temperature) and other factors. We systematically sampled the distribution of bull trout and brook trout in the upper Powder River basin in Oregon in the 1990s and resampled it in 2013–2015, examined temperature differences in the habitats of the two species and analysed trends in temperatures in the light of possible increases associated with climate change. The species' distributions are currently similar to those in the 1990s, except in one stream where bull trout declined. However, bull trout consisting of resident forms remain restricted to a few kilometres of habitat at the upper end of fish distribution. In streams where both species occur, the typical pattern was an intermediate zone of mixed bull trout, brook trout, and hybrids downstream of allopatric bull trout and allopatric brook trout extending farther downstream. Temperature differences between where bull trout and most brook trout occurred were small (0.5–1.0°C August mean). There were no statistical increases in water temperatures in nearby streams since the 1990s and no warming trends in air temperatures for the past 25–60 years. However, peak summer water temperatures are occurring about 3 weeks earlier than 25 years ago. Future effects of climate change, including possible increases in temperature, changes in timing and other factors (e.g. snowpack, flow and extreme events) remain a concern for the persistence of these populations. However, it is difficult to precisely predict where those changes will occur and what they will be.

KEYWORDS
brook trout, bull trout, climate change, species interactions, water temperature

1 | INTRODUCTION

Brook trout *Salvelinus fontinalis* have been introduced into many watersheds inhabited by native bull trout *Salvelinus confluentus*, which is listed as threatened under the US Endangered Species Act and by the Committee on the Status of Endangered Wildlife in Canada. Where their distributions overlap, the two species can hybridise (Kanda, Leary, & Allendorf, 2002), reducing the reproductive potential of the bull trout. Brook trout may mature earlier (Leary, Allendorf, & Forbes, 1993), providing a reproductive advantage. Brook trout are also more aggressive, out-compete bull trout for food and grow more rapidly (Gunckel, Hemmingsen, & Li, 2002; McMahon, Zale, Barrows, Selong, & Danehy, 2007). Both species are found in cold-water streams; however, brook trout have a wider range of temperature tolerances and can occupy habitats that are warmer (Benjamin, Heltzel, Dunham, Heck, & Banish, 2016; Hokanson, McCormick, Jones, & Tucker, 1973; Selong, McMahon, Zale, & Barrows, 2001). As a result of these interactions where both occur, over time, bull trout may be replaced by brook trout in some streams or displaced in some stream reaches (Rieman, Peterson, & Myers, 2006), particularly if streams warm due to climate or other habitat changes.

In the Powder River basin in Oregon, brook trout have been widely introduced since the early 1900s, including many of the streams occupied by bull trout. In the mid-1990s, when this study was initiated shortly following petitions to list bull trout under the Endangered Species Act, little was known about the distribution of bull trout and brook trout in Oregon, the extent of hybridisation, or other interactions. Consequently, we initially designed this study to determine the distribution of the two species and the occurrence of hybridisation (Bellerud, Gunckel, Hemmingsen, Buchanan, & Howell, 1997). Feeding interactions and growth were examined in a related study (Gunckel et al., 2002).

In the last decade, concern has increased regarding the potential effects of climate change on fishes (e.g. Paukert, Lynch, & Whitney, 2016 and accompanying papers), particularly increasing temperatures (Isaak, Wollrab, Horan, & Chandler, 2011; Isaak et al., 2012). It has been hypothesised that climate change may result in some species with lower temperature preferences, such as brook trout, retreating farther upstream to higher, cooler reaches as temperatures increase (Wenger et al., 2011) and local displacement or extirpations of bull trout due to increases in temperature and overlap with brook trout (Rieman et al., 2007). However, few studies have documented changes in fish distribution in response to climate change (Lynch et al., 2016), and only one involved bull trout (Eby, Helmy, Holsinger, & Young, 2014). Furthermore, few field studies have directly measured water temperatures relative to where bull trout and other species occur; and accurate assessments of fish distribution, including upstream and downstream extents, such as those in this study, are key to understanding how temperature and climate may influence that distribution (Al-Chokhachy, Wenger, Isaak, & Kershner, 2013; Isaak & Rieman, 2013). In 2013, a workshop sponsored by the *Salvelinus confluentus* Curiosity Society was held in the upper Powder River basin, which provided an impetus to resample bull trout and brook trout distributions after approximately 20 years and to examine those distributions in relation to water temperatures and in the context of recent analyses of regional temperature trends (NorWeST, 2015) and projected effects of climate change on water temperatures and fish habitat (Isaak, Young, Nagel, Horan, & Groce, 2015). Since the Powder River basin is in the southern portion of the range of bull trout, changes in distribution and temperature might be particularly evident.

1.1 | Study area

The Powder River in northeastern Oregon flows into the Snake River upstream of Brownlee Dam. Thief Valley Dam, built in 1931 on the Powder River at river kilometre (Rkm) 114, blocked passage to much of the spawning and rearing habitat of salmon and steelhead *Oncorhynchus* spp. and other migratory species, potentially including bull trout, in the upper basin. Completion of Brownlee Dam in 1958 and two other dams in Hells Canyon eliminated passage of migratory fishes to and from the Powder River and other upstream tributaries of the Snake River. Mason Dam, which created Phillips Lake, at Rkm 211 on the Powder River was completed in 1968, and a number of other irrigation reservoirs were constructed on other tributaries of the Powder River (Nowak, 2004). None of those dams has fish passage facilities.

Most of the surface and groundwater in the basin are used for irrigation, and stream flows are fully appropriated by water rights (Nowak, 2004). Consequently, besides passage barriers posed by dams, passage of migratory bull trout has been impeded by diversion structures, low flows during irrigation seasons and high temperatures in diverted reaches for much of the past century. Many of the diversions are not screened to bypass fish. Mining has also impacted bull trout habitat, particularly upstream of Phillips Lake.

Current bull trout populations consist of resident forms in some of the tributaries to the upper Powder River upstream of Phillips Lake, the North Fork Powder River and Wolf Creek, which drain the eastern and southern slopes of the Elkhorn Mountains (Bellerud et al., 1997). Although stocking of brook trout was discontinued in recent decades, naturally reproducing populations are well established in headwater streams and lakes in the basin.

2 | METHODS

In 1996, we used a systematic sampling design to determine bull trout and brook trout distribution (Bellerud et al., 1997). Sample sites consisted of 100 m reaches at 1-km intervals beginning at the mouth of the stream or 2 km below the lower limit of bull trout distribution based on previous sampling data (ODFW, unpublished). The sampling interval and reach length provided a 10% sampling rate which had been suggested for the detection of bull trout at low densities (Hillman & Platts, 1993). We sampled sites with a backpack electrofisher, pulsed DC and no blocknets. To determine the upper limit of fish distribution, sites were progressively sampled upstream until we sampled two adjacent sites where no fish were detected upstream of the uppermost occupied reach.

After capture, fish were identified to species, measured and released into the section in which they were captured. Bull trout, brook trout and bull x brook hybrids were identified based on dorsal fin banding and spotting and patterns on the back (Markle, 1992). Identification was not verified by genetic testing, but other comparisons (DeHaan, Schwabe, & Ardren, 2009) indicated an overall accuracy of 89% for similar visual classification. Some additional sites in those streams were also sampled in the early-mid-1990s by Oregon Department of Fish and Wildlife (ODFW) stream survey crews using similar methods (ODFW, unpublished).

During 2013–2015, we resampled the streams sampled in 1990s that contained bull trout or a mix of bull trout and brook trout. We also sampled some additional streams which were suspected to have bull trout based on anecdotal reports or previous spot sampling (ODFW, US Forest Service [USFS] or US Fish and Wildlife Service [USFWS], unpublished). We used basically the same sampling design and methods used in 1996; however, the downstream limit of the reaches sampled was the elevation which corresponded to an average annual maximum weekly maximum temperature (MWMT) of 17.5°C, the temperature at which the probability of bull trout occurrence becomes low (Isaak, Rieman, & Horan, 2009). The elevation for that temperature break (1,304 m) was derived from a linear regression of MWMT temperature versus elevation using water temperature and elevation data for 26 sites in the upper Powder River basin for 1995–2003 (USFS, unpublished) (MWMT = 32.407 − (0.0101×elevation), $p < .001$, $R^2 = 0.50$). Sampling sites were selected at 1-km intervals upstream from that point, which included the elevation corresponding to 15°C MWMT (1,550 m) and high probability of bull trout occurrence (Isaak et al., 2009). The sampled elevations included all of the sites where bull trout were detected in 1996 (Figure 1). In the North Fork Powder River, we also sampled upstream from the mouth to determine the downstream limit of brook trout distribution.

During July and August 2014 and 2015, temperature loggers (Onset HOBO Water Temp Pro v2) were placed in allopatric bull trout, mixed bull trout and brook trout, and allopatric brook trout zones of distribution. To calibrate and standardise the loggers, the loggers were immersed for 1 hr in an ice bath at approximately 0°C. The temperatures recorded by the loggers were then compared to the temperature measured by a National Institute of Standards and Technology thermometer. To correct for bias, the temperature data recorded by each logger deployed at the field locations were then adjusted by the differences between the logger and the NIST thermometer immersed in the ice bath prior to analysis.

Various metrics of the magnitude of summer water temperature have been associated with bull trout and brook trout distribution (Adams & Bjornn, 1997; Benjamin et al., 2016; Dunham, Rieman, & Chandler, 2003; Rieman et al., 2006) and reflect temperatures that could be stressful for cold-water species. I calculated August and July means and mean minima, MWMT and degree days for each logger location. However, because the metrics were all highly correlated (Pearson correlation, see Results), I used mean August temperatures and MWMT to describe differences in species distributions. August mean temperatures allow comparisons with metrics used in regional water temperature analyses (NorWeST, 2015) and projected effects of climate change on habitat suitability (Isaak et al., 2015). MWMT represent the highest temperatures sustained over the warmest week during the summer and are commonly used for water quality standards for bull trout and other fishes promulgated by the US Environmental Protection Agency and state agencies that administer water quality standards.

Since consistently collected data during the 1990s through 2015 were not available for water temperature monitoring sites in the Powder River basin, to examine trends in water temperatures for that period, I analysed temperature data using linear regression for 16 sites in similar streams in the upper Grande Ronde River basin immediately adjacent to the Powder River basin (USFS, unpublished). The sites in the Grande Ronde River basin were all unregulated (i.e. not influenced by dams or diversions), include bull trout streams and are comparable in geology, climate, precipitation and elevation to the streams sampled in the Powder River basin. I also similarly analysed longer term (1943–2015) air temperature data throughout the summer (June through August means) for Baker City, Oregon, located near the study streams (Western Regional Climate Center, 2015) since temperature patterns during periods as long 20 years (the span of the distribution sampling and available water temperature data) may not reflect long-term climate trends (Easterling & Wehner, 2009). Air temperature data are commonly used as a surrogate for water temperatures, when the latter are not available (e.g. Isaak et al., 2012; Rieman et al., 2007; Wenger et al., 2011), although its relationship to water temperatures can be imprecise (Isaak et al., 2016).

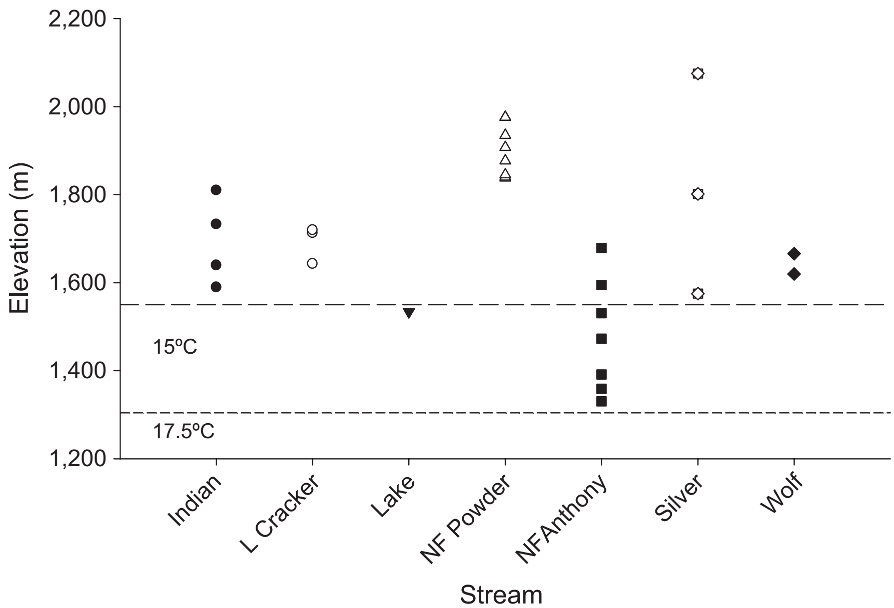

FIGURE 1 Elevations of sites in the upper Powder River basin where bull trout were detected in 1996 in relation to modeled elevations at which the mean weekly maximum temperatures were low probability (17.5°C) and high probability (15°C) for occurrence based on Isaak et al. (2009)

3 | RESULTS

During both sampling periods, the most common distribution pattern in streams containing bull trout and brook trout was the following. An allopatric bull trout reach was confined to 1–2 km at the upper end of fish distribution (Figure 2a). This transitioned downstream for a couple of km through a reach of mixed bull and brook trout and hybrids of the two species. Allopatric brook trout reaches extended as much as 19 km farther downstream. In bull trout streams with headwater lakes containing naturalised brook trout (Lake Creek and North Fork Powder River), brook trout were found in reaches downstream of the lakes or downstream of tributaries originating from the lakes. The only stream in which brook trout occurred upstream of bull trout was in Lake Creek downstream of Twin Lakes.

Distribution patterns in 2013–2015 were similar to those in the 1990s with a few exceptions. In Lake Creek, only one bull trout was found in a single reach, and only brook trout were found at sites farther upstream where only bull trout had previously occurred in the 1990s (Figure 2b). A single bull trout was also found in each of the two sites sampled in Fruit Creek, which was not sampled in the 1990s. Only one brook trout was collected in Cracker Creek downstream of Silver Creek.

We also documented a bull trout population in 2 km of Salmon Creek (Figure 2b). Sampling was limited by lack of access to private land downstream; however, those reaches were predicted by the temperature-elevation model to have low probability of bull trout occurrence. Stream flow in reaches upstream, where the temperature–elevation model suggested high probability of bull trout occurrence, was totally diverted for municipal water supply for Baker City. The upper occupied reach in Salmon Creek, about 1 km downstream from the diversion, had the highest catch per unit of effort (CPUE) of bull trout of all sample sites in the 1990s and 2013–2015 (Table S1).

In Wolf Creek in 2014, we found bull trout several km downstream of where they occurred in the 1990s. Bull trout were suspected to be in upper Anthony Creek (USFWS, unpublished); however, it contained only brook trout in sampled reaches that extended upstream to an 8–10 m falls below Anthony Lake that would have likely precluded historic upstream migration of bull trout. In Anthony Creek and the North Fork Powder River, current brook trout distribution extended to slightly downstream of the mouth of Anthony Creek (Figure 2a).

In streams with bull trout and brook trout, August mean temperatures differed slightly (0.5°C) between the allopatric bull trout, mixed bull and brook trout, and allopatric brook trout zones where the CPUE of brook trout was the highest; MWMT differed by about 1°C (Table 1). In streams without brook trout, allopatric bull trout distribution extended farther downstream into reaches with temperatures similar to mixed bull trout and brook trout reaches. Thus, the temperatures in reaches where bull trout occurred were similar whether brook trout were present or not. CPUE of bull trout in the lower reaches of bull trout distribution in all streams was relatively low (Table S1). Maximum annual August mean temperatures and MWMT at the downstream limits of bull trout distribution in streams without brook trout reached 11.5 and 16.5°C, respectively. August mean temperatures and MWMT in lower reaches of brook trout distribution in Anthony Creek and North Fork Powder River were about 14 and 19°C, respectively. The highest MWMT in those reaches was 23.5°C. In 2014, we initially sampled distribution in those lower brook trout reaches in July. Given the high temperatures in those reaches, we were uncertain if they would continue to be occupied by brook trout. However, when we resampled those same reaches in early September, we found similar numbers of brook trout.

Metrics other than maxima and August means for the temperature magnitude may be related to fish distribution, such as daily minima and degree days (cumulative temperature units) and for other months (e.g. June and July) (Adams & Bjornn, 1997; Arismendi, Johnson, Dunham, & Haggerty, 2013; Benjamin et al., 2016). However, other studies have found most temperature metrics of summer magnitude are highly correlated and statistically redundant (Dunham, Chandler, Rieman, & Martin, 2005; Dunham et al., 2003). This was also the case with our stream temperature data. For example, Pearson correlation coefficients for August means versus mid-July through August degree days and mean minima were both 0.98, $p < .00001$ ($n = 25$).

There has been largely no trend in annual August mean water temperatures and MWMT in nearby streams in the Grande Ronde River basin since the 1990s. For the 16 sites analysed, the mean p value (SE) of the linear regressions of mean August temperatures was 0.36 (0.05), and mean R^2 (SE) = 0.09 (0.02). Regressions using MWMT were similar: mean p (SE) = .38 (0.07), mean R^2 (SE) = 0.09 (0.02). Only two sites had significant trends, one indicating an increase in temperatures and one indicating a greater decrease ($p = .05$, coefficient = 0.08, $R^2 = 0.27$; $p = .03$, coefficient = −0.21, $R^2 = 0.31$). The strongest overall trend in the water temperature data was for the date of the MWMT (Figure 3). The MWMT is generally occurring almost 3 weeks earlier than it was 25 years ago.

These results suggested two related hypotheses. Since the MWMT is occurring earlier, streams may be experiencing an overall increase in heat loading during the summer that could be masked using only August mean temperatures or the MWMT temperature. For example, bull trout occurrence in the Klamath River basin was best predicted by the magnitude of June temperatures (Benjamin et al., 2016). Secondly, longer term temperature data prior to the 1990s may demonstrate an increase in temperatures not apparent by examining the past 25 years. However, available stream temperature data are limited to the past 25 years, and much of that is limited to August and to a lesser extent, July, including when the MWMT occurred.

To explore those hypotheses, I first analysed water temperature data for sites with complete records for July. Like August, July mean temperatures also showed lack of trends (mean p [SE] = .56 [0.09], mean R^2 [SE] = 0.05 [0.02], $n = 11$). There was also no trend in mean June–August air temperatures during 1990–2015 ($p = .85$, $R^2 = 0.001$), consistent with the stream temperature data; however, there was a significantly increasing trend in temperatures in the longer term data set since 1943 (Figure 4). That trend only explained 7% of the variability in the data, indicating low predictive power in the relationship. It was also driven by cooler temperatures during 1943–1957; there has been no trend in temperatures since then ($p = .21$, coefficient = −0.01,

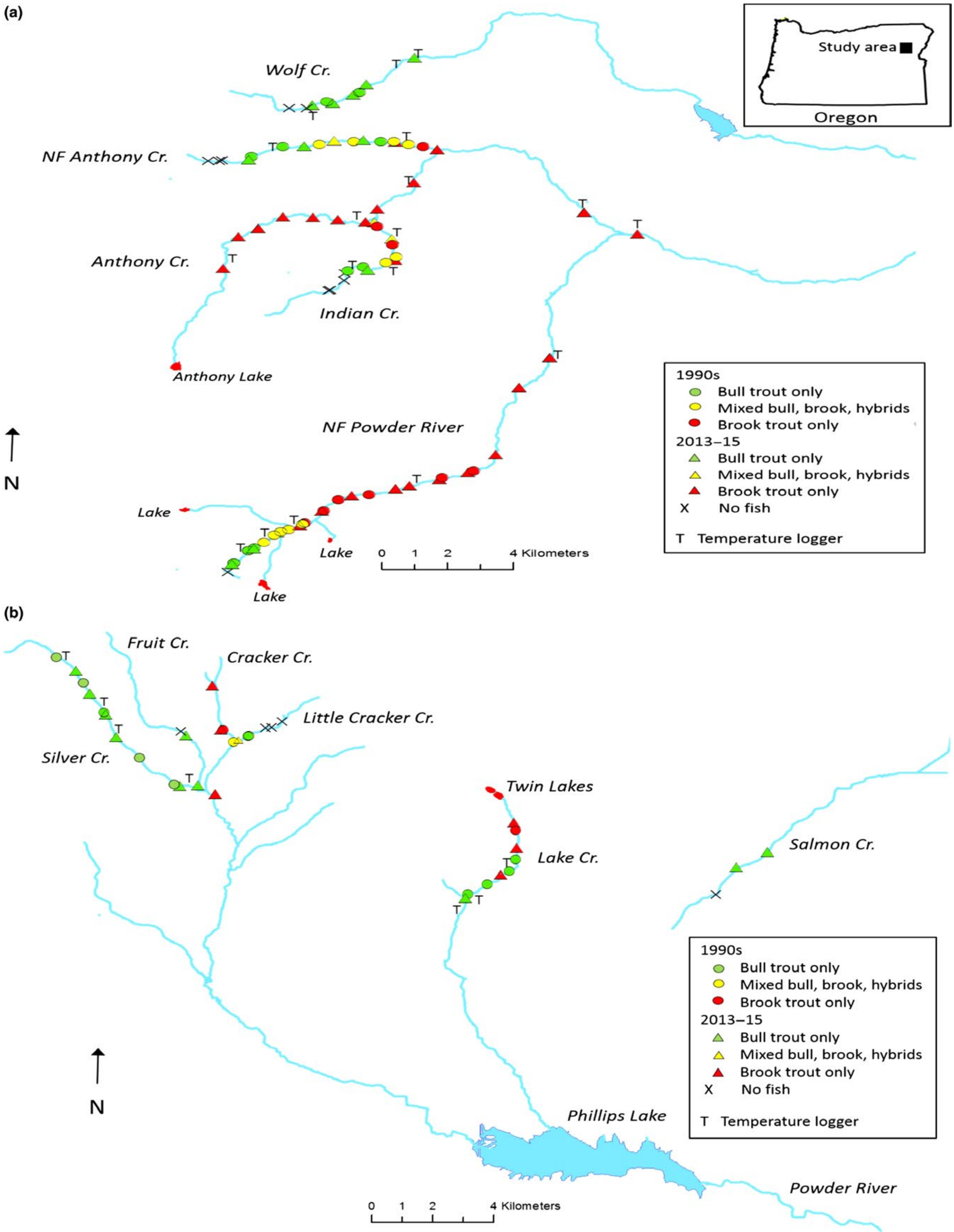

FIGURE 2 (a) Bull trout and brook trout distribution in Wolf and Anthony creeks and the North Fork Powder River from sample sites in the 1990s and 2013–2015. Lakes identified in red contain naturalized brook trout populations. (b) Bull trout and brook trout distribution in Salmon Creek and tributaries of the upper Powder River from sample sites in the 1990s and 2013–2015. Lakes identified in red contain naturalized brook trout populations

TABLE 1 Means (*SE*) of August mean and maximum weekly maximum temperatures (MWMT) in bull trout and brook trout distribution zones in bull trout streams with and without brook trout in the upper Powder River basin, 2014 and 2015. Loggers in upper allopatric brook trout zones were placed in reaches where catch per unit of effort was greatest; lower zones include two locations in the North Fork Powder River and one in Anthony Creek at the lower extent of brook trout distribution (Figure 2a)

	Distribution zone						
	Allopatric bull trout		Mixed bull and brook trout and hybrids		Allopatric brook trout		
	Aug. mean	MWMT	Aug. mean	MWMT	Aug. mean	MWMT	
Streams with bull trout and brook trout	9.5 (0.2)	12.9 (0.5)	10.0 (0.2)	13.9 (0.4)	10.5 (0.2)	15.1 (0.4)	Upper
					13.8 (0.5)	18.7 (1.2)	Lower
Streams with only bull trout	10.2 (0.3)	13.9 (0.5)					

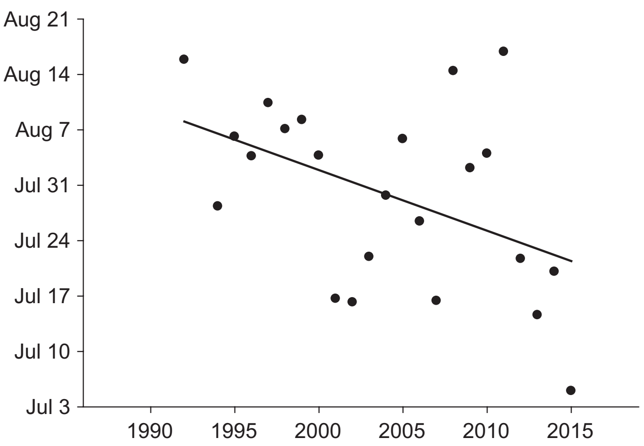

FIGURE 3 Mean annual date of the maximum weekly maximum temperature at 16 locations in streams in the upper Grande Ronde basin, 1991–2015 (Date = 2,459,501 − (0.77× year), *p* = .03, R^2 = 0.21) (Data from USFS, unpublished)

R^2 = 0.03). It is also possible that minimum temperatures rather than maximum temperatures may be more indicative of changes in climate patterns (Arismendi et al., 2013). However, minimum air temperatures during June–August since 1990 have significantly declined (p = .01, coefficient = −0.05, R^2 = 0.22). Longer term (1943–2015) minimum air temperatures revealed no significant trends (p = .17, R^2 = 0.03), nor did minimum water temperatures at the sites in the Grande Ronde River basin (mean p [*SE*] = .46 [0.13], mean R^2 [*SE*] = 0.05 [0.02]).

4 | DISCUSSION

In most streams with brook trout, allopatric bull trout distribution continues to be limited to a couple km of the uppermost fish-bearing reaches. These allopatric reaches are likely key to the persistence of those populations due to the absence of hybridisation and interspecific competition. The longitudinal distribution pattern of allopatric bull trout, mixed bull and brook trout, and allopatric brook trout in lower elevation and higher temperature reaches downstream is similar to the pattern in central Idaho where the two species co-occur (Adams & Bjornn, 1997; Rieman et al., 2006). Brook trout are the dominant char species in the Powder River basin in terms of distribution and likely abundance. In streams fed by lakes with naturalised brook trout populations, brook trout occur downstream of the lakes. This coupled with water temperatures may at least partially explain the absence of bull trout in upper Anthony Creek. Anthony Lake at the head of the drainage contains a naturalised brook trout population, and upper Anthony Creek just below the barrier falls where bull trout would most likely occur was similar to or warmer than other allopatric brook trout reaches. It was about 1°C warmer during August, and the MWMT was about 3°C warmer than the next logger site about 6 km downstream. Adams, Frissell, and Rieman (2001) found a similar example of a downstream brook trout invasion and a reverse temperature gradient in a headwater lake system in Montana.

There are only three streams with bull trout populations in the upper Powder River basin where brook trout do not occur (Silver, Wolf and Salmon creeks). In Silver and Wolf creeks, allopatric bull trout distribution extends farther downstream into slightly warmer reaches than in streams with brook trout. Similar patterns were found in Idaho (Rieman et al., 2006) and in the Klamath River basin (Benjamin et al., 2016). However, the lower abundance of bull trout in those reaches suggests they are less favourable to bull trout even in the absence of brook trout. Consequently, the narrow distribution of bull trout in the Powder River basin appears to be due to the limited availability of very cold-water habitat (≤10°C August mean) in all streams as well as interactions with brook trout in streams where they occur.

Although bull trout were found in Fruit Creek in 2015, only a single fish was found in each of the two reaches sampled to the upstream limit of fish distribution. Consequently, Fruit Creek probably does not support a self-sustaining population. Likewise, if there is a bull trout population in Little Cracker Creek, it is likely very small given the limited habitat, low numbers of bull trout captured and prevalence of brook trout and hybrids found during both 1996 and 2015. The population in Lake Creek also appears vulnerable to extirpation (one bull trout collected in a single reach in 2013). The reduction in distribution and low abundance of bull trout in Lake Creek is consistent with fish distribution and temperature elsewhere in the upper Powder River basin (Table 1). August mean temperatures in 2014 and 2015 in the upper

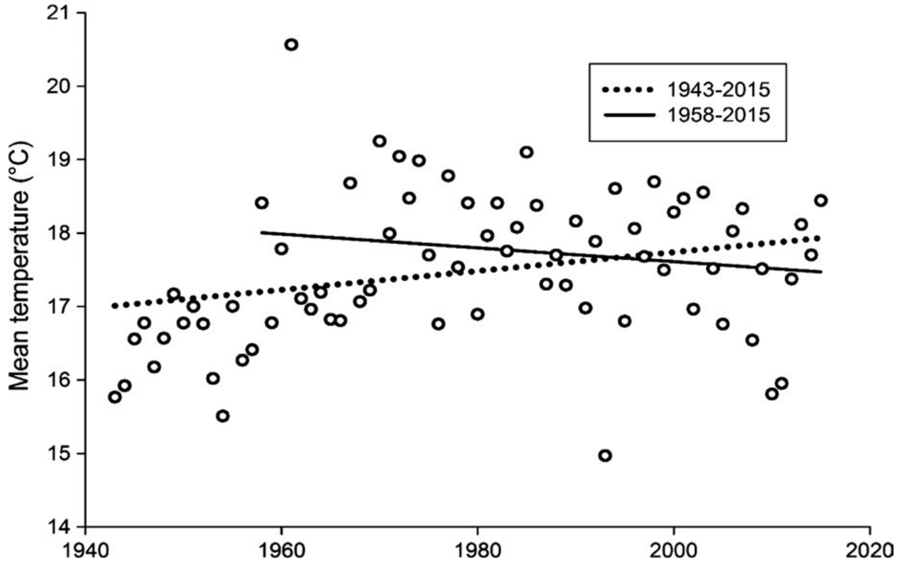

FIGURE 4 Mean June through August air temperatures, 1943–2015 versus 1958–2015, at the Baker City Airport (1943–2015 temperature = 17.912 + (0.02× year), p = .02, R^2 = 0.07) (1958–2015 temperature = 36.385 − (0.01× year), p = .21, R^2 = 0.03) (Data from Western Regional Climate Center 2016)

reaches formerly occupied by bull trout were 10.4 and 10.9°C, similar to other allopatric brook trout reaches; and August mean temperatures where the single bull trout was found downstream were 10.6–11.6°C. Twin Lakes, the headwaters of Lake Creek, is also a continuing source of brook trout. Although Silver Creek does not contain brook trout, there were large numbers of brook trout in nearby upper Cracker Creek. Since no other species were found in upper Cracker Creek and there are no upstream lakes that continually seed downstream reaches, eliminating the brook trout population there may be a management option to reduce the potential for brook trout invading Silver Creek.

Since all of the bull trout populations in the upper Powder River basin have very limited distribution, especially where brook trout occur, those populations are more vulnerable to stochastic events (e.g. high severity fires, floods and debris flows) that could also be exacerbated by climate change (Rieman et al., 2006; Isaak and Rieman, 2013). Since these populations appear to be resident forms and not migratory, there also is likely very low potential for demographic support or natural refounding from neighbouring populations following population depressions or extirpations from those events or other causes. Despite their limited distribution, the extent of bull trout distribution in the streams sampled has not declined except in Lake Creek, and no populations have become extirpated. Brook trout and hybrid distributions have not expanded since the 1990s, again with the exception of Lake Creek. Likewise, brook trout did not expand their range in most streams in the South Fork Salmon River basin over a similar time period (Adams, Frissell, & Rieman, 2002).

Bull trout distribution in the Powder River basin was consistent with the temperature–elevation model and the gradient of occurrence probabilities and temperature found in other studies (e.g. Isaak et al., 2009). CPUE of bull trout increased moving upstream to higher elevation/cooler sites, similar to that observed by Rieman et al. (2006). Salmon Creek was the exception. The somewhat anomalous location and occurrence of bull trout there, including the high CPUE, may be due at least in part to the effects of cold groundwater since all of the surface water upstream is diverted.

Water temperatures measured in bull trout reaches in 2014 and 2015 were similar to NorWeST (2015) modelled predictions for 2011 in those same reaches (August means [*SE*]: 10.0°C [0.2] and 9.7°C [1.3], respectively). If colder water temperatures are a key factor in segregating bull trout and brook trout (e.g. Dunham et al., 2003; Isaak et al., 2010), those differences between the upper temperature boundary of bull trout and the lower temperature boundary of brook trout in the upper Powder River basin are slight (~0.5°C August mean); and even small temperature increases associated with climate change could pose an additional risk to already small populations facing a variety of other threats. Water temperatures in current bull trout reaches are predicted by NorWeST (2015) models to increase 1°C by 2040. Although some populations elsewhere may be able to contract or retreat to cooler habitat at higher elevation, that is not possible in the upper Powder River basin since those populations are already restricted to the upper limits of fish distribution due to habitat constraints (falls, excessively high gradients, and small channels upstream). Although bull trout are generally found in the upper, colder reaches, there can be overlap in the temperatures associated with the distribution of the two species. Lower temperatures also appear to provide no growth or survival advantage for bull trout under laboratory conditions (McMahon et al., 2007). Thus, temperature alone may not alone be responsible for segregating the species (Isaak, Wenger, & Young, 2017); however, warmer temperatures do favour brook trout as shown by both laboratory studies (McMahon et al., 2007; Selong et al., 2001) and this and other field studies (Paul & Post, 2001; Rieman et al., 2006).

Brook trout occurrence and distribution also does not appear to have changed in the Powder River basin over the course of this study. Likewise, there has been little invasion by brook trout upstream or into other accessible streams in Idaho in recent decades (Adams et al., 2002), and the displacement of bull trout by brook trout is not inevitable (Rieman et al., 2006). However, future changes in conditions (e.g. increases in temperature) could favour continued upstream invasion by brook trout.

In the only other study of changes in bull trout distribution and relationships with trends in water temperatures (Eby et al., 2014), bull trout distributions in the East Fork Bitterroot River have contracted as temperatures have increased over a similar time period to this study. The differences in these two studies may be partially due to the absence of increasing temperatures in the upper Powder River basin. In addition, bull trout in the East Fork Bitterroot River primarily abandoned lower elevation sites. In the upper Powder River basin, bull trout were already absent at lower elevation sites 20 years ago likely due to a number of factors, including a legacy of migratory barriers, loss of migratory life histories, brook trout interactions and long-term changes in temperature regimes in downstream reaches due to diversions. Besides the Bitterroot River, bull trout have also declined at warmer sites (>10°C) in other parts of the Clark Fork River basin in Montana, while introduced brown trout abundance has been increasing in both migratory and spawning and rearing areas used by bull trout (Al-Chokhachy et al., 2016).

Those studies in Montana, including the Flathead River basin (Jones, Muhlfeld, Marshall, McGlynn, & Kershner, 2014), and the status of bull trout populations in the Powder River basin underscore the importance of life history diversity of the species and considering the habitat used by migratory forms. Much of the focus of temperature studies and analyses of potential climate effects on bull trout have been on headwater reaches where migratory bull trout spawn and rear and resident populations are found. Even if those areas are more resistant to temperature increases (Isaak et al., 2016) and expansion of introduced species, continuing declines and losses of migratory forms of bull trout from changes in habitat conditions in lower reaches of tributaries and main stem rivers and expansion of introduced brook trout and brown trout in those areas will continue to threaten the persistence of bull trout populations. Restoring connectivity and migratory bull trout populations in systems like the Powder River basin, where current remnant resident populations are fragmented and highly restricted in distribution, would help insure their persistence in view of continuing threats of climate change and introduced species. There may also be opportunities to maintain or improve water quality and quantity and to reduce the effects of seeding of brook trout from some lakes with naturalised brook trout populations.

Although water and air temperatures in the upper Powder River basin have not consistently increased, maximum water temperatures have generally been occurring earlier. Thus, metrics other than magnitude may be necessary to describe changes in thermal regimes over time affecting fish distribution (Arismendi et al., 2013). For example, the frequency of high temperatures and variability were also influential in explaining bull trout occurrence in the Klamath River basin (Benjamin et al., 2016). The importance of early summer temperatures and the timing of temperature increases (i.e. bull trout sites warmed more slowly) in that study also suggest possible detrimental implications of the trend towards earlier maximum temperatures in this study. Although the specific biological responses of bull trout are not clear, studies of other salmonids suggest earlier timing of temperature increases can shift life history patterns and influence food availability through changes in the development of aquatic invertebrates (Arismendi et al., 2013).

While much of the concern and investigation of the effects of climate change on bull trout and other fishes have centred on increasing temperatures, other studies suggest that changes in the distribution and composition of other fauna in relation to climate change are more closely linked to extreme weather events than to trends in temperature (Jentsch, Kreyling, & Beierkuhnlein, 2007). Climate change could also alter precipitation, snowpack, runoff, floods, debris flows, groundwater and other physical and biological influences on stream habitat (Wenger et al., 2011; Isaak et al., 2012; Luce et al., 2014).

Cold-water refugia have been proposed and identified to help insure the persistence of bull trout and other cold-water fishes in some areas as their suitable habitat shrinks from the future effects of climate change and to make the most efficient use of limited resources for conservation (Isaak et al., 2015; Wenger et al., 2011). The recovery plan for bull trout (USFWS 2015) likewise calls for focusing recovery efforts in areas with the coldest water. While such an approach is logical and strategic for addressing a broadscale issue, especially for bull trout, its implementation at the watershed level poses a number of challenges.

There is substantial uncertainty concerning future climate projections (Isaak et al., 2015; Wenger et al., 2013), and our understanding of the nature and extent of those changes continues to evolve. For example, NORWeST (2015) stream temperature modelling projected temperature increases bull trout reaches in the Powder River basin of 0.330°C/decade through 2040. Other and more recent studies (Isaak et al., 2016; Luce et al., 2014) indicate that the rate of temperature increase in cold headwater reaches, such as those where bull trout spawn and rear and where resident populations, like those in the Powder River basin occur, is slower than in lower elevation, warmer reaches and suggest a rate of 0.067°C/decade, approximately one-fifth of NorWeST (2015). Thus, temperature increases and loss of bull trout habitats in those areas may be less dire than previously projected (Benjamin et al., 2016). Although there is substantial evidence indicating a general increase in water temperatures in the Northwest (e.g. Isaak et al., 2012), there is considerable uncertainty about the specific watersheds where that will occur and the physical and biological effects (Eby et al., 2014; Rieman et al., 2007; Wenger et al., 2011). The Powder River basin is an example of that.

To the extent that a policy reduces efforts to conserve populations like those in the Powder River basin, it represents an additional risk to their persistence and potential loss of the diversity of the species. In bull trout, genetic diversity is high among populations but low within populations (Ardren et al., 2011; Spruell, Hemmingsen, Howell, Kanda, & Allendorf, 2003). Thus, the loss of populations would likely mean the loss of genetic and geographic diversity across the range of the remaining populations. Bull trout recovery could benefit from strategic, broadscale approaches to climate change. However, many conservation efforts are situational and opportunistic; and ultimately, their initiation and implementation depend on interested and willing agencies, organisations and individuals at the local level.

Think globally, act locally

Patrick Geddes (1915), biologist, sociologist, geographer, educator, town planner

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