

COLDWATER AS A CLIMATE SHIELD TO PRESERVE NATIVE TROUT THROUGH THE 21ST CENTURY

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Abstract—Native trout are culturally and ecologically important, but also likely to undergo widespread declines as the coldwater environments they require continue to shrink in association with global warming. Much can be done to preserve these fish but efficient planning and targeting of conservation resources has been hindered by a lack of broad-scale datasets and precise information about which streams are most likely to support native trout populations later this century. Using accurate stream temperature climate scenarios developed in the NorWeST project, we identify stream habitats for native Cutthroat Trout *Oncorhynchus clarkii* and Bull Trout *Salvelinus confluentus* across northern Idaho and northwestern Montana that are cold enough to serve as climate refugia and resist invasions by nonnative trout. Climate-safe coldwater habitats for Cutthroat Trout in the historical scenario encompassed 7,547 – 16,821 stream kilometers (depending on the local co-occurrence of Brook Trout *Salvelinus fontinalis*) and 12,189 kilometers for Bull Trout. The majority of coldwater habitats (77%-88%) currently occur on federal lands, a pattern that will become even more pronounced late in the century if the projected 63%-82% declines in coldwater habitats occur. The information developed for this project, and accompanying geospatial databases, are also available for a much larger area across the northwest U.S. to assist managers in strategic decision making about where to allocate conservation resources to best preserve native trout.

INTRODUCTION

From a societal perspective, the marquis freshwater fish in cold waters across the globe are salmonines—trout, salmon, and char in the subfamily Salmoninae. Not only do these fish have commercial, recreational, and cultural importance, they serve an array of ecological roles as predators, prey, hosts of freshwater mussels, and conduits of nutrients from oceans, lakes, and rivers to headwater tributaries and their associated riparian habitats. These fish evolved in and colonized waters throughout the Northern Hemisphere, but have also been widely introduced outside their native ranges in suitable waters of the Southern Hemisphere. Nevertheless, within their native ranges, every taxon of these fish has undergone declines over the last two centuries, coincident with our exploitation of them for food, their habitats for water extraction or development, and their watersheds for resources (e.g., Montgomery 2003; Williams et al. 2011). In North America, many taxa or conservation units within them have been designated as in need of conservation action e.g., listing under the U.S. Endangered Species Act, Canada's Species At Risk

Act, or state or provincial programs identifying species of concern. For some taxa, these declines have been arrested, but restoration to their former habitats has been difficult and costly, in many cases because invasive species, including salmonids introduced outside their historical ranges, now occupy those habitats (Fausch et al. 2009).

The relatively rapid and pervasive changes in global climate and stream temperatures (Webb and Nobilis 2007; Kaushal et al. 2010; Isaak et al. 2012) in recent decades constitute a further threat to the persistence of many salmonid populations. Growing evidence documents shifts in populations of these fishes (Comte et al. 2013; Eby et al. 2014) as they attempt to track the distribution of the cold waters on which they depend. In many cases, these changes are likely to constrain populations to smaller and more fragmented headwater habitats (Rieman et al. 2007; Wenger et al. 2011b). Given limited resources to conserve fishes that have already undergone broad-scale range reductions, further work that addresses the threat of climate change demands strategic planning. To that end, managers have begun to ask

which locations are likely to retain thermally suitable habitats of adequate size and connectivity for native salmonids despite anticipated changes in climate. If such climate refugia could be identified, it would allay fears of species losses this century and the refugia could serve as cornerstones in the development of strategic conservation networks. Moreover, because growth and survival of nonnative fishes are precluded in exceptionally cold streams where native salmonids often thrive, refugia with temperatures below certain thresholds would be resistant to invasions and require limited management intervention. In effect, cold water could be used as a “climate shield” to protect native salmonids against climate change and invasive species this century.

Accurately modeling the distribution of coldwater stream habitats is now possible because of the availability of nationally consistent stream geospatial data (Cooter et al. 2010; Wang et al. 2011), high-resolution climate scenarios for stream temperature and flow (Isaak et al. 2010; Wenger et al. 2010; Isaak et al. 2011), and new statistical models for stream data that enable development of unbiased information from large databases and accurate predictions of patterns throughout stream networks (Ver Hoef et al. 2006; Isaak et al. 2014; Ver Hoef et al. 2014). Our goal is to demonstrate how these data and tools may be used to identify current and future distributions of coldwater habitats for two species of native salmonid fishes—Bull Trout *Salvelinus confluentus* and Cutthroat Trout *Oncorhynchus clarkii*—across selected river basins in the upper Columbia River basin in Idaho and Montana. The work described herein is the initial phase of

delineating specific climate refugia for these species across a much broader area of the northwestern U.S.

METHODS

The study area included northern Idaho (north of the Salmon River basin) and northwestern Montana within the Columbia River basin (Figure 1). Stream elevations ranged from 200 to 2,500 m between the Continental Divide to the east and the mouths of major rivers to the west.

To delineate the fish-bearing stream network, geospatial data for the NHDPlus 1:100,000-scale stream hydrography layer (Cooter et al. 2010) were downloaded from the Horizons Systems website (<http://www.horizon-systems.com/NHDPlus/index.php>) and filtered by minimum flow and stream slope. Each reach in the NHDPlus hydrography layer already has many descriptive attributes calculated, among them stream slope (Wang et al. 2011). Stream reaches with slopes exceeding 10% were trimmed from the network because fish densities are low in these reaches, steep reaches are prone to post-fire debris torrents that can extirpate salmonid populations (Brown et al. 2001), and because they occur at the top of the network where slopes become progressively steeper. Summer streamflow values were downloaded from the Western US Flow Metrics website (http://www.fs.fed.us/rm/boise/AWAE/projects/modeled_stream_flow_metrics.shtml; Wenger et al. 2010) and linked to each reach in the hydrography layer through the COMID field. Summer flow values for three climate periods were available from that website: a

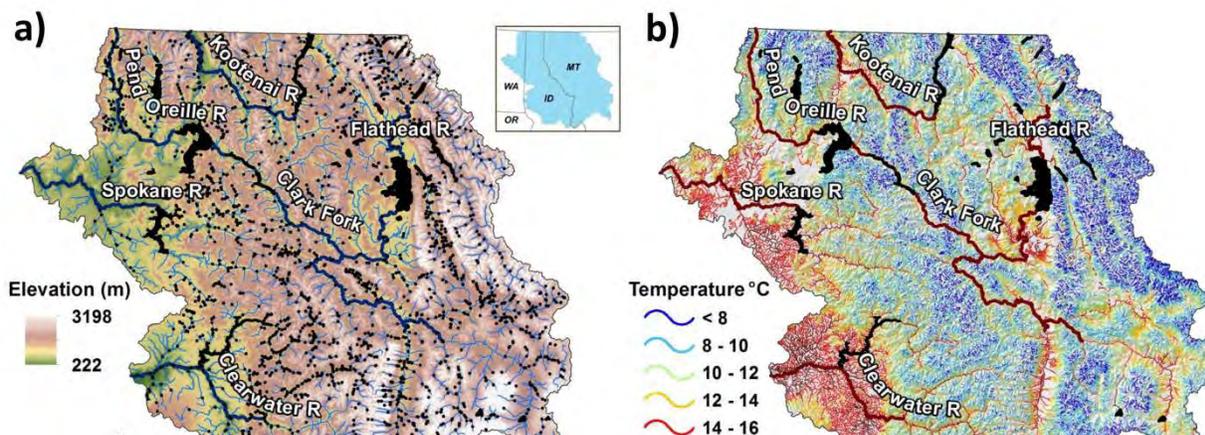


Figure 1. Stream temperature observations ($n = 9,969$) used to fit the NorWeST model in the study area (panel a) and an interpolated map of August mean temperatures representing the 1980s historical period (panel b).

historical period (1970–1999, hereafter referred to as 1980s) and two future periods (2030–2059, hereafter 2040s; 2070–2099, hereafter 2080s) associated with the A1B climate trajectory. Peterson et al. (2013b) described the relationship between summer flows and stream width and found that summer flows of 0.034 m³s (1.2 ft³s) approximated stream widths of 1.5 m. Trout presence in streams narrower than 1.5 m becomes sporadic due to small habitat sizes (Peterson et al. 2013a), so the network was also trimmed to exclude reaches with summer flows < 0.034 m³s. Application of the slope and flow criteria reduced the original set of blue-lines in the NHDPlus hydrography layer from 84,191 stream km to 35,850 km, the latter of which was used to represent fish habitat in the baseline 1980s period.

Summer stream temperature scenarios represented by August means were downloaded from the NorWeST website (www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html; Isaak et al. 2011) and used to attribute the baseline hydrography layer. The number of stream temperature observations used to fit the NorWeST model in the study area was 9,969 (Figure 1a) and the model had good predictive accuracy across these observed sites over a wide range of historical climate variation ($r^2 = 0.92$; RMSE = 0.78°C). NorWeST scenarios were available for the same A1B climate trajectory and future climate periods described above at a 1-km resolution for all streams in the study area.

Thermal niches for Bull Trout and Cutthroat Trout encompass colder temperatures than do those of nonnative salmonids such as Brook Trout *Salvelinus fontinalis*, Brown Trout *Salmo trutta*, and Rainbow Trout *O. mykiss* (Wenger et al. 2011a,b). Thus, important spawning and juvenile rearing habitats for allopatric populations of the native trout species are often upstream of the distribution of nonnative trout. Temperatures in Bull Trout natal habitats are so cold that overlap with nonnative trout is limited (Rieman et al. 2006; Isaak et al. 2010). However, Cutthroat Trout spawn over a wider temperature range and displacement by nonnative salmonids is common where species overlap in warmer streams. To estimate temperatures that delineated suitable natal Bull Trout habitats and buffered Cutthroat Trout populations against invasions, we referenced stream locations where juvenile trout of either species (<150 mm) had been sampled against mean August water temperature calculated using the NorWeST S1 historical scenario

(which represented the climate composite from 1993–2011) at the same location. For Bull Trout, the juvenile survey data came from longitudinal surveys of 74 streams across the interior Columbia River basin (Rieman et al. 2007). The mean stream temperature at the farthest downstream locations of juvenile Bull Trout in those streams was 10.9°C (99% CI, 10.7–11.1°C), so we used $\leq 11^\circ\text{C}$ to delineate natal Bull Trout habitats.

Locations of juvenile Cutthroat Trout in the study area were obtained from 863 reach surveys (Young et al. 2013; M. K. Young, unpublished data). Those data indicated juvenile Cutthroat Trout occurred most frequently in stream reaches with temperatures less than 10°C, but juveniles were not uncommon where August mean temperatures approached 14°C. Brown Trout and Rainbow Trout become more common in warmer streams (Wenger et al. 2011a), but those surveys did not include enough sites to reliably estimate temperatures at the upstream limits of these species. For that, we relied on information from a regional fish survey database that included approximately 20,000 site surveys (S. Wenger, unpublished data). Cross-referencing those surveys with the NorWeST S1 historical scenario indicated that Rainbow Trout and Brown Trout rarely occurred where temperatures were < 12°C so this value was used as one criterion for delineating Cutthroat Trout natal habitats. Another nonnative species, Brook Trout, has a colder thermal niche than Rainbow Trout or Brown Trout. The regional fish survey database and earlier research (Al-Chokhachy et al. 2013) indicate that Brook Trout are most common in reaches with mean August temperatures near 12°C and become relatively rare where temperatures are < 10°C. Hence, we used $\leq 10^\circ\text{C}$ to delineate Cutthroat Trout habitats that would resist Brook Trout invasions in streams where this nonnative also occurred.

To determine the amount of stream habitat that met the above criteria, we queried the trimmed hydrography layer to identify those reaches ≤ 10 , 11, and 12°C that also had summer flows > 0.034 m³s. The query was done for the historical and two future periods and the total length of coldwater streams summarized. Results from that query were cross-referenced with land ownership compiled for the ICBEMP project (Quigley and Arbelbide 1997) to determine the administrative status of coldwater refuge streams.

RESULTS

Considerable thermal heterogeneity existed across the study area due to the complex topography (Figure 1). Portions of the stream network with significant amounts of cold water occurred along the Continental Divide to the east and at high elevations scattered throughout various mountain ranges. August stream temperatures in the historical period ranged from 5.1°C to 24°C and averaged 12.5°C. Average temperatures were projected to increase by 1.4°C in the 2040s and 2.5°C in the 2080s. Application of the 12°C thermal criteria to the historical temperature scenario suggested that Cutthroat Trout had 16,821 km of streams cold enough to impede invasions by Brown Trout and Rainbow Trout (Table 1; Figure 2), but only 7,547 km if the more restrictive thermal criteria of 10°C was applied to limit Brook Trout invasions. Coldwater Bull Trout habitats were intermediate between these two extremes at 12,189 km.

Relative to the historical baseline, the amount of habitat in the 2080s that was $\leq 10^\circ\text{C}$ was predicted to decline by 82% to 1,355 km, whereas habitat $\leq 12^\circ\text{C}$ was predicted to decline by 63% to 6,169 km. Future habitat reductions reflected both summer flow declines that truncated headwater streams and summer temperature increases that shifted isotherms upstream. Of these two effects, temperature increases

accounted for most of the projected reductions (94–98%) in coldwater habitat length. The large majority of coldwater refugia streams in the historical period (77–88%) were on federal lands, and this will increase in the future because most non-federal lands are at lower elevations where streams are relatively warm. Approximately 23% of the historical coldwater habitats are considered protected based on special land designations (18.7% in Forest Service Wilderness Areas, 2.6% in Glacier National Park).

DISCUSSION

Consistent with many previous assessments (e.g., Rieman et al. 2007; Wenger et al. 2011b), our results indicate that coldwater habitats for salmonids will markedly decline as a consequence of climate change this century. Unlike many previous studies, however, our approach uses accurate stream temperature model scenarios and species-specific thermal criteria developed from large biological and temperature databases to greatly increase the precision of our projections. The approach is conservative in that it assumes nonnative species will invade all thermally suitable habitats and restrict the distribution of both native species. That is clearly not the case at present; Brook Trout, for example, are absent from large numbers of basins they could seemingly occupy

Table 1. Kilometers (% in parentheses) of stream habitat by land administrative status for Bull Trout and Cutthroat Trout that are cold enough to resist invasion by other trout species during historical and future periods.

Land status ¹	1980s			2080s		
	$\leq 10^\circ\text{C}$	$\leq 11^\circ\text{C}$	$\leq 12^\circ\text{C}$	$\leq 10^\circ\text{C}$	$\leq 11^\circ\text{C}$	$\leq 12^\circ\text{C}$
Private	691 (9.2)	1,655 (13.6)	3,200 (19.0)	82 (6.1)	217 (6.7)	556 (9.0)
Tribal	115 (1.5)	202 (1.7)	290 (1.7)	33 (2.4)	60 (1.9)	100 (1.6)
State/City	133 (1.8)	243 (2.0)	375 (2.2)	13 (1.0)	49 (1.5)	127 (2.1)
COE	2 (0.1)	2 (0.1)	2 (0.1)	0 (0.0)	2 (0.1)	2 (0.1)
BLM	59 (0.8)	111 (0.9)	149 (0.9)	0 (0.0)	7 (0.2)	34 (0.6)
FWS	0 (0.0)	0 (0.0)	4 (0.1)	0 (0.0)	0 (0.0)	0 (0.0)
NPS	149 (2.0)	321 (2.6)	456 (2.7)	21 (1.6)	65 (2.0)	136 (2.2)
FS-wilderness	1,674 (22.2)	2,274 (18.7)	2,688 (16.0)	452 (33.3)	871 (27.0)	1,329 (21.5)
FS-nonwilderness	<u>4,725</u> (62.6)	<u>7,380</u> (60.5)	<u>9,657</u> (57.4)	<u>754</u> (55.6)	<u>1,948</u> (60.5)	<u>3,885</u> (63.0)
Total	7,547	12,189	16,821	1,355	3,219	6,169

¹Abbreviations: COE, Corps of Engineers; BLM, Bureau of Land Management; FWS, Fish and Wildlife Service; NPS, National Park Service; FS, Forest Service.

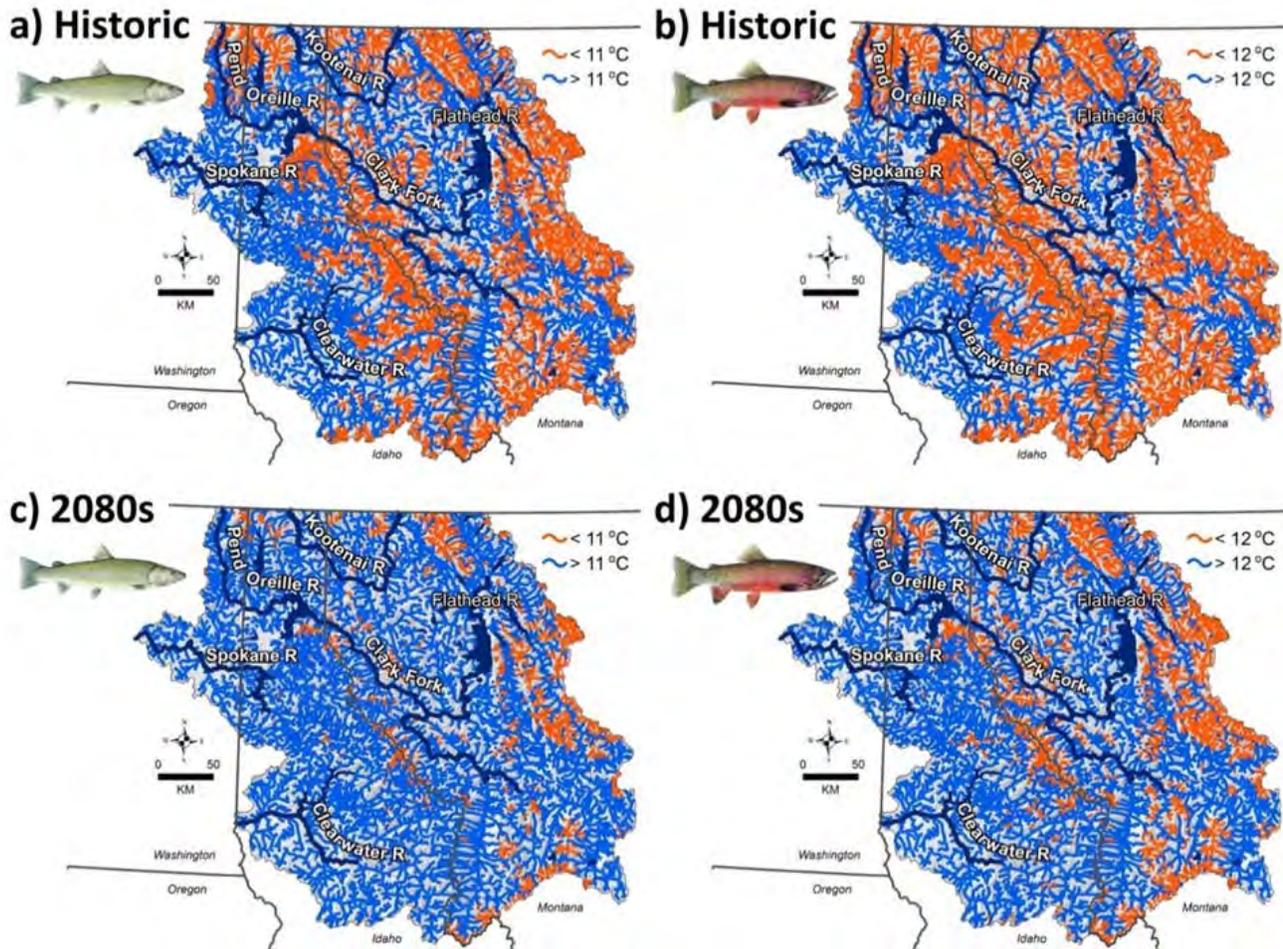


Figure 2. Streams for Bull Trout (panels a and c) and Cutthroat Trout (panels b and d) that are cold enough to resist invasion by other trout species during historical and future periods.

(Al-Chokhachy et al. 2013; M. K. Young, unpublished data; Wenger et al. 2011a). Nevertheless, the future spread of Brook Trout, Brown Trout, and Rainbow Trout—either by natural colonization or human-assisted (and generally illegal) transport—seems likely (Rahel 2004), and the coldwater streams highlighted here can serve as climate-safe and invasion-resistant refuge habitats.

Despite seemingly inevitable future declines, the long-term persistence of Bull Trout and Cutthroat Trout in the study area does not appear to be in jeopardy. There are thousands of stream kilometers that are cold enough to provide suitable habitats even with substantial future climate change and warming this century. Most of these coldwater habitats occur on federal lands at higher elevations, particularly the National Forests. Future climate change will only

enhance this pattern, emphasizing the role that federal land management can play in maintaining a climate shield to conserve native coldwater species. Many coldwater refuge streams already occur in designated wilderness areas and support disproportionate numbers of strong Cutthroat Trout and Bull Trout populations of (e.g., Rieman and Apperson 1989; Kershner et al. 1997), but wilderness designation may be insufficient insurance against climate change. For example, many portions of the Selway-Bitterroot Wilderness Area in Montana and Idaho are expected to warm beyond the thresholds acceptable to Bull Trout, and to favor more thermally tolerant trout species at the expense of Cutthroat Trout. Such areas will constitute a dilemma for biologists wishing to actively manage watersheds to retain coldwater species. However, coldwater habitats in adjacent non-wilderness public and private

lands have fewer restrictions and might be strategically targeted for conservation actions that bolstered native trout populations.

Identification of coldwater streams is only the beginning of climate-smart native trout conservation. The next steps in this process include developing demographically based estimates of habitat sizes needed for population persistence, implementing the approach across entire species ranges and large river basins, and providing climate refugia information in geospatial digital map formats for easy use with numerous native trout conservation initiatives, such as those sponsored by the multi-agency Western Native Trout Initiative. The approach taken is also generalizable in that it could be extended to other native headwater species that are dependent on cold water (e.g., Rocky Mountain Tailed Frog *Ascaphus montanus* or Coastal Giant Salamander *Dicamptodon tenebrosus*). In the northwestern U.S., doing so simply requires developing an estimate of habitat size needed for population persistence and species-specific thermal criteria, both of which can be derived using broadly available geospatial stream data and biological survey information. Coldwater climate refugia could also be delineated in other parts of the U.S. or globally where native organisms persist and thrive in cold environments that constrain nonnative species invasions. The primary limitation for identifying such areas currently is the limited availability of stream temperature data (and perhaps ecological data for poorly surveyed species), but monitoring networks and databases have begun to grow rapidly in recent years with the advent of inexpensive sensors and reliable protocols for data collection (Isaak et al. 2011; Isaak et al. 2013). In all cases, better information about the locations and likely persistence of coldwater climate refugia will contribute to more strategic allocation of limited conservation resources, help rally support among multiple stakeholders concerned about the future of coldwater fauna, and increase the odds of long-term species preservation.

REFERENCES

- Al-Chokhachy, R., S. J. Wenger, D. J. Isaak, and J. L. Kershner. 2013. Characterizing the thermal suitability of instream habitat for salmonids: a cautionary example from the Rocky Mountains. *Transactions of the American Fisheries Society* 142:793–801.
- Brown, D. K., A. A. Echelle, D. L. Propst, J. E. Brooks, and W. L. Fisher. 2001. Catastrophic wildfire and number of populations as factors influencing risk of extinction for Gila Trout (*Oncorhynchus gilae*). *Western North American Naturalist* 61:139–148.
- Comte, L., L. Buisson, M. Daufresne, and G. Grenouillet. 2013. Climate-induced changes in the distribution of freshwater fish: observed and predicted trends. *Freshwater Biology* 58:625–639.
- Cooter, W., J. Rineer, and B. Bergenroth. 2010. A nationally consistent NHDPlus framework for identifying interstate waters: Implications for integrated assessments and interjurisdictional TMDLs. *Environmental Management* 46:510–524.
- Eby, L. A., O. Helmy, L. M. Holsinger, and M. K. Young. 2014. Evidence of climate-induced range contractions for Bull Trout in a Rocky Mountain watershed, U.S.A. *PLoS ONE* doi:xxxxxxx
- Fausch, K. D., B. E. Rieman, J. B. Dunham, M. K. Young, and D. P. Peterson. 2009. Invasion versus isolation: trade-offs in managing native salmonids with barriers to upstream movement. *Conservation Biology* 23:859–870.
- Isaak, D. J., C. Luce, B. Rieman, D. Nagel, E. Peterson, D. Horan, S. Parkes, and G. Chandler. 2010. Effects of climate change and recent wildfires on stream temperature and thermal habitat for two salmonids in a mountain river network. *Ecological Applications* 20:1350–1371.
- Isaak, D. J., D. L. Horan, and S. P. Wollrab. 2013. A simple protocol using underwater epoxy to install annual temperature monitoring sites in rivers and streams. U.S. Forest Service General Technical Report RMRS-GTR-314.
- Isaak, D. J., E. Peterson, J. V. Hoef, S. Wenger, J. Falke, C. Torgersen, C. Sowder, A. Steel, M. J. Fortin, C. Jordan, A. Reusch, N. Som, and P. Monestiez. 2014. Applications of spatial statistical network models to stream data. *Wiley Interdisciplinary Reviews - Water* 1 doi: 10.1002/wat2.1023.
- Isaak, D.J., S. Wenger, E. Peterson, J. M. Ver Hoef, S. Hostetler, C. Luce, J. Dunham, J. Kershner, B. Roper, D. Nagel, D. Horan, G. Chandler, S. Parkes, and S. Wollrab. 2011. NorWeST: An interagency stream temperature database and model for the Northwest United States. Website: <http://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html>
- Isaak, D.J., S. Wollrab, D. Horan, and G. Chandler. 2012. Climate change effects on stream and river temperatures across the northwest US from 1980–2009 and implications for salmonid fishes. *Climatic Change* 113: 499–524.

- Kaushal, S. S., G. E. Likens, N. A. Jaworski, M. L. Pace, A. M. Sides, D. Seekell, K. T. Belt, D. H. Secor, and R. L. Wingate. 2010. Rising stream and river temperatures in the US. *Frontiers in Ecology and the Environment* 8:461–466.
- Kershner, J. L., C. M. Bischoff, and D. L. Horan. 1997. Population, habitat, and genetic characteristics of Colorado River Cutthroat Trout in wilderness and non-wilderness stream sections in the Uinta Mountains of Utah and Wyoming. *North American Journal of Fisheries Management* 17:1134–1143.
- Montgomery, D. R. 2003. *King of fish: the thousand-year run of salmon*. Westview Press, Boulder, Colorado.
- Peterson, D. P., B. E. Rieman, D. L. Horan, and M. K. Young. 2013a. Patch size but not short-term isolation influences occurrence of Westslope Cutthroat Trout above human-made barriers. *Ecology of Freshwater Fish*. DOI: 10.1111/eff.12108.
- Peterson, D. P., S. J. Wenger, B. E. Rieman, and D. J. Isaak. 2013b. Linking climate change and fish conservation efforts using spatially explicit decision support models. *Fisheries* 38:111–125.
- Quigley, T., and S. Arbelbide (editors). 1997. *An assessment of the ecosystem components in the Interior Columbia Basin and portions of the Klamath and Great Basins*. U.S. Forest Service General Technical Report PNW-GTR-405.
- Rahel, F. J. 2004. Unauthorized fish introductions: fisheries management of the people, for the people, or by the people? *American Fisheries Society Symposium* 44:431–443.
- Rieman, B. E., and K. A. Apperson. 1989. *Status and analysis of salmonid fisheries: Westslope Cutthroat Trout synopsis and analysis of fishery information*. Idaho Department of Fish and Game, Boise. Job Performance Report. Project F-73-R-11, Subproject II, Job 1.
- Rieman, B. E., D. Isaak, S. Adams, D. Horan, D. Nagel, C. Luce, and D. Myers. 2007. Anticipated climate warming effects on Bull Trout habitats and populations across the interior Columbia River basin. *Transactions of the American Fisheries Society* 136:1552–1565.
- Rieman, B. E., J. T. Peterson, and D. L. Myers. 2006. Have Brook Trout displaced Bull Trout along longitudinal gradients in central Idaho streams? *Canadian Journal of Fisheries and Aquatic Sciences* 63:63–78.
- Ver Hoef, J. M., E. E. Peterson, and D. Theobald. 2006. Spatial statistical models that use flow and stream distance. *Environmental and Ecological Statistics* 13:449–464.
- Ver Hoef, J. M., E. E. Peterson, D. Clifford, and R. Shah. 2014. SSN: An R package for spatial statistical modeling on stream networks. *Journal of Statistical Software* 56:1–47.
- Wang, L., D. Infante, P. Esselman, A. Cooper, D. Wu, W. Taylor, D. Beard, G. Whelan, and A. Ostroff. 2011. A hierarchical spatial framework and database for the national river fish habitat condition assessment. *Fisheries* 36:436–449.
- Webb, B. W., and F. Nobilis. 2007. Long-term changes in river temperature and the influence of climatic and hydrological factors. *Hydrological Sciences Journal* 52:74–85.
- Wenger, S. J., D. J. Isaak, J. B. Dunham, K. D. Fausch, C. H. Luce, H. M. Neville, B. E. Rieman, M. K. Young, D. E. Nagel, D. L. Horan, and G. L. Chandler. 2011a. Role of climate and invasive species in structuring trout distributions in the Interior Columbia Basin. *Canadian Journal of Fisheries and Aquatic Sciences* 68:988–1008.
- Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Neville, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, A. F. Hamlet, and J. E. Williams. 2011b. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proceedings of the National Academy of Sciences* 108:14175–14180.
- Wenger, S. J., C. H. Luce, A. F. Hamlet, D. J. Isaak, and H. M. Neville. 2010. Macroscale hydrologic modeling of ecologically relevant flow metrics. *Water Resources Research* 46, W09513, doi:10.1029/2009WR008839.
- Williams, J. E., R. N. Williams, R. F. Thurow, L. Elwell, C. P. Philipp, F. A. Harris, J. L. Kershner, P. J. Martinez, D. Miller, G. H. Reeves, C. A. Frissell, and J. R. Sedell. 2011. Native fish conservation areas: a vision for large-scale conservation of native fish communities. *Fisheries* 36:267–277.
- Young, M. K., K. S. McKelvey, K. L. Pilgrim and M. K. Schwartz. 2013. DNA barcoding at riverscape scales: assessing biodiversity among fishes of the genus *Cottus* (Teleostei) in northern Rocky Mountain streams. *Molecular Ecology Resources* 13:583–595.