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Perspective

Cold-water habitats, climate refugia, and their utility for conserving salmonid fishes

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Abstract

Anthropogenic climate change is warming global temperatures, with significant implications for salmonid fishes that depend on the availability of cold water during one or more life stages. Along the southern range extents of many species, and elsewhere that warm temperatures are increasingly problematic, identification and protection or restoration of habitats that may serve as climate refugia where local populations can persist is emerging as an important conservation tactic. In this perspective piece, we address the concept and utility of climate refugia—drawing a distinction with the more commonly considered thermal refuges—describe technological advances that enable accurate temperature mapping and species distribution modeling in lotic environments, and outline key uncertainties and opportunities to chart a constructive path forward on a topic that will continue to grow in importance. Identifying climate refugia is not a panacea for salmonid conservation, but we argue that there are tangible benefits to doing so, not the least of which are the options it affords for thinking and acting strategically within the context of a changing climate this century.

Key words: stream, climate change, climate refugia, thermal refuge, salmonid, species distribution model

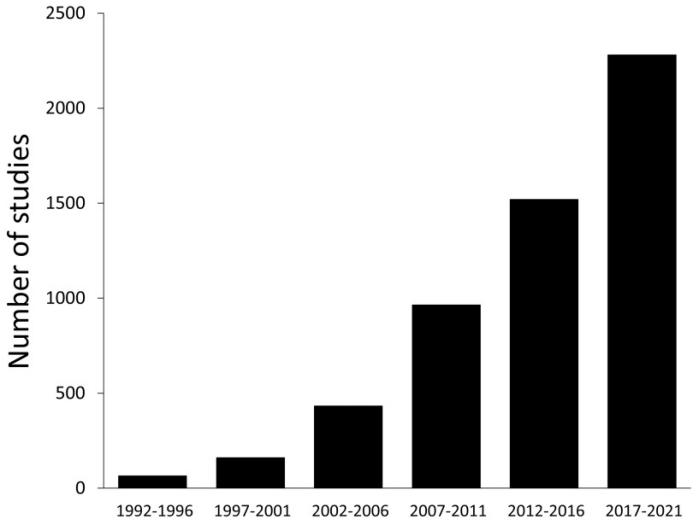
Introduction

Salmon, trout, char, lenok, whitefish, and taimen in the family Salmonidae (hereafter, salmonids) are commonly and often interchangeably referred to as cold-water fishes due to the temperatures of their preferred habitats. Like other ectotherms, the thermal environments experienced by salmonids strongly affect their metabolic rates, foraging behavior, stress responses, distributions and abundance, life histories, population structure, and evolution (Brett 1971; Brannon et al. 2004; Neuheimer and Taggart 2007; Angilletta and Angilletta 2009; Kingsolver 2009). Because salmonids are adapted to colder temperatures than most other fishes, however, they can exploit resources in environments that are unavailable to other species and have become broadly distributed within aquatic communities at higher latitudes across the globe. As is the case with many species native to the Northern Hemisphere (Hampe and Petit 2005), the prevalence of salmonids wanes along the southern margins of their ranges as the availability of suitably cold environments becomes seasonally limited, spatially fragmented, and increasingly constrained to mountainous terrain.

Stimulating discussions about thermal controls on salmonid populations in recent decades, of course, has been anthropogenic climate change that is increasing water temperatures globally (McCullough et al. 2009; van Vliet et al. 2013; O'Reilly et al. 2015; Isaak et al. 2018) and exacerbating habitat losses and productivity declines among salmonids and other aquatic species where warm conditions are limiting (Lynch et al. 2016; Gallagher et al. 2022). The potential for climate change to reduce the geographic extent occupied by salmonids was first recognized in late 20th-century bioclimatic assessments (Meisner 1990; Keleher and Rahel 1996; Nakano et al. 1996), which spawned many similar studies (reviewed by Comte et al. 2013) and, more recently, case histories that document species distribution shifts consistent with model predictions (Hari et al. 2006; Winfield et al. 2010; Almodóvar et al. 2012; Comte and Grenouillet 2013; Lemoine et al. 2020; Bell et al. 2021; Maitland and Latzka 2022; Svenning et al. 2022). Although climate-related extirpations of local populations in southern ranges are yet infrequent and may ultimately be limited in comparison to the historical losses already suffered by many species (Gustafson et al. 2007), projections of warming for the next several decades or longer (IPCC 2021) suggest that further population declines, range contractions, and occasional extirpations could become commonplace. As this dynamic unfolds, managers and conservationists may be forced to practice triage when deciding where to invest limited resources, which populations to save, and how to design and implement effective conservation strategies.

One concept drawing increasing attention for salmonid conservation as global temperatures warm is that of climate refugia, as evidenced by the growing number of studies that reference this and related terms (Fig. 1). Climate refugia

Fig. 1. Google Scholar search results for studies containing the words or phrases "climate change, refugia, and salmonid" published in 5 year intervals over a 30 year period.



were originally viewed as areas where populations, metapopulations, or lineages retreat to, remain in, and colonize from when environmental conditions are unfavorable for persistence elsewhere (Walker 1988; Keppel et al. 2012). This definition implies a temporal scale lasting generations, decades, or centuries, and an ecological scope involving entire populations and the suite of habitats necessary for their enduring persistence. Commensurate with this traditional view, many salmonid species in North America and Eurasia retreated during Pleistocene glacial maxima into refugia along the periphery of continental ice sheets and at lower elevations in mountain landscapes (Hamilton et al. 1989; Bernatchez and Wilson 1998; Shafer et al. 2010). As global air temperatures warmed 4–5 °C in the millennia after the last glacial maximum ~15–20,000 years ago (Lorius et al. 1990), salmonids dispersed from these areas to recolonize accessible hydrologic networks and also likely experienced thermal limitations associated with warm temperatures in portions of their ranges (Fig. 2). In recent years, the definition of climate refugia has expanded to include areas that may support populations through the current Holocene–Anthropocene transition (Gavin et al. 2014; Lewis and Maslin 2015) and a broader range of ecological attributes that apply to one or more life stages and individual species or entire communities and biomes (Ebersole et al. 2020; Morelli et al. 2020). Refugia are now also sometimes defined with an emphasis on physical rather than ecological attributes. In these cases, areas that are decoupled from or weakly linked to regional climate trends, e.g., places where temperature or precipitation isoclines shift particularly slowly, may be considered refugia (Loarie et al. 2009; Dobrowski 2011; Isaak et al. 2016; Briggs et al. 2018).

Two approaches to delineating refugia for contemporary salmonid conservation efforts have thus far been developed, and not surprisingly, they revolve around the availability and distribution of cold-water habitats where they are otherwise rare. The first approach, pioneered by Torgersen et al.'s (1999, 2001) seminal studies, used aircraft-mounted thermal infrared (TIR) sensors to delineate cold temperature anomalies along segments of the John Day River and describe the disproportionate use of these areas by migrating adult Chinook salmon (*Oncorhynchus tshawytscha*) during warm summer periods (Fig. 3). These and subsequent efforts, which expanded the approach to other species and geographies (Ebersole et al. 2001; Hillyard and Keeley 2012; Dugdale et al. 2013), identify refugia as localized areas, e.g., 1–10 m^2, within or adjacent to mainstem rivers that are associated with tributary confluences or groundwater upwelling zones, where a few or hundreds of individual salmonids concentrate to weather physiologically stressful peak temperatures before redistributing throughout a broader area or, in the case of migratory species, continuing unidirectional up- or downstream movements. Due to the short-term use and small scales of these cold-water anomalies, Sullivan et al. (2021) have classified them as thermal refuges rather than climate refugia, a distinction we support and recognize henceforth.

The second approach developed by Isaak et al. (2015) through application to native trout species uses network-scale stream temperature scenarios as elements of species distribution models (SDMs), which incorporate multiple covariates to describe species' ecological niches (Elith and Leathwick 2009). This approach is an adaptation of methods commonly applied to terrestrial taxa in which SDMs are used to model contemporary distributions and then predict future distributions in different climates with a goal of identifying climate refugia where target species are most likely to persist (Gavin et al. 2014; Singh et al. 2020; Brambilla et al. 2022). In Isaak et al.'s (2015) application, an emphasis was placed on predicting the locations and occupancy probabilities of particularly cold natal habitats throughout trout species' ranges that are less susceptible to non-native species invasions and are required for spawning, egg incubation, and juvenile rearing (Fig. 4; McCullough 1999; Dahlke et al. 2020). It was reasoned that these habitats are nonsubstitutable with regard to species persistence, and their identification could help focus limited conservation investments on critical source areas within the broader distributions typically occupied by salmonid fishes.

Both approaches have merit and provide information about habitats necessary for the persistence of salmonid populations or life histories within those populations. However, there are also inconsistencies in the literature concerning the distinctions between thermal refuges and climate refugia, as well as their potential interoperability, which need clarification. In this perspective piece, we address these issues by first revisiting how recent technological and analytical advances have improved the accuracy of stream and river temperature modeling and mapping at habitat unit to network scales. Because the SDM climate refugia approach is a more recent addition to the salmonid literature with less mature applications than those developed for thermal refuges, it is then illustrated with an example before its potential conservation benefits and perceived shortcomings are addressed. We conclude by discussing a series of key uncertainties, the resolution of which could improve the identification and

Fig. 2. The distribution and availability of salmonid habitats in North America and Eurasia have varied considerably during recent geological epochs. During the most recent Pleistocene glacial maxima ~15–20,000 years ago, many populations were forced into refugia along the periphery of continental ice sheets and at lower elevations within mountain landscapes (*a*). As global temperatures warmed into the Holocene, salmonids colonized newly available habitats and also experienced limitations associated with warm temperatures in some portions of their ranges (*b*). As the transition occurs between the Holocene and Anthropocene epochs, rapid global warming is occurring, cumulative effects from human land use and invasive species have reduced the biophysical complexity of available habitats, and many native salmonid species are confined to subsets of their former ranges (*c*).

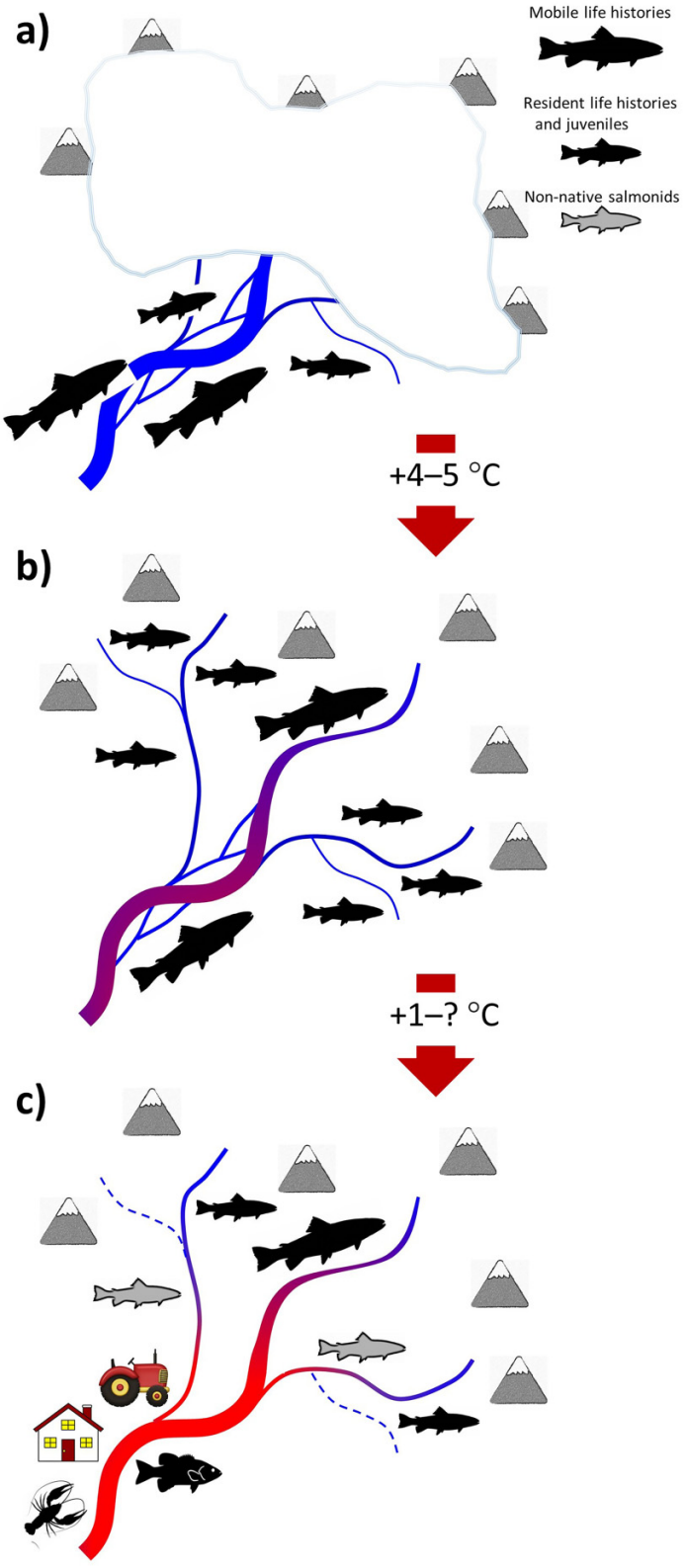
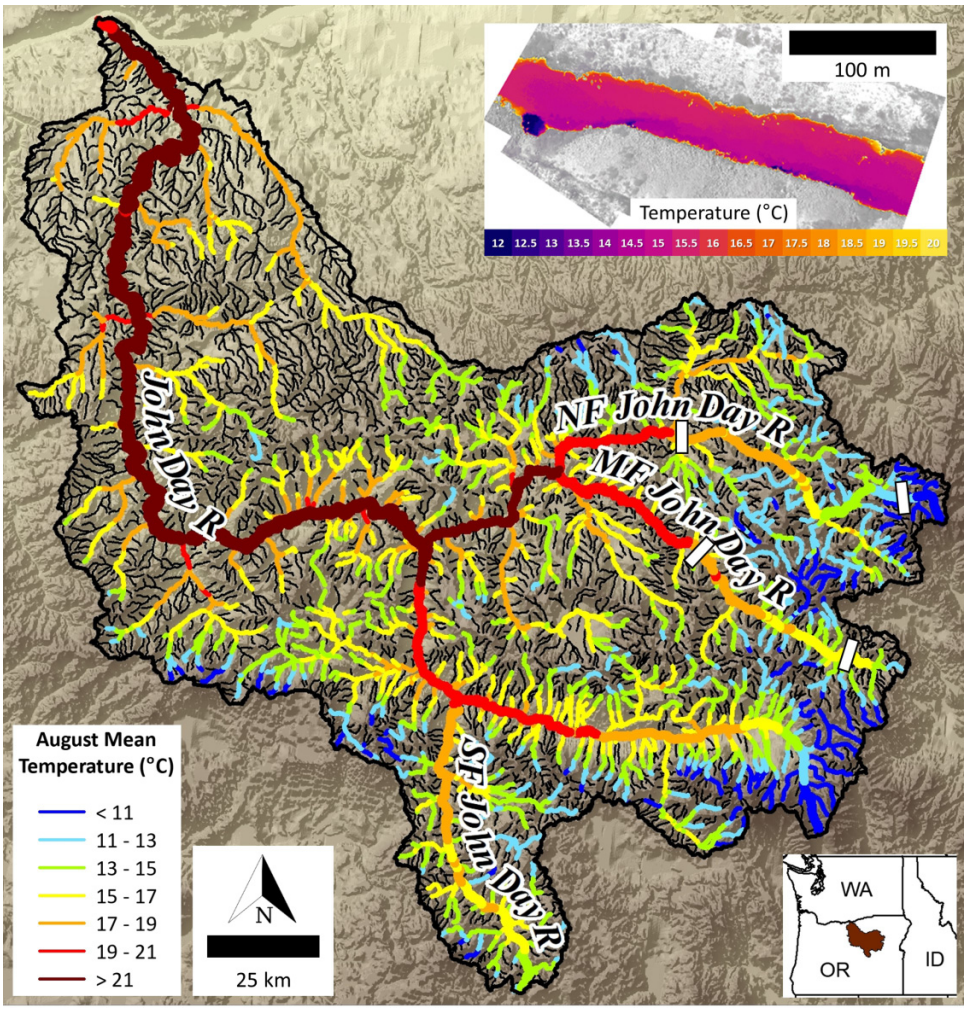


Fig. 3. The John Day River network in central Oregon showing contrasts between thermal refuges along a 250 m river reach (upper map inset; image provided by C. Torgersen) and broader network-scale temperature patterns predicted from a spatial statistical network model fit to temperature records as described in Isaak et al. (2017). The full network depiction is based on the medium-resolution NHD 1:100,000-scale hydrography layer (McKay et al. 2012) and encompasses 15,000 km but the reaches depicted as narrow black lines have slopes exceeding 15% or mean flows less than 0.03 $m^3 \cdot s^{-1}$ and are rarely occupied by salmonids or other fishes. A subset of the network encompassing 5622 km is color coded by mean August temperature for a climate scenario representing the 1993–2011 average (scenarios were downloaded from the NorWeST website: https://www.fs.usda.gov/research/rmrs/projects/norwest). White bars along two forks of the John Day River denote the upper and lower extents of the original TIR surveys conducted by Torgersen et al. (1999, 2001).

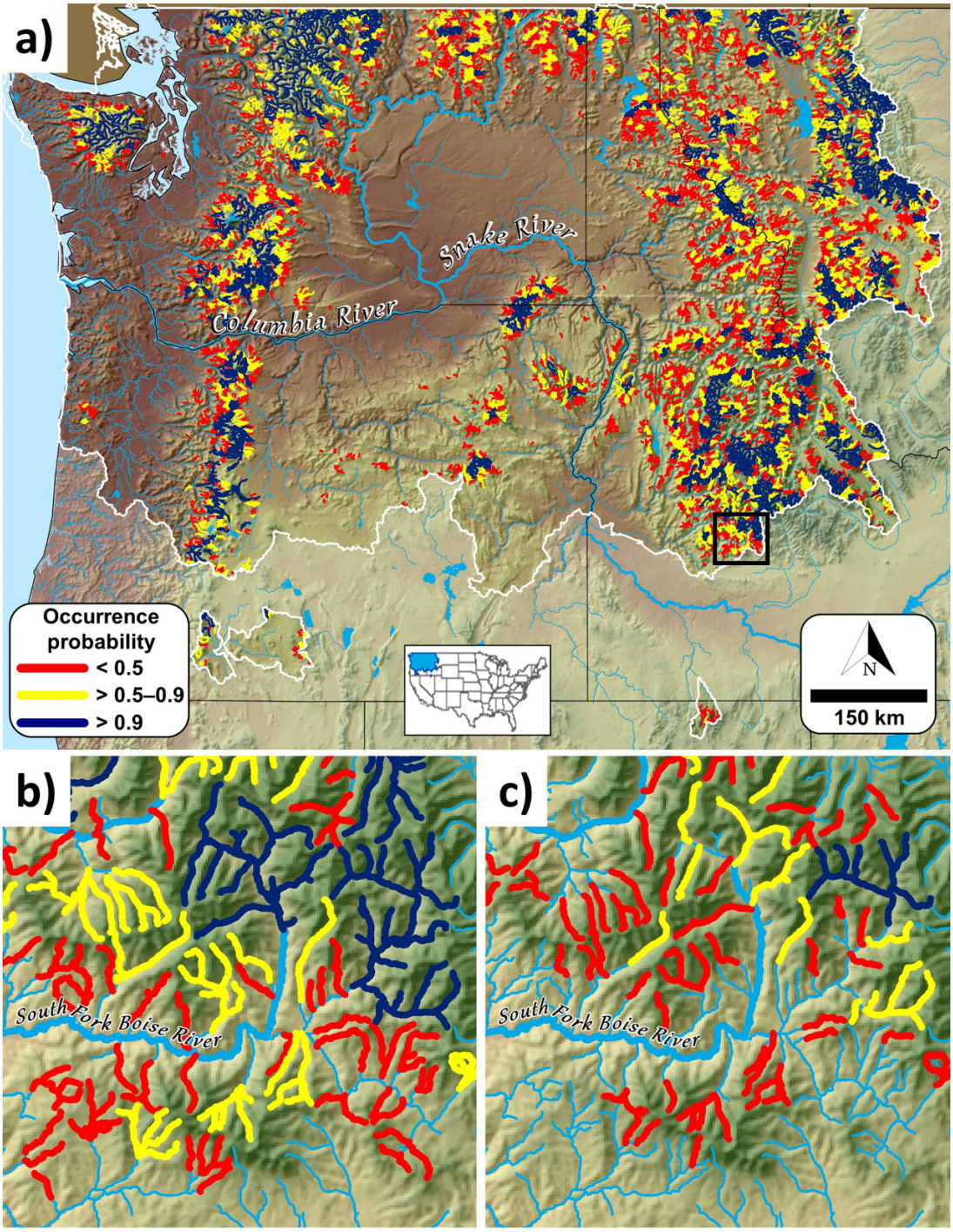


utility of climate refugia and thermal refuges for salmonid conservation efforts in the Anthropocene.

Technological enablers

Early bioclimatic assessments for salmonid fishes were important for raising awareness of the magnitude of habitat and population losses that could result from climate change. Loss estimates vary widely based on the species, geographic area, and climate change scenarios that were considered, but even lower end estimates implied substantial changes throughout the ranges of many species (Meisner 1990; Keleher and Rahel 1996; Comte et al. 2013). The utility of early assessments was tempered, however, by the imprecision stemming from the use of readily available but coarse surrogate measures for water temperature such as elevation, air temperature, or groundwater temperature. This imprecision meant that model outputs could not be used by managers to target conservation efforts at specific streams, watersheds, or portions thereof. This is critical because even in wilderness settings or when dealing with species designated for protection, numerous interests vie for land-use benefits, and fisheries managers do not have the authority or budgets to protect all populations. Consequently, climate-smart conservation efforts have to be targeted, scientifically grounded, and feasible. Fortuitously, the development of inexpensive, continuously recording water temperature sensors in the 1990s and their rapid adoption by aquatic resource professionals laid the foundation for developing precise information about thermal conditions in rivers and streams (Ouellet et al. 2020).

Fig. 4. Distribution of potential natal habitat patches for bull trout in the US portion of the species range color coded by occupancy probabilities that were predicted from a species distribution model for a baseline climate scenario representing the years 1993–2011 (*a*). Black box highlights habitat occupancy probabilities in the South Fork of the Boise River for the baseline climate scenario (*b*) and a scenario representing a 2 °C water temperature increase (*c*). Bull trout probability scenarios were downloaded from the Climate Shield website (https://www.fs.usda.gov/research/rmrs/projects/climate-shield) and overlaid on streamlines from the medium-resolution NHD 1:100,000-scale hydrography layer (McKay et al. 2012).



In the case of TIR river surveys for thermal refuge mapping, water temperature sensors are used in a complementary manner to collect instantaneous measurements coincident with survey flights, which are conducted over a few hours on a summer day when water temperatures are relatively high. The measurements provide calibration for TIR images, which then provide surface water temperature estimates that are accurate within ±0.5 °C of observed temperatures (Torgersen et al. 2001; Handcock et al. 2012). Because pixel widths in TIR images are 0.1–0.5 m, two-dimensional renderings

of river temperatures are possible, which include thermal patterns along the stream as well as anomalies associated with lateral inflows or point sources of midchannel groundwater upwelling if these are strong enough to register at the surface (Fig. 3; Dugdale et al. 2015). Individual TIR surveys encompass tens to hundreds of river kilometers, and multiple survey data sets may be collated into larger databases such as Fullerton et al. (2015) used to describe longitudinal thermal patterns in rivers of the northwestern US. Where TIR surveys are completed, the resulting data sets enable precise identification of thermal refuges that are often important for salmonids during warm temperature events, and which managers can enhance or protect (Kurylyk et al. 2015) while also reducing other stressors such as recreational fishing that sometimes targets aggregations of adults in these areas (Keefer et al. 2009). Primary limitations of the TIR refuge approach are high costs, the lack of a temporal dimension, and its applicability to subsets of river networks involving larger streams where water surfaces are not occluded by riparian vegetation. Use of unmanned aerial drones to collect TIR images can partially address limitations by reducing data acquisition costs, making survey reflights routine, and expanding the addressable portion of drainage networks (Dugdale et al. 2022). However, many tributary streams are heavily shaded and the large extent of most river networks (1000s–10,000s of kilometers), which may each comprise only portions of a species' range, means that developing comprehensive TIR temperature maps is not feasible.

The ease of acquiring temperature data with miniature sensors eventually translated to the availability of numerous water temperature records in many river basins across large portions of North America and Europe. This in turn provided opportunities to develop mechanistic and statistical approaches to temperature modeling, which have proliferated in recent decades (Gallice et al. 2015; Dugdale et al. 2017). Temperature models that are potentially useful in climate refugia applications are capable of accurately predicting temperatures throughout river networks and doing so at resolutions similar to or finer than the scale of local salmonid populations (e.g., 1–10s km) that managers often target for conservation purposes (Rieman and Dunham 2000; Bennie et al. 2014). Although multiple models potentially meet these needs, the spatial statistical network (SSN) models developed by Ver Hoef et al. (2006) have proven particularly useful for developing unbiased predictions from the large and often spatially clustered temperature data sets that are available in many areas. These models accommodate spatial autocorrelation among sites and employ prediction techniques adapted for the unique topology of stream networks to provide accurate, geographically referenced information.

Isaak et al. (2010) first used SSN models to develop accurate network temperature models (Root Mean Square Prediction Errors ~1.0 °C; r^2 ~0.9) that also incorporated temporal variability in air temperatures and stream discharge, thereby enabling linkages with outputs from global climate models and the downscaling of effects to river networks. This modeling approach was subsequently used with a database of stream temperature measurements from more than 23,000 unique sites to develop historical and future summer temperature scenarios for dozens of river basins and hundreds of thousands of network kilometers spanning the western US (Isaak et al. 2017*a*). More recently, FitzGerald et al. (2021) repurposed a portion of this database and used SSN models to develop annual monthly stream temperature scenarios for anadromous salmon streams along the US Pacific Coast. These temperature scenarios have been paired with a variety of biological data sets by multiple research groups and have helped expand and add precision to our understanding of thermal controls on salmonid distributions, patterns of abundance, genetic introgression, phenology, climate vulnerability, and population growth rates (Westley et al. 2015; Al-Chokhachy et al. 2016; Young et al. 2016, 2018*a*; Isaak et al. 2017*b*; Crozier et al. 2019; Mandeville et al. 2019; LeMoine et al. 2020; Bell et al. 2021; Bowerman et al. 2021; Cordoleani et al. 2021; FitzGerald et al. 2021, 2022).

To develop realistic SDMs that are representative of ecological niches, however, other aspects of stream systems beyond temperature must also be characterized. Critical in this regard was the development of nationally consistent vector networks depicting river drainages, such as the National Hydro Network in Canada (NHN; http://www.nrcan.gc.ca/home) and the National Hydrography Dataset in the US (NHD; https://www.usgs.gov/national-hydrography/national-hydrography-dataset; Moore and DeWald 2016). These provide geospatial representations of networks and the individual reaches composing them, and constitute powerful frameworks for organizing stream data. Each reach has a unique identifier that allows a suite of attributes to be assigned that describe stream conditions and may serve as model covariates (e.g., temperature, elevation, slope, discharge, watershed size, and many others; McKay et al. 2012; Hill et al. 2016). Geographic information systems (GIS) can be used to depict and query these networks, create data sets for analysis by cross-referencing biological and temperature observations with descriptive attributes, and apply model predictions throughout river networks to generate output data sets and maps.

A simple example illustrates how thermal conditions are relevant to salmonid distributions only after accounting for other network attributes. Looking at the mountainous John Day River basin in Oregon where Torgersen et al.'s (1999, 2001) original TIR surveys were conducted (Fig. 3), the NHD 1:100,000-scale medium resolution network there depicts 15,000 km of stream channels. However, much of this extent is inaccessible to salmonids or of marginal value due to channel steepness and limited flows in the smallest headwater reaches. Our observations from previous decades of field research, as well as results from studies that link thousands of species occurrence records to NHD reaches (Isaak et al. 2015, 2017*b*), indicate that salmonids and other fish species rarely occupy reaches in the upper portions of networks where flows are less than ~0.03 $m^3 \cdot s^{-1}$ (equivalent to ~1 m wetted width) or channel slopes consistently exceed ~15% because water depth, flow intermittency, or barriers prevent access at some point along channel profiles (Fransen et al. 2006). If these stream size and slope filters are applied within the John Day River basin using NHD reach descriptors, 9378 km of the network are excluded, and 5622 stream km

remain where fish occurrence is likely and temperatures may affect distributions.

Within the potential habitat networks so delineated, SDMs are useful for estimating the joint effects of multiple covariates on species occurrence or abundance, and as with temperature models, the number of statistical and mechanistic analytical approaches is extensive (Elith and Leathwick 2009; Guillera-Arroita et al. 2015; Briscoe et al. 2023). Specialized models exist to address different types of biological survey information (e.g., presence-only data, presence–absence data, or abundance data), but all share the capacity to link this information to habitat covariates and describe these relationships with predictive equations. Care is required in model development to avoid under- or overfitting models and to maintain interpretability by using covariates that are biologically meaningful (Merow et al. 2014; Fourcade et al. 2018), but by jointly considering factors that represent different aspects of species' ecological niches, SDMs provide a means of accurately estimating the marginal effects of covariates, including temperature, on biological outcomes. Once an SDM is developed, the predictive equation becomes a tool for use with a GIS and geospatial representations of stream covariates to map predictions about species distributions throughout river networks.

An example modeling climate refugia for native trout

Drawing on the availability of the NHD, extensive species occurrence surveys, and GIS data sets representing temperature and other habitat covariates, Isaak et al. (2015) developed SDMs to predict native bull trout and cutthroat trout distributions in the northwestern US for a baseline period and future conditions associated with the A1B warming trajectory for mid- and late 21st-century periods (IPCC 2013). Rather than developing models for the occurrence of any life stage that would have yielded prediction maps of limited specificity, a focus was placed on modeling occurrence within potential natal habitats. These habitats are restricted in ecological scope and geographic extent, especially with regard to temperature because reproductive life stages, i.e., mature adults, incubating eggs, and juveniles, require colder conditions than subadults and prespawn adults, which may range widely through warmer environments (McCullough 1999; Dalke et al. 2020). Natal habitat "patches" have previously been defined for salmonid fishes as discrete portions of river networks that meet these restrictive thermal requirements and are usually associated with the distributions of juvenile fish (McElhany et al. 2000; Rieman and Dunham 2000; Dunham et al. 2002). Acknowledged in this definition is that natal habitat patches are also often occupied by resident individuals and populations, but that some proportion of individuals may exhibit migratory life histories and emigrate after one to several years of rearing (Northcote 1992; McPhail and Baxter 1996). Upon maturation, however, these individuals return to cold natal areas for spawning, and because salmonids are philopatric, genetic structure indicative of local breeding populations commonly emerges at the patch scale (Whiteley et al. 2006; Schtickzelle and Quinn 2007).

Isaak et al. (2015) operationalized the definition of natal habitat patches for bull trout and cutthroat trout by applying the reach slope and flow criteria described in the previous section with a mean August temperature criterion of 11 °C to delimit the downstream extent of potential natal patch habitats. The temperature criterion was chosen from a frequency histogram describing the occurrence of juvenile cutthroat trout <125 mm at 2269 survey sites and bull trout <150 mm at 1102 sites relative to a baseline stream temperature scenario representing conditions during the survey years. Large majorities of these juvenile occurrences, i.e., 90%–99%, were restricted to stream reaches where mean August temperatures were colder than 11–13 °C, despite frequent observations of the adults of both species in reaches where summer temperatures approach 20 °C (Howell et al. 2010; Schoby and Keeley 2011). Choosing the lower end of the 11–13 °C range for patch delineation was also influenced by a desire to provide the native trout with a buffer against deleterious interactions with other species. Especially cold streams, for example, are largely outside the thermal niche of non-native brown trout (*Salmo trutta*), a widespread competitor and predator that often displaces cutthroat trout and bull trout from warmer stream and river reaches (Wenger et al. 2011; Budy and Gaeta 2018; Bell et al. 2021). Likewise, in river basins where rainbow trout (*Oncorhynchus mykiss*) are present and hybridization with cutthroat trout is a concern, the incidence of genetically pure cutthroat trout increases rapidly in reaches where mean August temperatures are less than 11 °C (Young et al. 2016) because hybrids are better adapted to warmer temperatures (Rasmussen et al. 2012).

The descriptors of the cold-water habitat patches that were used in SDM development consisted of patch slope averaged across the reaches composing a patch, mean or minimum August temperature, patch size estimated as stream length, and the prevalence of brook trout (*Salvelinus fontinalis*), a non-native species also favoring cold headwater habitats. Logistic regression models were used to parameterize the SDMs from data sets that included more than 500 habitat patches where species status was known, and the models correctly classified native trout occurrence in 78% of the bull trout patches and 85% of the cutthroat trout patches. The SDMs were then used with a GIS to predict occupancy probabilities in potential natal habitat patches throughout the US portions of the species' ranges under different climate scenarios and levels of brook trout invasion (Fig. 4). As expected, habitat occupancy probabilities decreased broadly as available cold-water areas in future scenarios contracted into headwater areas and fragmented. Under both moderate and extreme climate change scenarios, however, tens to hundreds of natal habitat patches with occupancy probabilities >0.5 (a threshold commonly used to denote occupancy) were predicted to remain for both species, and those with probabilities >0.9 were designated as climate refugia (Isaak et al. 2015). There was nothing sacrosanct about the higher probability level in terms of refugia; the intent was merely to highlight subsets of patches within the full range of possibilities that retained high odds of future occupancy. Because previous climate assessments for these species based on coarse covariates and simpler models predicted substantially greater range reductions and risks

of population losses (Rieman et al. 2007; Williams et al. 2009), the results were novel both due to their less dire nature and, more importantly, a precision that enabled the identification of specific streams where species occurrence and persistence were most likely.

Conservation benefits

An array of practical benefits arose from this exercise, perhaps foremost of which was a cause for cautious optimism. The presence of one or more occupied refugia within a river basin or subdrainage often helped alleviate the concerns of local managers that a species would disappear from landscapes within their jurisdiction. In areas where climate refugia were rare, their identification led to efforts at greater protections, either through special administrative designations, discretionary decisions to direct detrimental land uses away from these areas, or by rallying support among stakeholders to target conservation resources and maximize population support (S. Spaulding, U.S. Forest Service regional fisheries manager (personal communication in 2022)). Equally relevant from a management perspective, the SDMs used a consistent and replicable approach to delineate potential habitat patches and assign probabilities at a scale commensurate with local populations across significant portions of the species' ranges. This was important for bull trout and cutthroat trout because hundreds of extant populations are spread among multiple administrative jurisdictions and thousands of habitat kilometers in five US states, which at some level, through either formal or informal means, must be ranked and prioritized for limited funding and conservation efforts. In this broader matrix, climate refugia—and habitat patches with higher occupancy probabilities in general—could also ultimately emerge as redoubts around which climate-smart conservation strategies are someday designed (e.g., Cabeza and Moilanen 2001; Verboom et al. 2001). For example, if populations in the future are increasingly extirpated from small, isolated habitats with low occupancy probabilities, managers could choose to prioritize investments in higher probability habitats (or those which restoration could significantly improve) that are proximal to occupied refugia which may provide demographic support through local dispersal (Rieman and Dunham 2000; Isaak et al. 2022).

Another valuable outcome from the native trout SDMs was the design of an efficient population inventory program predicated on the distribution of suitable habitats (Guisan et al. 2006). Such programs are often needed in headwater areas where the large network extents and remote settings mean that many potential habitats have not been adequately surveyed (Bishop et al. 2008). Even for a high-profile species like bull trout in the intensively studied southern portion of its range, this remained true until recently when SDM predictions were used to guide a regional environmental DNA sampling campaign that assessed bull trout status at thousands of sites where occurrence was uncertain (McKelvey et al. 2016; Young et al. 2017). Some of these surveys led to the discovery of new populations, whereas others targeted habitats where populations historically occupied only a few stream kilometers and had not been resurveyed in decades (Nelson et al. 2002; Rieman et al. 2006). The results typically confirmed that these populations remained and suggested a degree of resilience that is encouraging in light of ongoing environmental change and range contractions in this species (Lemoine et al. 2020; Bell et al. 2021; Isaak et al. 2022). Finally, the SDM predictions and subsequent sampling highlighted unoccupied habitats with high probabilities of supporting populations that could be potential candidates for establishing new populations. In one instance, this led to state and federal management agencies planning the establishment of a native fish climate refugium in the upper North Fork Blackfoot River in Montana, which is isolated above a geological barrier and was historically fishless (S. Spaulding (personal communication)).

Criticisms of cold-water climate refugia

The native trout SDMs are not without uncertainties and limitations, but their application to delineate potential climate refugia has also drawn criticisms that are useful to address because they help highlight several important and underappreciated considerations. Most prominently, Armstrong et al. (2021) suggest that climate refugia, when focused on cold habitats, devalue warmer, more productive downstream environments that mobile individuals may exploit to attain larger body sizes and greater fitness. Further, because conservation is a zero-sum game, the allocation of resources to these cold areas reduces investments elsewhere and may result in a maladaptive response. While these arguments have some merit and we readily acknowledge the importance of warm, productive environments as their relationships with life history expression and abundance have long been a foundation of salmonid research (Allen 1951; Chapman and Bjornn 1969; Gross et al. 1988; Elliott 1994), we also observe that for many nonanadromous species, such areas are not strictly required for persistence and instead constitute a complementary habitat element. Evidence of this is provided by resident populations of many salmonid species that have persisted for decades, centuries, or longer in headwater streams isolated above geologic or anthropogenic barriers (McCart and Craig 1973; Hindar et al. 1991; Propst et al. 1992; Sato and Harada 2008; Morita et al. 2009; Northcote 2010; Whiteley et al. 2010; Pujolar et al. 2011; Torterotot et al. 2014; Duda et al. 2021; Harvey et al. 2021; Kovach et al. 2022). It is also frequently the case in developed river basins that mobile life histories and the larger fish that exploit warmer environments have declined significantly or been lost while many headwater populations composed of resident individuals endure (Rieman and Dunham 2000; Morita and Yamamoto 2002; Nelson et al. 2002; Hudy et al. 2008; Donadi and Näslund 2023).

Moreover, in southern range extents where the threats from climate change are greatest, the warmer growth environments emphasized by Armstrong et al. (2021) are not a limiting resource. To the contrary, they are widespread, increasing with climate change, and abundant relative to the cold habitats that support the reproductive life stages required for species persistence. To demonstrate the magnitude

of this disparity, we calculated the length and volume of streams and rivers in four mean August temperature categories throughout the southern portions of the bull trout and westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) ranges in the northwestern US. These areas constitute ~30%–50% of the species' ranges, which also extend far north into western Canada (Reist et al. 2002; Young et al. 2018*b*). Calculations were done using the NHD network (filtered by the reach slope and flow criteria described previously) with stream temperature scenarios obtained from the NorWeST website (https://www.fs.usda.gov/research/rmrs/projects/norwest). The potential ranges of both taxa encompassed large portions of mountainous drainage networks in this region (156,000 km for bull trout and 84,000 km for westslope cutthroat trout), but in a baseline climate scenario representing the years 1993–2011, only 25%–30% of the network lengths were colder than the 11 °C criterion we used to delimit natal habitat areas (Table 1). On a volumetric basis, however, these suitable areas were dramatically smaller, constituting <0.58% of the networks because the coldest streams usually occur in small headwater basins. Future scenarios representing 1 °C and 2 °C stream temperature increases, which are likely to be achieved sometime in the 21st century given historical warming rates and future projections for this region (Wu et al. 2012; Isaak et al. 2017*a*, 2018), further reduced these cold areas to less than 13% of the network lengths and 0.17% of the network volumes under the more extreme scenario. In comparison to other salmonid species, these percentages are likely to be relatively small, but even species with warmer thermal niches will be confined to subsets of their ranges at times by the availability of suitably cold temperatures for reproduction, thus creating a thermal bottleneck and key climatic vulnerability highlighted by Dahlke et al. (2020).

Other reasons for focusing on cold-water habitats are equally pragmatic in light of the fact that native salmonids in many areas are already restricted to relict headwater habitats by their exclusion from warmer, historical habitats through a complex of factors that are difficult, if not impossible, to remedy. For example, patterns of human landscape occupation and degradation of fluvial systems are usually concentrated in floodplains along major river and stream valleys (Fang et al. 2018). Multiple factors associated with human development result in warmer stream temperatures (e.g., reduced riparian shading, flow withdrawals, dam and reservoir development, paved surfaces, and urban heat sinks)—now exacerbated by climate change and contributing to rapid warming and exceedance of maximum temperature tolerances for salmonid species in larger portions of the Northern Hemisphere each decade (Kaushal et al. 2010; van Vliet et al. 2013; Arora et al. 2016; Isaak et al. 2018).

Equally important, these altered habitats and their warmer thermal regimes often host well-established populations of non-native invasive aquatic mussels, plants, crustaceans, disease organisms, and fishes (Sanderson et al. 2009; Olden et al. 2021). Unlike the depauperate fauna that can be successful in the coldest streams, the species pool capable of invading warmer waters is vast, and introductions are ongoing (Gallardo et al. 2016; Seebens et al. 2017; Rahel and Smith 2018; Hartman and Larson 2023). Through direct competition, predation, epizootics, and trophic alterations, these invasions make it more difficult for native cold-water species to navigate and exploit the warmer portions of their ranges. Moreover, several of the most widely introduced non-native fish species such as brown trout, rainbow trout, lake trout (*Salvelinus namaycush*), smallmouth bass (*Micropterus dolomieu*), and northern pike (*Esox lucius*) are sportfishes that are directly implicated in the declines of native salmonids (Stafford et al. 2002; Lawrence et al. 2012; Hesthagen et al. 2015; Walrath et al. 2015; Budy and Gaeta 2018). Where these species are supported by angling communities, their removal is often contentious, not to mention logistically impossible in larger rivers, lakes, and reservoirs. Collectively, therefore, we expect warm, downstream portions of many river networks to continue warming at accelerated rates, perhaps undergo additional degradation if important and ongoing habitat restoration efforts prove insufficient (Poff and Matthews 2013; O'Connor et al. 2015), and to host growing assemblages of non-native species, thereby making these areas increasingly hostile environments for mobile salmonids that venture from colder waters.

The other main criticism of the Isaak et al. (2015) SDMs is that stream thermal regimes are so complex that focusing on a single descriptive metric such as mean August temperature misses ecologically important details (Steel et al. 2016, 2017). Although plausible and the use of multiple thermal regime metrics is encouraged when appropriate, it is also the case that many metrics are strongly correlated (Rivers-Moore et al. 2013; Steel et al. 2016), convey similar information when used as model covariates, and would therefore have minor effects on the spatial patterns of predicted occurrence probabilities that help inform conservation decisions. Mean August temperature, for example, is highly correlated, i.e., $r > 0.9$, with several additional measures of summer maxima, mean fall and spring temperatures, annual temperature, growing degree days, and measures of annual and short-term thermal variability, among others (Isaak et al. 2018, 2020). Additionally, when developing SDMs, it is problematic if two or more highly correlated covariates are included in the same model—the redundancy potentially causing issues with multicollinearity that degrade parameter estimates and lead to spurious inference (Dormann et al. 2013). Multivariate data reduction techniques such as principal components analysis may be useful in these circumstances to summarize large sets of regime metrics into scores that describe a small set of orthogonal axes, which can then be used in lieu of the original metrics to represent distinct aspects of thermal regimes. Doing so, however, often decreases model interpretability and may offer only marginal improvements in predictive performance if the axis scores are strongly correlated with simpler metric descriptors.

Future uncertainties

In our view, there are more salient issues and uncertainties associated with delineating climate refugia, which include multiple aspects of downscaling the effects of climate change on stream hydroclimates, the description of important habitat covariates at sufficient scales and resolutions, and

Table 1. Summary of network length and stream volume by summer temperature categories throughout the US portions of the bull trout and westslope cutthroat trout ranges for three climate scenarios.

		Bull trout		Westslope cutthroat trout	
Scenario	Mean August temperature	Stream length (km)	Stream volume (m^3)	Stream length (km)	Stream volume (m^3)
Baseline*	<11 °C	46,448† (29.8%)	3.94×10^7 (0.58%)	20,866 (24.9%)	9.38×10^6 (0.49%)
	>11 to <15 °C	63,030 (40.4%)	1.89×10^8 (2.77%)	17,558 (20.9%)	4.62×10^7 (2.40%)
	>15 to <19 °C	37,860 (24.3%)	2.61×10^9 (38.2%)	43,920 (52.3%)	1.46×10^9 (75.9%)
	>19 °C	8610 (5.50%)	3.99×10^9 (58.4%)	1587 (1.89%)	4.07×10^8 (21.2%)
+1 °C	<11 °C	32,192 (20.6%)	2.08×10^7 (0.31%)	15,043 (17.9%)	5.11×10^6 (0.27%)
	>11 to <15 °C	60,012 (38.5%)	1.33×10^8 (1.95%)	19,945 (23.8%)	3.74×10^7 (1.96%)
	>15 to <19 °C	49,539 (31.8%)	1.39×10^9 (20.5%)	46,176 (55.0%)	9.78×10^8 (51.2%)
	>19 °C	14,205 (9.10%)	5.26×10^9 (77.3%)	2767 (3.30%)	8.88×10^8 (46.5%)
+2 °C	<11 °C	19,551 (12.5%)	1.16×10^7 (0.17%)	9286 (11.1%)	2.93×10^6 (0.15%)
	>11 to <15 °C	56,339 (36.1%)	9.30×10^7 (1.36%)	21,446 (25.6%)	3.02×10^7 (1.57%)
	>15 to <19 °C	58,012 (37.2%)	5.37×10^8 (7.88%)	48,704 (58.0%)	9.59×10^8 (49.9%)
	>19 °C	22,046 (14.1%)	6.18×10^9 (90.6%)	4495 (5.36%)	9.30×10^8 (48.4%)

Note: Values in parentheses are percentages of the totals for a scenario.
*Baseline climate period is 1993–2011.
†Network extents are estimated from the NHD 1:100,000-scale stream layer filtered by 15% reach slope and 0.03 $m^3 \cdot s^{-1}$ summer flow in the baseline climate period.

limitations associated with biological data sets and model inferences (Potter et al. 2013; Urban et al. 2016; Briscoe et al. 2023). Challenges in these areas, however, are common to many fields and addressed elsewhere in the literature, so here we focus on topics that we believe are particularly relevant for salmonid researchers and managers to consider.

First, the issues outlined above regarding warm environments and salmonid growth have an important corollary: a warming climate is likely to increase selection against larger body sizes and, in some cases, mobility. Warmer temperatures are nearly universally associated with decreases in adult body size of aquatic ectotherms (Atkinson 1994; Pörtner 2021), although the specific causes of this trend remain an area of active research (Verberk et al. 2021; Lindmark et al. 2022; Wootton et al. 2022). To this point, there is evidence of widespread and long-term declines in adult body sizes of Pacific and Atlantic salmon, which, despite complex underlying mechanisms (Todd et al. 2008; Oke et al. 2020), are similar to the declines observed in a broad range of other fish taxa for which temperature increases are implicated (Sheridan and Bickford 2011; Baudron et al. 2014; Ikpewe et al. 2021). Moreover, water temperature and growth during the first year of life often dictate life history strategies in salmonid fishes (Ferguson et al. 2019), and juveniles of nonanadromous species that experience warm temperatures and faster growth are more likely to adopt resident life histories (Jonsson and Jonsson 2009; Morita et al. 2014; Nevoux et al. 2019; Archer et al. 2020). For anadromous species, faster growth typically results in earlier smoltification and outmigration but still may translate to smaller adult body sizes through decreases in age at maturity (Holtby 1988; Todd et al. 2008; Jonsson and Jonsson 2009; Oke et al. 2020).

A related factor of potential relevance for delineating stream climate refugia in mountainous areas is oxygen availability (as measured by the oxygen supply index, OSI; Jacobsen 2020), which reflects a complex interaction between altitude, water temperature, and boundary layer thickness at the gill–water interface. As thermally suitable habitats at high elevations warm, they may increasingly lack sufficient oxygen to support the metabolic demands of all life history types. For example, the OSI for fish or other aquatic organisms at an elevation of 4000 m is less than a third of that available at sea level (Jacobsen 2020) and because oxygen demand increases with fish size, the elevational limit for small (and likely resident) fish may be higher than for large (and probably migratory) individuals (Verberk et al. 2011, 2021, but see Audzijonyte et al. 2019 and Scheuffele et al. 2021 for differing viewpoints). Similarly, warming temperatures that limit oxygen availability at low-elevation sites are expected to disproportionately affect the largest individuals within populations (Pauly and Cheung 2018; Rubalcaba et al. 2020), a pattern that appears to apply to salmonids (Meyer and Schill 2021) and would be most problematic for large, migratory adults nearing maturity. Collectively, the factors mentioned here and earlier suggest that migratory species and life history types are exposed to risks that are only partially addressed by SDMs that focus exclusively on natal habitat patches, and more sophisticated models are required to address life stages outside these areas (Crozier et al. 2021; FitzGerald and Martin 2022).

If warmer temperatures increasingly favor smaller body sizes, salmonids will be faced with a complex of interacting challenges. For mobile species and life histories, these may include decreases in fecundity and greater difficulty in completing migrations due to insufficient energy reserves (Todd et al. 2008; Lennox et al. 2018; Howard and von Biela 2023) or increased exposure to hydroclimatically extreme conditions (Luce and Holden 2009; Mantua et al. 2010). Because facultative residency is not an option in these circumstances, management actions may have to increasingly focus on maintaining suitable thermal conditions in migratory corridors where warm temperatures are limiting to ensure life cycle completion. Thermal refuges will be vital

for temporarily harboring migrants along these corridors, and efforts to describe and inventory cold-water anomalies with TIR surveys (Dugdale et al. 2015; Fullerton et al. 2015) may need to become more predictive to aid in the design and implementation of projects that create stepping-stone habitats that meet the ecological requirements of target species (Hannah et al. 2014; Kurylyk et al. 2015; Snyder et al. 2022).

Resident life history types lack the exposure risks associated with migration, but resident individuals also grow slowly, mature at smaller sizes, and have lower fecundity than their migratory counterparts (Rieman and McIntyre 1993; Letcher et al. 2007). Moreover, a diminution of mobile life histories is equivalent to increasing levels of isolation among populations, and the effects can range from a loss of the portfolio effects that prevent regional extinction to the potential for inbreeding depression or greater vulnerability to extirpation from small-scale disturbances in local populations (Dunham et al. 2003; Haak and Williams 2012; Kovach et al. 2022). A critical uncertainty, therefore, is how long populations can persist largely or solely by expressing resident life histories. As already noted, there are many examples of long-term persistence in isolated trout and char populations, and physical isolation from invasions by non-native species is even a management strategy in some locations (Rahel 2013). And although concerns exist that the loss of migratory life history components will be permanent, there are many examples of the opportunistic re-expression of migratory life histories despite decades of anthropogenic isolation (e.g., Thrower et al. 2004; Quinn et al. 2017; Al-Chokhachy et al. 2020). Regarding a species like bull trout, there is some pessimism that populations consisting solely of residents can persist (Fausch et al. 2009), to the extent that the loss of the migratory forms has been equated with population collapse (Kovach et al. 2018). Whether this concern is legitimate, however, is unclear because most studies and status assessments have focused on larger migratory forms because resident individuals are more difficult to study (Howell and Sankovich 2012). Consequently, the abundance, distribution, and demographic characteristics of resident life histories often represent a critical gap in our understanding (Rieman and Dunham 2000), as does the likelihood of persistence should the migratory component of populations be lost (Budy et al. 2017).

Second, as environmental trends reduce the cold habitats that salmonids require, climate-related disturbances within these areas are likely to increase in both frequency and severity. Evidence already exists that extreme floods, droughts, heatwaves, and wildfires are increasing (Dettinger et al. 2015; Abatzoglou and Williams 2016; Williams et al. 2020), while simultaneously advancing into higher elevations and contacting larger portions of stream networks (Alizadeh et al. 2021; Ball et al. 2021). Future projections suggest that climatic trends in precipitation and air temperatures, which underpin these disturbance elements, will continue and perhaps worsen this century (IPCC 2021). Although salmonid species evolved in disturbance-prone environments and are often adept at navigating short seasonal or even multiyear perturbations, biological resilience has its limits, which may become more apparent as no-analog climates and disturbance regimes are imposed on smaller and more fragmented populations. As a result, future populations may require larger habitats to persist than are reflected in modeled relationships developed with historical occurrence data. Nonstationarity in these relationships means that the traditional conservation question of "how much is enough?" will change over time as conditions shift in concert with the climate. To accommodate this potential bias in habitat occupancy predictions from SDMs, a precautionary principle is warranted when forecasting or protecting areas that may serve as climate refugia, and larger habitats will almost always be better.

Third, invasions by non-native species into climate refugia may also affect modeled occurrence relationships and the persistence of native salmonid populations but the extent and consequences of future invasions are unclear. Fortunately, the global vertebrate species pool capable of invading cold aquatic environments is relatively limited and largely restricted to other salmonids (Parkinson et al. 2016; Mandeville et al. 2019) or to sculpins in the genus *Cottus*, which have minor effects on salmonids in natural settings (Moyle 1977). Because the stocking of nonnative salmonids is declining or has been eliminated in waters supporting many native salmonid populations (e.g., Love Stowell et al. 2015; Nordberg et al. 2021), and because the historical use of sculpins as baitfish (probably the primary mode of their introduction to new waters) is now banned in many areas, extensive state-sanctioned invasions by novel cold-water species are less likely in the future.

Nonetheless, nonnative salmonids are already widespread in many regions; illegal translocations may further extend their distributions; and we anticipate that the invasion fronts of two of the most problematic global invaders, rainbow trout and brown trout (Stanković et al. 2015; Budy and Gaeta 2018), will advance upstream in association with slowly shifting temperature isotherms that delimit their distributions (Wenger et al. 2011; Isaak et al. 2016; Bell et al. 2021). These potential invasions, and the desire to reduce distributional overlap with cutthroat trout and bull trout, were part of the rationale for choosing a relatively cold 11 °C thermal criterion when delimiting potential habitat patches in our models (Isaak et al. 2015, 2022). Segregation along a thermal gradient, however, may not provide a protective buffer against invasive salmonids with colder thermal niches. In these circumstances, the invasive species may be included as a covariate in SDM development to better understand and quantify the degree of habitat overlap and interactions with native species. In our native trout SDMs, this approach revealed that although the increasing prevalence of brook trout was associated with lower cutthroat trout and bull trout occurrence in small habitat patches, the effect was negligible in large patches. This suggested that co-occurrence with the native species was contextually dependent and provided a means of further refining predictions about which habitats were most likely to retain high probabilities of occupancy.

Fourth, despite an extensive literature linking climate change and many aspects of salmonid ecology, it remains unclear whether the dire predictions concerning extirpations of local populations are transpiring or whether adaptive capacity has thus far limited changes to shifts along distributional

boundaries. The first studies documenting climate-related range contractions in European grayling (*Thymallus thymallus*) and brown trout were completed at least a decade ago (Hari et al. 2006; Almodóvar et al. 2012; Comte and Grenouillet 2013) but subsequent accounts have not been published concerning local population losses. Further north in Norway and Iceland, Svenning et al. (2022) described similar range contractions and reduced abundances of Arctic char (*Salvelinus alpinus*) but also that brown trout had become more abundant in streams where cold temperatures were previously limiting. In the western US, Bell et al. (2021) described losses of 18% for bull trout and 6% for cutthroat trout (both westslope and Yellowstone cutthroat trout *O. c. bouvieri* subspecies) from historical occurrence sites between 1993 and 2018. Despite these reductions, however, recent eDNA inventories in the same region found no evidence of patch-scale bull trout extirpations when compared with earlier surveys (Young et al. 2017; Isaak et al. 2022). Nonetheless, many small bull trout populations and those of other salmonid species (Morita et al. 2009; Torterotot et al. 2014; Kovach et al. 2022) are currently restricted to a few kilometers of headwater habitat, and it grows increasingly likely that ongoing warming trends will either eliminate these thermal habitats or reduce them to such an extent that catastrophic disturbances or perhaps a series of smaller climatic perturbations begin to cause population extirpations.

Continued population monitoring, therefore, will be critical to document extirpations when they occur and to understand and describe the potentially complex interactions among factors that result in population loss (Jackson et al. 2009; Durance and Ormerod 2010; Cahill et al. 2013). Surveys conducted with environmental eDNA will be an important monitoring tool, given their logistical simplicity and high reliability, to definitively determine the absence of a population when an extirpation occurs (Thomsen et al. 2012; Wilcox et al. 2016). There may also be opportunities for researchers to collaborate with managers to develop anecdotal accounts of population losses into detailed case histories. Managers often have a familiarity with the extent and history of local populations within their jurisdictions and may have already observed extirpations but lack the time or incentives to publish the accounts. Documenting population losses will serve an important role in understanding habitat size thresholds, below which the danger of extirpation increases to the point that populations may represent "the living dead" and become poor places to invest. It would also highlight the stakes raised by climate change and perhaps ultimately provide greater freedom for managers to make difficult decisions about which populations to save beyond the current conservation paradigm of saving them all (Kuussaari et al. 2009).

Delineating climate refugia for other species

Climate refugia models have thus far been developed for only a few of the salmonid species globally that may be at risk from climate change this century (Kovach et al. 2019). Those we developed for bull trout and cutthroat trout focused on particularly cold stream habitats that are unsuitably cold for most other fish species. In these biologically depauperate headwater systems, relatively simple models with covariates representing major environmental gradients in temperature, habitat size, and topographic slope provided accurate predictions of habitat occupancy. Subsequent efforts to improve the bull trout model by considering a broader suite of covariates led to only small improvements in predictive performance (Isaak et al. 2022) and suggest that a limited number of key factors, if accurately rendered and available throughout broad portions of species' ranges, may be sufficient to provide an initial foundation for delineating potential habitats and climate refugia. There are attractive opportunities to further test this idea and refine the SDM refugia approach for other salmonids within the data-rich native ranges of brook trout in eastern North America (Hudy et al. 2008; Torterotot et al. 2014), brown trout and Arctic char in Europe (Filipe et al. 2013; Svenning et al. 2022), and white-spotted char (*Salvelinus leucomaenis*) in Japan (Nakano et al. 1996), where many remaining populations appear dependent on cold headwater areas upstream from their primary competitors and invasive species. Parameterization of SDMs for these or other species is likely to reveal interspecific differences that are important to understand and integrate into forecasts so that climate refugia are tailored to address specific ecological requirements and conservation risks. In the Isaak et al. (2015) models, for example, bull trout required cold habitat patches that were approximately five times larger than cutthroat trout to reach the same probability of occurrence, which meant that climate refugia for bull trout were much rarer despite otherwise similar habitat requirements and wide distributional overlap of the two species.

From a broader biodiversity perspective, there are a variety of non-salmonid fishes (Troia et al. 2019; Cussac et al. 2020; Sharma et al. 2021; Ishiyama et al. 2023), macroinvertebrates, and amphibian species (Milanovich et al. 2010; Hotaling et al. 2017) that are restricted to cold headwater streams, considered to be climate sensitive, and could also be good candidates for SDMs to delineate climate refugia. It is unknown how accurately the distributions of these species could be predicted based on the environmental gradients that appear relevant to salmonids, but exploratory analyses would be intriguing and may yield encouraging results. The limitation for many of these species is sparse occurrence data sets that hinder model development although the rapid adoption of eDNA sampling and growing databases that can be repurposed for multiple species are alleviating this deficiency in many areas (Dysthe et al. 2018; Young et al. 2018*c*, 2022).

Delineating climate refugia for anadromous salmonid species presents greater challenges because their habitats encompass broad geographies and diverse conditions from headwaters to marine environments. This complexity is usually addressed using life-cycle models with stage-dependent habitat capacities and survival rates to understand population dynamics and extinction risks. In these models, the dominant influence of survival during oceanic life stages is well established (Mantua et al. 1997; Mueter et al. 2002), and recent results suggest that climate-related declines in ocean productivity could threaten the persistence of some populations (Di Lorenzo and Mantua 2016; Crozier et al. 2021). If these worst-case predictions fail to materialize,

however, population persistence could still be threatened by climate change effects on freshwater life stages, so attempts to identify climate refugia seem prudent. Moreover, there are strong parallels between the pressures imposed on the natal areas of anadromous species and on those of native trout that originally motivated our SDM-based refugia approach. For example, the invadability of spawning and rearing areas of several anadromous salmonid species by non-native predatory smallmouth bass and Sacramento pikeminnow (*Ptychocheilus grandis*) in the western US is mediated by temperature (Rubenson and Olden 2020; FitzGerald et al. 2022). Smallmouth bass, in particular, are widely established and expanding in rivers across this region but thermal restrictions on the growth and survival of juvenile bass appear to significantly curtail invasions where mean summer temperatures are colder than 17–18 °C (Lawrence et al. 2015; Rubenson and Olden 2020). Recent empirical and theoretical studies also provide evidence of decreased exposure and mortality risks for multiple salmon life-stages in populations with access to particularly cold spawning and rearing areas (Bowerman et al. 2021; FitzGerald et al. 2021; FitzGerald and Martin 2022), and highlight the role that cold habitats already play in preserving some high-risk populations (Cordoleani et al. 2021).

The other important contribution that network temperature scenarios could have for anadromous species conservation is identifying temporal climate refugia, or "windows in time", when migrating adults or juveniles in thermally exposed populations will retain access to safe migrating conditions in future climates. Warm summer temperatures currently interrupt salmon migrations in many rivers and can trigger mass mortalities of adults (Hinch et al. 2012; Crozier et al. 2020; Hutchins et al. 2021; von Biela et al. 2022) or complete losses of juvenile outmigrant year classes (Cordoleani et al. 2021) when the capacity of thermal refuges is exceeded during extreme heat events. Because the frequency and duration of extreme temperatures are predicted to grow rapidly in the future (Meehl and Tebaldi 2004; Mantua et al. 2010), these mortality events could become frequent or extensive enough to threaten the persistence of some stocks or populations. Extreme heat events typically occur over the span of days and weeks, however, and therefore require hourly and daily stream temperature models to resolve. Numerous options exist to develop network temperature scenarios at fine temporal resolutions (Wu et al. 2012; McNyset et al. 2015; Santos-Fernandez et al. 2022) but significant research investments will be required to adequately calibrate and broadly scale these approaches given their computational intensity, number of data processing steps, and size of output data sets that would require archiving and interpretation. If comprehensive archives of hourly or daily network temperatures were developed, this information could be used to describe the thermal histories and tolerances of anadromous fishes, or even the mobile life histories of nonanadromous species, during all freshwater life stages, changes in response to climatic variation, and probabilistic forecasts made regarding which populations or stocks would retain temporal refugia and which may experience thermal conditions that interrupt life cycle completion. Finely resolved thermal information could also be integrated with conventional life-cycle models (Crozier et al. 2021) or approaches that more specifically address thermal performance (FitzGerald and Martin 2022) to refine predictions about stage-dependent survival, the relative success of different phenotypes, and other population parameters key to persistence.

Concluding thoughts

At this point in the Holocene–Anthropocene transition, global air temperatures have increased ~1 °C due to anthropogenic forcings, warming is occurring at rates which have few precedents in the geological record (IPCC 2021), and stresses upon many salmonid populations are increasingly evident. These trends are likely to continue throughout much of the 21st century, and wisdom dictates an organized retreat in some areas, aided by forecasting abilities to understand which populations may occur in defensible redoubts so that conservation investments can be targeted accordingly (Moore and Schindler 2022). Increasing data availability and new technologies enable the development of accurate stream temperature scenarios and SDMs with good predictive power at resolutions approximating those of local populations. These models are not a panacea but the next logical step from early bioclimatic models and provide useful frameworks that can help organize our thinking and actions strategically across salmonid ranges where risks from climate change are significant. Spatially explicit predictions from SDMs concerning habitat occupancy probabilities also lend themselves to integration with formal decision support tools that may further refine the process of making conservation investments (Peterson et al. 2013; Thompson et al. 2021). Although urgency is advisable to address climate-related factors that pose immediate threats to particularly valuable populations, we also believe time exists to develop key information and learn adaptively as events unfold over multiple fish generations and the careers of fisheries scientists and managers. Therefore, SDMs should be viewed as working hypotheses about the biophysical factors that affect the distributions of target organisms and, as such, should be tested and updated with new information describing important habitat covariates, species interactions, genetic attributes, or food resources if this information can be developed at useful scales and adds predictive power to models.

These tasks will be made more challenging by the overarching unknowns associated with the speed and magnitude of future climate change. Much attention has focused on the potential for accelerating warming trends, despite evidence indicating trend consistency in recent decades (Rahmstorf et al. 2017). Regardless, the vagility of most salmonid fishes should enable tracking of suitable habitats where spatiotemporal connectivity along fluvial networks does not impede movements or preclude key life history stages. Looming larger, in our opinion, is the ultimate magnitude of anthropogenically induced change in Earth's climate system before a new quasi-equilibrium is hopefully reached this century or next, as this level will largely determine the amount of biodiversity loss (Kaiho 2022). Contingent on those future conditions are the fates of populations along southern range extents

and elsewhere that warm temperatures are increasing limiting to salmonids (Daigle et al. 2015; Donadi and Näslund 2023; Howard and von Biela 2023), and it seems worthwhile to enhance our ability to discern which populations may be doomed and which are most likely salvageable with conservation interventions. Climate refugia have played important roles in maintaining salmonid biodiversity during major climatic perturbations in the past and are poised to do so again through the current crisis.

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Data availability

No new data were generated for this work. Data sets used in the examples were downloaded from websites associated with the NorWeST project (https://www.fs.usda.gov/research/rmrs/projects/norwest), Climate Shield project (https://www.fs.usda.gov/research/rmrs/projects/climate-shield), and National Hydrography Dataset (https://www.usgs.gov/national-hydrography/national-hydrography-dataset).

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