FEATURE ARTICLE

Can thermal refuges save salmonids? Simulation of cold-pool benefits to salmonid populations

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Abstract

Objective: The literature on thermal refuges has focused on when fish use what kinds of refuge, but we address how refuge availability and characteristics affect population abundance and persistence under warming.

Methods: Population benefits of thermal refuges are very difficult to assess empirically, so we used InSTREAM, an individual-based trout population model. InSTREAM represents several ways temperature affects survival and growth, as mediated by behaviors such as deciding when and where to feed. The model's credibility was established by showing that it closely reproduced 10 observed patterns in how refuge use varied with temperature, time of day, and trout size and in how refuge availability affects populations. We then simulated four levels of refuge availability in four increasingly warm temperature regimes, examining (1) survival and growth over summer periods of prolonged high temperatures and (2) population abundance and persistence over 22 years.

Result: In the simulation experiments, summer refuge use acted as a population bottleneck: the number of surviving trout increased with refuge area and decreased with temperature. During prolonged summer high temperatures, mortality was high until abundance dropped to a level sustainable by the refuges. The model predicted reduced but persistent populations under high warming when thermal refuges made up 2% or more of stream area.

Conclusion: The concept of salmonids "hanging on" in refuges, losing weight but surviving peak temperatures, was not supported by our experiment. The value of potential refuges to salmonid populations appears determined not just by temperature and area, but also by other characteristics that affect growth and survival, such as the availability of food and habitat for feeding and predator avoidance.

KEYWORDS

modeling, salmonids, stream temperature, thermal refuges, trout, warming

INTRODUCTION

As streams warm and populations of coldwater species such as salmonids continue to decline, fisheries scientists and managers are increasingly interested in the potential for thermal refuges to buffer populations from high temperatures (e.g., Howell et al. 2010; Fullerton et al. 2018). Here, we specifically address stream salmonid populations, and by "thermal

refuge," we refer to small areas (e.g., a few tens to hundreds of square meters) within a stream or river that are distinctly cooler than the mean water column during periods of high temperature ("coldwater patches," per Sullivan et al. 2021). Such refuges can occur in deep pools as a result of stratification and groundwater inflow and at the mouths of tributaries that have lower summer temperatures due to processes like shading, spring flow, and prolonged snowmelt (we do not address cool tributaries themselves as large refuges).

Even when thermal refuges hold high densities of fish, many questions about their ability to sustain individuals and populations remain. Can refuges significantly increase summer survival by reducing acute temperature mortality, chronic mortality, and other consequences of weight loss resulting from high metabolic demands or the predation that results from foraging at risky times and places necessary to keep up with high metabolic rates? Or is refuge use a perilous trade-off between the risks of high temperatures and risks of refuges, such as intense competition and predator attraction? If refuges can keep individuals alive, how widespread must they be to sustain population abundance or persistence?

While the literature on thermal refuges is extensive, little of it addresses such questions about population benefits. Much of the literature appears focused on the question of when fish use refuges (e.g., the studies by Brewitt and Danner 2014 and Ebersole et al. 2001 that we use below). Sullivan et al. (2021) reviewed numerous studies of thermal refuges and identified characteristics of coldwater patches affecting their value as refuges (e.g., proximity to and connection with high river temperatures, dissolved oxygen concentrations, habitat characteristics). Ebersole et al. (2001, 2003) examined empirical relationships between refuge availability and salmonid abundance across stream reaches, providing invaluable evidence for the benefits of refuges. However, such empirical studies provide limited ability to predict population responses to warming at specific sites or to elucidate the mechanisms and refuge characteristics linking population abundance and persistence to refuge availability.

The question of how refuge availability affects salmonid populations typifies management problems that are very difficult to answer conclusively via field studies alone but addressable using a combination of modeling and empirical research. We use InSTREAM, an individual-based simulation model of stream salmonids that incorporates empirical knowledge of multiple ways temperature affects individuals and theory for adaptive behavior to simulate the fate of individuals and the resulting population dynamics.

We specifically address thermal refuges provided by deep pools cooled by groundwater inflow. Several characteristics of such pool refuges could affect their benefits to salmonid populations: their availability (e.g., as

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Impact statement

A simulation experiment indicates that pools cooled by groundwater can let salmonid populations persist under substantial warming, but population size can be limited by the area of refuges and their food and risk conditions.

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percentage of total stream area) and their characteristics, such as temperature and depth. Here we address the first of these, thermal refuge availability.

We used simulation experiments to address these questions: (1) To what extent can pool refuges offset the effects of increasing temperatures on salmonid survival and growth over prolonged summer periods?, (2) How do the benefits of refuges to individuals depend on their availability as a percentage of stream area?, (3) How does refuge use affect salmonid activity patterns, especially when they feed?, and (4) How does refuge availability affect long-term population abundance and persistence in increasing warm temperature regimes? First, however, we evaluated the credibility of our simulations by assessing the model's ability to reproduce 10 patterns in the extensive empirical data on stream temperature and refuge use reported by Brewitt and Danner (2014) and Ebersole et al. (2001).

METHODS

Population model and site

Model description

We used version 7 of the InSTREAM individual-based stream salmonid population model (Railsback et al. 2021a, 2021b), modified to represent thermal refuges in pools. Railsback et al. (in press) provide a complete description of the model and how it was developed, including the extensive literature and original research supporting the following assumptions. InSTREAM represents the salmonid population of a river reach by simulating each individual fish. Habitat is represented as a collection of polygonal cells, each with its own depth, velocity, and availability of three cover types: velocity shelter for drift feeding, escape cover that reduces predation risk when feeding, and concealment cover for use when not feeding. Each day is represented with four time steps representing night, dawn, day, and dusk. On each time step, each fish (1) selects its habitat cell and activity, deciding whether and where to feed or conceal, (2) grows (or loses weight) as a consequence of its habitat and activity, and (3) survives or dies

from each of several mortality risks (especially predation, starvation, and disease from excess weight loss and acute temperature stress) that also depend on habitat and activity. Spawning and egg incubation are also represented, allowing multigeneration simulations.

The primary adaptive behavior, habitat and activity selection, considers the potential growth and predation risks of available habitat and the growth (or weight loss) and risk experienced in the three preceding time steps. These activity and habitat selection decisions of individual fish balance growth and predation risk; normally, fish behavior over a full day yields positive growth while otherwise minimizing predation risk (Railsback et al. 2020). The model represents two kinds of feeding: drift feeding, which usually provides positive growth over a range of intermediate velocities but less at night, and active searching, which provides some food intake in low velocities and low light. InSTREAM assumes a length-based hierarchy among individuals: the choice of where to feed or conceal is executed from the largest to smallest fish, and each depletes the resources (food, concealment cover) available to smaller individuals. Because of these habitat- and activity-selection assumptions, a simulated fish uses a thermal refuge if, and only if, the refuge provides a better trade-off between growth and survival than other habitat, given the food and concealment cover left available by larger fish.

InSTREAM represents multiple effects of temperature. Energetic effects are represented using a standard bioenergetics approach described by Railsback and Rose (1999). As temperature increases, metabolic rates increase, so growth decreases. Because InSTREAM represents growth–risk foraging trade-offs, lower growth results in lower survival: as growth becomes negative, fish become vulnerable to mortality due to disease and starvation and due to predation when they feed more often, or in riskier places, to avoid further weight loss. The risk of acute mortality due to disease and thermal stress increases sharply as temperatures exceed ~22°C. Risk of predation by fish (here, cannibalism on small juveniles) increases with temperature. Maximum sustainable swimming speed, which affects drift-feeding success, peaks at 14°C. Temperature also affects reproductive timing and success: fish can spawn only between 8°C and 15°C, and eggs incubate more rapidly at higher temperatures. Eggs are increasingly vulnerable to disease and direct mortality as temperatures increase above ~15°C.

While InSTREAM is a complex model, it still lacks many mechanisms through which habitat and temperature can affect individuals and populations. Especially relevant here is that InSTREAM does not represent energy allocation among growth, storage, and reproduction as an adaptive trait, individual- or population-level variation in temperature responses, or effects of temperature on salmonid food availability.

TABLE 1 Observed daily flow (m³/s) and temperature (°C) means and ranges by warm-season month, 2001–2011.

Month	Mean flow (min–max)	Mean temperature (min–max)
May	8.4 (4.0–87.2)	13.7 (10.5–17.8)
June	5.3 (2.9–21.1)	16.2 (12.0–20.3)
July	3.1 (2.0–6.2)	19.2 (15.9–21.7)
August	2.7 (1.9–3.9)	18.8 (16.3–21.2)
September	4.2 (2.1–7.8)	16.0 (12.9–20.0)
October	5.8 (2.8–15.8)	12.9 (9.8–17.2)

Site and input

We simulated a hypothetical population of Rainbow Trout *Oncorhynchus mykiss* at a study site based on lower Clear Creek, near Redding, California. The habitat input used hydraulic simulations from a restoration project design (for a site near the one evaluated by Railsback et al. 2013 using a related salmonid model). The simulated site is approximately 1000 m long with a wetted area of 24,449 m² at a typical summer flow of 4.0 m³/s. Flow and temperature scenarios were based on observed values from 2001 to 2011. Flows and temperatures in lower Clear Creek are controlled by an upstream reservoir; inflows below the reservoir are minor except during winter–spring storms. Instream flow releases from the reservoir were similar across 2001–2011, which yielded less-than-natural variation in flow and temperature among years. The observed values (Table 1) indicate moderate flows and nonstressful temperatures for summer months, with lowest flows and highest temperatures in July and August. We used the same simulated population (parameter values, initial abundance and size, but different habitat) as Railsback et al. (2021b). Because the study site is artificial, we based the initial population structure on values output from long-term simulations; model runs started with 20,000 fish of age 0 (2.6–3.0 cm fork length), 500 fish of age 1 (7–13 cm), and 500 of age 2 and older (age 2+; 18–24 cm).

Simulation experiments

Model evaluation experiments

The credibility and validity of complex models like InSTREAM depend on demonstration that the models adequately represent the mechanisms driving individual- and population-level responses to the habitat variables of interest (Augusiak et al. 2014). Evaluating a model's ability to reproduce observed patterns driven by those mechanisms is a practical and convincing way of demonstrating validity

(Grimm and Railsback 2005). Previous experiments of this type have demonstrated InSTREAM's ability to predict how various habitat characteristics affect when and where salmonids feed (e.g., Railsback and Harvey 2002; Railsback et al. 2020). To evaluate InSTREAM's ability to represent thermal refuge effects, we examined how well it reproduced 10 patterns in refuge use observed by Brewitt and Danner (2014) and Ebersole et al. (2001).

Brewitt and Danner (2014) used temperature-reporting tags to infer when juvenile steelhead (anadromous Rainbow Trout) occupied thermal refuges provided by tributary inflows to the Klamath River. They observed six patterns useful for model evaluation: (1) fish used refuges across the full range of summer temperatures, ~15–27°C, and (2) fish also used nonrefuge habitat across the full range of summer temperatures, except that (3) all fish occupied refuges at temperatures above about 25°C; (4) refuge use varied widely among individuals, with different individuals spending all, some, and none of their time in refuges; (5) there was no obvious relationship between fish size and refuge use, but smaller fish spent more time in refuges at night than did larger fish; and (6) at temperatures below ~22°C, refuge use was higher at night than during the day for both small and large fish. We looked for the same patterns in model results comparable to Brewitt and Danner's (2014) observations: the temperatures experienced by each adult (ages 1 and older) at each time step, which indicate when each fish occupied a refuge. We simulated the summer of 2002 with observed temperatures multiplied by 1.1 to produce a range (~15–26°C) similar to the field observations of Brewitt and Danner (2014) and the medium refuge availability scenario (explained below).

We also used four patterns observed by Ebersole et al. (2001) in Rainbow Trout use of small coldwater patches at river temperatures of ~17–25°C: (7) strong effects of temperature regime on reach-scale fish abundance at refuge availabilities <7%, (8) refuge use increasing gradually with temperature instead of rapidly at a threshold temperature, (9) many fish using nonrefuge habitat at daily temperatures up to at least 22°C, and (10) no use of refuges at relatively low summer temperatures (below ~18°C).

Temperature and refuge scenarios

The scenarios we used to evaluate refuge benefits included four levels of refuge availability and four temperature regimes. We used simple thermal refuge and temperature scenarios to elucidate general insights, instead of attempting precise site-specific predictions.

We used a definition of refuge habitat that (1) represents "coldwater patches" (Sullivan et al. 2021) produced by groundwater inflow to stratified pools and (2) lets us vary refuge availability in a straightforward way. We assumed that any cell with velocity below 30 cm/s and depth above a threshold D_T (cm) was a groundwater-fed pool refuge. Our refuge scenarios used values of 230, 175, and 150 cm for D_T. At a typical summer flow of 4.0 m³/s, the resulting refuge availability, as percentage of wetted stream area, is 2% (the "low" scenarios), 6% ("medium"), and 10% ("high"). From low to high, these scenarios provide two, three, and four pool refuges (Figure 1). We also simulated zero refuge availability.

The temperature scenarios included observed temperatures and three warming scenarios. The observed temperature scenario used daily mean water temperatures recorded near the study site. However, instead of assuming constant temperatures within each day, we represented realistic within-day temperature variation using diurnal ranges based on observed hourly temperatures: we assumed that temperatures during dawn and dusk time steps equal the daily mean but temperatures during day time steps are 1.14× the daily mean and night temperatures are 0.884× daily mean. We generated the warming scenarios by simply multiplying observed temperatures by a constant temperature multiplier (TM), which had values of 1.0 (observed), 1.1, 1.2, and 1.3. Therefore, an observed temperature of 15°C became 16.5, 18.0, and 19.5°C under the three warming scenarios and 20°C became 22, 24, and 26°C. We did not vary salmonid food availability among temperature scenarios.

Water temperature in refuge cells was set to $15 \times TM$ on any time steps when the river temperature exceeded $15 \times TM$. We neglected groundwater effects on pool temperature when the river is colder than groundwater because that condition—common except in July–September—does not induce stratification. The observed-conditions refuge temperature of 15°C approximates the mean annual air temperature near lower Clear Creek; because the aquifer is alluvial and shallow, we assumed that future warming will cause groundwater temperatures to increase in proportion to river temperatures (Taylor and Stefan 2009).

Simulated population responses

We used two kinds of simulation experiment to evaluate thermal refuge benefits. First, we evaluated effects of refuge availability on summer survival and growth by simulating all combinations of temperature and refuge scenarios over the summers (May–October) of 2001 through 2005, treating each year as a separate observation. May through October includes rising, peak, and declining summer temperatures. We report survival as the percentage of initial fish still alive at the end of the simulation, with separate analyses for age-0, -1, and -2+
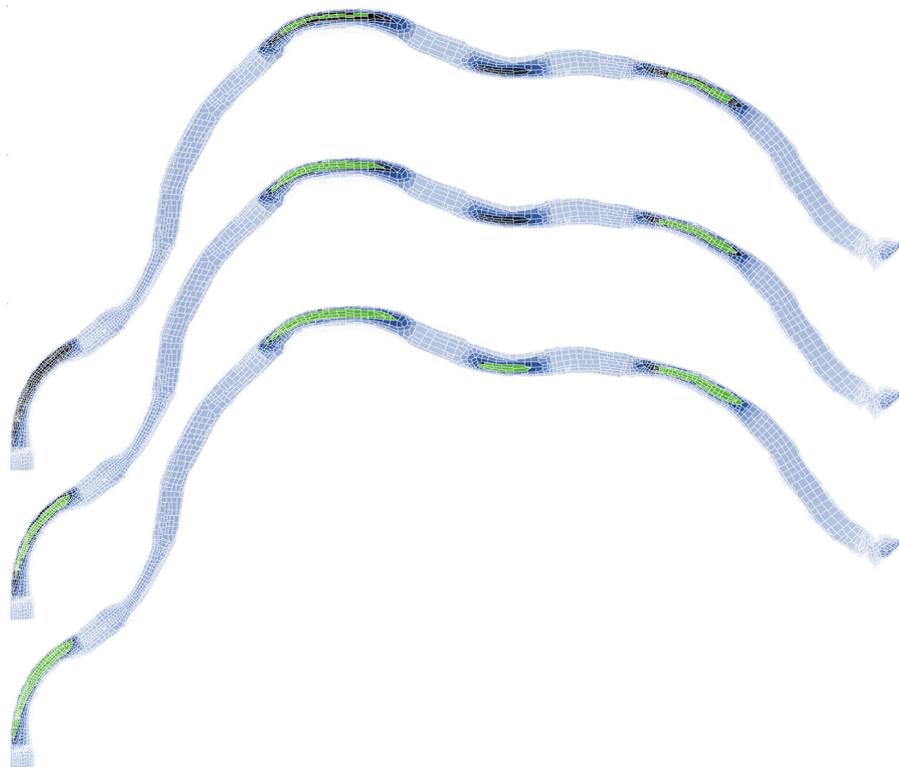
FIGURE 1 The simulated stream reach under (top to bottom) low, medium, and high refuge availability. Cells are shaded by depth, with darker being deeper; cells providing thermal refuge at a flow of $4.0\,\mathrm{m}^3$/s are green.

fish. Reported growth is the percent increase in mean weight between the initial population and the individuals alive at the end of the simulation, so it includes effects of size-dependent survival as well as individual growth. InSTREAM's assumed length-based hierarchy in habitat selection gives larger individuals more access to feeding or concealment habitat in refuges, making size-dependent survival likely. These simulations also provided output on fish activity to address how refuge use affects diurnal activity patterns.

The second experiments evaluated long-term population persistence with 22-year simulations. Input for these simulations was generated by using observed flow and temperature data from 2001 to 2011 twice and randomly shuffling the sequence of water years (October to September). Five replicate simulations were produced by rerandomizing the water years.

RESULTS

Model evaluation experiments

Our simulations largely reproduced the 10 observed patterns we identified to evaluate InSTREAM's validity for predicting effects of thermal refuges. Figure 2 illustrates correspondence with patterns 1–3. Over river temperatures
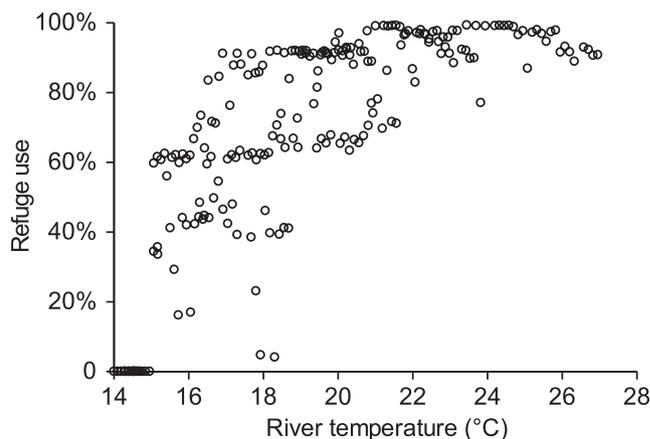
FIGURE 2 Simulated refuge use versus river temperature, May–August 2002, with a temperature multiplier of 1.1. Each point represents one time step; the *x*-axis is the temperature outside thermal refuges, and the *y*-axis is the percentage of adult (age 1 and older) salmonids in a refuge.

between about 15°C and 26°C, fish used both refuge and nonrefuge habitat, but above 22°C, use of nonrefuge habitat was rare. Our simulated fish did not use refuges when the river temperature was below 15°C, and refuge use was never 100% even at the highest temperatures.

Patterns 4–6 were also reproduced. Some individuals never used refuges and others used refuges frequently, and there
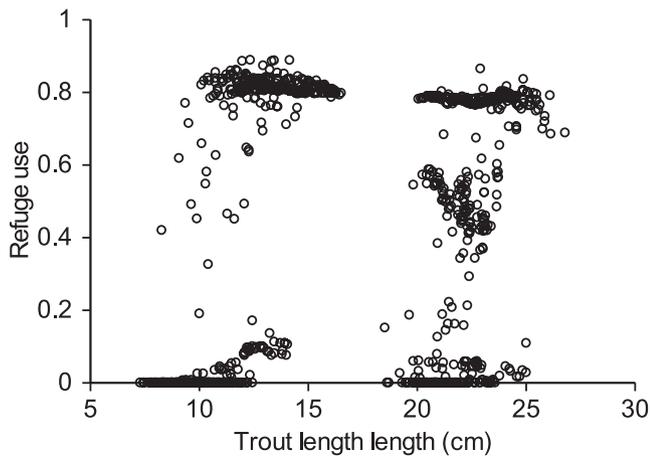
was no clear relationship between fish size and refuge use (Figure 3). (The individuals that never used refuges died before peak temperatures were reached; mortality is addressed in the following subsection). Age-1 fish used refuges more than older fish at night (Figure 4). At temperatures below 22°C, both age-1 and age-2+ fish used refuges more during night (and dawn and dusk) time steps than during day (Figure 4).

Model consistency with pattern 7 (strong effects of temperature regime on fish abundance at refuge availabilities <7%) is illustrated below by the population abundance and persistence results. Correspondence with patterns 8–10 (gradual increases in refuge use with temperature, many fish using nonrefuge habitat at daily temperatures up to at least 22°C, and no use of refuges at relatively low temperatures) is illustrated in Figure 2 and below in the results for how refuge use varied with temperature scenario over the summer.

Effects of refuge availability on summer survival and growth

Under the observed temperature regime ($TM = 1.0$), the simulated thermal refuges provide a slight benefit to survival (Figure 5). For all the warming scenarios, even the lowest refuge availability offered higher survival than none. For age-1+ fish, the two highest refuge availability scenarios largely buffered the effects of warming on summer survival, but survival of age-0 fish—already much lower than survival of older fish—decreased sharply in all refuge availability scenarios.

Abundance time series (Figure 6) show that survival decreased rapidly at the onset of summer high temperatures then recovered after mid-July. The early mortality
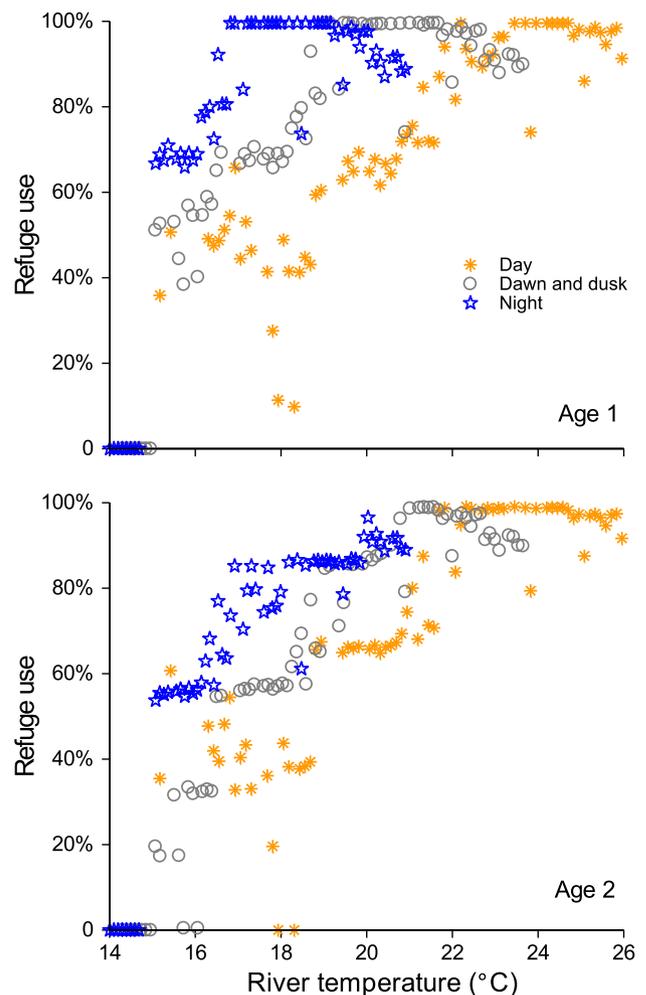
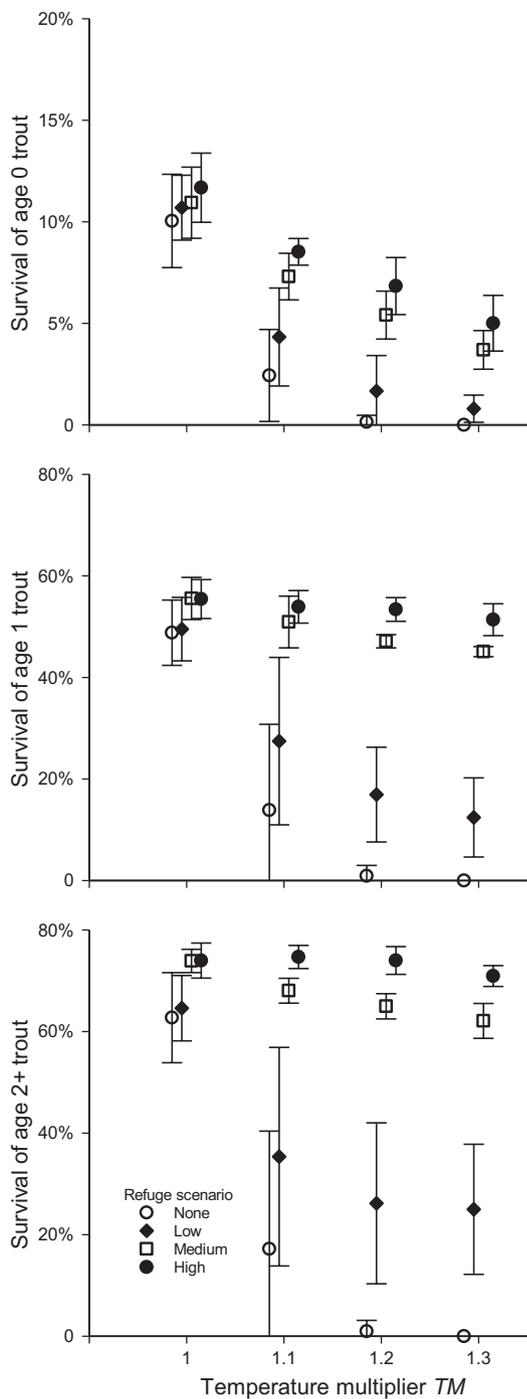appears to be thinning of the population down to a level that the refuges can support.

Under observed temperatures ($TM = 1.0$), simulated mortality was largely caused by predation and, less so, poor condition (Figure 7). At the higher temperature scenarios, acute temperature stress increasingly dominated mortality. Refuges substantially reduced temperature mortality, with their benefit increasing with refuge availability. In the two warmest temperature scenarios, predation mortality increased slightly with refuge availability.

Refuges provided less benefit in growth than they did in survival (Figure 8) and especially little benefit for age-2+ fish.

Even under the warmest temperature regimes, simulated fish made relatively little use of thermal refuges except in the June to mid-September period of highest temperatures (Figure 9). Especially when refuges were scarce (left panels of Figure 9), the percentage of fish using refuges increased steadily as TM increased. Refuge use varied little among times of day during the warmest season, but in the less-warm periods (May–June, mid-September

FIGURE 3 Refuge use by individual simulated fish; each point represents one fish, indicating (*y*-axis) the percentage of time steps it spent in refuges over the May–August simulation period versus (*x*-axis) its mean length during the simulation. Fish <16cm are age 1, and fish >16 cm are age 2. Results include fish that died during the simulation.
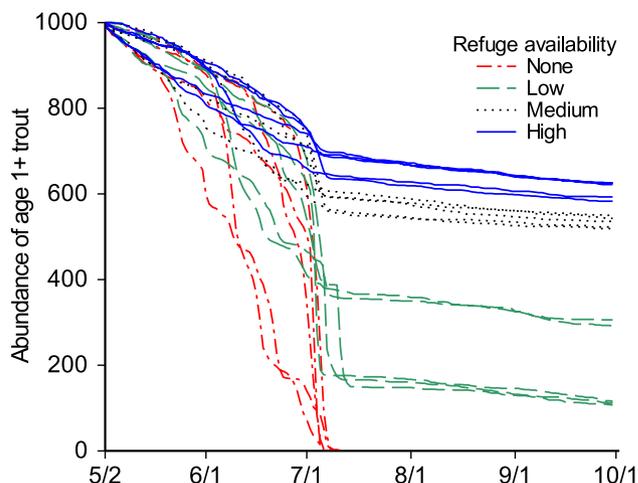

FIGURE 4 Refuge use versus river temperature, categorized by fish age and time of day.

FIGURE 5 Survival results for (top to bottom) ages 0, 1, and 2+. Symbols and error bars indicate the mean and standard deviation, respectively, over the five simulated years. Points are offset around the temperature multiplier (TM) values to increase clarity.

FIGURE 6 Time series of age-1+ salmonid abundance over May–September for the four refuge availability scenarios and warmest temperature scenario ($TM = 1.3$). Separate lines represent the 5 years simulated for each refuge scenario.

season of highest temperature (Figure 10, left panel). With high refuge availability, warming produced little change in feeding time; almost all fish fed during day and about half also fed during the other times of day.
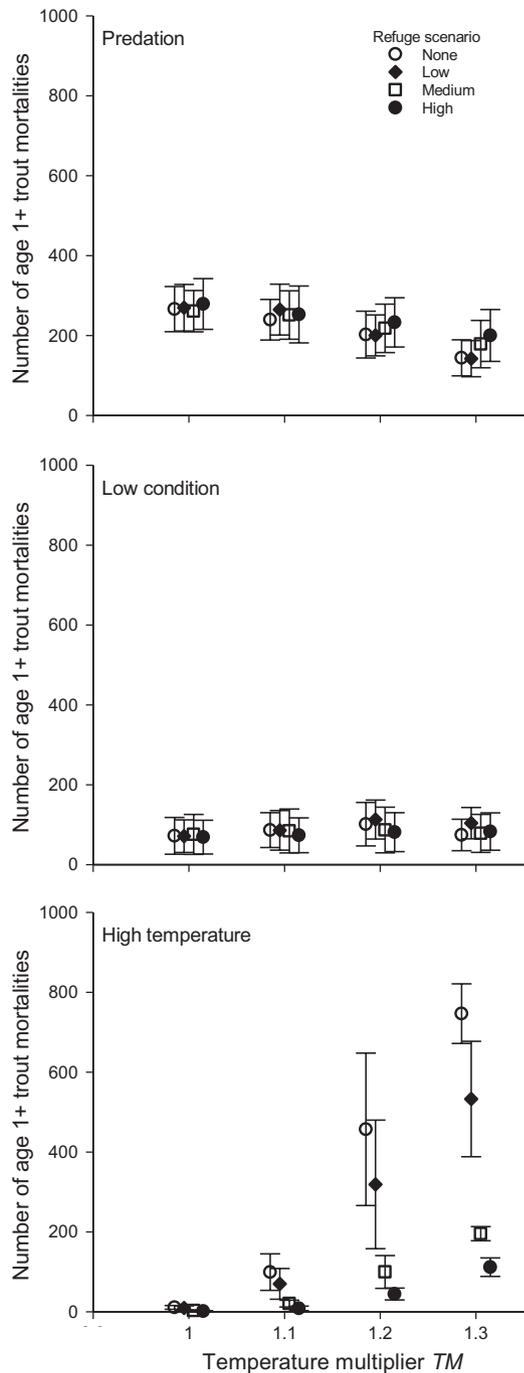
Effects of refuge availability on population abundance and persistence

The 22-year simulations indicated that the model Rainbow Trout population is robust and persistent under the observed temperature regime ($TM = 1.0$), with or without thermal refuges (Figure 11). With $TM = 1.1$, the population died out in two of five simulations with no refuges, but even low refuge availability provided persistence. In the two warmest temperature scenarios, the population died out quickly in the absence of refuges and persisted in all three refuge scenarios, but abundance was higher with higher refuge availability. In fact, mean adult abundance over all simulated years except the first two (during which abundance was strongly affected by initial population size) decreased roughly linearly with increasing TM, with a lower rate of decrease with increasing refuge availability (Figure 12).
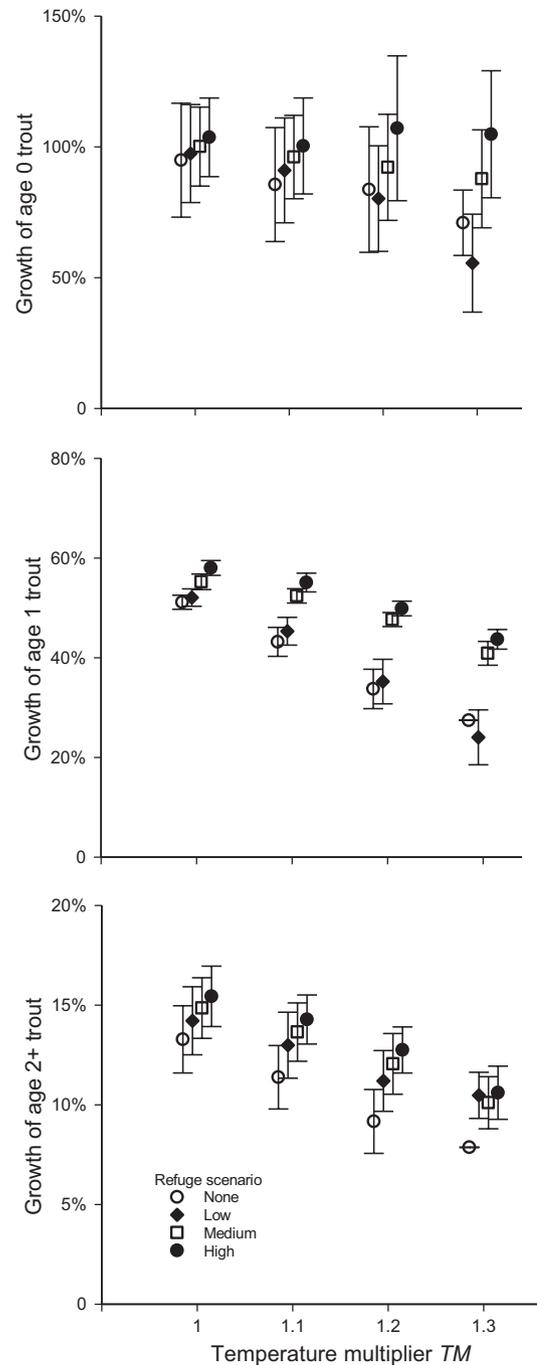
DISCUSSION

The simulation approach

The extensive literature on thermal refuges (recently reviewed by Sullivan et al. 2021) clearly illustrates the anticipated importance of refuges to salmonid populations facing climate change. However, this literature has largely

through October), refuge use was highest in day and lowest at night. However, for $TM = 1.1$, refuge use was more common at night, dawn, and dusk than during day, corresponding to Figure 4.

In the absence of refuges, warming produced a modest transition from feeding during day to increased feeding during dawn, dusk, and night in the July–September

FIGURE 7 Causes of mortality: number of simulated salmonids age 1 and older dying of predation, poor condition (disease and starvation), and acute temperature stress. Format is as in Figure 5 except that ages 1 and 2+ are combined as adults (age 1+).

FIGURE 8 Simulated March–October growth. Format as in Figure 5.

focused on short-term phenomena, such as when fish use refuges and how that use is affected by characteristics of refuges, surrounding habitat, and the fish (e.g., Ebersole et al. 2001; Brewitt and Danner 2014; White et al. 2019). The population benefits of thermal refuges, from summer survival to long-term persistence, are difficult to evaluate in the field and therefore remain largely unexplored. The

model InSTREAM embodies much of our knowledge of how temperature and other habitat characteristics affect individual salmonids in a framework that makes long-term population predictions, making simulation studies such as this one a way to explore such important yet difficult questions. The simulation approach has been used before; Snyder et al. (2022a, 2022b) used a larger-scale individual-based model to evaluate thermal refuge benefits for upstream-migrating salmonids.
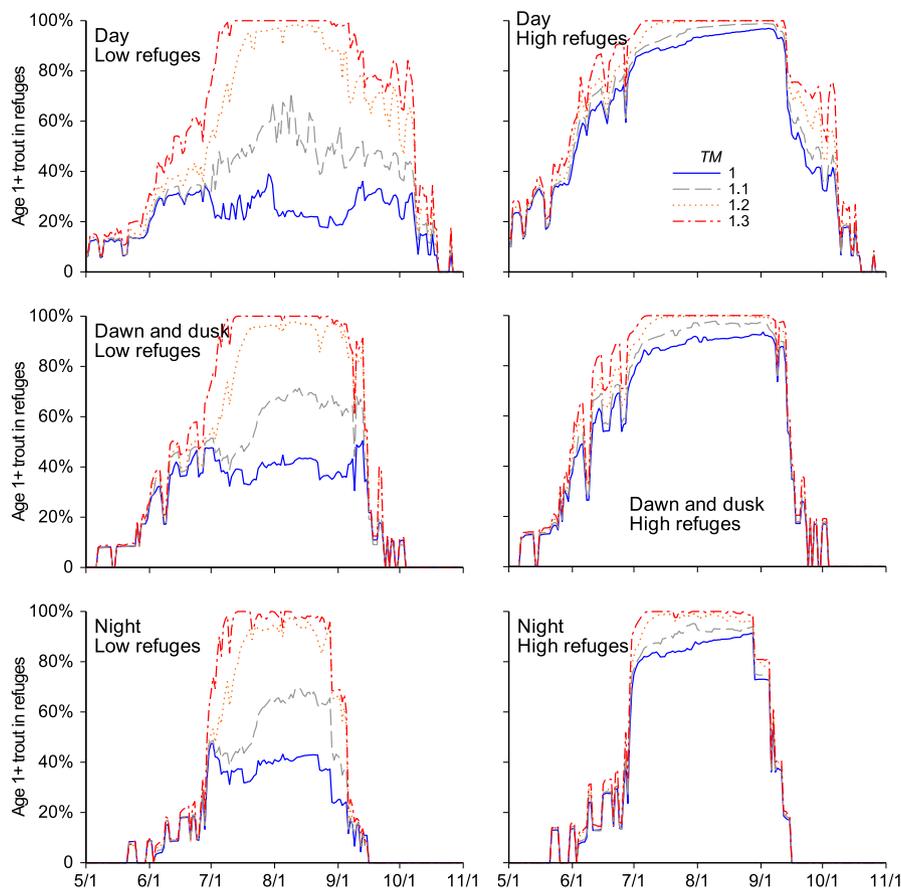
FIGURE 9 Refuge use: percentage of salmonids age 1 and older occupying refuge pools in low (left panels) and high (right panels) refuge availability scenarios during the three daily light conditions. Combined results over all five simulated years.

Using simulation, as with field studies, we need to consider the limitations of our analysis and evidence for its validity and then look for conclusions of general relevance to understanding and managing fish populations.

Limitations of our analysis

While our low and medium refuge availability scenarios appear realistic, the high scenario does not. Our simulations were designed to represent relatively small, in-channel patches of deep habitat cooled by groundwater. Ebersole et al. (2001) looked for such cold patches in 12 small streams of the lower Snake River basin; they found cold patches to make up 0% to 6.6% of stream area, with only one stream having > 4% cold patches. In comparison to these observations, our medium refuge scenario (6% of area) actually appears to represent unusually high refuge availability and our high scenario may represent unrealistically abundant pool refuges.

Our results indicate that the benefits of refuges depend in part on the feeding and growth opportunities they provide. The pools we simulated probably offer less

food than typical tributary-mouth refuges, which can receive food from the tributary and provide better drift-feeding conditions. On the other hand, we assumed that refuge pools have velocities up to 30 cm/s, and our model provides positive growth via daytime drift feeding at velocities as low as 10 cm/s for all the fish we simulated; our simulated refuges are therefore more profitable than very still pools.

We made the simplest assumptions about how warming and refuge use affect food availability and predation risk. To avoid overestimating refuge benefits, we ignored any increase in food availability that could result from warming. We also ignored potential effects of aggregation in refuges on predation risk; InSTREAM does not (without modification) include effects of local fish density on survival of predation, either positive (e.g., via schooling or predator swamping) or negative (e.g., by attraction of predators to fish concentrations).

Our simulations do not represent any adaptive mechanism other than habitat- and activity-selection behavior that could make individuals or populations less affected by temperature; to avoid underestimating effects of warming, the version of InSTREAM we used does not represent
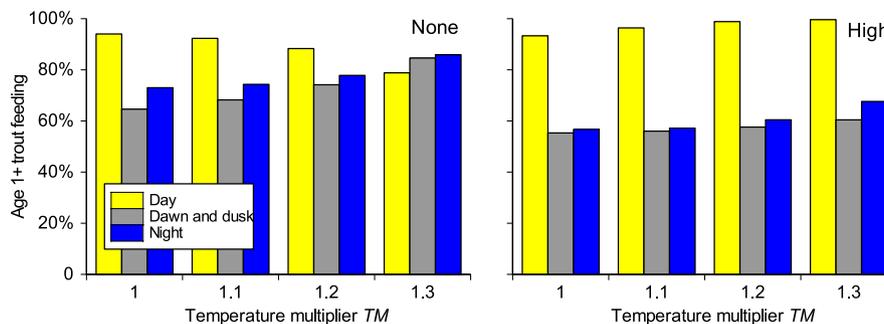
FIGURE 10 Example effect of refuges on when salmonids feed, with no (left panel) and high (right panel) refuge availability. Bars indicate the mean percentage of age-1+ fish feeding by time of day in July–September of five simulated years.

any kind of acclimation or local evolution (but see Ayllón et al. 2019).

Model evaluation

The simulation experiments examining how well our model reproduced 10 patterns observed in the field by Brewitt and Danner (2014) and Ebersole et al. (2001) were conducted to evaluate InSTREAM's ability to predict thermal refuge use and its consequences to salmonids. This evaluation was surprisingly successful, with the model at least partially reproducing all 10 patterns.

Two differences between the observed patterns and our results appear explained by differences between tributary-mouth and cold-pool refuges. Our simulated fish did not use refuges when the river temperature was below ~15°C, which conflicts with pattern 1 but is consistent with pattern 10. Refuge use was never 100%, even at the highest temperatures, conflicting with pattern 3. These differences are presumably because our pool refuges, unlike the tributary mouths observed by Brewitt and Danner (2014) but like the groundwater-fed cold patches observed by Ebersole et al. (2001), provide neither especially productive feeding habitat nor abundant concealment cover for individuals not feeding. Consequently, our refuges are not desirable habitat at low temperatures and, during high temperatures, require simulated fish to occasionally leave to feed. White et al. (2019) observed such behavior in a laboratory experiment that presented Brook Trout *Salvelinus fontinalis* with separate foraging and refuge habitat patches.

The ability of InSTREAM to reproduce these diverse patterns gives us confidence that it adequately represents the mechanisms driving salmonid use of small thermal refuges and so could be generally useful for modeling effects of thermal heterogeneity. InSTREAM also appears useful for investigating the effects of refuge characteristics not explored here, such as temperature, food and feeding habitat availability, and predation pressure.

Refuge analysis

Overall, our simulated thermal refuges provided population persistence under rather severe warming scenarios. Under even our lowest (and probably most realistic) refuge availability scenario, simulated populations were reduced but persistent even at 1.3 times current temperatures, while without refuges the population was severely reduce at $TM = 1.1$ and rapidly died out at $TM = 1.2$ and 1.3. These results are not surprising given that the refuges provided substantial areas of relatively safe and moderately productive habitat throughout the summers. Our results agree with the empirical evidence of Ebersole et al. (2001, 2003) for positive relationships between refuge availability and salmonid abundance.

We found lower survival benefits of refuges for juveniles and younger adults, presumably because smaller fish are less able to compete for the limited resources in refuges. (Ebersole et al. [2001] observed larger salmonids excluding smaller individuals from refuge space; Morgan and O'Sullivan [2022] found smaller salmonid juveniles occupying warmer refuge temperatures, presumably explained by competition.) Increased cannibalism on the smallest juveniles could be an additional risk not represented in our simulations. However, it was not clear from the long-term simulations that lower juvenile survival strongly affected population persistence. In extreme cases of juvenile competition with adults, InSTREAM has produced interannual population cycles: recruitment is suppressed until the adult population falls and then rebounds until adult density again is high enough to limit recruitment. Such cycles were not apparent in this study.

Our results that warming and refuges had less effect on growth than on survival may seem anomalous, but InSTREAM commonly produces inverse relationships between abundance and growth due to competition for safe and productive feeding sites; the fewer fish that survive, the greater access the survivors have to such sites. Further, thermal refuges provide limited feeding opportunity due
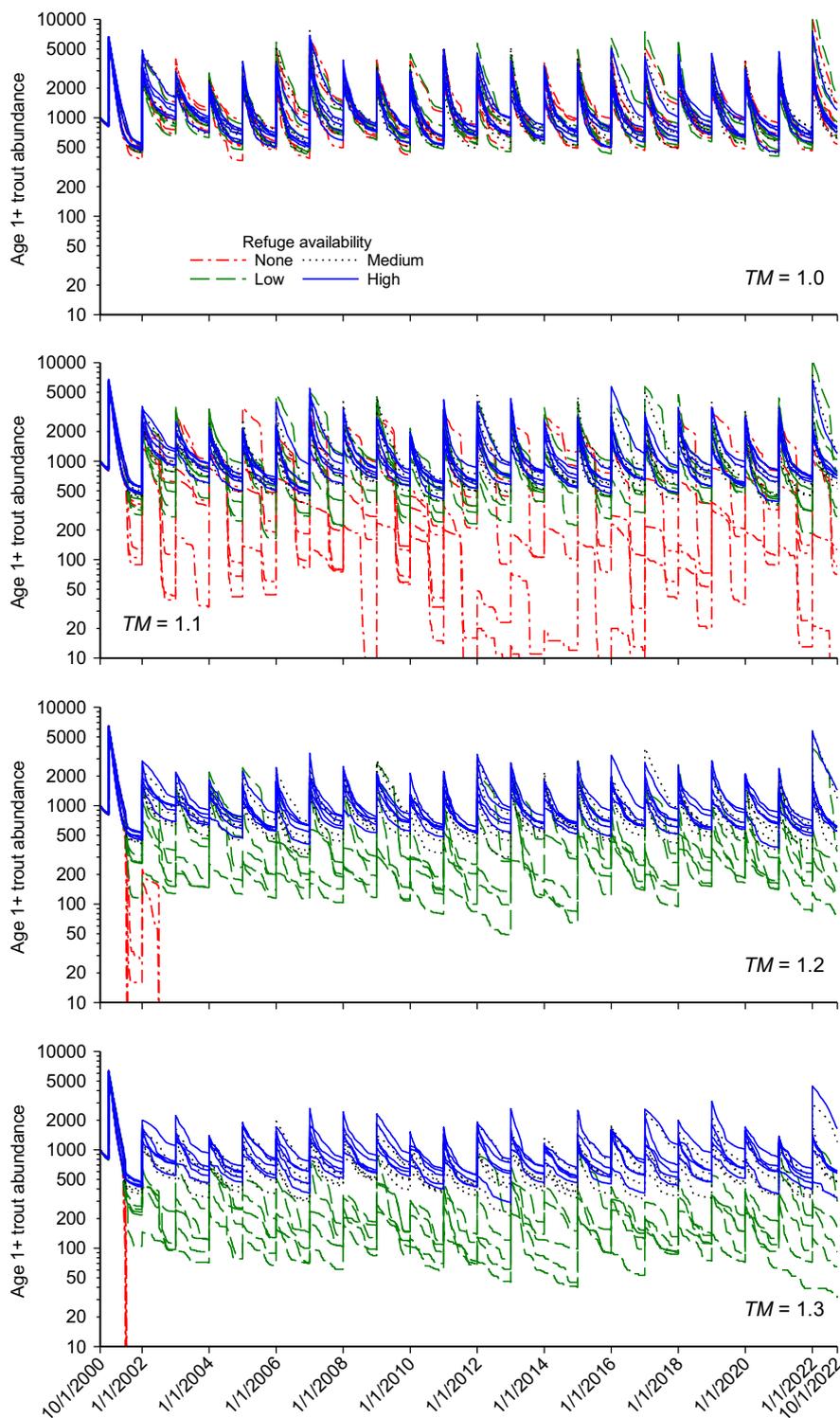
FIGURE 11 Long-term simulation results. Each line represents the results of one of five simulations for each refuge scenario. From top to bottom, panels report results for the *TM* from 1.0 to 1.3.

to intense competition among the many fish in each refuge and, in pool refuges, low velocities and light levels that reduce drift-feeding success. Size-dependent mortality could also contribute to the apparently small benefit of refuges for growth; InSTREAM's length-based hierarchy in habitat selection makes smaller individuals less likely to survive.

Conceptual models of refuge benefits

Our results supported the general assumption that cold-patch thermal refuges can allow stream salmonid populations to persist in substantially warmed temperature regimes. They also helped us evaluate several conceptual models of refuge effects.
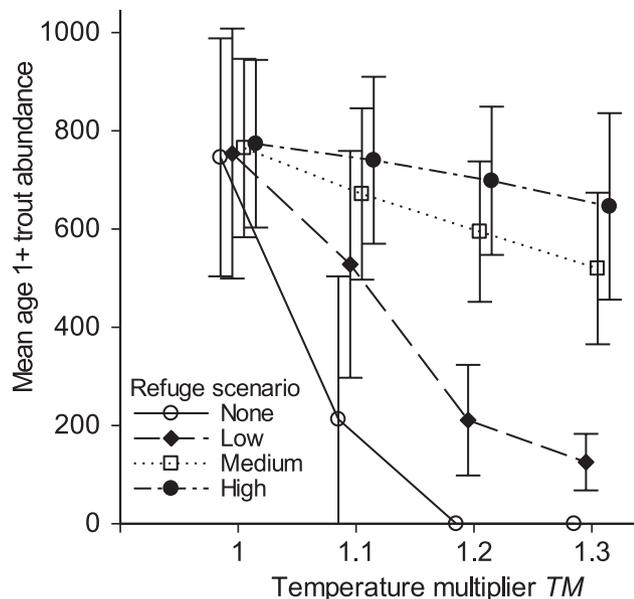
FIGURE 12 Response of long-term mean salmonid abundance to temperature regime and refuge availability. The *y*-axis is the mean of adult abundance on September 30 over simulated years 2003–2022. Error bars represent standard deviation over the 20 annual values of five replicate simulations.

One potential conceptual model of refuge benefits is "hanging on": refuges allow fish to stay alive by losing weight in crowded refuges during the times when river temperatures are too stressful. This model was not supported by our simulations; instead, simulated abundance rapidly dropped to a level that allowed the survivors to maintain weight by feeding in the refuge and leaving only occasionally to feed elsewhere. That outcome resulted in part from InSTREAM's algorithm for deciding when and where to feed, which assumes a strong incentive to maintain weight and condition instead of losing weight to avoid other risks (Railsback et al. 2020). Even if we do not represent the trade-offs accurately, the important point is that crowded refuges create trade-offs between the risks of losing weight in the refuge (lower growth and fecundity, susceptibility to disease) and the risks of leaving to feed in dangerously warm water. This trade-off is illustrated in Figure 9; the number of fish in refuges and the range of dates over which they used refuges depended strongly on refuge availability, indicating that refuges could support a limited density of fish instead of letting any number of fish "hang on." This conceptual model seems even less useful if we assume that predation risk is higher in refuges. Keep in mind that our warming scenarios represented steady summer-long high temperatures; the "hanging on" conceptual model may be much more applicable to short-term events such as the one observed by Morgan and O'Sullivan (2022).

Our experiment also did not fully support a conceptual model of daytime refuge use, where fish primarily use refuges during the warmest part of the day and leave to feed at night. While Figures 4 and 9 indicate that there were times when more fish used refuges during day than in dawn, dusk, and night, the opposite was sometimes true. Figure 10 indicates that the majority of feeding occurred during day in peak temperatures, even though almost all fish were in refuges. One explanation for the importance of daytime feeding at high temperatures is its higher efficiency; even though fish can feed at low light levels, drift feeding during the day is most efficient. Feeding efficiency is especially important at high temperatures due to higher metabolic demands. Further, the refuges we simulated were relatively deep pools, and depth reduces light levels; this mechanism reduces feeding efficiency in InSTREAM substantially at night and in crepuscular periods (and in elevated turbidity) but not during daytime. The alternative to feeding in InSTREAM is to conceal in cover to reduce predation risk, but concealment cover is limited and competition for it is undoubtedly another reason why refuges supported limited salmonid densities. Complete understanding of refuge use may require observations at night as well as in day.

Our results did support a conceptual model of summer peak temperatures acting as a population bottleneck, with the number of surviving fish decreasing with the level of warming and increasing with refuge availability; Ebersole et al. (2001) proposed this model from their field observations. Figure 12 best illustrates this conceptual model. The rapid mortality at the onset of summer peak temperatures illustrated in Figure 6 caused this bottleneck to act rapidly. We use the term "bottleneck" to mean a period when mortality is especially high and density dependent. We do not mean that refuges have a carrying capacity that abundance is limited to; the number of surviving fish depends on many processes, both inside and outside of refuges, that vary among years.

Finally, our results supported the assertion (also supported by empirical studies, e.g., by Ebersole et al. 2001; Stevens and DuPont 2011; Kurylyk et al. 2015) that size and temperature are not the only important characteristics of refuge habitat. Our results implied that any characteristics providing higher food intake, lower energy costs, or reduced predation risk are also important to refuge value. Such characteristics include hydraulics and velocity shelter that provides efficient drift feeding, depth that reduces predation risk, and concealment and escape cover. For adult salmonids, feeding is not important, but reducing energy costs and avoiding predation are. The importance of safe and productive habitat for small juveniles was not clear in our experiments but deserves consideration; Morgan and O'Sullivan (2022) observed small juvenile salmonids using refuge habitat too shallow to be safe and productive for larger fish. Deep pools and tributary mouths may have similar thermal characteristics while

differing strongly in other ways, especially food input and hydraulics. These important characteristics should be considered in inventorying and evaluating refuge availability.

CONFLICT OF INTEREST STATEMENT
The authors state no conflicts of interest.

ETHICS STATEMENT
No animals were used in this research.

DATA AVAILABILITY STATEMENT
No field data were collected in this study. The simulation model and input are available in the Zenodo repository (https://doi.org/10.5281/zenodo.7255605). The InSTREAM model and documentation are available at: www.humboldt.edu/ecomodel.

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REFERENCES
Augusiak, J., Van den Brink, P. J., & Grimm, V. (2014). Merging validation and evaluation of ecological models to 'evaludation': A review of terminology and a practical approach. *Ecological Modelling*, *280*, 117–128. https://doi.org/10.1016/j.ecolmodel.2013.11.009

Ayllón, D., Railsback, S. F., Harvey, B. C., Quirós, I. G., Nicola, G. G., Elvira, B., & Almodóvar, A. (2019). Mechanistic simulations predict that thermal and hydrological effects of climate change on Mediterranean trout cannot be offset by adaptive behaviour, evolution, and increased food production. *Science of the Total Environment*, *693*, Article 133648. https://doi.org/10.1016/j.scitotenv.2019.133648

Brewitt, K. S., & Danner, E. M. (2014). Spatio-temporal temperature variation influences juvenile steelhead (*Oncorhynchus mykiss*) use of thermal refuges. *Ecosphere*, *5*(7), Article 92. https://doi.org/10.1890/ES14-00036.1

Ebersole, J. L., Liss, W. J., & Frissell, C. A. (2001). Relationship between stream temperature, thermal refugia and Rainbow Trout *Oncorhynchus mykiss* abundance in arid-land streams in the northwestern United States. *Ecology of Freshwater Fish*, *10*(1), 1–10. https://doi.org/10.1034/j.1600-0633.2001.100101.x

Ebersole, J. L., Liss, W. J., & Frissell, C. A. (2003). Thermal heterogeneity, stream channel morphology, and salmoid abundance in northeastern Oregon streams. *Canadian Journal of Fisheries and Aquatic Sciences*, *60*(10), 1266–1280. https://doi.org/10.1139/f03-107

Fullerton, A. H., Torgersen, C. E., Lawler, J. J., Steel, E. A., Ebersole, J. L., & Lee, S. Y. (2018). Longitudinal thermal heterogeneity in rivers and refugia for coldwater species: Effects of scale and climate change. *Aquatic Sciences*, *80*, Article 3. https://doi.org/10.1007/s00027-017-0557-9

Grimm, V., & Railsback, S. F. (2005). *Individual-based modeling and ecology*. Princeton University Press. https://doi.org/10.1515/9781400850624

Howell, P. J., Dunham, J. B., & Sankovich, P. M. (2010). Relationships between water temperatures and upstream migration, cold water refuge use, and spawning of adult Bull Trout from the Lostine River, Oregon, USA. *Ecology of Freshwater Fish*, *19*(1), 96–106. https://doi.org/10.1111/j.1600-0633.2009.00393.x

Kurylyk, B. L., MacQuarrie, K. T. B., Linnansaari, T., Cunjak, R. A., & Curry, R. A. (2015). Preserving, augmenting, and creating cold-water thermal refugia in rivers: Concepts derived from research on the Miramichi River, New Brunswick (Canada). *Ecohydrology*, *8*(6), 1095–1108. https://doi.org/10.1002/eco.1566

Morgan, A. M., & O'Sullivan, A. M. (2022). Cooler, bigger; warmer, smaller: Fine-scale thermal heterogeneity maps age class and species distribution in behaviourally thermoregulating salmonids. *River Research and Applications*, *39*(2), 163–176. https://doi.org/10.1002/rra.4073

Railsback, S. F., Ayllón, D., & Harvey, B. C. (2021a). InSTREAM 7: Instream flow assessment and management model for stream trout. *River Research and Applications*, *37*(9), 1294–1302. https://doi.org/10.1002/rra.3845

Railsback, S. F., Gard, M., Harvey, B. C., White, J. L., & Zimmerman, J. K. H. (2013). Contrast of degraded and restored stream habitat using an individual-based salmon model. *North American Journal of Fisheries Management*, *33*(2), 384–399. https://doi.org/10.1080/02755947.2013.765527

Railsback, S. F., & Harvey, B. C. (2002). Analysis of habitat selection rules using an individual-based model. *Ecology*, *83*(7), 1817–1830. https://doi.org/10.2307/3071767

Railsback, S. F., Harvey, B. C., & Ayllón, D. (2020). Contingent tradeoff decisions with feedbacks in cyclical environments: Testing alternative theories. *Behavioral Ecology*, *31*(5), 1192–1206. https://doi.org/10.1093/beheco/araa070

Railsback, S. F., Harvey, B. C., & Ayllón, D. (2021b). Importance of the daily light cycle in population-habitat relations: A simulation study. *Transactions of the American Fisheries Society*, *150*(1), 130–143. https://doi.org/10.1002/tafs.10283

Railsback, S. F., Harvey, B. C., & Ayllón, D. (In press). *InSTREAM 7 user manual: Model description, software guide, and application guide*. U.S. Forest Service.

Railsback, S. F., & Rose, K. A. (1999). Bioenergetics modeling of stream trout growth: Temperature and food consumption effects. *Transactions of the American Fisheries Society*, *128*(2), 241–256. https://doi.org/10.1577/1548-8659(1999)128<0241:BMOSTG>2.0.CO;2

Snyder, M. N., Schumaker, N. H., Dunham, J. B., Ebersole, J. L., Keefer, M. L., Halama, J., Comeleo, R. L., Leinenbach, P., Brookes, A., Cope, B., Wu, J., & Palmer, J. (2022a). Tough places and safe spaces: Can refuges save salmon from a warming climate? *Ecosphere*, *13*(11), Article e4265. https://doi.org/10.1002/ecs2.4265

Snyder, M. N., Schumaker, N. H., Dunham, J. B., Keefer, M. L., Leinenbach, P., Brookes, A., Palmer, J., Wu, J., Keenan, D., & Ebersole, J. L. (2022b). Assessing contributions of cold-water refuges to reproductive migration corridor conditions for adult salmon and steelhead trout in the Columbia River, USA. *Journal of Ecohydraulics*, *7*(2), 111–123. https://doi.org/10.1080/24705357.2020.1855086

Stevens, B. S., & DuPont, J. M. (2011). Summer use of side-channel thermal refugia by salmonids in the north fork Coeur d'Alene River, Idaho. *North American Journal of Fisheries Management*, *31*(4), 683–692. https://doi.org/10.1080/02755947.2011.611037

Sullivan, C. J., Vokoun, J. C., Helton, A. M., Briggs, M. A., & Kurylyk, B. L. (2021). An ecohydrological typology for thermal refuges in streams and rivers. *Ecohydrology*, *14*(5), Article e2295. https://doi.org/10.1002/eco.2295

Taylor, C. A., & Stefan, H. G. (2009). Shallow groundwater temperature response to climate change and urbanization. *Journal of Hydrology*, *375*(3–4), 601–612. https://doi.org/10.1016/j.jhydrol.2009.07.009

White, S. L., Kline, B. C., Hitt, N. P., & Wagner, T. (2019). Individual behaviour and resource use of thermally stressed Brook Trout *Salvelinus fontinalis* portend the conservation potential of thermal refugia. *Journal of Fish Biology*, *95*(4), 1061–1071. https://doi.org/10.1111/jfb.14099