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RESEARCH ARTICLE

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InSTREAM 7: Instream flow assessment and management model for stream trout

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Abstract

Mechanistic, individual-based simulation models have been used for >25 years to overcome well-known limitations of "habitat suitability" models. InSTREAM 7 is the latest of our individual-based models for predicting the effects of flow and temperature regimes on stream salmonid populations. Unlike PHABSIM (or other methods based on habitat "quality," e.g., as net rate of energy intake), inSTREAM mechanistically represents specific effects of flow and temperature on all life stages, and how those effects combine into testable predictions of population measures such as abundance, relative abundance of multiple trout species, and persistence. InSTREAM 7 is the first version to also represent the daily light cycle (dawn, day, dusk, and night) and how feeding, predation risk, and individual behavior vary among light phases. An example assessment illustrates the importance of inSTREAM's multiple mechanisms: predicted trout population response to flow and temperature regimes depended on the effects of sub-lethal temperatures on feeding behavior and effects of temperature on egg survival and development, as well as how depth and velocity affected growth and predation risk. While its input data requirements are comparable to PHABSIM's, inSTREAM provides a more comprehensive framework for thinking about and predicting specific, well-known effects of flow and temperature. It has also proven useful for designing and evaluating restoration projects and for prioritizing alternative management actions. InSTREAM 7 is free, open-source, completely updated with recent literature, and implemented in the popular NetLogo software platform that makes customization easy.

KEYWORDS
inSTREAM, instream flow, population model, salmonids, stream temperature, trout

1 | INTRODUCTION

InSTREAM is a family of individual-based stream salmonid population models descended from the first attempt to use this modeling approach for river management (Van Winkle et al., 1998). These models simulate how individual fish behave, grow, survive or die, and reproduce over time in a virtual stream. By tracking what happens to individuals each day for many years, inSTREAM predicts how long-term population status (e.g., abundance, biomass, persistence) depends on channel morphology; flow, temperature, and turbidity regimes; and habitat characteristics such as cover for feeding and escaping predators.

We have been using, testing, and improving inSTREAM for 22 years; it has now been applied at over 50 sites on 3 continents and in over 25 publications. InSTREAM's original purpose was to provide instream flow and temperature assessment methods that overcome the well-known limitations of PHABSIM (Bovee et al., 1998) with reasonable cost and effort, in part by explicitly incorporating ecological processes widely recognized as critical to population dynamics (Anderson et al., 2006). In our experience, inSTREAM not only serves that purpose but has also led to important changes in how we think about, model, and conduct river management.

Here we introduce InSTREAM 7, a new version that implements additional concepts of modern salmonid ecology and major improvements in usability. We describe the new features of InSTREAM 7 and summarize how it differs from other instream flow assessment methods. We then use an example application to illustrate how inSTREAM can provide a more comprehensive understanding of how management actions, such as alternative flow and temperature regimes, affect salmonid populations.

2 | WHAT IS NEW IN InSTREAM 7

Previous versions of inSTREAM (and the closely related inSALMO salmon model) and their applications to river management were described by Harvey and Railsback (2007, 2021), Railsback and Harvey (2002), and Railsback, Harvey, Jackson, and Lamberson (2009); Railsback, Gard, Harvey, White, and Zimmerman (2013); Railsback, Harvey, and White (2014). InSTREAM 7 differs from previous versions in these major ways:

2.1 | Explicit representation of the daily light cycle and its effects on feeding, predation risk, and behavior

Trout biologists now understand circadian cycles in activity—what times of day fish feed vs. conceal themselves—as adaptive behavior that depends on characteristics of individual fish, habitat, and fish populations (e.g., Fraser & Metcalfe, 1997; Fraser, Metcalfe, & Thorpe, 1993; Metcalfe, Fraser, & Burns, 1998). InSTREAM 7 recognizes this important behavior by simulating four time steps per day, representing night, dawn, day, and dusk; and the light intensity in each habitat cell, which depends on depth and turbidity. Light intensity is among the factors inSTREAM uses to determine potential food intake and predation risk in each cell: low light—during the night or crepuscular periods, or in deep cells or high turbidity—reduces both predation risk and the ability to capture drift. We model how each trout decides whether to feed or hide and where to do so, on each time step, as a function of potential growth, predation risk, and competition among individuals. We showed that this method reproduces a variety of ways real salmonids adapt activity cycles (Railsback, Harvey, & Ayllón, 2020), and that considering the light cycle can strongly affect conclusions of instream flow assessments (Railsback, Harvey, & Ayllón, 2021).

2.2 | Updated assumptions, methods, and parameter values

InSTREAM 7 includes updates and improvements throughout the model, developed from a careful review of recent literature. Examples include new assumptions and parameters for respiration at high swimming speeds and temperatures to improve the prediction of growth under stressful conditions. The InSTREAM 7 user manual (Railsback et al., in preparation) provides thorough documentation of the model formulation.

2.3 | New software in a modern platform

Unlike previous versions, InSTREAM 7 is programmed in NetLogo (Wilensky, 1999), a popular and powerful software platform for individual-based models. NetLogo provides a high-level programming language with highly optimized commands, a complete graphical interface (Figure 1), a tool for automating simulation experiments for parallel execution, and links to statistical software for analysis of results. Consequently, InSTREAM 7 is simple to install and use on any operating system, and easy for users to customize (e.g., by modifying output files to use a desired format, replacing assumptions or equations). The software supports simulation of multiple species and multiple linked stream reaches. InSTREAM 7 also provides better integration with GIS, importing cell shapes and habitat variables directly from a GIS shapefile. It can accept depth and velocity input from a wide range of hydraulic models. The software is comprehensively tested and includes extensive run-time error checking.

3 | HOW INSTREAM DIFFERS FROM OTHER MODELS

Our experience illustrates important differences between using inSTREAM and other models used for instream flow assessment and other river management decisions. By "other models" we especially refer to the PHABSIM physical habitat model (Bovee et al., 1998) and the use of temperature criteria (e.g., evaluating how often a criterion of 20°C is exceeded). We also include the mechanistic models of drift feeding and energetics that have appeared more recently. These models (like inSTREAM) predict a trout's net rate of energy intake (NREI, often treated as equivalent to growth potential) as a function of hydraulic conditions, food availability, temperature, and fish characteristics. NREI models are used as an alternative way to evaluate habitat in PHABSIM-like models, by treating NREI as a measure of "suitability" (e.g., Jowett, Hayes, & Neuswanger, 2021; Naman et al., 2020; Naman, Rosenfeld, Neuswanger, Enders, & Eaton, 2019) and, combined with models of drift transport, to predict the "carrying capacity" of stream reaches (e.g., Hayes, Hughes, & Kelly, 2007; Wall, Bouwes, Wheaton, Saunders, & Bennett, 2015).

Other spatially explicit individual-based salmonid models have been developed for a variety of purposes. Landguth et al.'s (2017; see also Mims et al. 2019) metapopulation demogenetic model examines how factors such as stream network topology, habitat variability over time and space, individual migration, and migration barriers affect demography and gene flow among resident populations. Fullerton et al.'s (2017) model (also used by Armstrong et al., 2021) links

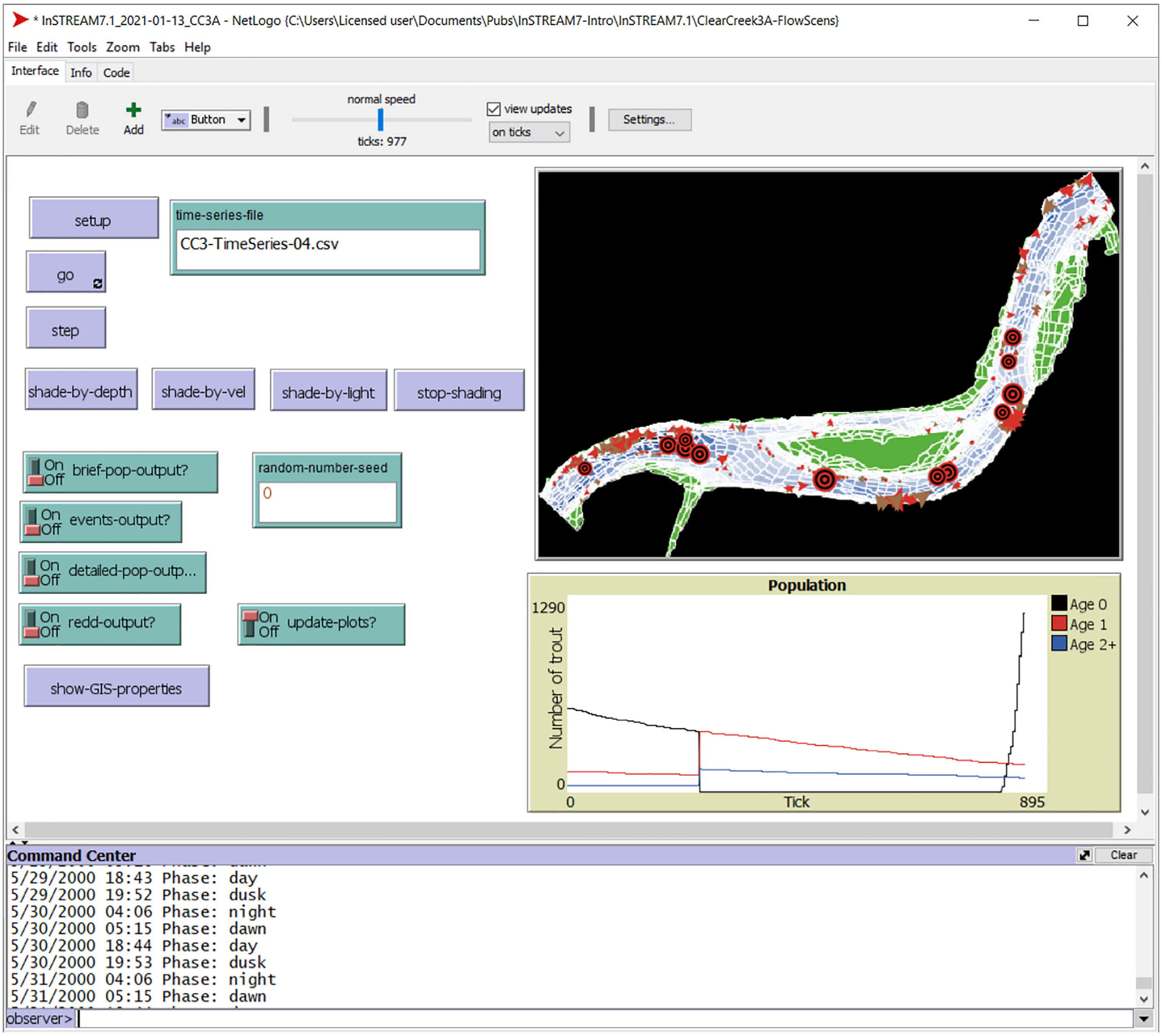

FIGURE 1 InSTREAM 7 interface. The model imports cell geometry and habitat variables from GIS, and cell depth and velocity relations can be imported from any hydraulic model. The display represents individual fish as triangle-like symbols colored by species; the round symbols represent redds. Interface controls let users pause and restart a simulation, turn output files on and off, and select which cell variable (depth, velocity, light intensity) to display. The NetLogo platform makes the software easy to understand and customize [Color figure can be viewed at wileyonlinelibrary.com]

juvenile salmon growth and phenology to network complexity and spatial variation in temperature regime. Snyder et al. (2019) modeled how upstream migration of adult salmon is affected by spatial configuration and temperature distributions of the migration path. However, none of these other individual-based models are directly comparable to inSTREAM because none are designed for assessing instream flows by predicting population responses to flow and temperature regimes and physical habitat at the microhabitat to reach and reach-network scales.

Here we identify important specific differences between InSTREAM 7 and traditional assessment methods, specifically the use of PHABSIM and NREI models and temperature criteria. These differences are further illustrated in the example application below. In the conclusion, we consider how these differences change the way we think about and conduct decision support for river management.

3.1 | InSTREAM considers flow and temperature *regimes*, not just minimum flows and peak temperatures

By simulating many years at daily or shorter time steps, inSTREAM automatically considers seasonal changes in flow and temperature, periods of uncontrolled flow, low as well as high-temperatures, etc.

This ability is in contrast to habitat selection models such as PHABSIM, which do not include time. Habitat selection models can address effects of changes in flow over time only via ad hoc and limited methods such as habitat time series analysis. Traditionally, water temperature effects are evaluated only by considering how often a high-temperature threshold is exceeded. Because of these limitations, traditional assessments have focused only on minimum (often, summer) flows and maximum temperatures. In contrast, inSTREAM lets us predict the effects of variable flow regimes and year-round temperatures. Temperature can have strong effects during seasons other than summer (Armstrong et al., 2021; Railsback & Rose, 1999).

3.2 | InSTREAM considers the interacting effects of multiple stressors and factors

Traditional methods generally neglect the interacting effects of flow and temperature, and rarely consider turbidity. InSTREAM simulates how flow, temperature, and turbidity combine to affect individual trout growth and survival and, therefore, their cumulative, interacting effects on populations. Interactions among these factors are important. For example, temperature strongly affects fish metabolic rates and food intake requirements; therefore, higher temperatures can cause trout to feed more often, more often in daytime instead of night, and in riskier places (e.g., Fraser, Heggenes, Metcalfe, & Thorpe, 1995; Vondracek, Spence, & Longanecker, 1992). Harvey and Railsback (2007) examined three stressors (wet-season turbidity, summer temperature, and channel modification) in a set of inSTREAM simulation experiments and found strong, nonlinear interactions in their effects on trout abundance. Ayllón, Nicola, Elvira, and Almodóvar (2021) used a custom version of inSTREAM to examine interactive effects of angler harvest and climate change on the eco-evolutionary trajectories of trout populations.

3.3 | InSTREAM represents multiple effects of temperature

The traditional use of thresholds provides an easy way to assess effects of water temperature, for example by assuming that temperature has important effects on trout only if it exceeds 20°C. However, temperature affects fish in many ways, over ranges well below those causing conspicuous effects such as mortality or feeding impairment (some illustrated by our example assessment below). InSTREAM represents the following direct effects of temperature, which typically have complex consequences for population dynamics and instream flow assessment. One is the control of metabolic rates and food demand mentioned above; changes in cool-season temperatures can cause trout to switch from nocturnal to daytime feeding and thus expose themselves to higher predation risk. (NREI models also represent some of these effects: how temperature-driven metabolic rates affect habitat selection.) The risk of predation by piscivorous fish is assumed to increase with temperature, reflecting increased predator metabolic rates. Temperature also has a nonlinear effect on sustainable swimming speeds so that trout are less able to use high velocities at both low and high-temperatures. Temperature is one of the cues salmonids use to determine when to spawn, and egg development rates are strongly temperature-driven; therefore, temperature regimes can strongly affect when spawning occurs, when fry emerge, and what flows fry experience. Salmonid eggs can be killed (directly or by disease) by temperatures either above or below an optimal incubation range much narrower than the range adults can tolerate.

3.4 | InSTREAM produces testable predictions of population responses

Unlike models that predict only habitat suitability indices or carrying capacity for separate life stages, inSTREAM predicts long-term population characteristics (abundance, biomass, persistence) resulting from what happens throughout the life cycle. This ability makes inSTREAM's results directly applicable to management decisions, without further interpretation. Because its predictions are at the same scale that trout populations are typically censused, this ability also means that inSTREAM results can be tested with field observations.

3.5 | InSTREAM represents interactions among trout species

Interactions among salmonid species are a common management concern; a common example is how alternative flow and temperature regimes affect native vs. introduced trout species. InSTREAM represents multiple species explicitly, typically by using species-specific values for parameters that control when spawning occurs (e.g., spring- vs. fall-spawning species) and how temperature affects egg mortality and incubation rates. Even with such minimal differences among simulated species, inSTREAM can illustrate complex and unexpected ways in which flow management alternatives affect relative abundance (e.g., Bjørnås, Railsback, Calles, & Piccolo, 2021).

3.6 | Both growth and predation risk drive habitat selection in InSTREAM

While bioenergetics-based drift foraging models (Hayes et al., 2007; Jowett et al., 2021; Naman et al., 2020) are a more mechanistic and general representation of habitat selection than traditional suitability measures based only on empirical observations, they neglect a potentially important consideration: trout habitat selection can also be strongly driven by risk avoidance. Harvey and White (2017) found that even unlimited food did not entice juvenile Steelhead Trout into shallow habitat where they are especially vulnerable to overhead predators. Fear of fish predators may make very small juveniles just as reluctant to use deep habitat. InSTREAM represents habitat selection as a trade-off between growth and predation risk; model trout typically select feeding times and locations to maintain positive growth while otherwise minimizing predation risk. The model reproduces a variety of observed behavior patterns that depend on the trade-off (Railsback et al., 2020; Railsback & Harvey, 2002; Railsback, Harvey, Hayse, & LaGory, 2005).

3.7 | InSTREAM explicitly considers fish activity and habitat use throughout the circadian cycle

Its ability to simulate behavior, growth, and survival throughout the daily light cycle lets inSTREAM represent additional kinds of habitat that trout need, such as for night feeding and for concealment, and the consequences of not providing that habitat. Traditional methods are almost always based only on daytime observations or feeding models that assume daytime conditions; ignoring habitat use during lower-light conditions is likely an important source of bias (Railsback et al., 2021; Rosenfeld & Naman, 2021).

3.8 | InSTREAM is easily extended

Many applications of inSTREAM are enhanced by modifying or extending the model to address especially important or unique issues. Several characteristics of inSTREAM make it easy to customize: its individual-based and mechanistic nature, its modular design, and (for InSTREAM 7) the ease of programming in NetLogo. We have already produced specialized versions of InSTREAM 7 that represent flow fluctuations from peaking hydropower and how the accessibility of off-channel pools varies with the flow. Previous versions of inSTREAM have been modified to represent effects of: angler harvest and angling regulations (Ayllón et al., 2021; Ayllón, Nicola, Elvira, & Almodóvar, 2019), drift food availability that varies with temperature and the rate of flow change (unpublished), evolution of life history traits (Ayllón et al., 2016), passage barriers (Harvey & Railsback, 2012), and a contaminant that affects reproductive physiology (Forbes et al., 2019). InSALMO is a modification of inSTREAM to represent freshwater life stages of salmon and Steelhead Trout (Railsback et al., 2013, 2014). These models have also proven uniquely useful for designing and evaluating habitat restoration projects, for example, by assessing the relative benefits of alternative actions such as augmenting spawning gravel versus providing feeding and hiding cover (e.g., Railsback et al., 2013).

4 | EXAMPLE ASSESSMENT OF FLOW REGIMES

We illustrate inSTREAM's use via an example assessment of alternative reservoir release rules. We model two reaches of Clear Creek below Whiskeytown Reservoir, Shasta County, California, also used by Railsback et al. (2013, 2021) and Gard (2014). One simulated reach ("RESTORED," illustrated in Figure 1) represents an extensive project that restored meanders and riffle-pool morphology, while the second ("DEGRADED") represents a relatively uniform, straight, steep-sided channel that resulted from gravel mining. The simulated trout population is artificial: the real site is managed primarily for Chinook Salmon spawning, but for this example we simulate a single species, Rainbow Trout.

We used the same set of hypothetical flow and temperature scenarios examined by Railsback et al. (2021), which were synthesized from observed flows and water temperatures. These scenarios include minimum reservoir releases ranging from 3 to 15 m^3/s, with much higher flows during the winter–spring high-runoff season due to tributaries (Figure 2). Because the reservoir releases are much cooler than the air in summer, we assume that water temperature regime varies among the instream flow scenarios, with low minimum flows resulting in higher summer water temperatures. We used the same daily flows and temperatures at both sites.

We also used the same model parameterization and calibration reported by Railsback et al. (2021) for their "four-phase" model version. Our simulations started with three "warm-up" years ignored in the analyses (to reduce effects of initial population characteristics). The primary result used for comparing flow scenarios is the mean abundance of age 1 and older trout, on September 30th of water

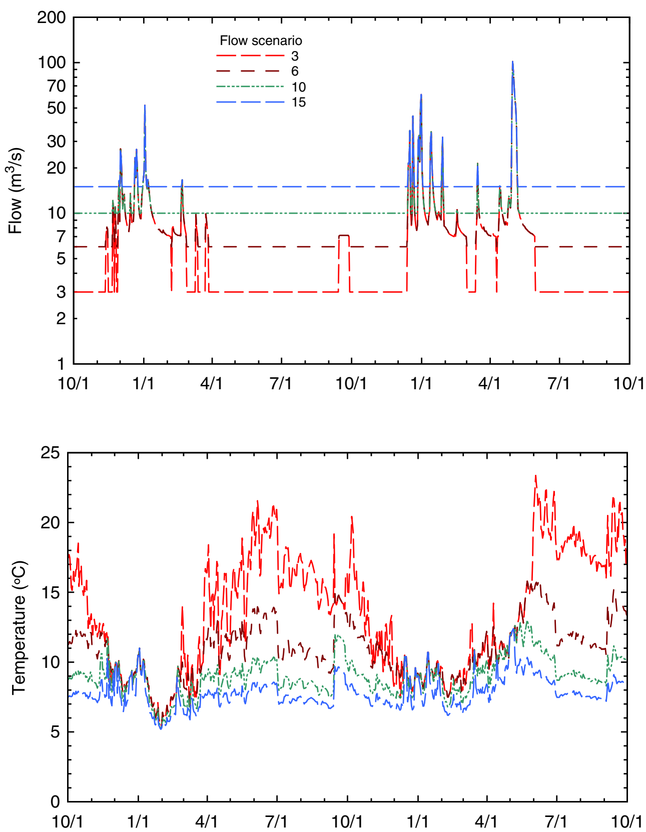

FIGURE 2 Example instream flow scenarios: Daily flows and temperatures over 2 years. Scenarios are labeled by their minimum reservoir release, in m^3/s. All scenarios include winter–spring high flow periods when tributary inflows augment reservoir releases [Color figure can be viewed at wileyonlinelibrary.com]

years 2002–2011. We executed five replicate simulations of each flow scenario to consider inSTREAM's stochasticity.

For the RESTORED site, InSTREAM 7 predicted trout abundance to increase with minimum flow up to the 6 m^3/s scenario, then decreases only slightly at higher minimum flows (Figure 3). At DEGRADED, predicted abundance increases with flow up to the 10 m^3/s scenario. To obtain the real value of inSTREAM, however, we need to investigate why it produced these results and what it says about the effects of flow and temperature regime at these sites.

What caused the predicted trout abundance to increase with flow and then peak? Several of inSTREAM's mechanisms relating abundance to flow are driven by drift feeding. First, higher flows deliver more food because inSTREAM assumes a constant concentration of drift (g of food per m^3 flowing through a cell). Second, inSTREAM (like other drift feeding models, e.g., Naman et al., 2020) assumes that drift feeding efficiency increases with velocity and depth, up to a peak that depends on fish size and (in inSTREAM) light intensity. A key difference from other models is that inSTREAM explicitly represents whether drift-feeding trout use velocity shelter to reduce their swimming speeds; velocity shelter lets trout feed efficiently at higher cell velocities.

The drift feeding component of inSTREAM explains why *growth* increased with flow, but not why *abundance* increased; increased abundance requires increased survival or reproduction. Flow can affect survival by creating more places where trout can feed productively and in relative safety, so fewer individuals are at high risk of predation or starvation. Higher growth is translated to abundance via fecundity: bigger spawners produce more eggs. The most important mechanisms relating growth to survival in inSTREAM, however, are behaviors: better feeding conditions allow simulated trout to feed in safer habitat and at times with lower light and less predation, and to spend more time concealed instead of feeding. As flow increased from the lowest scenario in summer, simulated adult trout fed less in daytime and (at RESTORED) spent less total time feeding (Figure 4). Transitions in the prevalence of daytime feeding in InSTREAM 7 results are good indicators of overall feeding and growth conditions: if the percentage of adult trout feeding in daytime (or the total amount of feeding in a day) decreases over a range of flow, it usually indicates improving conditions that let more trout meet their energetic demands with less risk.

The predicted differences among flow scenarios were not due only to flow: temperature also had strong effects. A traditional temperature assessment that only considered an upper temperature criterion would identify temperature concerns only at the lowest flows: a criterion of 20°C was exceeded on 8.0, 1.0, and 0.03% of days in the 3, 4, and 5 m^3/s scenarios and never at higher flows. InSTREAM in fact predicted acute temperature mortality to cause 3% of all trout mortality in the 3 m^3/s scenario, 0.2% in the 4 m^3/s scenario, and none at higher flows. However, sublethal effects of temperature via growth were likely more important: in warmer water trout must feed more, and at riskier times and places, to maintain body condition and grow. As a consequence of behavior to balance growth and risk, higher metabolic rates increase predation mortality.

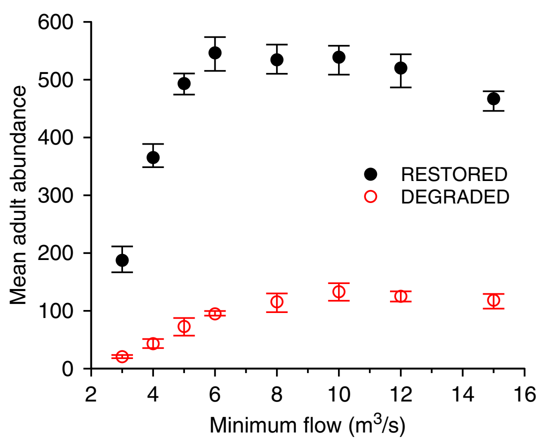

FIGURE 3 Adult trout abundance predicted by InSTREAM 7 for the eight flow scenarios (the X axis is the flow except during uncontrolled high flows). The dots and error bars indicate the mean, minimum, and maximum over five replicate simulations of mean September 30 abundance [Color figure can be viewed at wileyonlinelibrary.com]

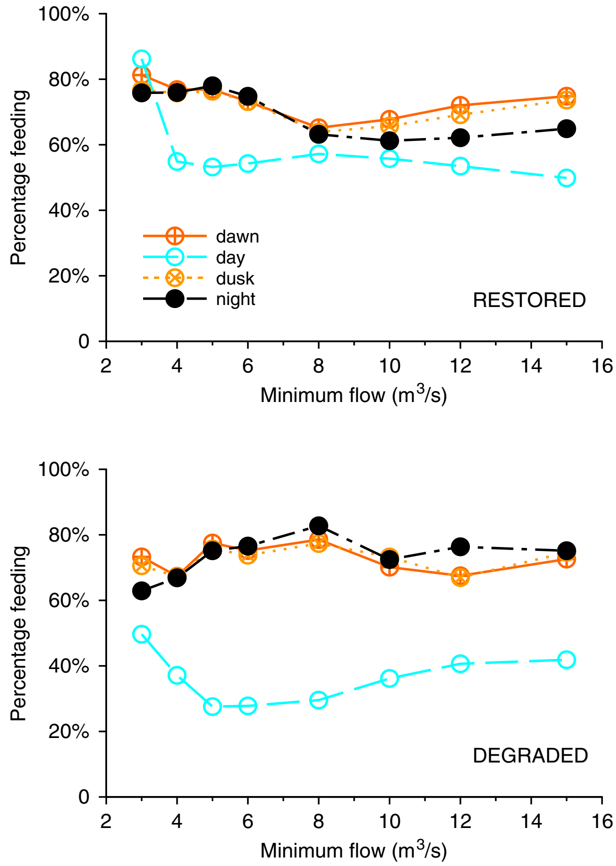

FIGURE 4 Response of simulated trout activity to minimum flow in summer, at the RESTORED and DEGRADED sites. The Y axis is the percentage of age 1 and older trout predicted to be feeding during each of the four daily light phases, averaged over August of 1 year [Color figure can be viewed at wileyonlinelibrary.com]

Temperature effects on egg survival and development are well-understood but typically neglected by assessment methods other than inSTREAM. These effects were strong in this example. In particular, temperature caused much higher mortality of eggs than fish. InSTREAM predicted that high temperature and associated disease killed 30% of eggs in the 3 m^3/s scenario, decreasing to 21, 16, and 10% of eggs in the 4, 5, and 6 m^3/s scenarios, and continuing to decrease at higher flows. (Because of density-dependent survival, effects on adult abundance were less than these egg mortality rates.) Egg development rate increases with temperature, so fry emerged earlier in the lower-flow scenarios. From the lowest to highest flow scenario, the mean date of emergence increased from late May to mid-July (Figure 5). Later emergence partly explains the predicted decrease in trout abundance in the highest flow scenarios: trout in the highest flow scenarios were smaller at the end of their first year and had lower survival to the following spring (smaller size increases vulnerability to predation by fish and reduces ability to feed in high winter flows).

The different responses to flow regime predicted by inSTREAM for the RESTORED vs. DEGRADED sites (explored further by Railsback et al., 2021) appear driven by the lack of deep habitat and concealment cover at DEGRADED. That lack makes the site more dangerous for feeding, especially in daytime, but high summer temperatures in low flow scenarios forced trout to feed more in daytime to meet metabolic demands. As flow increased, InSTREAM 7 predicted that trout switch from feeding in daytime to nighttime and crepuscular periods, which increased their survival. In contrast, the greater habitat diversity at RESTORED allowed more trout to feed safely at all times of day, over all flows. For example, feeding in deep pools in daytime can be almost as safe as feeding at night.

All of these mechanisms use assumptions and parameter values that we based on thorough literature review and tested to the extent possible, but uncertainty remains an important concern. Analyzing robustness to parameter values is one practical way to estimate the effects of uncertainty on conclusions drawn from mechanistic models like inSTREAM. We repeated the flow scenario analysis nine times, using all combinations of low, standard, and high values of two parameters that are especially uncertain and expected to have strong effects (using the methods of Railsback et al., 2021). These parameters control the effect of light intensity on drift feeding ability and predation risk and, therefore, the relative benefits of feeding during day vs. dawn, dusk, or night.

Across the nine parameter combinations, the relative rank of flow scenarios (which scenarios produced the fewest, second-fewest, … most adult trout) changed little except among scenarios producing very similar abundances (Figure 6). So far in our experience with this kind of analysis (e.g., Railsback et al., 2009), inSTREAM's results of management relevance—which scenarios are substantially better or worse than the others—have never been sensitive to parameter values. Railsback et al. (2021) documented another kind of robustness in InSTREAM 7: they showed that flow scenario rankings varied little when drift food availability was increasingly concentrated in dawn and dusk.

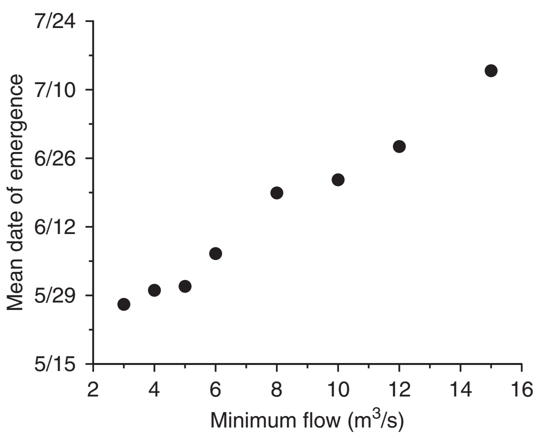

FIGURE 5 Timing of fry emergence from redds in simulations of the eight flow scenarios. The Y axis is the mean day on which emergence was completed, over all simulated redds

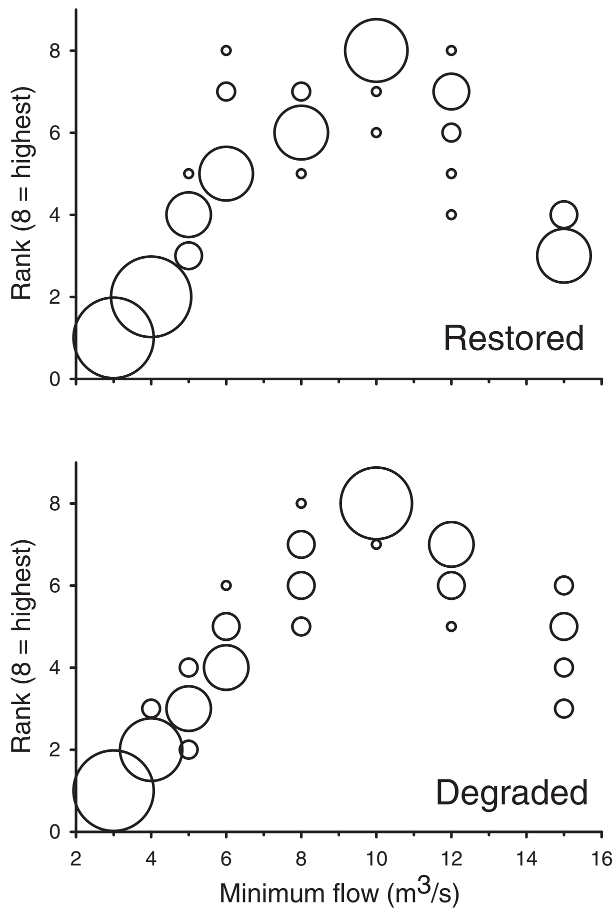

FIGURE 6 Parameter robustness analysis results: Symbol size represents the number of times the flow scenario on the X axis had a given trout abundance rank (1 = fewest trout, 8 = most trout) out of the nine combinations of parameter values. Comparison to Figure 3 shows that rank varied little among parameter combinations except among the scenarios producing nearly equal abundance

5 | CONCLUSIONS

InSTREAM was designed to provide a more comprehensive approach to instream flow and temperature assessment than traditional methods, without substantially higher input requirements or costs. It has evolved over 20+ years to incorporate more salmonid ecology and improved technology.

One unexpected benefit of inSTREAM is that it changes the way biologists and managers think about instream flows and river management. The traditional focus on habitat "suitability" and temperature criteria provide only abstract, simplified ways to think about river habitat that may not be well-linked to fish populations (Railsback, Stauffer, & Harvey, 2003). Using mechanistic models like inSTREAM shifts the focus to real, observable processes that directly affect fish fitness: food production and feeding, energetics and growth, competition for food and habitat, predation by fish and by terrestrial animals, spawning, and egg incubation. Our example assessment identified as important a number of mechanisms that are well-understood by salmonid biologists yet ignored in conventional assessment methods. InSTREAM 7's mechanisms include all those identified by Rosenfeld and Naman (2021) as causing systematic underprediction of instream flow needs when ignored by PHABSIM-like models. InSTREAM provides a framework for thinking about such mechanisms and a rigorous way to explore their consequences.

Using inSTREAM also changes the way we think about and deal with uncertainty. Uncertainty is a natural concern for large, complex models, but there are important ways that inSTREAM helps us reduce and understand uncertainties. The results of habitat models like PHABSIM can be informative but are not directly translatable into management recommendations: getting from habitat availability for various life stages to a decision about which flow scenario is best requires a great deal of interpretation, for example, What flow is best when juvenile WUA decreases as adult WUA increases? How do we assess flow regimes with natural seasonal variation? How will multiple competing species respond? This interpretation must be based on assumptions, judgment, or additional modeling assumptions (e.g., Ayllón, Almodóvar, Nicola, Parra, & Elvira, 2012), which may or may not be tested or even documented. In contrast, inSTREAM predicts population responses using tested and documented methods. Its user manual (Railsback et al., in preparation) provides in-depth information and analysis on parameter sensitivity, uncertainty, and the multiple ways we have tested inSTREAM's components and overall predictions. When inSTREAM produces results that appear to conflict with observations (or beliefs), we can determine why and perhaps consider alternative assumptions.

Finally, inSTREAM's ability to produce testable predictions of population abundance provides a fundamental difference from traditional approaches: it allows the cycle of model testing and improvement that is essential to both science and adaptive resource management. This cycle has been conspicuously lacking in instream flow biology and is in fact impossible unless we use models that predict observable and meaningful phenomena. Even though we have not yet had the opportunity for multiple, large-scale, or lengthy tests, we have steadily improved inSTREAM from lessons learned in field applications and controlled experiments designed to address specific model components.

InSTREAM 7 is available at Humboldt State University's ecological modeling web site: https://ecomodel.humboldt.edu. The model and its software platform are free and open-source. Potential users are encouraged to contact the authors about training and support.

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DATA AVAILABILITY STATEMENT

This study produced no original data. The models and input used to generate Figures 3–6 are available from the corresponding author, SFR, upon reasonable request.

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