ARTICLE

Importance of the Daily Light Cycle in Population–Habitat Relations: A Simulation Study

Steven F. Railsback*

Lang Railsback and Associates, 250 California Avenue, Arcata, California 95521, USA

Bret C. Harvey

U.S. Forest Service, Pacific Southwest Research Station, 1700 Bayview Drive, Arcata, California 95521, USA

Daniel Ayllón

Department of Biodiversity, Ecology and Evolution, Faculty of Biology, Complutense University of Madrid, Madrid 28040, Spain

Abstract
    Salmonids adaptively select when in the daily light cycle to feed, and they use different habitat at different times of day; however, the data and methods used to evaluate management actions like instream flows and restoration projects typically consider daytime only. Our new model, inSTREAM 7, lets us investigate how management decisions might change if we consider the full daily light cycle. The model explicitly represents the effects of light intensity on feeding efficiency, predation risk, and, therefore, foraging behavior. We simulated trout population response to a range of flows at restored and unrestored sites by using model versions that represented one (daytime only), two (day and night), and four (dawn, day, dusk, and night) light phases per day. Inclusion of night and crepuscular phases in the model produced important changes in results: it allowed model trout to convert improved growth conditions to increased survival by feeding less often during the day. This adaptive ability produced sharper population responses to habitat improvements. Crepuscular phases can be important because they let trout feed in the same higher-velocity habitat used in daylight but with reduced predation risk. Analyses of parameter uncertainty and circadian cycles in food availability indicated that simulated population responses of management importance are not sensitive to details of how light affects feeding and predation risk. We suggest ways to consider night and crepuscular periods in management decision making and monitoring even without complex simulations.

Fish ecologists have long recognized diel variation in the behavior and habitat use of fishes, including salmonids (Edmundson et al. 1968), yet this variation is rarely considered in management models and methods, such as those commonly used to support instream flow decisions. Patterns of variability in when fish feed as well as where they feed have been widely observed and explained as adaptive trade-off behaviors. Examples include feeding less often—and more nocturnally—at lower temperatures (e.g., Fraser et al. 1995; Bradford and Higgins 2001), feeding more often in daytime when food availability or fish condition is low (Metcalfe et al. 1998, 1999), less daytime feeding by adults than juveniles (Bradford and Higgins 2001; Gries and Juanes 1998), and the prevalence of nocturnal versus diurnal feeding depending on habitat variables such as flow (Bradford and Higgins 2001) and the availability of hiding places (Larranaga and Steingrímsson 2015). These patterns are understood as adaptive responses to how light

affects both predation risk and feeding success; less light makes fish less visible and less vulnerable to predators but also less able to see and capture their own prey. Therefore, light intensity interacts with other factors driving growth and risk in determining what times of day and kinds of habitat are good for foraging versus remaining concealed (Metcalfe et al. 1999).

The potential importance of diel variation in behavior and habitat use to instream flow assessment also has been long recognized: if fish use different habitat for different essential activities (feeding and concealment) at different times of day, should assessment methods and models not consider all of these needs (Heggenes et al., 1999; Orth 1987)? In fact, Harris et al. (1992) and Davey et al. (2011) found differences in habitat preferences between day and night and concluded that the differences should not be ignored in instream flow studies. However, consideration of circadian light cycles in instream flow assessment and related management studies appears to remain rare; for example, the topic was not addressed in a recent review of habitat selection modeling for instream flow assessment (Nestler et al. 2019). Neglecting how habitat use and activity vary throughout the day (as well as seasonally) has obvious risks; models and decisions based on observed habitat selection only during daytime feeding cannot be accurate if many fish or if critical individuals (such as the oldest and largest) feed primarily at night or during crepuscular periods. Neglecting circadian variation can also lead to misunderstanding of population responses to instream flow changes: if an increase in flow enhances feeding conditions such that adult fish can switch from daytime to nocturnal feeding, then the counts of feeding individuals during day (e.g., using standard snorkel survey methods) could misleadingly indicate a decrease in abundance. A management change that reduces feeding and growth conditions could force fish to switch from nocturnal to daytime feeding, resulting in a misleading increase in daytime abundance.

Population models that incorporate diel variation in the behavior and habitat use of stream salmonids exist. Railsback et al. (2005) presented a spatially explicit, individual-based model of stream salmonids that distinguished day versus night behavior and habitat use; the model reproduced a variety of within-day patterns in habitat use observed in nature. Harvey et al. (2014) applied this model to the problem of predicting the effects of stream diversion on a trout population. Comparison of the model that represented both day and night to a simpler model that included only daytime behavior and habitat use revealed that the former predicted lesser sensitivity of the population to reductions in streamflow.

Might even more detailed representation of the circadian light cycle be useful to address questions about the effects of environmental alterations on fish populations? Crepuscular periods in particular are short but unique and potentially important times of day because they offer light levels sufficient for fish to feed but low enough to reduce predation risk and sometimes provide a higher availability of invertebrate drift (Hynes 1970; Kreivi et al. 1999). Bradford and Higgins (2001) and Roy et al. (2013) observed that juvenile salmonids fed primarily during crepuscular periods at some sites and seasons. Although the potential importance of crepuscular periods for salmonids (and their anglers) is widely recognized, we know of no previous attempt to include them in habitat assessment models or to evaluate their influence on habitat–population relations.

We offer a spatially explicit, individual-based model of stream trout that subdivides the day into four phases and treats light as a driving variable. The added complexity over existing individual-based models of trout that simulate one or two periods each day will have costs in the form of additional assumptions and parameters, increased computational requirements, and, perhaps, difficulty of calibration. This paper is an initial effort to determine whether the added complexity is justified.

Our objective is to learn more about how and why analyses of river management effects on fish populations change when we explicitly consider the circadian light cycle in increasing resolution. Here, we examine the effects of environmental conditions typically altered by resource managers: (1) channel morphology, by contrasting a degraded channel to a restored one; and (2) flow and temperature regimes, by contrasting a range of minimum flow releases from a reservoir. We simulate the effects of these scenarios using three individual-based model versions that represent (1) day only, (2) day and night, and (3) dawn, day, dusk, and night. Contrasting the results of these three alternative models allows us to draw conclusions about the importance of considering nighttime and crepuscular activity of fish when evaluating river management effects. To better understand the feasibility and costs of explicitly considering crepuscular periods, we also examine the sensitivity of management-relevant model results to the details of how those periods are modeled.

METHODS

Model description.— This simulation experiment used version 7.0 of inSTREAM, the newest of a family of individual-based salmonid population models that are designed for river management applications (e.g., Railsback and Harvey 2001; Railsback et al. 2009). InSTREAM 7 is a complete revision of the model, with an updated formulation and new software platform. The Supplement (available in the online version of this article) provides a complete description of the model; the

following summary focuses on parts that are especially relevant to this application. (Throughout this article, "trout" and "fish" refer to virtual trout in the model.)

The most fundamental difference between inSTREAM 7 and previous versions is that it explicitly represents the circadian light cycle as one driver of feeding success, predation risk, and, therefore, trout behavior. The circadian cycle is represented via separate time steps for each of the four "phases" of the cycle: dawn, day, dusk, and night. The two crepuscular phases start and end when the sun is 6° below and above the horizon, as determined from date and latitude. Light intensity (as irradiance, W/m^2) at the water surface for dawn, day, and dusk is calculated from a model of mean irradiance over part of a day; surface irradiance at night is assumed a constant 0.9 W/m^2. Irradiance in the water decreases exponentially with depth, with the rate of this decrease determined by turbidity. The model assumes that simulated fish experience the irradiance at half the depth of the habitat cells they occupy.

InSTREAM 7 retains the basic structure of previous versions, representing habitat dynamics and the full life cycle of individual trout. Habitat is represented as one or more linked stream reaches, which each have daily input for flow, temperature, and turbidity. Habitat cells—irregular polygons with variables for depth and velocity (which depend on flow), light irradiance, and the availability of cover for drift feeding and hiding—represent habitat variation within reaches.

The model represents each trout as an individual, with variables for length, weight, condition, age, sex, and species. On each time step, each fish executes three actions: habitat and activity selection, survival, and growth. These three actions are all executed by one trout at a time, in order from the largest to the smallest trout, thus representing a size-based hierarchy.

The habitat and activity selection action (fully described and tested in our previous work, Railsback et al. 2020) determines which habitat cell a trout occupies and which activity—feeding or hiding—the trout uses. The trout are assumed to be able to sense the characteristics of cells and move only to cells within a radius that increases with their length (e.g., within 12.5 m for a 5-cm trout, within 50.0 m for a 10-cm trout). A trout examines each such cell and calculates the growth rate and survival probability it would experience in the cell over the upcoming time step, for both feeding and hiding. The trout then decides which combination of cell and activity, in combination with the growth and survival it experienced in the previous three time steps (to represent a full 24-h d), would give it the best probability of surviving both predation and starvation until a time horizon 90 d in the future. This decision depends on the trout's current state, the options available to it in the upcoming phase, and its experience in preceding phases. For example, a trout in

good condition that accumulated its daily energy demand during night and dawn will be much less likely to feed during the following day. This approach causes simulated trout to make good trade-offs between growth and survival, and inSTREAM has been shown to reproduce a wide variety of patterns in how trout adapt their habitat and activity selection to changes in variables such as food availability, predator and competitor density, temperature, and hiding cover availability (Railsback and Harvey 2002; Railsback et al. 2005, 2020).

The survival action determines whether each trout survives each of several kinds of mortality, the most important of which are predation by other fish and predation by terrestrial animals. Predation is very difficult to observe and quantify, but because these relations appear to strongly affect habitat use, inSTREAM assumes that predation risk depends on trout length, depth, velocity, light level, and several kinds of cover. The risk functions are based on literature when possible and otherwise are inferred from trout behaviors or simply estimated. Risk from terrestrial predators is assumed highest for large fish (Harvey and Stewart 1991) but is reduced by depth (Harvey and Stewart 1991; Harvey and White 2017), low light intensity (Harvey and Nakamoto 2013), and proximity to escape cover (Harvey and White 2017). The risk of predation by fish is, in this case, due to cannibalism and is therefore highest for small trout but reduced in habitat that is shallow enough to place piscivorous trout at risk of terrestrial predation. Trout that choose the hiding activity instead of feeding are assumed to have (1) 60% less risk of predation by fish, a relatively low benefit of hiding reflecting the scarcity of hiding cover for small fish (e.g., substrate crevices) at the study sites; and (2) 80% less risk of predation by terrestrial animals, reflecting that some predators (e.g., otters) can extract fish from hiding cover, whereas most cannot.

Feeding and growth are simulated using standard drift feeding and bioenergetics approaches (e.g., Hughes and Dill 1990; reviewed by Piccolo et al. 2014) plus an alternative "search" feeding method (Nakano et al. 1999). Drift food intake increases with water velocity and trout length and decreases with turbidity. On the basis of evidence such as that provided by Hansen et al. (2013), the model assumes that light has no effect on drift feeding at irradiances of 20 W/m^2 or greater but that the distance over which trout can detect prey decreases by half as irradiance decreases to night levels. The energy cost of drift feeding increases with water velocity, so the growth rate is highest at an intermediate velocity. Search feeding represents actively searching the streambed or the surface for prey. Search feeding intake is assumed to be independent of irradiance. Food intake from both feeding methods (drift feeding and search feeding) is subject to competition in a size-based hierarchy (e.g., Hughes 1992; Nakano et al.

1999): each cell has limited amounts of drift and search food available at each time step (these amounts depend on cell size), and each trout choosing to feed in a cell reduces the amount of food that is left for the remaining smaller trout. Therefore, the choice of which cell to feed in—and even of whether to feed or hide—depends on the choices of larger trout. For these simulations, we assumed that food availability (as concentration of drift in the flow and the per-area rate of search food production) is constant over space and time.

InSTREAM also represents spawning and egg incubation, allowing it to depict the effects of habitat management and flow regulation on reproductive success and long-term population dynamics.

InSTREAM 7 is implemented in NetLogo, a specialized software platform for spatial and individual-based models (Wilensky 1999). The inSTREAM software was tested comprehensively by reimplementing each submodel independently in Microsoft Excel; a set of approximately 18 documented code tests is available from the authors.

Study site and input.— We simulated two reaches that were previously used with a related Chinook Salmon *Oncorhynchus tshawytscha* model (Railsback et al. 2013, which provides additional site description) to evaluate habitat restoration effects. The reaches are on lower Clear Creek downstream of Whiskeytown Reservoir in Shasta County, California. The simulation analyses presented here are strictly hypothetical and of no direct relevance to the management of Clear Creek because in reality the site is managed for salmon spawning and rearing, whereas our simulations assumed that the two reaches support only resident trout—our simulation results for adult trout are not meaningful for juvenile salmon. Although inSTREAM can simulate multiple species, we simulated only Rainbow Trout *O. mykiss.*

The two reaches were designated as "RESTORED" and "DEGRADED." The RESTORED reach resulted from an extensive channel restoration project that built bends, shallow bars, a backwater, and deep pools and added hiding cover. The RESTORED site is 490 m long and an average of 27 m wide. The DEGRADED reach represents degraded conditions caused by gravel mining. Its channel, which is 460 m long and averages 14 m wide at base flow, is straight and lacking in hydraulic complexity. The scarcity of shallow habitat in DEGRADED provides little area where small juvenile trout are safe from predation by other fish, while its lack of pools means that larger trout have less refuge from visual predators, such as birds (Harvey and White 2017). The RESTORED reach provides high availability of moderate depths and velocities over a wide range of flows. In contrast, at DEGRADED, with its U-shaped channel, the availability of moderate depths and velocities varies sharply with flow;

for example, only 22% of the wetted area has a depth greater than 50 cm at a flow of 3 m³/s, but 52% of the wetted area exceeds 50 cm at a flow of 5 m³/s. The two sites have similar availability of hiding cover. We used the same parameter values for both sites with one exception: RESTORED is relatively wide and unshaded, while DEGRADED is overgrown with trees, so the parameter representing how much sunlight reaches the water surface was set to 90% for RESTORED and 60% for DEGRADED.

Flow, temperature, and turbidity regimes at the RESTORED and DEGRADED sites are typical of reservoir-controlled instream flow assessment sites. These regimes are controlled by reservoir releases during the summer–fall dry season and by tributary inflows during the winter–spring season of precipitation and snowmelt. Because of a low-elevation reservoir release and high shading between the reservoir and the study sites, water temperatures are characteristically much more moderate than the air temperatures; historically, in summer when air temperatures typically range from 25°C to 30°C, observed water temperatures range from 15°C to 20°C.

With one exception, we used the site input from Railsback et al. (2013), which was based on two-dimensional hydrodynamic modeling and extensive habitat surveys conducted by the U.S. Fish and Wildlife Service. The exception is that inSTREAM 7 differs from previous versions by treating hiding cover—places used by adult trout that choose to hide instead of feed for a time step —as discrete "hiding places": concealed locations, such as crevices or undercut banks, that trout appear to defend from other trout (Harvey and White 2016). The number of hiding places in a cell limits the number of trout that can hide. We estimated the number of hiding places per cell from direct observations and photographs of the sites.

Scenarios.— Our simulation analyses were designed to mimic a typical instream flow assessment; we formulated a range of alternative flow release scenarios and modeled their consequences. We developed the scenarios from a baseline scenario representing observed conditions. (Because of the sites' proximity, daily flows and temperatures did not differ between DEGRADED and RESTORED.) The baseline scenario uses daily mean flows measured by the U.S. Geological Survey gauge (11372000) upstream of the study site and temperatures observed by the U.S. Fish and Wildlife Service at the study site. We established a gradient of eight flow scenarios to represent minimum reservoir release alternatives that might be considered in an instream flow assessment. These scenarios simply differ in the flow and temperature on days when tributary inflows have negligible influence, which typically occur in June–November. Turbidity input was not varied among flow scenarios; turbidity remained

below the threshold for affecting feeding and survival (5 NTU) when reservoir releases dominated streamflow.

The scenarios represent the 10-year period from October 2001 through September 2011. We used a flow of 7.0 m³/s as the threshold between conditions dominated by reservoir releases versus tributary inflow. The historic flow data indicate that controlled flows were almost always below this threshold. Our eight scenarios represented minimum flow releases of 3, 4, 5, 6, 8, 10, 12, and 15 m³/s. To create flow input for the 3-, 4-, 5-, and 6-m³/s scenarios, the flow was set to the scenario flow on any day when the observed flow was less than 7.0 m³/s; daily flows exceeding 7.0 m³/s were unchanged. For the 8-, 10-, 12-, and 15-m³/s scenarios, any daily flow less than the scenario flow was replaced with the scenario flow. These scenarios (Figure 1) are simpler than the actual release regime, which includes separate minimum flows for spring, summer, and fall to enhance salmon spawning, incubation, and rearing success.

We assumed that water temperature is highly flow dependent because air temperatures at the sites are typically much higher than observed water temperatures. In lieu of a calibrated water temperature model, we used a simple approximation of water temperatures for each flow scenario. Observed water temperatures were used for the scenario days that used observed flow. On days when a scenario's flow was less than the observed flow, we adjusted water temperature by assuming that the difference between water and air temperatures decreases as flow decreases. The daily water temperature was increased by (1) the fractional decrease in flow from the day's observed flow multiplied by (2) the difference between observed daily mean air and water temperatures. In other words, we assumed that water temperature linearly approaches the air temperature as flow approaches zero. On days when the scenario's flow was greater than the observed flow, we used a similar approach but assumed that water temperature approaches 5°C (approximately the lowest temperature in the historic record) as flow increases. On such days, we adjusted the temperature by decreasing the difference between the observed temperature and 5.0°C by the ratio of observed flow to scenario flow (i.e., to simulate a day with flow three times the historic observed flow, the daily temperature input was set to one-third of the difference between 5.0°C and the observed temperature). This approach produces strong differences among flow scenarios in summer temperature (Figure 1), which may not be completely realistic but are useful for evaluating modeled population responses.

Model versions.— We simulated trout populations under each flow scenario using three versions of inSTREAM that differ only in how they treat the circadian cycle. All three versions represent how the length of each phase of the cycle changes through the year. The standard version of inSTREAM 7 explicitly simulates the circadian cycle as four phases: dawn, day, dusk, and night. We refer to this as the four-phase version.

The second version represents the cycle as only day and night. This "two-phase" version was produced by (1) making dawn and dusk very short by defining them as the time that the sun is between −0.1° and +0.1° of the horizon (instead of the standard ±6°), and (2) assuming that trout always experience no growth or mortality risk during dawn and dusk. Hence, a trout selects its activity and habitat at the beginning of each day and night considering its current state, the options available in the upcoming phase, and its experience during the previous night or day.

The third, "one-phase," version assumes that fish behavior, growth, and survival are driven only by what the fish experience during daylight. Therefore, this version explicitly embodies the implicit assumption of instream flow methods and models that are based entirely on daytime observations: that we can safely ignore what happens during dusk, night, and dawn. Like previous daytime-only versions of inSTREAM (e.g., Railsback et al. 2005), the one-phase version assumes that trout always feed during daytime and hide during other phases. Growth is
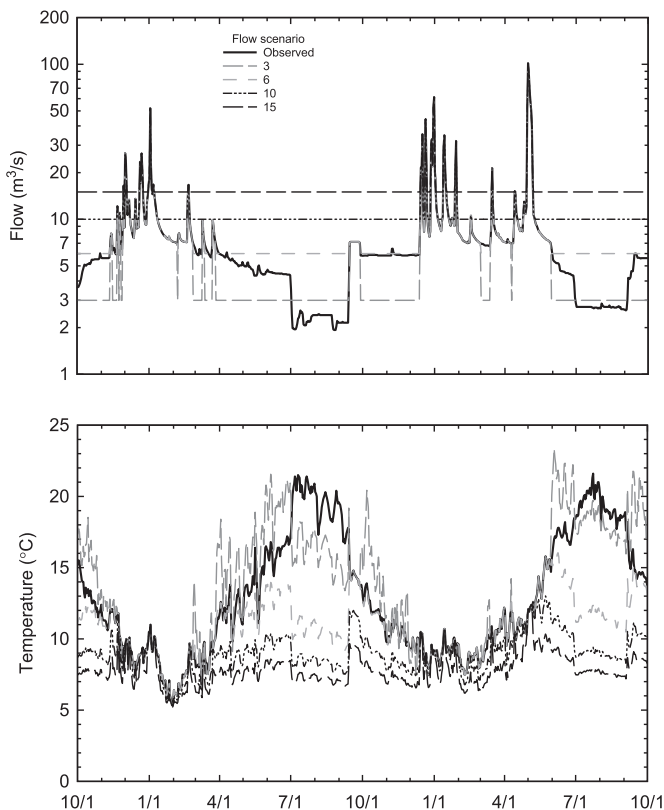

FIGURE 1. Daily flow and temperature input for four of the eight alternative instream flow scenarios (m³/s) and observed values for the first two simulated years (October 2001–September 2003).

determined by food intake and metabolic costs during the day plus resting metabolism during other phases. Trout are subject to predation and other risks only during the day phase. Trout select habitat at the start of each day phase considering only their current condition and the options available in the upcoming day.

Calibration.— Because each model version makes different assumptions about when trout can feed, the model versions were calibrated independently to make trout abundance and size reasonable under baseline conditions. We designed the calibration process to be simple and limited (1) to avoid the comparison of model versions being biased by excessive calibration; (2) because the simulated population is hypothetical, so there are no data to support detailed calibration; and (3) to make it consistent and reproducible among the three model versions.

In calibration, we adjusted three parameters that are especially uncertain and have especially strong effects. We adopted calibration targets from another site where we have collected an extensive data set: the lower main-stem site on Little Jones Creek (LJC), a tributary of the Smith River in Del Norte County, California (e.g., Harvey and Railsback 2012). The LJC site has complex, natural habitat more similar to the RESTORED site used here, so we used observations from LJC to calibrate inSTREAM 7 to the RESTORED site and then applied the calibrated parameter values to the DEGRADED site. (Calibrating the model to each site would risk the calibration masking differences between the sites.) Typical trout densities at LJC in fall censuses (~October 1) are 0.054 trout/m^2 for age 1 and 0.016 trout/m^2 for age 2 and older (age 2+). Typical mean lengths are 12 cm for age 1 and 17 cm for age 2+. Because the RESTORED site has a much lower percentage of complex habitat than the LJC site, we assumed that it could support half the LJC densities, producing calibration target abundances of 350 age-1 trout and 100 age-2 + trout.

Calibration used two simulation experiments. First, we varied food availability, executing 11 simulations in which the density of drift food and the production rate of search food were varied together, from 0.5 to 1.5 times their standard values. The two parameters controlling the intensity of predation (*terr-pred-min-survival*, the daily probability of surviving terrestrial predators for the most at-risk individuals and habitat; and *fish-pred-min-survival*, the daily probability of surviving fish predation for the most at-risk individuals and habitat) were both held constant at a typical value of 0.95. The calibrated food parameter values were those in the simulation that produced (1) mean trout lengths within 2 cm of the target values of 12 and 17 cm for ages 1 and 2+, respectively, and (2) the lowest sum of absolute differences between model results and target abundances for the two age-classes.

The second calibration experiment held food availability constant at the calibrated values while running the model for all combinations of *terr-pred-min-survival* from 0.92 to 0.97 and *fish-pred-min-survival* from 0.92 to 0.99, each varied in steps of 0.01. The calibrated values of these two parameters are those from the simulation producing the smallest total absolute difference between model results and target abundances for age 1 and age 2+ while generating lengths that were still within the target range.

Our calibration experiments started with an assumed initial population on October 1, 2001, and ended on September 30, 2006. Results from the first 2 years were ignored to reduce the influence of initial conditions. Mean results from September 30 of the last three simulated years were compared to the target values.

Contrast of model versions.— Our analysis of the importance of night and crepuscular periods to management decision making was based on a contrast among the three model versions of the predicted trout population response to the flow scenarios. For each model version, we executed five replicate simulations (differing only in the random number sequences that drive stochastic model events) of each flow scenario at both sites. The model result used for analysis was the abundance of adult trout, defined as those age 1 or older on September 30. We averaged abundance over the last 8 years of the 2001–2011 simulations, ignoring the first 2 years to avoid the effects of initial conditions.

The contrast of model versions focused not on the magnitude of simulated population responses, but instead on the qualitative patterns of predicted population response: the ranges of instream flow over which trout abundance increased, decreased, or stayed relatively constant. We assume that such qualitative patterns are likely to provide the foundation for instream flow decisions by allowing identification of flows that provide good trade-offs between fishery and other benefits. We also looked at how these patterns differed between the RESTORED and DEGRADED sites to examine how the differences between sites in channel shape and resulting depth and velocity distributions might influence the predictions of different model versions.

Understanding the importance of considering non-daylight phases requires some understanding of the differences produced by the three model versions. Explaining these differences is challenging. Results of inSTREAM are complex outcomes of how physical habitat and temperature vary among flow scenarios; how habitat and temperature affect individual trout growth, survival, and reproductive success; how model trout adapt to changes by deciding when and where to feed; and competition among trout. Instead of trying to understand all of these mechanisms, we focus here on what differed among model versions—that is, what

model trout did at different times of day. To understand these differences, we present results from the four-phase model version showing the percentage of trout feeding during the four daily phases under each flow scenario. These results were averaged over the month of September 2003 for one model run after the model had run for over a year. We chose September to represent the warmest months because earlier in summer, the feeding behavior of some adults is dominated by the need to regain weight that had been lost during spring spawning.

Parameter uncertainty analysis.— We conducted a simple parameter uncertainty analysis of the four-phase model version to investigate the extent to which its predictions are robust to differences among phases in feeding success and predation risk. We simulated the population response to the eight minimum flow scenarios at RESTORED using all nine combinations of three values of the two parameters described below. The parameter controlling the distance over which model trout can see and capture drift food at low light levels was set to 50, 100, and 150% of its standard value, which results in drift intake at night being 6, 25, and 56% of daytime and crepuscular intake. A parameter controlling the nonlinear function for how the risk of predation by terrestrial animals (the most important risk for adult trout) depends on light was set to values below, at, and above its standard value so that (1) risk at night was 10, 19, and 50% of daytime risk; and (2) risk during crepuscular periods was 39, 50, and 71% of daytime risk. We evaluated uncertainty by how it affects model results that are likely to drive management decisions: the relative rank of the eight minimum flow scenarios by predicted adult trout abundance. For each of the nine parameter value combinations, we determined the rank (1 = lowest predicted abundance; 8 = highest predicted abundance) of each flow scenario. We then examined the variation in these ranks across parameter combinations.

Crepuscular food availability experiment.— A major motivation for including the crepuscular phases in inSTREAM 7 was the potential importance of circadian cycles in trout food availability; would higher availability of drift food during dawn and dusk change relations such as those between minimum flow and trout abundance? Our last analysis examined whether our conclusions about the four-phase model version would be different if drift was higher during crepuscular phases. We repeated (one replicate each) the minimum flow scenario simulations for the RESTORED site with higher drift food availability. In the 200, 300, and 400% crepuscular food scenarios, drift concentrations during dawn and dusk were two, three, and four times higher than the daily mean concentration; night and day concentrations were reduced so that daily mean concentration remained at the calibrated value.

RESULTS

Calibration

Our calibration process produced reasonable values of calibrated parameters and relatively close correspondence between model results and the target values of trout abundance and length, considering that it calibrated only three parameters (Table 1). However, the one-phase version was less able to reproduce the target lengths and abundances. For that version, none of the food scenarios produced both age-1 and age-2+ lengths within 2 cm of the target values (age-1 fish were too small unless food availability was so high that older fish were too large), although at 0.9× standard food availability both age-classes were within 3.1 cm of the target lengths. We therefore accepted that value as the calibrated food availability. The one-phase version also fit the abundance targets less well than the other versions; it consistently produced too many age-2+ fish and not enough age-1 fish.

The differences among model versions in calibrated parameter values appeared to be small (Table 1). (However, small differences in daily survival probability produce large differences in long-term survival.) As the model is simplified by reducing the number of periods per day in which fish can decide whether and where to feed or hide, the fish's adaptive ability declines such that higher survival and food availability should be required to maintain the same population. However, for the one-phase version, that reduced adaptive ability is partly offset by the fish being exposed to predation only during the daytime.

Simulated Effects of Minimum Flow

The three model versions produced different responses to minimum flows in both abundance and trout size for both DEGRADED and RESTORED (Figure 2). We disregard the magnitude of the results because the magnitude depends in part on the calibration parameter values; instead, we focus on relative differences that could be meaningful for management decisions. We observed four noteworthy relative differences among model versions.

The first difference is clearest at the RESTORED site (Figure 2, left panels). Each model version predicted adult trout abundance to increase rapidly with minimum flow from 3 m³/s up to 6–8 m³/s. However, the four-phase and two-phase versions exhibited much sharper responses to increasing minimum flow; the one-phase version produced relatively little increase in abundance between 4 and 6 m³/s. The DEGRADED site also exhibited this difference (Figure 2, top right panel).

TABLE 1. Results of inSTREAM 7 model calibration, including values of parameters controlling the intensity of predation by terrestrial animals and piscivorous fish (daily survival probabilities for the most at-risk fish); the concentration of drift food; and the sum of the difference between target abundance and calibrated model results (abundance error) for age-1 and age-2 and older trout.

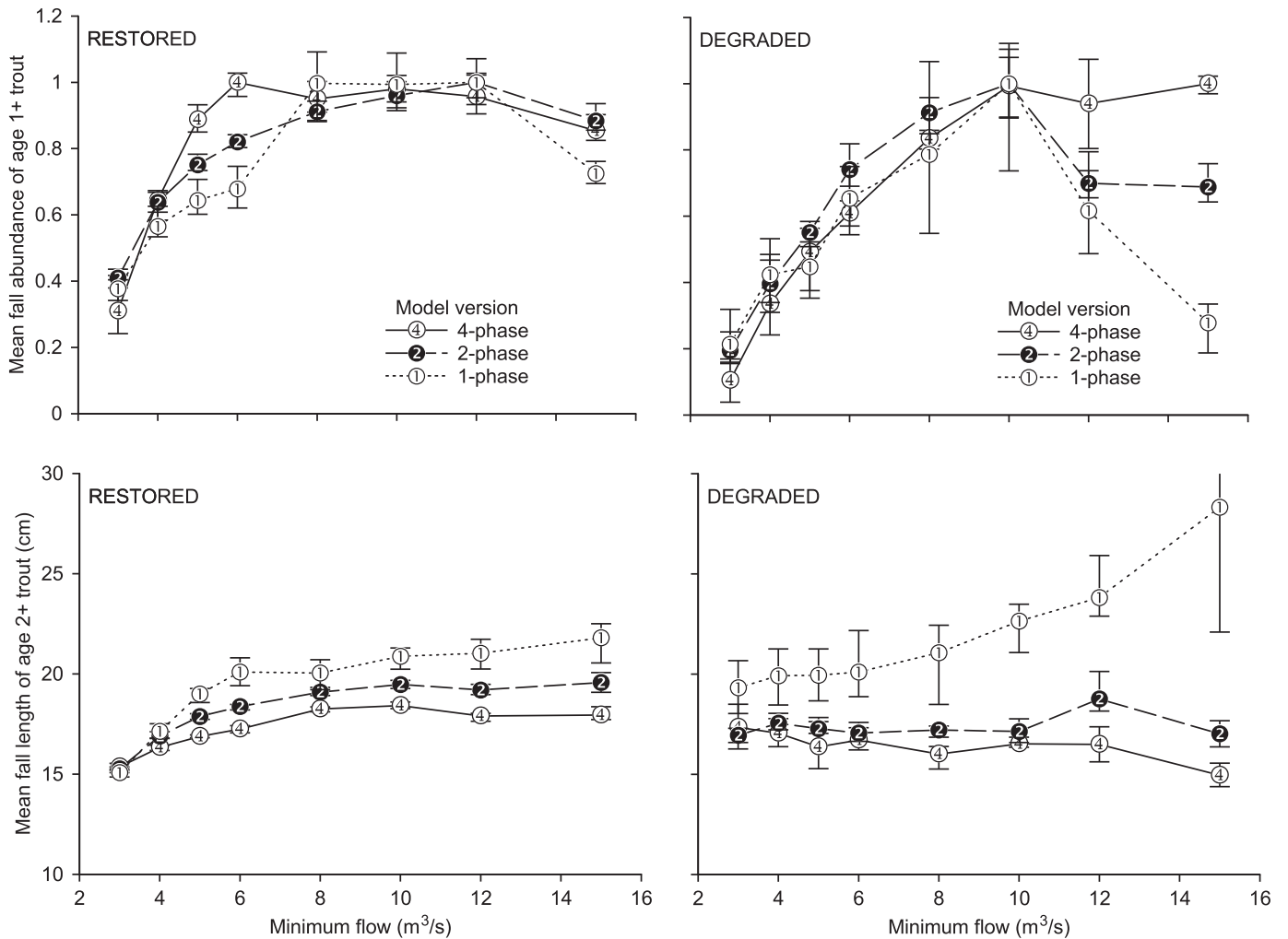| Model version	Minimum survival of terrestrial predation	Minimum survival of fish predation	Drift food concentration (g/m³)	Abundance error
Four phases	0.94	0.97	3.2×10^{-4}	57
Two phases	0.95	0.96	3.2×10^{-4}	57
One phase	0.95	0.99	3.6×10^{-4}	165

FIGURE 2. Simulated trout population responses to minimum flow scenarios for the RESTORED (left panels) and DEGRADED (right panels) sites (described in Methods). Top panels present the mean abundance of age-1 and older (age-1+) trout on September 30 of simulated years 2004–2011, with abundance expressed as a fraction of the maximum abundance across all flow scenarios. Bottom panels show the mean length of age-2+ trout on the same dates. Symbols and error bars indicate the mean, minimum, and maximum values over five replicate simulations that differed only in random number sequences.

The second difference among versions is in the higher flow scenarios at DEGRADED: the two-phase and one-phase versions predicted abundance to decrease substantially at flows from 10 to 15 m³/s, while the four-phase version predicted no such decrease.

Third is the difference in abundance response for RESTORED between the four-phase and two-phase versions (Figure 2, top left panel). The four-phase version predicted maximum abundance at minimum flows about half of those predicted by the two-phase version. This difference could lead to quite different instream flow recommendations.

The fourth difference concerns prediction about trout length. All versions predicted increases in mean adult length with flow for RESTORED, but at flows above 8 m³/s the increases were much lower for the four-phase and two-phase versions. For DEGRADED, the one-phase version predicted a consistent increase in length with minimum flow, especially at the highest flow scenarios, but the other two versions produced no clear response in length.

Analysis of when trout fed in the four-phase version is useful for explaining differences among the versions. The two sites exhibited the same trends in the timing of summer feeding by age-2+ trout (Figure 3, top panels). Most individuals fed during the day, but the percentage of individuals feeding during the day decreased gradually with increasing minimum flow. The number of individuals feeding during crepuscular phases and at night decreased sharply as flow increased from 3 to 5 m³/s. The more numerous, subdominant age-1 trout exhibited quite different feeding patterns. At the RESTORED site (Figure 3, lower left panel), there was a transition from most fish feeding during all phases at low flows to fish feeding more commonly during crepuscular periods at higher flows. At the DEGRADED site (Figure 3, lower right panel), there was much less feeding except during the day at low flows; as flow increased, daytime feeding decreased sharply as night and crepuscular feeding increased.

We also analyzed September feeding in the two-phase model, looking at how the percentage of model trout feeding during day and night varied with flow (Figure 4). Almost all age-1 and age-2+ individuals fed during daytime at all flows at both sites. At DEGRADED, there was a small decrease in daytime feeding over flow scenarios from 3 to 10 m³/s, but then daytime feeding increased again up to the 15-m³/s scenario. However, at RESTORED the percentage feeding at night dropped rapidly as minimum flow increased from 3 to 8 m³/s.

Parameter Uncertainty Analysis

Our parameter uncertainty analysis revealed robustness in the results of the four-phase model version to specific assumptions about how feeding success and predation risk differ among circadian phases (Figure 5). Even across wide ranges of parameter values, there was little variation in how the model ranked minimum flow scenarios by predicted trout abundance. The ranks varied substantially for scenarios in the 6–12-m³/s range, but this variation means little because the model predicted very little difference among those scenarios (Figure 2, top left panel).

Crepuscular Food Availability Experiment

This experiment predicted that a higher concentration of food availability during dawn and dusk in the four-phase model version would strongly reduce daytime feeding by adult trout (Figure 6, right panel), resulting in major increases in abundance across the entire range of flow scenarios (left panel). However, these effects were consistent across flow scenarios such that they did not change the qualitative relation of abundance versus minimum flow.

DISCUSSION

The question of how important it is to consider night and crepuscular periods in assessing effects of habitat change, including instream flow management, on fish populations has been raised for decades (e.g., Orth 1987; EPRI 2000; Davey et al. 2011), yet little has been done previously to address it. The difficulty of addressing this question makes the lack of progress unsurprising—it is one of the many fisheries management questions that are virtually impossible to address via field studies alone. Models that explicitly represent the population effects of how fish use habitat during all phases of the circadian cycle have not been available before. The model we applied, inSTREAM 7, can address this question because it explicitly represents the effects of light and habitat on the feeding, survival, and adaptive behavior of individual trout and the resulting population dynamics.

Previous simulation experiments have shown that inSTREAM 7 reproduces a variety of observed patterns in how the circadian feeding cycle of trout responds to factors such as flow and temperature (Railsback et al. 2020). However, those experiments also showed that predicted feeding behaviors can depend on a variety of factors and that multiple behaviors often provide almost equal benefits to trout. The empirical literature also shows that circadian feeding patterns can depend in complex and interacting ways on conditions such as food availability (Metcalfe et al. 1998, 1999; Sato and Watanabe 2014), temperature (Fraser et al. 1995), inter- and intraspecific competition (Harwood et al. 2001; Sato and Watanabe 2014), and flow (Bradford and Higgins 2001). Therefore, we should not expect the specific results reported here to be general. Instead, we focus on general lessons illustrated by our experiment that seem important for understanding how river management effects on salmonid populations can
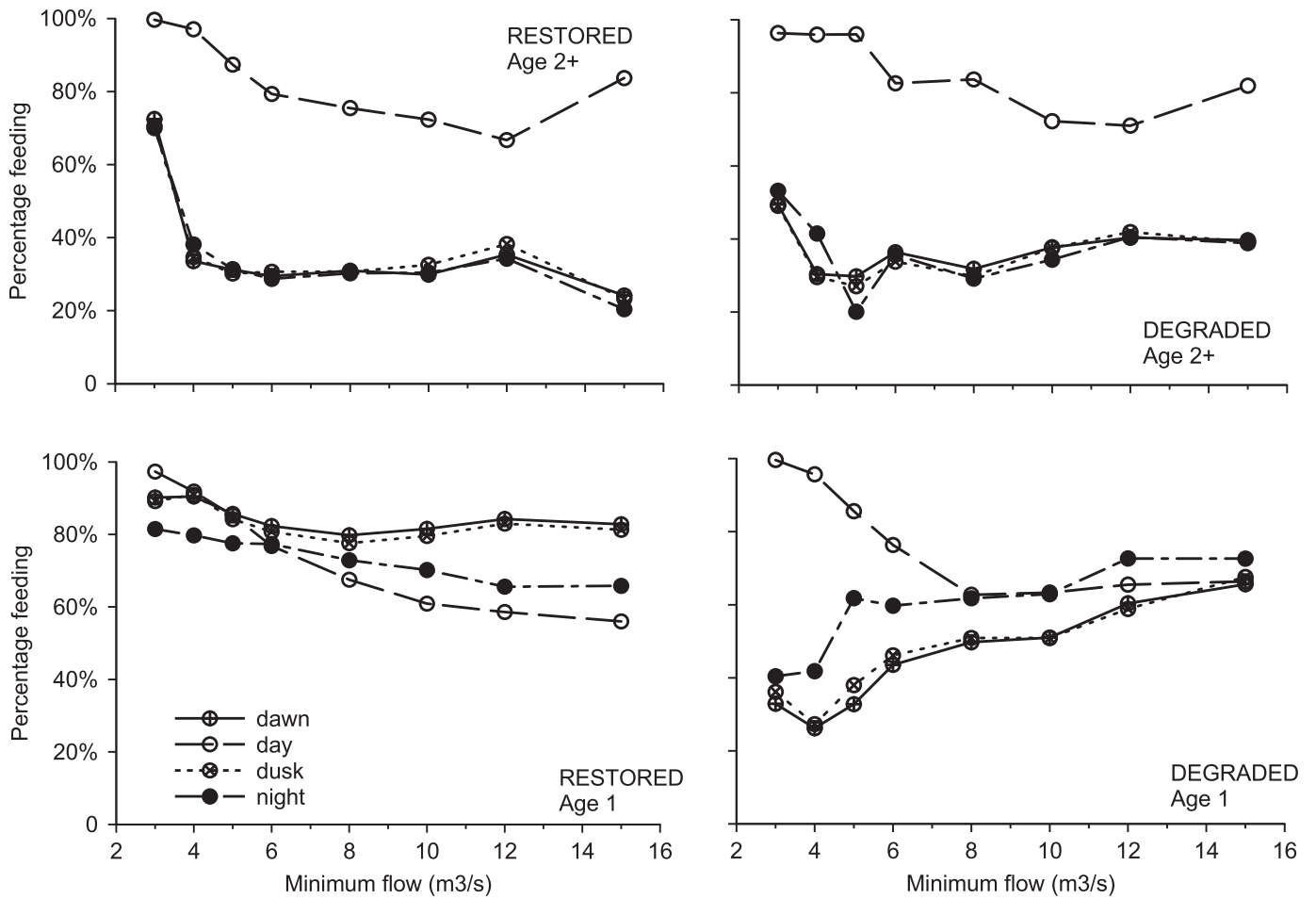
FIGURE 3. Summer feeding behavior (percentage feeding) of trout (age 1 and age 2 and older [age 2+]) in the four-phase version of the inSTREAM 7 model at RESTORED (left) and DEGRADED (right) sites (described in Methods). Values are means over all days of September 2003.
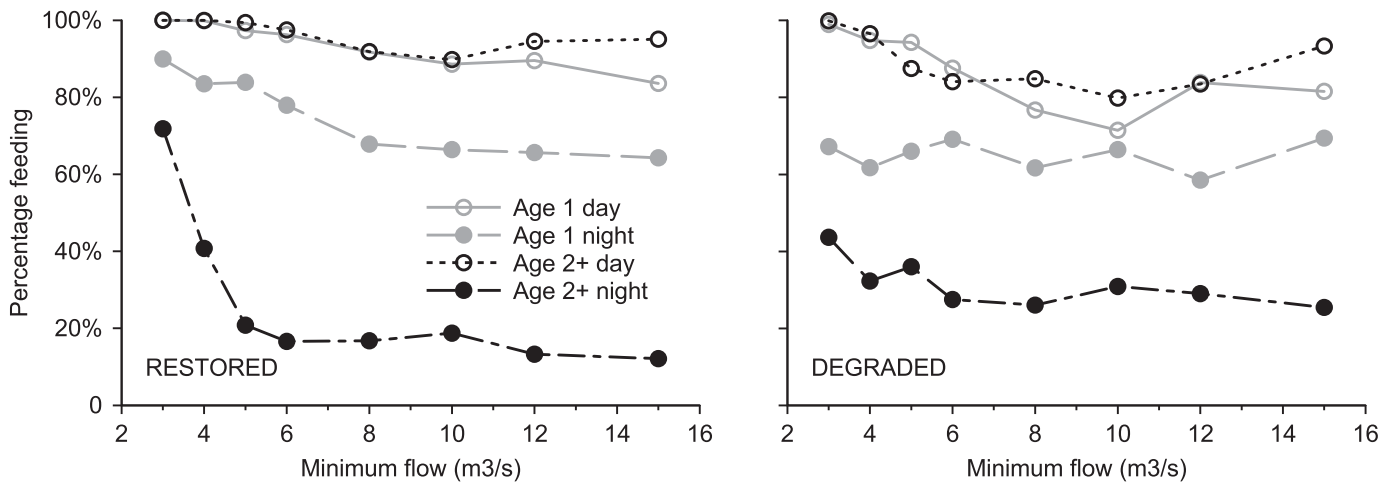

FIGURE 4. Summer feeding behavior (percentage feeding) of trout (age 1 and age 2 and older [age 2+]) in the two-phase version of the inSTREAM 7 model. The format matches that of Figure 3 except that both age-classes are shown on the same panel.
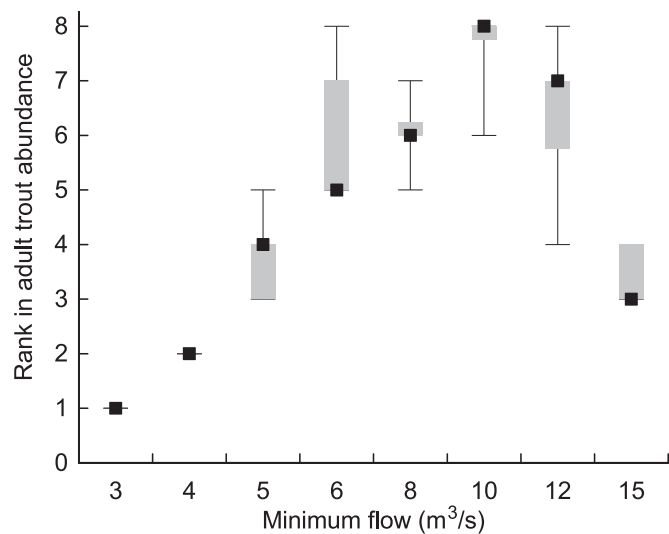
FIGURE 5. Parameter uncertainty analysis results depicting the distribution of ranks in predicted trout abundance (1 = lowest; 8 = highest) for minimum flow scenarios over the nine parameter value combinations. The black squares indicate the median rank, the whiskers indicate the minimum and maximum ranks, and the gray boxes indicate the central five ranks.

depend on the ability of fish to adaptively select when to feed as well as where to feed.

One lesson is illustrated by the first difference among model versions identified above (in Results): when we assume that trout adaptively select when to feed, the model predicts sharper population responses to habitat improvements such as (in this case) increased minimum flows and moderated temperature regimes. While the

increases in flow from 3 to 6 m³/s produced more growth in the one-phase version (Figure 2, lower panels), trout in the other versions reduced feeding (Figures 3 and 4) and therefore experienced less predation and higher abundance. This result implies that the benefits of habitat improvements can be undervalued when we consider only what happens during daytime.

A second lesson is that crepuscular periods may be especially important where shallow, high-velocity habitat is widespread, such as at the DEGRADED site during high flows (Figure 2). Shallow habitat is risky for daytime feeding, and high velocities are inefficient for feeding at night (when trout can capture drift food only over short distances, making it hard to offset the energy costs of swimming; Metcalfe et al. 1997). Under such conditions, crepuscular feeding is especially valuable; at dawn and dusk, trout can still detect food well enough to use higher velocities, providing several hours per day when feeding is more profitable than at night and safer than in daytime. This lesson seems especially important for streams degraded in ways (e.g., excess sediment) that reduce deep and slow habitat. The strong effects of crepuscular drift concentration on simulated trout abundance (Figure 6) provide further evidence of the importance of treating dawn and dusk as unique parts of the circadian cycle.

The third lesson concerns simulated growth. Our one-phase version produced consistently larger adult trout than the two-phase and four-phase versions did, especially for the DEGRADED reach at the highest flows (lower right panel, Figure 2). This difference occurred in part because the one-phase model forces simulated trout to feed in the daytime, when drift feeding intake is higher. Basing
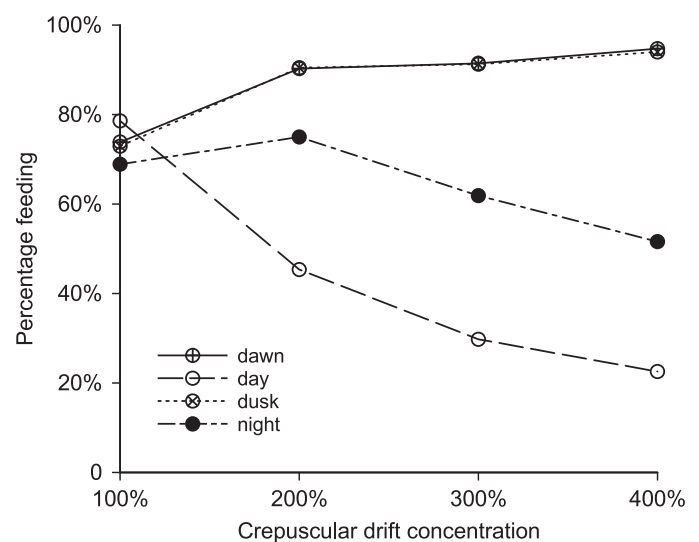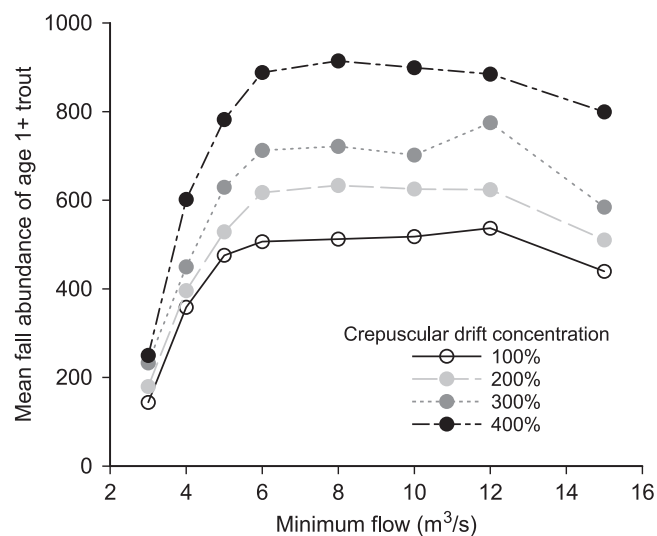

FIGURE 6. Results of four-phase inSTREAM 7 model simulations at the RESTORED site (described in Methods), with drift food concentration assumed higher during crepuscular phases. The left panel depicts the abundance of age-1 and older (age-1+) trout. The right panel shows the percentage of those trout feeding during each circadian phase in September.

growth predictions on the assumption that trout always feed during daytime is questionable because it ignores the possibility that rapid (or adequate) growth could let trout switch to feeding at less-risky times. This lesson is of management interest because bioenergetics-based models that are proposed for evaluating habitat by the growth it provides via drift feeding (e.g., Rosenfeld et al. 2016; Naman et al. 2020), although they offer a more mechanistic and rigorous alternative to observation-based habitat selection models, typically ignore the circadian cycle and assume that fish feed only during daytime.

A fourth lesson that can be inferred from our results is that habitat diversity is important. Traditional approaches to instream flow assessment (e.g., Bovee et al. 1998) focus only on habitat for daytime feeding. Acknowledging that fish use different habitat for different activities (concealment as well as feeding; Harvey and White 2016; Harwood et al. 2002) at different times of day and that patterns of habitat use can change in response to how we manage flows means that (1) there is no single "optimal" habitat type and (2) it is not easy to predict what habitat fish will use under changed conditions. Maximizing the availability of habitat that is considered "optimal" for daytime feeding could be counterproductive if it forces high-value individuals to switch to riskier daytime feeding from night or crepuscular periods. Instead, we can consider habitat used for both feeding and concealment during all phases of the circadian cycle.

Considering the ability of salmonids to adaptively select when to feed can be valuable for management measures other than instream flows. Management actions that reduce the time needed for feeding, such as by reducing temperature and, hence, metabolic rates or by providing velocity shelters for drift feeding, can reduce the need for trout to feed during the day, when predation risk is higher. On the other hand, management actions that reduce predation risk, such as restoration projects that provide deep pools or cover, can allow more trout to feed during daytime with less risk.

How can we incorporate night and crepuscular phases into instream flow assessment or restoration project design? One option is to apply, test, and improve models that explicitly incorporate these phases, such as inSTREAM 7. Fortunately, our parameter uncertainty analysis and crepuscular drift experiment indicate that such models (or perhaps even simpler ones) can usefully represent the effects of the circadian cycle without extremely precise representation of how feeding success and predation risk vary with light. Relatively tractable studies, such as those of Hansen et al. (2013) on drift feeding and Harvey and Nakamoto (2013) on predation risk, can provide sufficient understanding to make useful predictions, and circadian variation in drift need not be understood in detail.

Even without using complex models, instream flow studies and habitat evaluations can address the full light cycle in several ways. Perhaps the most basic thing we can do is to make observations at night and in crepuscular periods to determine how many fish and which sizes of fish feed at times other than daylight and what habitat they use. For example, if such observations indicate that nighttime or crepuscular feeding is dominant, then an instream flow study should focus on habitat suitable for feeding at those times (and providing concealment cover at other times). However, we must remain aware that fish feeding is adaptive and variable: the numbers and sizes of fish feeding at different times of day must be expected to vary seasonally and with conditions such as flow or temperature.

Observations during crepuscular periods and at night also seem important for monitoring the effects of flow regime changes, restoration projects, and other management actions. Our simulations predicted that increasing minimum flows would produce increasing trout abundance but a decreasing rate of daytime feeding; monitoring only during the daytime would therefore underestimate the actual population response. Management actions that improve overall growth conditions (e.g., augmenting depleting flows; Bradford and Higgins 2001) can allow for more nocturnal feeding; a daytime-only monitoring program could mistake a shift to nocturnal feeding for a decrease in abundance. To avoid such problems, monitoring programs should be designed to distinguish population responses from changes in when fish feed.

We can also consider the timing of fish feeding and its consequences for growth and predation risk in the conceptual models, study designs, and decision processes that are used to evaluate instream flows and other management actions. We suggest four examples here. First, for sites where safe feeding habitat is scarce (e.g., at our DEGRADED site, with its lack of deep pools), we can reasonably assume that night feeding is more important and therefore give more weight to habitat that provides efficient feeding at night. Second, we can also give more weight to night feeding during periods of low metabolic demands, especially cold seasons. Management actions that reduce temperature may make nocturnal feeding relatively more important. Third, daytime feeding may be especially important when metabolic demands are high, such as during warm seasons and as adults prepare for and recover from spawning. Fourth, we can quantify variation in drift food availability over the circadian cycle; habitat availability during any peaks in food availability deserves special consideration.

ACKNOWLEDGMENTS

(Project CGL2017-84269-P). There is no conflict of interest declared in this article.

REFERENCES

Bovee, K. D., B. L. Lamb, J. M. Bartholow, C. B. Stalnaker, J. Taylor, and J. Henriksen. 1998. Stream habitat analysis using the instream flow incremental methodology. U.S. Geological Survey, Biological Resources Division, Report USGS/BRD-1998-0004, Fort Collins, Colorado.

Bradford, M. J., and P. S. Higgins. 2001. Habitat-, season-, and size-specific variation in diel activity patterns of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences 58:365–374.

Davey, A. J. H., D. J. Booker, and D. J. Kelly. 2011. Diel variation in stream fish habitat suitability criteria: implications for instream flow assessment. Aquatic Conservation: Marine and Freshwater Ecosystems 21:132–145.

Edmundson, E., F. E. Everest, and D. W. Chapman. 1968. Permanence of station in juvenile Chinook Salmon and steelhead trout. Journal of the Fisheries Research Board of Canada 25:1453–1464.

EPRI (Electric Power Research Institute). 2000. Instream flow assessment methods: guidance for evaluating instream flow needs in hydropower licensing. EPRI, Technical Report 1000554, Palo Alto, California.

Fraser, N., J. Heggenes, N. B. Metcalfe, and J. E. Thorpe. 1995. Low summer temperatures cause juvenile Atlantic Salmon to become nocturnal. Canadian Journal of Zoology 73:446–451.

Gries, G., and F. Juanes. 1998. Microhabitat use by juvenile Atlantic Salmon (*Salmo salar*) sheltering during the day in summer. Canadian Journal of Zoology 76:1441–1449.

Hansen, A. G., D. A. Beauchamp, and E. R. Schoen. 2013. Visual prey detection responses of piscivorous trout and salmon: effects of light, turbidity, and prey size. Transactions of the American Fisheries Society 142:854–867.

Harris, D. D., W. A. Hubert, and T. A. Wesche. 1992. Habitat use by young-of-year Brown Trout and effects on weighted usable area. Rivers 3:99–105.

Harvey, B. C., and R. J. Nakamoto. 2013. Seasonal and among-stream variation in predator encounter rates for fish prey. Transactions of the American Fisheries Society 142:621–627.

Harvey, B. C., R. J. Nakamoto, J. L. White, and S. F. Railsback. 2014. Effects of streamflow diversion on a fish population: combining empirical data and individual-based models in a site-specific evaluation. North American Journal of Fisheries Management 34:247–257.

Harvey, B. C., and S. F. Railsback. 2012. Effects of passage barriers on demographics and stability properties of a virtual trout population. River Research and Applications 28:479–489.

Harvey, B. C., and A. J. Stewart. 1991. Fish size and habitat depth relationships in headwater streams. Oecologia 87:336–342.

Harvey, B. C., and J. L. White. 2016. Use of cover for concealment behavior by Rainbow Trout: influences of cover structure and area. North American Journal of Fisheries Management 36:1308–1314.

Harvey, B. C., and J. L. White. 2017. Axes of fear for stream fish: water depth and distance to cover. Environmental Biology of Fishes 100:565–573.

Harwood, A. J., N. B. Metcalfe, J. D. Armstrong, and S. W. Griffiths. 2001. Spatial and temporal effects of interspecific competition between Atlantic Salmon (*Salmo salar*) and Brown Trout (*Salmo trutta*) in winter. Canadian Journal of Fisheries and Aquatic Sciences 58:1133–1140.

Harwood, A. J., N. B. Metcalfe, S. W. Griffiths, and J. D. Armstrong. 2002. Intra- and inter-specific competition for winter concealment habitat in juvenile salmonids. Canadian Journal of Fisheries and Aquatic Sciences 59:1515–1523.

Heggenes, J., J. L. Baglinière, and R. A. Cunjak. 1999. Spatial niche variability for young Atlantic Salmon (*Salmo salar*) and Brown Trout (*S. trutta*) in heterogeneous streams. Ecology of Freshwater Fish 8:1–21.

Hughes, N. F. 1992. Ranking of feeding positions by drift-feeding Arctic Grayling (*Thymallus arcticus*) in dominance hierarchies. Canadian Journal of Fisheries and Aquatic Sciences 49:1994–1998.

Hughes, N. F., and L. M. Dill. 1990. Position choice by drift-feeding salmonids: model and test for Arctic Grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Canadian Journal of Fisheries and Aquatic Sciences 47:2039–2048.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto.

Kreivi, P., T. Muotka, A. Huusko, A. Mäki-Petäys, A. Huhta, and K. Meissner. 1999. Diel feeding periodicity, daily ration and prey selectivity in juvenile Brown Trout in a subarctic river. Journal of Fish Biology 55:553–571.

Larranaga, N., and S. Ó. Steingrímsson. 2015. Shelter availability alters diel activity and space use in a stream fish. Behavioural Ecology 26:578–586.

Metcalfe, N. B., N. H. C. Fraser, and M. D. Burns. 1998. State–dependent shifts between nocturnal and diurnal activity in salmon. Proceedings of the Royal Society of London Series B: Biological Sciences 265:1503–1507.

Metcalfe, N. B., N. H. C. Fraser, and M. D. Burns. 1999. Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. Journal of Animal Ecology 68:371–381.

Metcalfe, N. B., S. K. Valdimarsson, and N. H. C. Fraser. 1997. Habitat profitability and choice in a sit-and-wait predator: juvenile salmon prefer slower currents on darker nights. Journal of Animal Ecology 66:866–875.

Nakano, S., K. D. Fausch, and S. Kitano. 1999. Flexible niche partitioning via a foraging mode shift: a proposed mechanism for coexistence in stream-dwelling charrs. Journal of Animal Ecology 68:1079–1092.

Naman, S. M., J. S. Rosenfeld, J. R. Neuswanger, E. C. Enders, J. W. Hayse, E. O. Goodwin, I. G. Jowett, and B. C. Eaton. 2020. Bioenergetic habitat suitability curves for instream flow modeling: introducing user-friendly software and its potential applications. Fisheries 45:605–613.

Nestler, J. M., R. T. Milhous, T. R. Payne, and D. L. Smith. 2019. History and review of the habitat suitability criteria curve in applied aquatic ecology. River Research and Applications 35:1155–1180.

Orth, D. J. 1987. Ecological considerations in the development and application of instream flow-habitat models. Regulated Rivers: Research and Management 1:171–181.

Piccolo, J. J., B. M. Frank, and J. W. Hayes. 2014. Food and space revisited: the role of drift-feeding theory in predicting the distribution, growth, and abundance of stream salmonids. Environmental Biology of Fishes 97:475–488.

Railsback, S. F., M. Gard, B. C. Harvey, J. L. White, and J. K. H. Zimmerman. 2013. Contrast of degraded and restored stream habitat using an individual-based salmon model. North American Journal of Fisheries Management 33:384–399.

Railsback, S. F., and B. C. Harvey. 2001. Individual-based model formulation for Cutthroat Trout, Little Jones Creek, California. U.S. Forest Service General Technical Report PSW-GTR-182.

Railsback, S. F., and B. C. Harvey. 2002. Analysis of habitat selection rules using an individual-based model. Ecology 83:1817–1830.

Railsback, S. F., B. C. Harvey, and D. Ayllón. 2020. Contingent tradeoff decisions with feedbacks in cyclical environments: testing alternative theories. Behavioral Ecology 31:1192–1206.

Railsback, S. F., B. C. Harvey, J. W. Hayse, and K. E. LaGory. 2005. Tests of theory for diel variation in salmonid feeding activity and habitat use. Ecology 86:947–959.

Railsback, S. F., B. C. Harvey, S. K. Jackson, and R. H. Lamberson. 2009. InSTREAM: the individual-based stream trout research and environmental assessment model. U.S. Forest Service General Technical Report PSW-GTR-218.

Rosenfeld, J., H. Beecher, and R. Ptolemy. 2016. Developing bioenergetic-based habitat suitability curves for instream flow models. North American Journal of Fisheries Management 36:1205–1219.

Roy, M. L., A. G. Roy, J. W. A. Grant, and N. E. Bergeron. 2013. Individual variability of wild juvenile Atlantic Salmon activity patterns: effect of flow stage, temperature, and habitat use. Canadian Journal of Fisheries and Aquatic Sciences 70:1082–1091.

Sato, T., and K. Watanabe. 2014. Do stage-specific functional responses of consumers dampen the effects of subsidies on trophic cascades in streams? Journal of Animal Ecology 83:907–915.

Wilensky, U. 1999. NetLogo. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, Illinois. Available: http://ccl.northwestern.edu/netlogo/. (May 2020).

SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.