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ARTICLE

Effects of Streamflow Diversion on a Fish Population: Combining Empirical Data and Individual-Based Models in a Site-Specific Evaluation

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Abstract

Resource managers commonly face the need to evaluate the ecological consequences of specific water diversions of small streams. We addressed this need by conducting 4 years of biophysical monitoring of stream reaches above and below a diversion and applying two individual-based models of salmonid fish that simulated different levels of behavioral complexity. The diversion of interest captured about 24% of streamflow between June and October but had little or no effect over the remainder of the year. The change in biomass of Rainbow Trout *Oncorhynchus mykiss* and steelhead (anadromous Rainbow Trout) over the dry season (June–October) favored the upstream control over the downstream diversion reach over 4 years (2008–2011). Dry-season growth did not differ consistently between the two reaches but did exhibit substantial annual variation. Longer-term observations revealed that in both reaches most fish growth occurred outside the period of dry-season diversion. After calibration to the upstream control reach, both individual-based models predicted the observed difference in fish biomass between control and diversion reaches at the ends of the dry seasons. Both models suggested the difference was attributable in part to differences in habitat structure unrelated to streamflow that favored the upstream reach. The two models both also reproduced the large seasonal differences in growth, small differences between reaches in individual growth, and natural distributions of growth among individuals. Both the empirical data and simulation modeling suggested that the current level of diversion does not threaten the persistence of the salmonid population. In multiyear simulations using the two models, the model incorporating greater flexibility in fish behavior exhibited weaker population-level responses to more extreme reductions in dry-season streamflow. We believe the application of individual-based models in this case has placed resource managers in a relatively strong position to forecast the consequences of future environmental alterations at the study site.

Resource managers commonly face the need to evaluate the effects of site-specific, ongoing physical alterations of ecosystems. This can be challenging for several reasons, including (1) "after-the-fact" evaluation precludes use of accepted experimental designs such as before–after, control–impact designs, or intervention analysis (Stewart-Oaten and Bence 2001); (2) in many cases, the environmental alteration of interest may be small but the spatio-temporal scales of interest larger than those of relevant experiments; (3) physical alterations commonly affect ecosystems through a variety of processes; and (4) site-specific management questions often incorporate the contemporary or future influences of pervasive

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issues such as climate change and invasive species, creating the need to make predictions about interactions among factors and novel future conditions.

The challenge outlined above is exemplified by the desire to evaluate the ecological effects of historic diversions of small streams: (1) many diversions have been in place for decades or centuries; (2) some divert a small fraction of streamflow on a seasonal basis, while most studies of the ecological effects of diversions involve more substantial reductions in streamflow (Poff and Zimmerman 2010); (3) streamflow alterations can have multiple physical consequences—including effects on depth, water velocity, stream temperature, and sediment deposition—which, in turn, affect multiple ecological responses; and (4) the consequences of streamflow diversions may be compounded by climate changes that also affect streamflows and temperatures. Physical factors such as streamflow and water temperature can affect the probability of success for invasive fishes and other alien species which can, in turn, affect physical regimes and native taxa.

Evaluations of the effects of stream diversions commonly focus on salmonid fishes within their geographical range because many salmonids are of special concern for conservation or commercial reasons. Stenothermic, drift-feeding fishes such as salmonids seem likely to be both directly and indirectly affected by streamflow. For example, streamflow influences foraging efficiency (Nislow et al. 2004; Kemp et al. 2006) and possibly predation risk through effects on depth (Harvey and Stewart 1991) and water velocity. Any effects of streamflow on the productivity of invertebrate prey and their availability are likely to have significant consequences for salmonid populations. Relatively large reductions in streamflow generally have been found to reduce the abundance of aquatic invertebrates (Poff and Zimmerman 2010), with some inconsistency in results. A variety of studies have documented significant effects of streamflow variation on salmonids (e.g., Nislow et al. 2004; Harvey et al. 2006; Davidson et al. 2010; Teichert et al. 2010), but the current state of knowledge leaves open the question of the ecological significance of modest changes in streamflows (Poff and Zimmerman 2010).

Where focus on a particular taxon is appropriate, spatially explicit, individual-based population models (IBMs) can be used to evaluate site-specific alterations of ecosystems such as stream diversions. Because these models represent particular sites, it may be possible to make comparisons between sites of interest and control sites that take into account "nuisance" differences between them, thereby allowing the effects of specific physical alterations to be estimated. The underlying assumption of IBMs is that population-level outcomes emerge from interactions between individuals and their environment. This assumption sets the stage for mechanistic model formulations focused on key behaviors and processes which, in turn, enhance the potential for the models to capture the effects of interactions among factors and predict outcomes under novel conditions. One obvious challenge in the formulation of these models is determining an appropriate level of model complexity, specifically which behaviors and processes should be included to maximize the model's ability to address management questions and produce predictions that can be tested against observations. Grimm et al. (2005) suggested that the payoff of IBMs will commonly be maximized at intermediate levels of complexity, but to our knowledge this issue has not been extensively addressed.

In this study, we made empirical observations of fish density and growth over 4 years to directly address the effects of a small-scale, historic diversion of a small stream in northwestern California. We then used these data to explore the ability of two spatially explicit, individual-based salmonid population models of different complexity to predict fish density and growth below the diversion. Finally, we used the models to estimate the population-level consequences of seasonal streamflow diversion greater than we observed.

METHODS

Study site.—West Weaver Creek is a second-order tributary of the Trinity River in the southern portion of the Klamath Mountain Province in northwestern California. At the study site (40°44′45.55″ N, 122°58′13.35″ W–NAD83, UTM), West Weaver Creek drains approximately 14 km^2 on the southern edge of the Trinity Alps Wilderness. The maximum elevation in the watershed exceeds 2,200 m, while the study site lies between 730 and 760 m. Climate in the region is marked by cool wet seasons (commonly November to May) and hot dry seasons (June to October). The study site is in an open, mixed-conifer and hardwood forest, with an overstory of ponderosa pine *Pinus ponderosa*, Douglas fir *Pseudotsuga menziesii*, and occasional western hemlock *Tsuga heterophylla* and an understory of bigleaf maple *Acer macrophyllum* with scattered white alder *Alnus rhombifolia* and redosier dogwood *Cornus sericea*. The study site was hydraulically mined in the late 1800s and early 1900s; mining-caused scarps and mounds of cobbles and boulders remain apparent. Mean daily water temperatures in West Weaver Creek ranged from 0.2°C to 14.5°C (mean = 6.6°C) from October 16 to June 14, and from 6.8°C to 17.5°C (mean = 13.0°C) from June 15 to October 15. Daily turbidities ranged from 0 to 179 NTU (mean = 2.5 NTU) from October 16 to June 14, and from 0 to 14 NTU (mean = 1.4 NTU) from June 15 to October 15.

We focused on two study reaches, approximately 300 m each, upstream and downstream of a diversion that has provided water for domestic and irrigation use for 150 years. Dry-season wetted width averages about 4 m in both reaches. For the simulation modeling, we focused on subsections of the two 300-m reaches: a 110-m subsection below the diversion and a 106-m section upstream of the diversion. Gradient is 3.4% over the downstream subsection and 3.7% over the upstream subsection. The subsections contained a similar number of pools, but two pools in the upstream section were noteworthy for having both substantial cover for fish and maximum depths exceeding 60 cm.

The diversion does not currently involve any permanent structures in the stream channel; it instead relies on temporary boulder dams partially covered in plastic fabric. It is not a complete barrier to upstream or downstream movement by fish. The diversion takes an average of 24% of the dry-season streamflow. The study reaches are accessible to anadromous fish. A population of *Oncorhynchus mykiss* appears to include both resident and anadromous individuals (hereafter Rainbow Trout and steelhead, respectively). Other aquatic vertebrates were less abundant than steelhead and Rainbow Trout in the study area; these included Brown Trout *Salmo trutta* (one individual captured during the entire study), lamprey *Lampetra* spp. ammocoetes, larval coastal giant salamanders *Dicamptodon tenebrosus*, and coastal tailed frogs *Ascaphus truei*.

Fish sampling.—To estimate fish biomass, density, and growth in the two study reaches, we sampled fish twice each year from 2008 to 2011, at approximately the beginning and end of the dry season. Within-year periods between sampling efforts ranged from 92 to 133 d. We timed sampling to approximately correspond with the operation of the diversion but also sought to avoid low sampling efficiency during high streamflows. Fish were captured by electrofishing. We inserted PIT tags into the body cavities of individuals >70-mm FL on all sampling occasions to quantify individual growth rates. Sampling consisted of three-pass depletion sampling in subsections of both reaches that we simulated in the models and single-pass collections over the remainder of each reach. The main goal of the single-pass efforts was to increase sample sizes for the estimation of individual growth rates. We used the three-pass depletion data to generate maximum likelihood population estimates (Van Deventer and Platts 1989) for the subsections included in the simulation models. Biomass estimates for the subsections incorporated the measured mass of all captured fish and an estimate of the mass of uncaptured fish. While we collected age-0 steelhead and Rainbow Trout in spring–early summer of all 4 years, their small size (mean FL = 35 mm) at that time precluded effective sampling.

Physical data.—To characterize the physical environment, we measured water temperature, turbidity, and streamflow in the two study reaches. In both reaches, we collected water temperature data, at 60-min intervals, using Onset HOBO pendant data loggers (Onset Computer, Bourne, Massachusetts) and water level data, at 30-min intervals, using Onset HOBO Model U20 data loggers beginning in October 2007. Water level data were corrected for fluctuations in barometric pressure using a data logger mounted on the bank in the upper reach. To estimate streamflow in each reach, we employed a set of relationships between water level readings and concurrent measurements of discharge. To improve the accuracy of our reach-specific streamflow estimates, we developed separate relationships for low-flow and high-flow periods. In all cases, R^2 exceeded 0.98 for the stage versus streamflow relationships. We also monitored turbidity beginning in October 2007 with a Forest Technology Systems DTS-12 turbidity sensor (Forest Technology Systems, Victoria, British Columbia) installed in the upstream reach. The turbidity sensor was placed in an aluminum housing anchored to a large boulder in the channel. Flotation at the downstream end of the housing and a hinge at the anchor point allowed the turbidity probe to self-adjust in both the horizontal and vertical planes in response to streamflow. A Campbell Scientific CR10X data logger (Campbell Scientific, Logan, Utah) recorded turbidity at 60-min intervals. From July 2, 2008, to October 9, 2008, and June 16, 2009, to October 20, 2009, we also operated the same type of turbidity sensor in the downstream reach. Data records for temperature, streamflow, and turbidity were summarized as daily means for use in the IBMs.

Individual-based modeling.—We applied two IBMs developed for stream salmonids that have been described in detail elsewhere (Railsback et al. 2005; Railsback et al. 2009). The daily model has reproduced a variety of patterns exhibited by individual trout (Railsback and Harvey 2002; Harvey and Railsback 2009) and trout populations (Railsback et al. 2002). The more complex subdaily model (Railsback et al. 2005) includes simulation of both day and night, and explicitly includes the trout behavior variously described as hiding, refuge use, or concealment (e.g., Hartman 1963). We briefly describe the models here, emphasizing their properties directly related to the influence of streamflow on fish and the differences between them. The resources (e.g., fieldwork, computer time) required to apply these models are comparable to those required for an instream flow study that includes collection of site-specific biological data. While the two models we used differ in complexity, implementation of the more complex model requires only that one additional habitat characteristic be recorded during fieldwork.

The trout IBMs retain many spatial and temporal complexities of real rivers. In both models, stream reaches are represented as sets of two-dimensional cells. These cells have unique dimensions and values for parameters representing the availability of cover that influences short-term avoidance of predators, velocity shelter that influences the benefits of feeding on drifting prey, and spawning gravel. The subdaily model also uses habitat cell-specific information on the availability of cover that allows complete concealment of fish. Site-specific hydraulic models are used to estimate cell-specific depths and water velocities from streamflow. At West Weaver Creek, the 110-m reach modeled below the diversion included 139 cells arranged along 20 transects perpendicular to the streamflow, while the 106-m upstream control reach included 127 cells along 18 transects. Reach-scale variables in addition to streamflow include water temperature and turbidity. In the simulations presented here, fish do not have the option of moving among reaches and more generally cannot emigrate from reaches they occupy. While these assumptions do not strictly apply in the field, 94% of recaptured fish were caught in the reaches where they were tagged. We therefore concluded these assumptions do not prevent useful characterization of the reaches' capacities to support fish survival and growth.

Trout growth is the difference between energy intake and metabolic costs. Trout may acquire food by drift feeding or

search feeding. For drift feeding, intake varies nonlinearly with water velocity: increasing velocity carries more food but makes the food harder to capture. Metabolic costs increase with trout size, swimming speed, and temperature. Consequently, for drift feeding fish growth peaks at an optimal velocity that delivers sufficient food while not requiring excessive energy for swimming; this optimal velocity increases with trout size. The availability of drifting prey is represented as a concentration (mass of food/volume of water). The assumption of a constant drift food concentration means that availability varies with streamflow and among habitat cells, increasing with cell cross-sectional area and water velocity. The efficiency of search feeding is assumed to be independent of streamflow, while the cost, like the cost for drift feeding, depends on water velocity. The availability of food acquired by search feeding is represented as mass of food per area per time. In general, for both daily and subdaily models, over broad ranges of food availability for the two types of feeding, drift feeding is more profitable for adult trout than search feeding. Competition can limit food intake: model trout follow a size-based feeding hierarchy such that in a given cell, a trout has access only to food not consumed by larger trout. In the subdaily model, trout that choose to hide rather than feed experience slightly negative growth, as food intake and swimming costs are both zero but resting metabolism produces an energy loss. Also in the subdaily model, trout that choose to feed at night have reduced intake because food is harder to detect and capture.

The models assume predation risks vary among cells because of the effects of increasing depth and water velocity, which presumably make trout harder to detect and capture, and the value of cover in reducing predation risk. The approach to quantifying predation risk includes a parameter that characterizes the maximal predation risk for fish at the reach scale; this parameter is commonly varied in model calibration. Maximal predation risk is reduced for individuals to varying extents depending on their size and features (depth, water velocity, cover) of the habitat cells they occupy. The subdaily model includes the assumption that risk is 70% lower at night when visibility is lower and some potential predators less active. Also in the subdaily model, trout that choose to hide rather than feed are assumed to be almost immune to predators. In both models, trout are assumed to have accurate knowledge of predation risks and how they vary with habitat. The survival of individuals in each time step is determined by comparison of a random number between 0 and 1 with the survival probabilities for each of several sources of mortality, including predation risk and starvation.

In both models, females must meet size and condition thresholds to spawn. Spawning is restricted to appropriate dates and physical conditions (streamflow and temperature). Whether a female spawns on a particular day with appropriate conditions is determined stochastically using a spawning probability. This probability is set to yield a realistic temporal pattern of spawning. The timing of spawning is important because both models simulate the mortality of eggs and embryos as a result of streamflow and temperature fluctuations.

At each time step, the models conduct the following actions: (1) habitat is updated with the current cell depths and velocities, temperature, and turbidity; (2) female fish able and allowed to spawn select a spawning cell, create a redd, and incur spawning weight loss; (3) in order from largest to smallest each trout selects its current activity and habitat cell using methods described below, and the trout's consumption of food or hiding cover is subtracted from that available to smaller trout in its cell; (4) all trout grow, or lose weight, according to their resource consumption and energy costs; and (5) survival probabilities for each fish are determined from its current state and features of the habitat cell it occupies, and survival is determined.

Behavior.—In the daily model, fish select habitat once per day and are assumed to feed during daylight hours. In the subdaily model, fish select habitat and make the decision to feed or hide each day and night. (In all habitat selection decisions in both models, trout evaluate both the drift and search feeding options.) Trout consider four activity alternatives in the subdaily model: feeding during day and night, feeding during day and hiding at night, feeding at night and hiding during day, and hiding both day and night. Each of these activity alternatives is considered for each available habitat cell by evaluating a fitness measure for that combination of cell and activity. Both models assume the radius over which fish are familiar with habitat, and therefore the number of habitat cells they evaluate in each time step, increases with fish size. The fitness benefits of behavioral alternatives are represented as the expected probability of surviving both predation and starvation over a sliding time horizon—the next 90 d—multiplied by a term that estimates the size-specific benefit of growth for fitness. Basing the fitness measure on survival of both predation and starvation causes individuals to balance growth and risk: they feed enough to keep starvation from being a greater risk than predation. The growth term represents the fitness benefits of reaching reproductive size and of continued growth for adults (e.g., higher fecundity and ability to compete for feeding and spawning habitat; growth is given decreasing weight as a fish approaches the size of its largest competitor). To evaluate the fitness measure for a behavior alternative, model trout must predict the growth and survival probability they would experience over the 90-d time horizon. They do so by simply assuming that habitat and competitive conditions occurring at the current time step—and thus the predation risk and growth rate they would experience under the behavior alternative—will persist unchanged over the time horizon. Therefore, survival of predation over the time horizon is S^{90}, where S is the probability of surviving predation for the current day, under the behavior being considered. Starvation survival and growth over the time horizon depend on the individual's current length, weight, and net energy intake rate; starvation is more likely if the individual is currently underweight or if its net energy intake is negative.

Analytical approach.—We used data from the upstream reach to calibrate the models, then applied calibrated values for three key parameters in simulations of the downstream reach. We first attempted to separately calibrate both models to the 4 years of

within-year, dry-season empirical results (total biomass [g/m], numbers, mean growth) for the upstream control reach. Because the two food availability parameters and the maximum predation risk parameter are difficult to measure empirically yet very important to population dynamics, they were the variables used in calibration. The calibration process contrasted scenarios with values for these three parameters cross-classified because the influence of the three parameters on survival and growth are not independent. Because calibration to within-dry-season observations for the upstream reach produced a relatively broad range of combinations of parameter values yielding similar results, we added to the calibration process year-round simulations of the upstream reach and focused on the mean size of fish of different ages at the end of the dry seasons. We then simulated the downstream reach with both models, assuming upstream calibration values for predation risk and food availability, under both the measured streamflow regime downstream and the flow regime upstream. The last scenario, downstream-reach habitat with upstream-control streamflows, was designed to distinguish the effects of streamflow from those of reach-specific habitat structure. For all within-year simulations, populations were initialized to the abundance and size distributions in each reach from our first fish sampling in each year.

While the study area is influenced to an unknown extent by the reproductive contributions of anadromous individuals, the second element of our approach was to complete year-round simulations that assumed purely resident populations. To include several generations of fish in this exercise, we conducted 8-year simulations by repeating the available 4-year records for physical data; simulations began with the initial populations sampled in the first year of the study. The goals of these simulations were to (1) test the models' ability to reproduce seasonal patterns in individual growth, and (2) explore multiyear, population-level consequences of seasonal flow diversions. For both within-year and multiyear simulations, we summarized 50 replicate simulations of all scenarios. Replicates vary because of stochasticity in the determination of the initial sizes of individuals, the survival of individuals at each time step, and, for the multiyear simulations, the occurrence and timing of spawning.

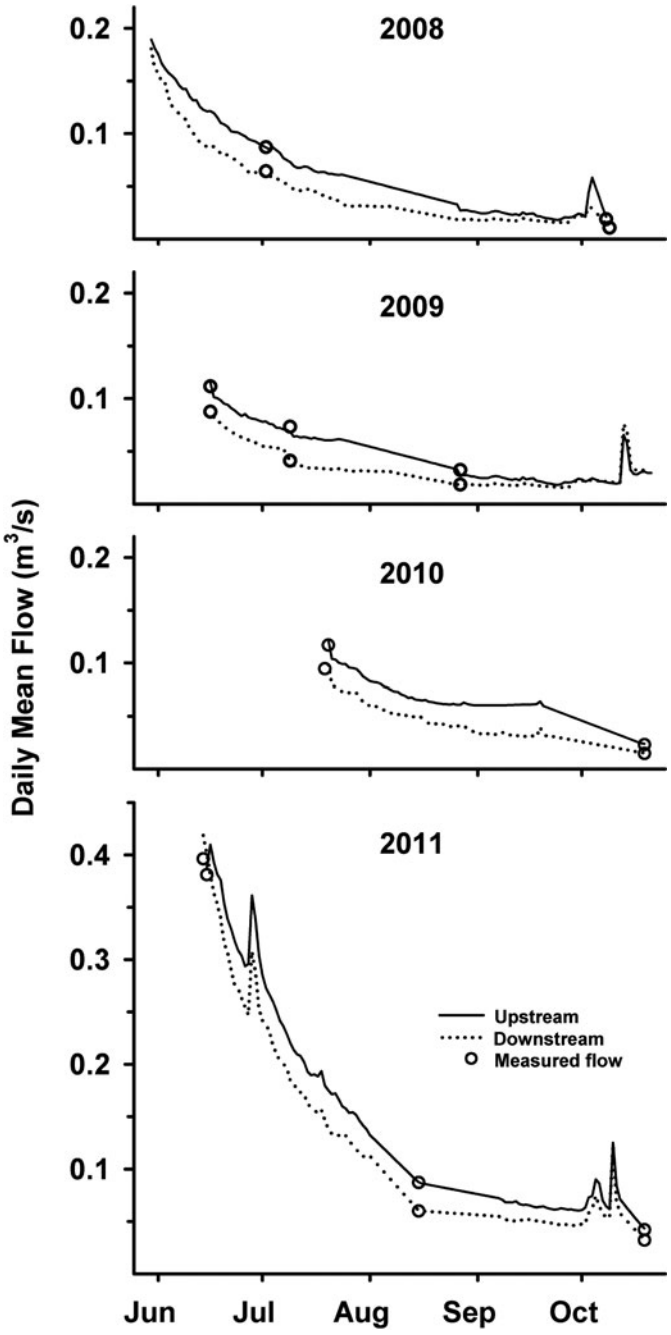

FIGURE 1. Streamflow records (as inferred from stage–discharge relationships) for two study reaches above and below a water diversion on West Weaver Creek in northwestern California, during four successive dry seasons. Curves span the periods between spring–early summer and fall fish sampling efforts in each year.

RESULTS

Field Observations

The diversion on West Weaver Creek yielded modest but consistent differences in streamflow between the two study reaches during the dry season (Figure 1). Predictably, wet-season streamflows were higher in the reach below the diversion point when the diversion was either not functional or insignificant (Figure 2). During the dry-season study periods, differences in water temperature between the upstream and downstream reaches averaged 0.2°C and never exceeded 1.1°C. Similarly, over two dry seasons, the two reaches exhibited negligible differences in turbidity (mean difference = 0.1 NTU [within the precision of the instruments]; maximum difference = 1.7 NTU).

Number and biomass of steelhead and Rainbow Trout were similar in the upstream control and downstream reduced-flow study reaches in the first samplings of the year, although the downstream reach held more fish per meter in June 2009 and

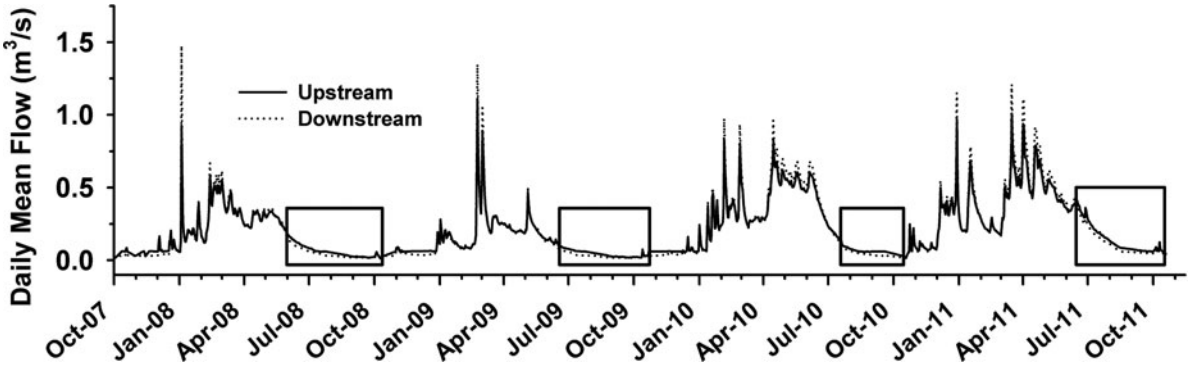

FIGURE 2. Continuous streamflow records for two study reaches above and below a water diversion on West Weaver Creek in northwestern California. Rectangles contain dry-season periods between spring–early summer and fall fish sampling events illustrated in Figure 1.

the upstream control more fish than the downstream reach in June 2010. At the end of the dry season, the upstream control supported a higher number and biomass of fish age 1 and older in all 4 years, while the two reaches supported similar densities of age-0 fish (Figure 3). The change in biomass over the dry season that most favored the upstream reach, 2009, was unexplained by any of our field observations. Mean growth rates during the dry season varied strongly among years, but less so and inconsistently between reaches (Figure 4). In all 4 years, individuals within reaches exhibited substantial variation in growth (Figure 5, top row). For both reaches, growth of tagged fish captured in the spring–early summer revealed that growth rates from fall to spring far exceeded growth rates during the dry season (Figure 6, top panel).

Model Results

Calibrations of the daily and subdaily models to empirical observations for the upstream reach appeared similarly successful (Figure 7). The calibration process produced comparable values for predation risk for the two models: a higher minimum probability of survival of predation risk in the subdaily model offset the fact that fish must face predation mortality risk twice each day in that model. However, calibration yielded a greater relative availability of search food versus drift food in the subdaily model. While the calibration value for search food availability was the same for the two models, fish in the subdaily model have the option of feeding during both day and night, while fish in the daily model are restricted to feeding during daylight hours. The drift food concentration value for the daily model was approximately twice that of the subdaily model. This difference is reasonable given the differences in feeding opportunities for fish in the two models. As a calibration parameter, drift concentration is designed to capture the effects of a variety of processes not in the models.

Using upstream calibration values for food availability and predation risk, both models applied to the downstream diversion reach yielded patterns that generally corresponded with fish biomass at the end of the dry season for the downstream reach (Figure 7) and observed differences in fish biomass between the

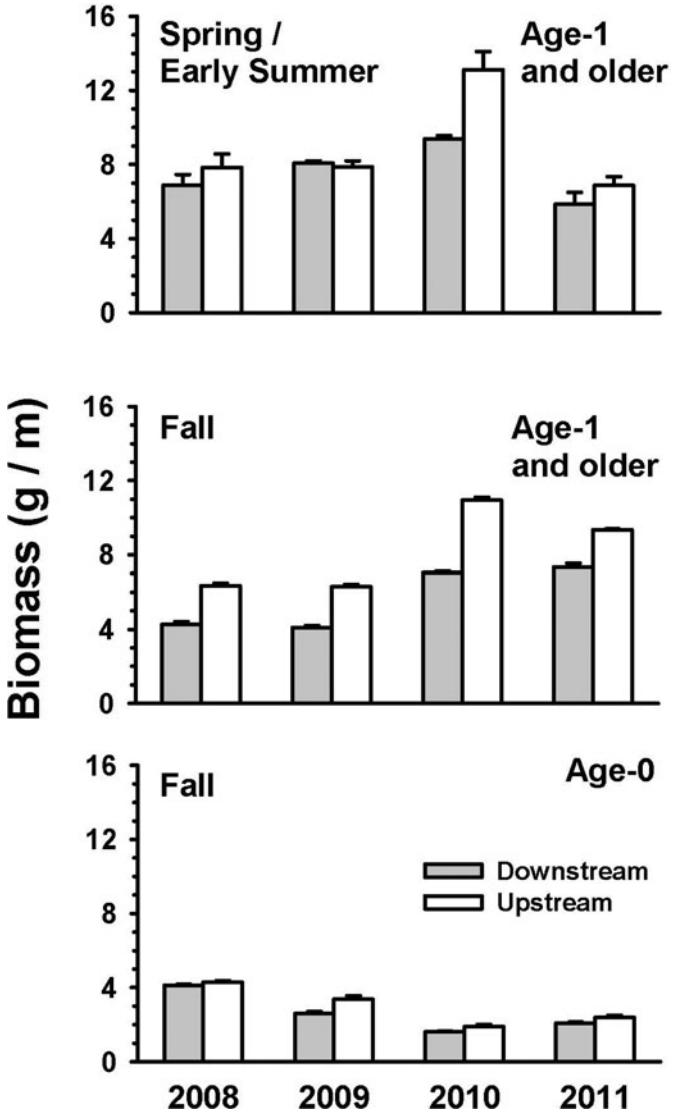

FIGURE 3. Biomass of steelhead and Rainbow Trout at the beginning and end of the dry season over 4 years in two reaches of West Weaver Creek, California, upstream and downstream of a water diversion. Error bars indicate SE derived from depletion estimates.

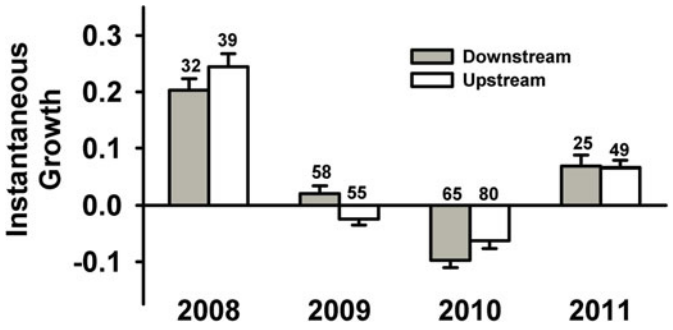

FIGURE 4. Steelhead and Rainbow Trout growth during four dry seasons in two reaches of West Weaver Creek, California, upstream and downstream of a water diversion. Numbers above bars indicate sample sizes; error bars indicate SE.

control and diversion reaches (Figure 8). However, both models underestimated the difference between reaches in 2009, and the direction of their variation from observed values differed for the last 2 years. Simulation of the downstream reach using the undiverted flow regime of the upstream reach suggested a substantial effect of differences between reaches in physical habitat (i.e., nonflow-related characteristics) on the differences in fish biomass at the end of the dry season for 3 of the 4 years (2008, 2010, and 2011). That is, the model simulations predicted differences in end-of-dry-season biomass between reaches even when their flow regimes were identical (Figure 8). For both models, the estimated effects of reduced streamflow per se on fish biomass (the difference in the effects of flow + habitat versus habitat alone) were consistent across all 4 years; the estimated effect of reduced streamflow per se was greater for the daily model (about 1 g/m) than for the subdaily model (about 0.5 g/m).

Both models also produced realistic patterns in fish growth that were not outcomes of the calibration process, which did not involve the distributions of growth among individuals, used information only from the end of the dry season, and included only the upstream reach. Distributions of within-year individual growth rates in the models had levels of variability similar to those observed in the field (Figure 5). Both models also reproduced the empirical result that the majority of growth occurred outside of the dry season (Figure 6). Finally, with the

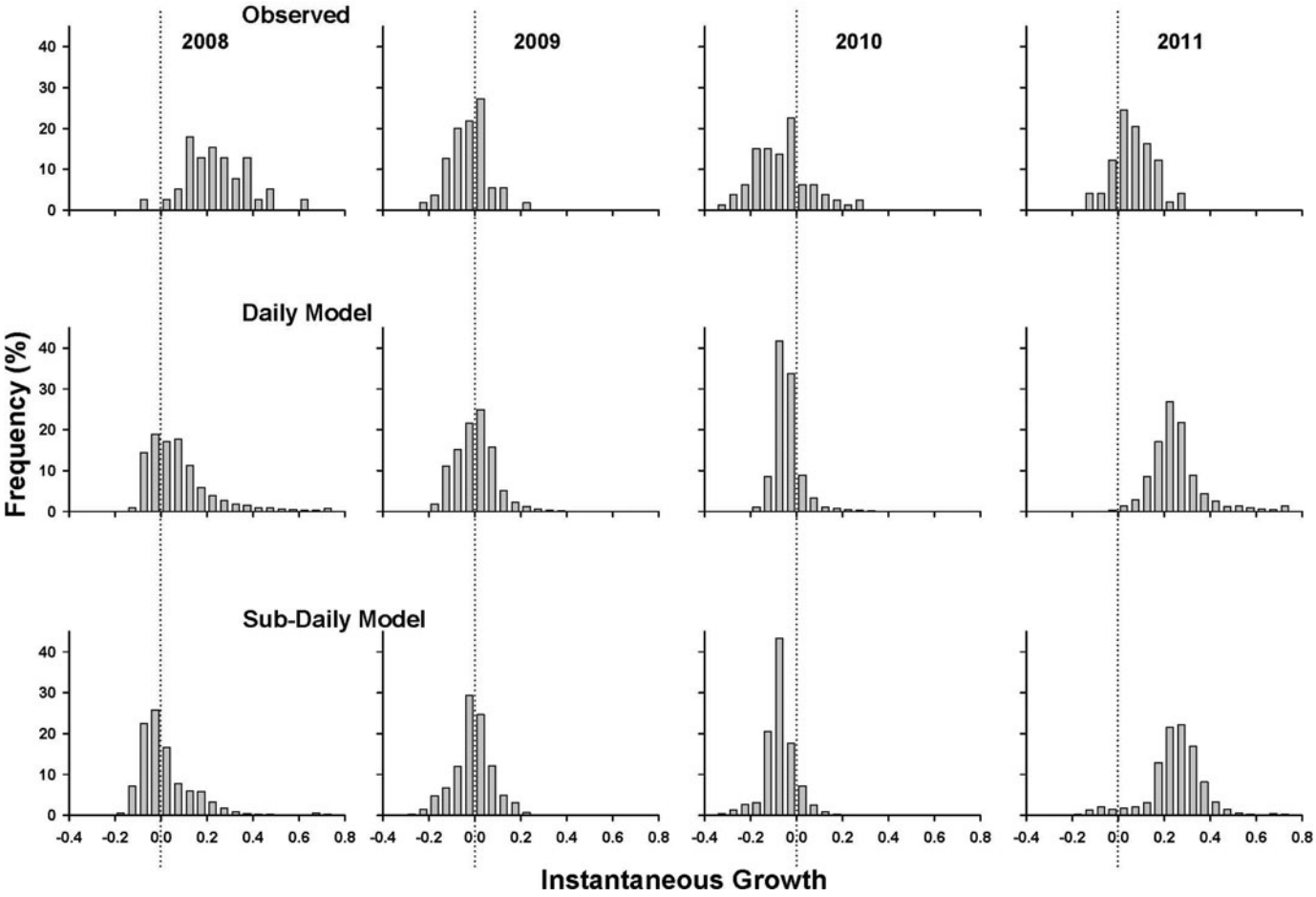

FIGURE 5. Observed and modeled patterns of individual dry-season growth over 4 years for steelhead and Rainbow Trout in the upstream control reach of West Weaver Creek, California. Model results summarize 50 replicate simulations.

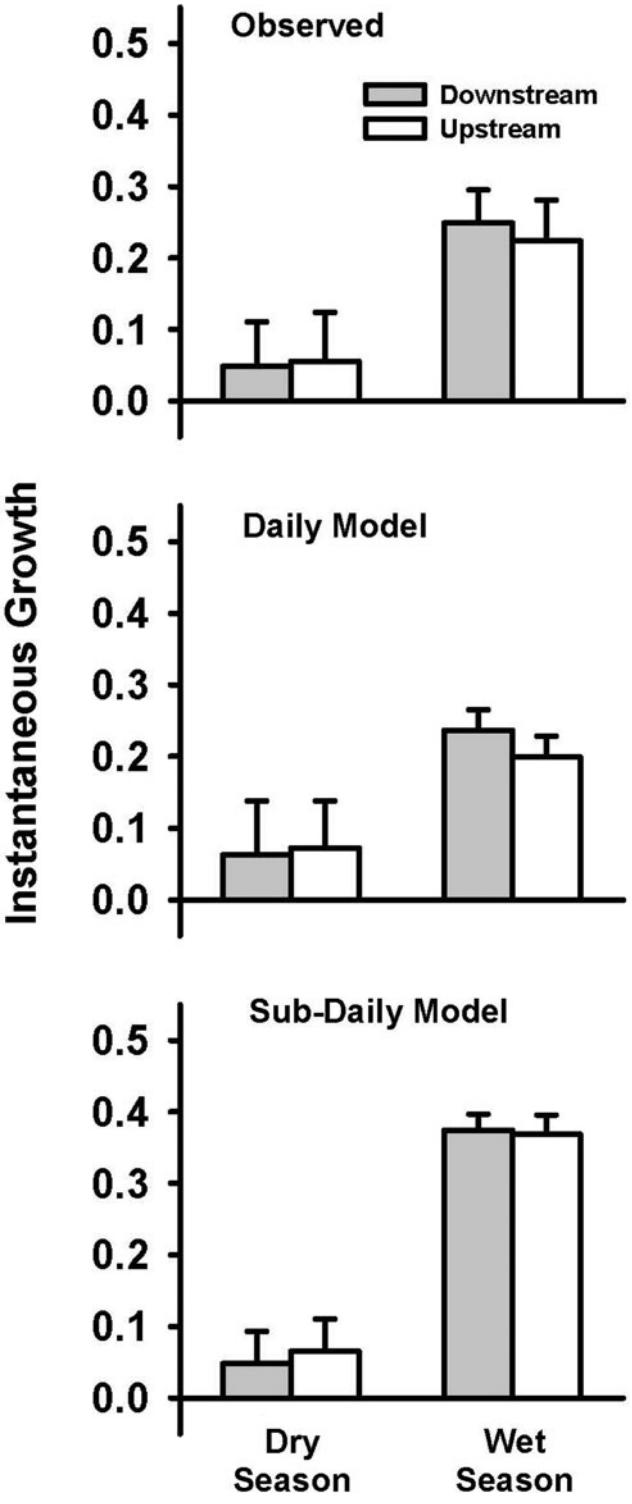

FIGURE 6. Observed and modeled patterns of dry season versus wet season growth for steelhead and Rainbow Trout in two reaches of West Weaver Creek, California. Error bars indicate SEs based on annual means ($n = 4$ for the dry season, $n = 3$ for the wet season.). For model results, annual means were themselves the means of 50 replicate simulations.

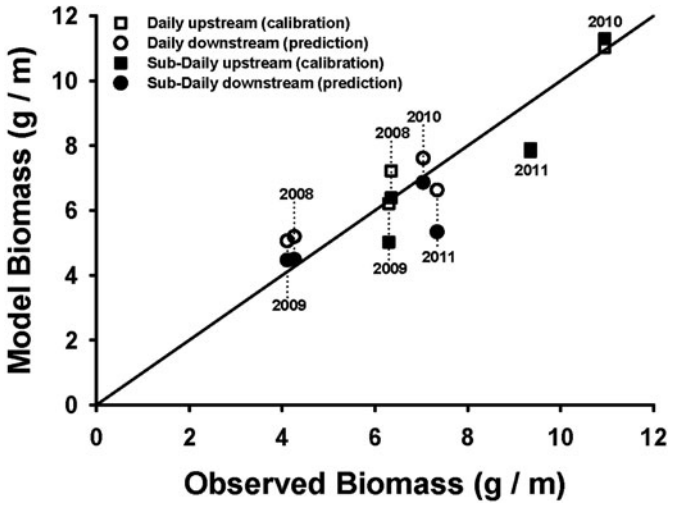

FIGURE 7. The relationship between observed and model results for two individual-based models (daily, subdaily) of steelhead and Rainbow Trout in two reaches of West Weaver Creek, California. The two models were calibrated using 4 years (2008–2011) of data from the upstream control, then applied to a reach downstream of a diversion.

exception of 2009 when dry-season growth was relatively low in the upstream control reach, both models yielded small observed differences in growth rates between reaches (Figure 9).

Eight-year simulations of the upstream reach across a range of dry-season flow regimes produced somewhat different results for the two models. Both models predicted that further reductions of dry-season streamflows below those we measured (with measured wet-season streamflows unaltered) would further reduce salmonid biomass. However, in comparison to the subdaily model, the daily model predicted a stronger effect of reduced streamflows on fish biomass and population persistence (Figure 10). This difference is partially explained by the higher relative availability of food obtained by search feeding in the subdaily model, and the insensitivity of search food to variation in streamflow. Indeed, relatively large trout did very little search feeding in the daily model even at very low streamflows, while in the subdaily model about 20% of such fish used search feeding during the day and 50% at night, although those percentages did not increase with decreasing streamflows. Search feeding by smaller fish increased with decreasing streamflows in the daily model, while it remained relatively high and insensitive to streamflow for those fish in the subdaily model. In the subdaily model, both day and night hiding behavior declined with streamflow, as drift food availability declined.

DISCUSSION

Our field observations above and below a stream diversion that reduces dry-season streamflow by about 24% detected persistently higher abundance and biomass of steelhead and Rainbow Trout at the end of four dry seasons in an upstream control

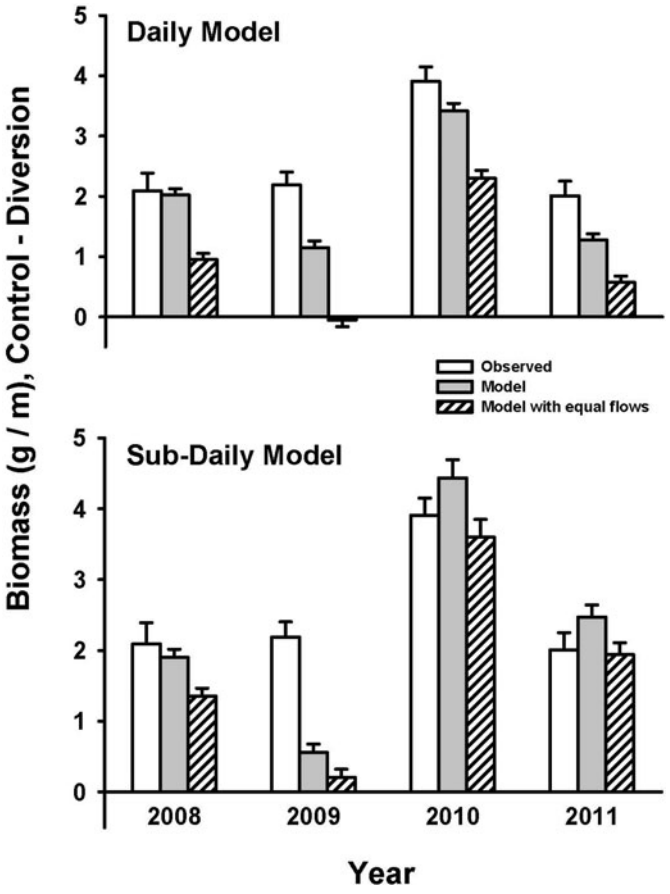

FIGURE 8. Observed and modeled biomass of steelhead and Rainbow Trout in two reaches of West Weaver Creek, expressed as the difference between an upstream control reach and a downstream diversion affected during the fall sampling. Error bars for the observed data reflect SE from the depletion sampling. For the model results, bars indicate the differences between the means of 50 replicate simulations of the upstream (control) and downstream (diversion) reaches. Error bars for the model results reflect the sum of the SE for 50 replicate simulations of the control reach and the SE for an equal number of replicate simulations of the diversion reach.

reach than in a reach below the diversion. Observed differences between the reaches in dry-season growth were modest and inconsistent. Importantly, these unreplicated observations do not control for differences between reaches in habitat availability; our spatially explicit simulations suggested the upstream control reach contained somewhat superior habitat. It is difficult to place these results in the context of current scientific knowledge because few studies have addressed the effects on stream fish of relatively minor changes in streamflow. While the consequences of larger changes in streamflow for fish abundance have been often negative (Poff and Zimmerman 2010), several observations suggest the importance of site-specific factors in determining outcomes (Bradford and Heinonen 2008). Observations of significant effects on fish growth in experimental (e.g., Harvey et al. 2006) and extensive observational studies (e.g., Ebersole et al. 2009; Davidson et al. 2010) covered larger differences in streamflow than we addressed here.

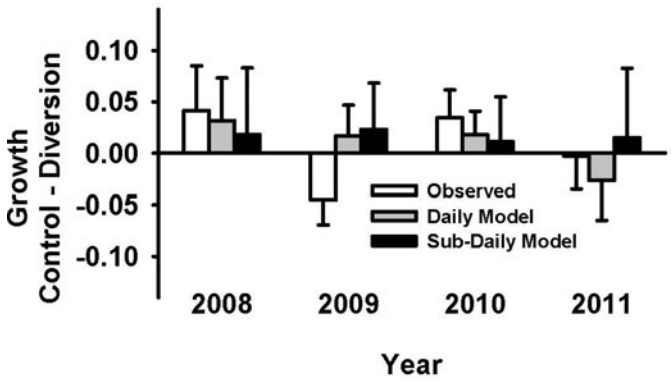

FIGURE 9. Observed and modeled dry-season growth rates for steelhead and Rainbow Trout in two reaches of West Weaver Creek, expressed as the difference between an upstream control reach and a downstream diversion-affected reach. Error bars for the observed data indicate SE. Error bars for the model results represent the sum of the SE of mean growth for 50 replicate simulations of the control reach and the SE for an equal number of replicates for the diversion reach.

While between-reach differences in fish growth and abundance were small (Figures 3, 4), annual variation was more dramatic, particularly for growth. This variation was to some extent explained by variation in dry season streamflow and fish density (as indicated by our model results), but particularly high growth rates in the dry season of 2008 were not. Annual variation in food availability provides one possible explanation. While we assumed constant food availability over time, the abundances of many aquatic and terrestrial invertebrates likely exhibit substantial annual variation (e.g., Levings 1983). In

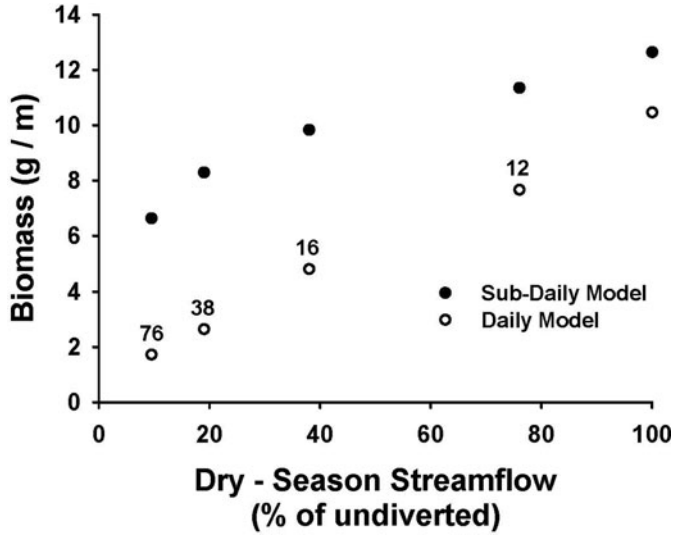

FIGURE 10. Results of 8-year simulations of a population of steelhead and Rainbow Trout in the upstream control reach of West Weaver Creek, over a range of dry-season streamflow regimes. Points show mean results for 50 replicate simulations. Numbers above points indicate the percent of replicate simulations in which the population did not persist over the simulation, in all cases where the population did not persist in all 50 replicates.

addition to annual variation in invertebrate abundance, variation in the inputs of terrestrial prey to streams may occur, driven by patterns of streamflow and its consequences for abundances of terrestrial vegetation and invertebrates along streams. Spring streamflows preceding the dry season marked by exceptional fish growth (2008) were milder than in the other 3 years; perhaps this pattern of streamflow allowed greater colonization of stream margins by terrestrial invertebrates.

The two IBMs we applied to the study reaches produced results with similar levels of correspondence with empirical observations. However, the modest differences in physical conditions and biological outcomes between reaches limited our ability to distinguish the performances of the two models in this case. Results of the calibration process were apparently important to the lower sensitivity to streamflow exhibited by the more complex, subdaily model in that calibration yielded greater availability of search food in the subdaily model and search food is relatively insensitive to streamflow in the models. However, it is important to recognize that results of the calibration process are a product of model formulation. The greater behavior flexibility of fish (e.g., having the options of feeding at night and hiding during the day) in the subdaily model makes search feeding a more attractive option, which could lead to higher calibration values for the search food parameter. In addition, search feeding cannot be calibrated precisely in the daily model because search feeding is relatively rare in that model. The choice between the two models in this case should perhaps be driven less by their relative complexity per se but rather by which model better captures the key ecological processes affecting the population's response to streamflow. The latter remains unresolved.

Both the models we applied seem complex from the perspective of traditional ecological modeling. What alternatives are available for the scale of resolution and complexity of the management questions addressed here? Effective general approaches to conceptually linking flow regimes and their ecological consequence designed for larger scales of resolution (Poff et al. 2010) cannot readily address the fine-scale difference in flow regimes that we studied. To our knowledge, models other than mechanistic IBMs do not make the kinds of predictions we tested: the responses of measurable population characteristics such as abundance and biomass to changes in physical habitat. Also, simpler ecological models seem unlikely to be able to make use of the site-specific data available in this study (in which small differences in habitat structure between adjacent reaches were important to data interpretation) or to address the outcomes of interactions among factors of interest in this example (water diversion, climate-driven changes in streamflow and temperature, invasive species).

This study suggested several specific benefits to the application of IBMs to site-specific management questions concerning fish populations. First, the general step of modeling population dynamics leads to greater emphasis on longer time spans than the original dry-season focus of the empirical observations. Second, the models incorporate real-world temporal variation in key physical factors (such as streamflow and temperature), thereby allowing evaluation of specific physical regimes with relevance to resource management. Third, mechanistic models that reasonably represent real-world conditions and processes offer the opportunity to explore the consequences of multiple environmental changes: we can now address the combined effects of streamflow alterations and additional environmental alterations on fish populations. Fourth, mechanistic inclusion of food availability in the models requires consideration of multiple trophic levels in evaluating the effects of environmental alterations. Finally, comparison of two models highlighted key processes we otherwise might not have considered. In this case, the comparison exposed the need for better understanding of the extent to which steelhead and Rainbow Trout rely on drift feeding versus search feeding in small streams.

The last two points highlight an additional key uncertainty important to our simulations: the effect of streamflow alteration on the production of aquatic invertebrates. We assumed a constant concentration of drift food, meaning that the percent change in total invertebrate drift was equal to the percent change in streamflow. Streamflow affected search food availability in the models only to the extent lower streamflow reduced wetted area. The combination of these two assumptions means that streamflow reduction had modest negative effects on food availability in our simulations. Once again, relevant studies generally address larger changes in streamflow than we observed and do not address food availability at the detailed level of drifting versus nondrifting prey. The review by Poff and Zimmerman (2010) documented declines in the abundance of aquatic invertebrates with streamflow reductions $> 50\%$, although percent declines in invertebrate biomass were less than the declines in streamflow. Walters and Post (2011) quantified a significant negative linear relationship between total log-transformed insect biomass and summer streamflow expressed as a measure of exceedance in an experimental study in which summer streamflow was diverted from 100-m reaches for 2 months. However, Dewson et al. (2007) observed increases in insect densities in 100-m stream sections subject to diversion for 1 month. While our assumptions about streamflow effects on the availability of drift and nondrifting prey for fish lack detailed empirical support, in this case they yielded model results that corresponded well with the observed effects of lower streamflows on fish.

CONCLUSION

Empirical observations of growth and abundance, combined with simulation modeling that took habitat availability into account, suggested a modest effect of a small dry-season diversion on the abundance of salmonids in a small stream. The effect of the current timing and extent of diversion on the probability of population persistence appears minimal. The current situation combines streamflow diversion with dramatic changes in channel morphology due to historic hydraulic mining but does not include factors that may become important in the future, such as additional changes in streamflow, temperature regimes, or the

influences of invasive species. The mechanistic model approach presented allows the combined effects of such factors to be estimated. While such estimates of outcomes under possibly novel conditions would necessarily be uncertain, alternatives for addressing situations where interactions among factors are likely are not apparent to us, with the exception of subjective "expert judgment."

Concerning our attempt to identify an optimal level of individual-based model complexity for the issue at hand, neither of the two models we used was clearly superior in matching short-term empirical observations. However, in our simulations virtual fish populations composed of individuals with the ability to feed both day and night and to engage in concealment behavior were more resistant to streamflow reductions than populations exhibiting lesser behavioral complexity.

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