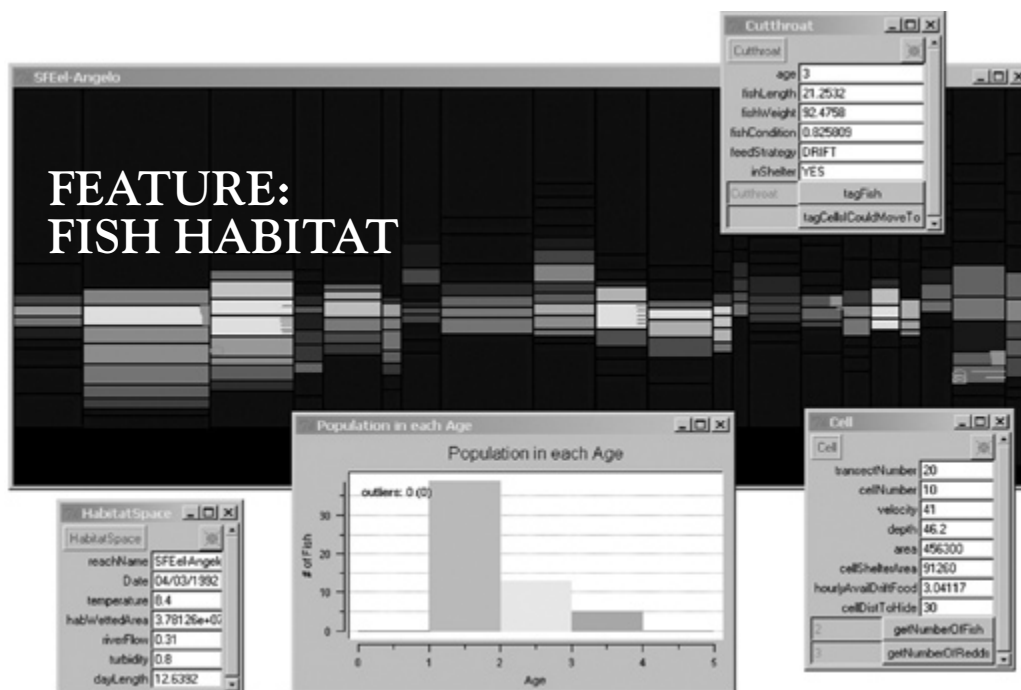


FEATURE: FISH HABITAT



inSTREAM's graphical interface illustrates the model's structure. The "HabitatSpace" window shows the daily inputs: flow, temperature, and turbidity. The main animation window is a top-down depiction of the habitat cells, with flow from right to left and cells shaded by depth (lighter is deeper). Fish appear as lines scaled by fish length, and redds as ovals. Depth and velocity of each cell vary daily with flow. Fish select the cell offering the best trade-off between growth and predation risk, a decision affected by temperature and turbidity as well as competition. Population status (illustrated in the age histogram) is determined by spawning and mortality of individuals. Users can open additional windows (via mouse clicks) to see habitat variables within a cell and the status of an individual fish; here: the fish tagged green and its current cell are shown. The tagged fish has low condition because it just spawned.

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Estimating Multi-Factor Cumulative Watershed Effects on Fish Populations with an Individual-Based Model

ABSTRACT: While the concept of cumulative effects is prominent in legislation governing environmental management, the ability to estimate cumulative effects remains limited. One reason for this limitation is that important natural resources such as fish populations may exhibit complex responses to changes in environmental conditions, particularly to alteration of multiple environmental factors. Individual-based models hold promise for estimating cumulative effects in these situations. We present an example application of an individual-based model of stream trout to the problem of estimating the cumulative effects of multiple environmental changes: elevated wet-season turbidity, elevated dry-season stream temperature, and reduced pool frequency. Each of these physical changes had multiple consequences for individual fish in the model, reflecting existing information. The simulations exhibited non-linear and non-multiplicative population responses to the multiple stressors. The results indicate the value of the individual-based approach for estimating cumulative effects and challenge the assumption that consequences for animal populations of increasing or multiple environmental changes are readily estimated from responses to modest changes in single factors.

Estimación de Efectos Multi-factoriales Acumulados de una Cuenca Hidrográfica en Poblaciones de Peces mediante Modelos Basados en el Individuo

RESUMEN: Si bien el concepto de efectos acumulados es importante en la legislación ambiental, su estimación aún es limitada. Una de las razones de dicha limitación es que recursos naturales de primera importancia como las poblaciones de peces pueden mostrar respuestas complejas ante los cambios ambientales, particularmente a la alteración de diversos factores. Los modelos basados en el individuo (MBI) son una alternativa promisoriosa para la estimación de efectos acumulados. En el presente trabajo se aplica un MBI a la trucha de río para estimar los efectos acumulados de distintos cambios ambientales: elevación de la turbidez durante la época húmeda, elevación de la temperatura del agua durante la época seca y un menor número de estanques disponibles. Cada uno de estos cambios físicos tuvo diversas respuestas en los organismos dentro del modelo, lo cual es un reflejo de la información existente. Ante los distintos factores forzantes, las simulaciones mostraron respuestas poblacionales no lineales y no multiplicativas. Los resultados ponen de manifiesto la utilidad de los MBI para estimar efectos acumulados y cuestionan la suposición de que las consecuencias que los cambios ambientales múltiples o crecientes tienen sobre las poblaciones animales, son fácilmente estimables a partir de respuestas a cambios individuales y de poca intensidad.

INTRODUCTION

The cumulative effects concept is fundamental to environmental policy and management, by virtue of its inclusion in key legislation such as the U.S. National Environmental Policy Act and the Canadian Environmental Assessment Act. However, many cumulative effects analyses focused on consequences for animal populations may not help achieve management goals, in part because of the inability to estimate biological responses to complex environmental changes (Duinker and Greig 2006). Most cumulative effects analyses must incorporate a variety of complicating aspects. For example, spatial variation can be important in cumulative effects: even within a watershed, the downstream transport of water, heat, and other watershed products may lead to accumulation of physical changes along stream networks (Li et al. 1994; Bolstad and Swank 1997). Temporal variation is often important: for example, significant cumulative effects may be undetectable until triggered by rare events such as extreme weather, and environmental changes separated in time may, as in the simulations we present, have cumulative impacts. Human activities often affect multiple environmental features important to the resource of interest. For example, changing the operation of a dam can alter not only flow but also water temperature and geomorphic processes downstream (Ligon et al. 1995), while timber harvest can affect temperature, turbidity, channel morphology, and possibly food production (Hartman et al. 1996). Finally, different kinds of human influences on the environment (e.g. habitat alteration and invasive species) commonly overlap (Allan 2004).

What tools are available to resource managers seeking to predict cumulative effects on key biological resources such as fish populations? Many of the models and tools fishery managers typically use for impact assessment are designed to evaluate static conditions and often best suited for evaluating effects of single factors. These approaches might be useful in cumulative effects analyses if one can assume that impacts are linear (e.g., a 50% decrease in preference-weighted habitat area reduces abundance by 50%) and that multiple impacts act independently. However, cumulative effects analysts whose qualitative reasoning suggests non-linear responses and interactions among factors have few tools to explore and expand their understanding.

Spatially explicit, individual-based models appear well-suited to support cumulative impact assessments. In these models, the consequences of environmental conditions on

populations emerge from the effects of those conditions on individuals, which can often be effectively simulated. For example, Goss-Custard et al. (2006) used an individual-based model to identify critical thresholds of disturbance for wading birds by quantifying the energetic cost of disturbance and its consequences for over-winter mortality while incorporating spatial and temporal variation in food supply, the cost of thermoregulation, and other key factors controlling the energetics of individuals. Because they explicitly incorporate spatio-temporal variation in the environment and the mechanisms by which the environment affects individuals, the interacting effects of environmental variables on population dynamics can be directly estimated. Rose et al. (2000) described an individual-based model of striped bass (*Morone saxatilis*) in the Sacramento and San Joaquin river system that incorporates possible effects of diversion mortality, changes in prey composition that reduced food availability, and increased adult mortality on population dynamics. In that example, the combined effect of the three factors on the virtual population significantly exceeded the effect predicted by multiplying their separate effects.

One specific area where the individual-based approach may be useful to decision-makers is in the analysis of cumulative effects within watersheds, where human activities can influence a variety of physical factors and fish populations are often the foci of impact assessments (e.g., Hughes et al. 2006). Our objective in this study was to explore the use of an individual-based model in estimating cumulative watershed effects on stream trout, using realistic scenarios reflecting alteration of physical factors commonly influenced by human activities: water temperature, turbidity, and habitat structure.

METHODS

We used a spatially explicit, individual-based model (IBM) of cutthroat trout (*Oncorhynchus clarki*) in Little Jones Creek, northwest California, to explore the cumulative effects of physical changes commonly associated with human disturbance of forested watersheds. Little Jones Creek is a third-order tributary of the Middle Fork of the Smith River. The reach we simulated drains about 2,500 ha of forest, about 30% of which has been logged in the last 50 y. We used *inSTREAM*, an IBM we designed for assessment of changes in physical habitat on stream trout populations. This IBM has been described in detail elsewhere (Railsback and Harvey 2001; see also www.humboldt.edu/~ecomodel) and several examples of its use are available (Railsback and Harvey 2002; Railsback et al. 2003).

Brief description of the model

inSTREAM tracks the survival and growth of model fish within simulated stream reaches, using a one-day time step. Habitat is represented two-dimensionally as rectangular cells several square meters in size. In this example, we simulated one 372-m stream reach using habitat cells arranged along 42 transects. Variables representing the availability of hiding cover and velocity shelters for feeding are input for each cell and assumed constant over time. An external hydraulic model uses channel geometry and streamflow to determine the depth and velocity in each habitat cell. The model requires daily reach-scale values for streamflow, temperature, and turbidity.

Model trout may conduct four major processes in each time step: habitat selection, feeding and growth, mortality, and reproduction. Trout select the habitat cell they forage in considering habitat features and their own condition. Fish select the habitat cell, within a limited radius, that maximizes their probability of surviving (and, for juveniles, reaching reproductive size) over a future time horizon of 90 days (Railsback and Harvey 2002). This probability depends both on short-term risks such as predation, and on food intake (if food is inadequate, then starvation becomes a significant risk over the time horizon). The condition of individuals influences habitat selection by affecting starvation probability. Thus, a fish in poor condition might occupy a habitat cell with relatively high mortality risk if that cell also offers high food intake.

Feeding and growth (for which we adapted existing bioenergetics models) are affected by a variety of factors, including fish size, hydraulic conditions, turbidity, temperature, and competition. The model simulates two kinds of food: the concentration of drifting invertebrates and the production rate of benthic invertebrates are assumed constant on the reach scale.

Higher velocities carry more drifting food to the fish, but reduce the distance over which fish can see and capture food, and increase metabolic costs of swimming. Velocity shelters reduce swimming costs. Turbidity reduces the distance over which fish can capture drifting food, but does not affect benthic feeding. Fish compete for the food available in each habitat cell. This competition is assumed to be size-based: smaller fish only have access to food not consumed by the larger fish in their cell. Simulating competition for food has proven essential for reproducing a variety of realistic behaviors (Railsback and Harvey 2002; Railsback et al. 2002). Overall, growth is a function of food intake, metabolic activity, and temperature.

Mortality from specific sources is modeled by treating daily survival probability as a deterministic function of each fish's state and habitat; random numbers are then used each day to determine whether each fish survives. We model several different mortality risks, including predation, high temperature, starvation, and stranding. Predation by terrestrial animals is modeled separately from predation by fish because the risks of these two kinds of predation vary differently with habitat (e.g., water depth) and fish size. We assume elevated turbidity reduces predation risk from both terrestrial animals and fish.

Spawning is included in *inSTREAM* so that impacts of stressors on reproduction can be included and simulations much longer than one life span can be conducted. When environmental conditions are appropriate, model fish of adequate size in good condition can spawn. The nests of fish eggs are treated as individuals. Redds are vulnerable to several kinds of mortality: extremely high or low temperature, scouring in high flows, and dewatering in low flows. Egg development rate is controlled by temperature.

The model's software includes tools to thoroughly observe and understand the model. Graphical and file outputs are easily modified as needed to test and understand simulations. An animation window displays habitat conditions and fish locations. Thorough documentation and testing have been completed, including detailed user guides and a variety of rigorous testing procedures (Railsback and Harvey 2001). The software allows *inSTREAM* to be easily modified for new species and sites. Finally, an "experiment manager" automatically generates and executes model runs that compare scenarios and include replicate simulations.

The model requires several kinds of input. Parameter values are based on review of the literature and data on the process they represent (Railsback and Harvey 2001). Physical habitat input is site-specific. Using an established set of field procedures, a study site is selected and a grid of rectangular cells established. Variables representing feeding and hiding cover and spawning gravel are evaluated in the field. Depth and velocity in each cell is measured at several flows to calibrate a hydraulic model used to predict depth and velocity in each cell at each simulated flow rate. (We used PHABSIM hydraulic models for this study; alternative versions of *inSTREAM* interpolate depth and velocity directly from field measurements, or use two-dimensional hydrodynamic models.)

Time-series input includes daily values for stream flow, temperature, and turbidity. Here, we use 15-year records (October 1990–September 2005). Baseline conditions for Little

Jones Creek represent actual measurements for 1998–2005. We estimated the discharge record for 1990–1998 using a strong linear relation between Little Jones Creek streamflow and Smith River streamflow at a USGS gage downstream ($R^2 = 0.96$ with a 1-h lag between sites). Also for the simulation period preceding direct measurements, we estimated temperature by establishing monthly relations between Little Jones Creek water temperature and the air temperature at a weather station in Cave Junction, Oregon. The coefficients of determination (R^2) ranged 0.5–0.8 for these regressions. Finally, to estimate turbidity for 1990–1998, we used a linear relationship ($R^2 = 0.68$) between turbidity and discharge at the study site. We chose not to use power functions to describe the relationship between turbidity and stream discharge, because of their tendency to overestimate turbidity at low discharge.

We calibrated the model using parameters representing especially important but uncertain environmental processes: food availability and predation risk. Five variables (representing drift food concentration, drift regeneration rate, benthic food production rate, maximum aquatic predator risk, and maximum terrestrial predator risk) each dominate one model output (adult growth, adult density, juvenile growth, juvenile mortality, and adult mortality). Typically the only calibration *inSTREAM* needs is adjustment of these five variables to produce realistic values for the related five outputs. We do not consider the IBM's sensitivity to these uncertain variables a flaw: it is a reflection of the reality that food availability and predation risk are very important drivers of fish populations yet they are inherently difficult to estimate. Note that while these variables are constant at the reach scale (e.g., the model assumes a constant concentration [mg of prey/m³ of water] of drift food throughout a reach), variation in physical conditions among habitat cells produces strong differences in food availability and predation risk within simulated reaches.

In general, individual-based models predict the effects of stressors by simulating: (1) how the stressors affect an individual; (2) how individuals respond behaviorally to the stressor (here, primarily by selecting different habitat), considering their current habitat and competitive conditions; and (3) the consequent survival, growth, and reproduction of individuals, which when summarized over time yields an estimate of the population-level response (Grimm and Railsback 2005). Consequently, the effects of stressors on simulated populations can be complex and unexpected. Consider the effects of a stressor (e.g., sublethal but high temperature) that reduces individual growth.

An individual exposed to the stressor would experience reduced growth, causing it to adapt by shifting habitat to sites with higher growth but higher mortality risk. Thus, the population-level result may be lower abundance (because more fish use riskier habitat and get eaten) as well as (or instead of) a decrease in average body size. Alternatively, mean body size could increase if a severe reduction in abundance reduced intraspecific competition to the point that the direct effect of sublethal high temperature on individuals was more than offset.

Models as complex as *inSTREAM* naturally raise concerns about uncertainty, especially the extent to which conclusions from the model could be artifacts of detailed assumptions and parameter values. While we do not analyze uncertainty in the results presented here, we have taken a number of steps to deal with the issue. The assumptions and parameters in the model are based to the extent possible on published information and thoroughly documented. A study of parameter uncertainty (Cunningham 2007) found the model highly sensitive to only a few parameters other than those either estimated via calibration or with values well-established in the literature, and no evidence of unpredictable or strong "error propagation." The same study also found a relative comparison of scenarios (the approach used here) robust to parameter uncertainty.

Simulation of cumulative watershed effects

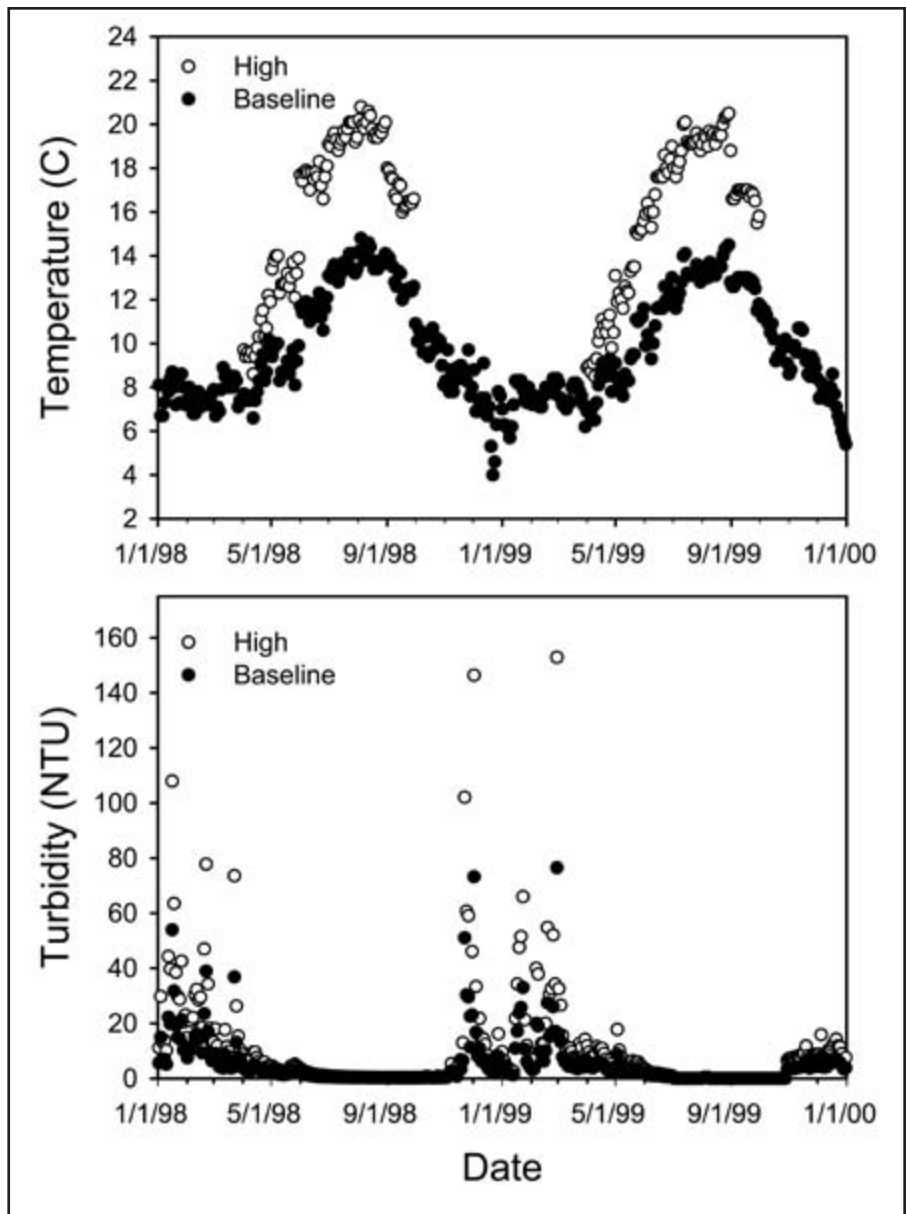
Here we explore the cumulative effects of three physical changes commonly associated with human activities in temperate forested watersheds: increased dry season temperature (Moore et al. 2005), increased wet season turbidity (Gomi et al. 2005), and reduced pool frequency (McIntosh et al. 2000). For each of these changes, we establish three regimes: baseline (current conditions at Little Jones Creek), moderate (halfway between the baseline and high regimes), and high (a major change that is still well within observed conditions in the region). The high temperature regime (Figure 1) was derived from our unpublished data for disturbed streams in northwestern California. We created alternative turbidity regimes by increasing the slope of the turbidity–discharge relationship at Little Jones Creek by 50 and 100%. These alternatives are modest in comparison to turbidity–discharge relationships for some streams in the region of similar size, one of which has a turbidity–discharge relationship with a slope 720% higher than Little Jones Creek. While the modified temperature regimes only differed from the baseline regime during five months in the dry season, the ele-

vated turbidity regimes have meaningful differences from baseline only during winter and occasionally spring stormflows (Figure 1). Finally, we reduced pool frequency in the simulated reach by 50% (the high impact regime) and 25%, replacing habitat cells along transects through pools with cells from adjacent run habitat. When cross-classified, these alternative regimes (including baseline conditions for all three factors) yielded 27 different scenarios.

Each physical alteration included in the simulations has multiple consequences for fish in the model. Temperature affects bioenergetics (the relation between food intake and growth) and some mortality risks. The model also simulates the potentially important effects of temperature on the duration and success of egg incubation, which can affect population size. Moderate turbidity can have both negative and positive effects on fish. By reducing visibility, turbidity reduces the amount of food fish can capture by reducing their reactive distances to drifting prey but also reduces the risk of fish being captured by some predators. Both of these mechanisms are represented in *inSTREAM*. Availability of pool habitat influences the survival and growth of fish in the model through effects of water velocity and depth on the energetics of feeding and on predation risk.

We contrasted simulation results by quantifying median population biomass over the last 10 years of the 15-year simulation period, for 10 replicates of each of the 27 scenarios. We also quantified population persistence as the percent of replicates in which the population did not go extinct. We increased the level of replication when persistence varied substantially. Variation among replicates in this case indicates only the influence of stochastic processes affecting individual fish. The main stochastic process in the model is mortality: the daily probability of survival for each trout is a deterministic function of its state and its habitat, but whether the trout actually lives or dies each day is a stochastic event. Given the relatively small length of stream simulated here, persistence is basically a measure of the population declining to a very low abundance, at which the probability of chance "extinction" is magnified. To explore non-linearities and interactions among factors, we compared results for population biomass and persistence to the results predicted by assuming effects are linear and multiplicative. For example, the predicted effect of the high temperature regime, assuming linearity, was twice the effect of the intermediate regime, while the predicted combined effect of high temperature and high turbidity regime was the product of their separate effects.

Figure 1. A two-year example of the input data for different temperature and turbidity regimes used in simulations of a resident trout population using an individual-based model. While the model uses a daily time step, for clarity the graph shows data from every other day.



RESULTS

Simulations of cutthroat trout abundance under baseline conditions at Little Jones Creek yielded a relatively stable population, similar to our population estimates for the site over the last eight years (B. C. Harvey, unpublished data). This result in part simply reflects successful calibration, but the multi-year results suggest the model also captured the influence of annual variation in patterns of streamflow, temperature, and turbidity. The moderate temperature, turbidity, and pool reduction alterations separately yielded modest biomass reductions (25% or less) compared to the baseline scenario, but the severe alteration regimes and the combined effects of multiple

factors produced more dramatic effects (Figure 2). Both non-linear and non-multiplicative effects emerged from the simulations.

All noteworthy departures from predictions assuming linear, multiplicative effects were negative. The IBM predicted that doubling the change in each single factor more than doubled the impact on population biomass. The effects of multiple factors on mean biomass were often stronger than predicted by assuming each factor acts independently. Treatment combinations including increases in both water temperature and turbidity yielded particularly large departures from expected results assuming multiplicative effects (Figure 3), even though the within-year timing of these alterations did not overlap. Also, when

combined with decreased pool frequency, the interaction of temperature and turbidity effects occurred even when both were only moderately altered. Departure from multiplicative results over the last 10 years of the simulations was greatest under the most challenging environmental conditions that yielded very low mean biomass, suggesting that differences in population persistence influenced these results.

The strongly non-multiplicative results for population persistence (Figure 4) make clear their influence on the biomass results. None of the simulated populations went extinct in scenarios with just one factor altered to either a moderate or high level. Thus, the assumption of multiplicative effects would predict 100% persistence in all scenarios. However, the fish in simulations with multiple factors altered commonly did not persist over the 15-year simulation period. The most severe scenario, combining high temperature, high turbidity, and 50% pool reduction, yielded no persistence.

DISCUSSION

The IBM simulations presented here yielded frequent non-linear and non-multi-

plicative outcomes, particularly for population persistence. These results appear germane for decision-makers facing questions about the consequences of additional human activities in previously altered systems: the effects of additional alterations may often be greater than predicted by the system's response to prior changes. While providing a general illustration of the potential complexity of cumulative effects, the variable outcomes in these simulations also suggest the usefulness of specific analyses for particular populations and scenarios.

Why the preponderance of non-linear, non-multiplicative effects, particularly for population persistence? The IBM suggests two reasons. First, many of its relationships for how physical factors affect individuals are non-linear. Examples include the relationships between metabolism and temperature and between drift feeding success and turbidity. Because population-level responses to altered physical conditions arise from such individual-level relations, there is good reason to expect these responses will be non-linear. Second, non-linear relations between physical factors and the fitness of individuals are likely to produce complex patterns in the amount of useful living space when envi-

ronmental conditions create increasing physiological challenges. Deteriorating environmental conditions can eventually reach thresholds: populations crash when conditions degrade to the point that little or no habitat allows individuals to survive, grow, and accumulate energy for reproduction. Consequently, predictions based on small perturbations become less reliable as the level of perturbation increases.

The simulations presented also suggest that process linkages between environmental changes and individual fitness should be considered when estimating cumulative effects. Different kinds of environmental change may be more likely to produce non-multiplicative results if they produce similar consequences for individuals, even if those consequences are separated in time. In this case, both elevated temperature and elevated turbidity had energetic costs to individuals, although these effects generally did not overlap within years. These factors combined to produce the most strongly non-multiplicative results.

To be useful, even complex models like *mSTREAM* must simplify reality. Therefore, uncertainties concerning the effects of environmental variables on individuals require

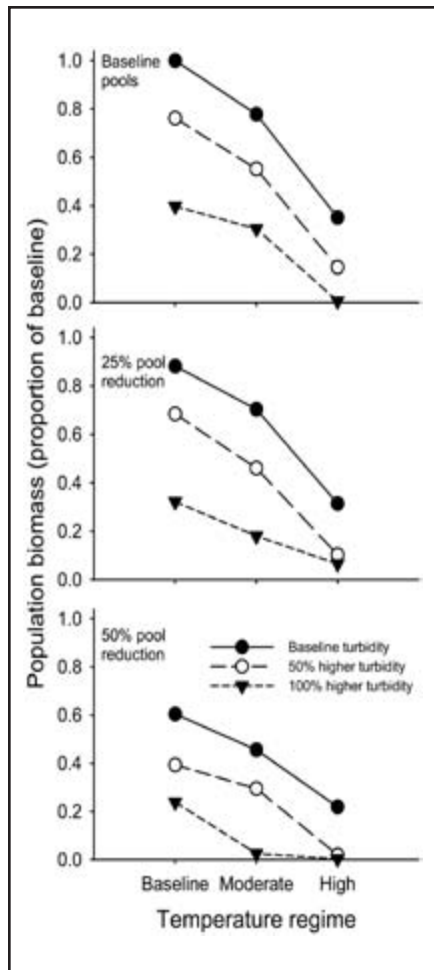
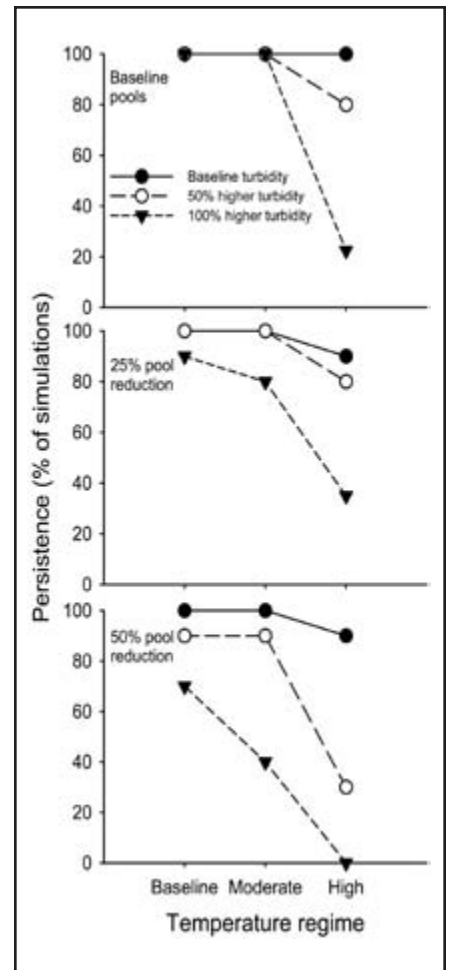
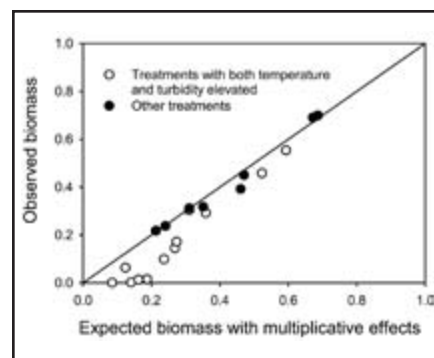


Figure 2. (left) Results of IBM simulations of a resident trout population under 27 different scenarios varying in turbidity, temperature, and pool frequency. The response variable reflects median biomass for 10 replicate runs of each treatment combination over the last 10 years of a 15-year simulation period, expressed as a proportion of the median biomass under baseline conditions.

Figure 3. (below) Comparison of IBM results for median biomass versus those expected given multiplicative effects of individual factors. Twenty treatment combinations included two or three altered environmental factors, thus allowing computation of an expected multiplicative effect. The graph distinguishes treatments in which both temperature and turbidity were altered from other treatments involving two altered factors.

Figure 4. (right) Results of simulations of a resident trout population showing the proportion of populations persisting for 15 years under 27 different treatment combinations. Sample size ranged 10–40. We completed more replicate runs for scenarios with intermediate levels of persistence.



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caution in interpreting the quantitative results of simulations such as these. For example, we assumed trout cannot reproduce unless their weight is above 95% of "normal" for their weight, a substantial simplification of reproductive energetics. However, the potential significance of such uncertainties is readily addressed with sensitivity analyses. For example, completely eliminating the weight threshold for reproduction still yielded only 30% persistence under the most challenging scenario; our conclusion that persistence is much less than expected from assuming impacts are multiplicative therefore appears robust to how reproductive energetics are modeled.

Another key question in modeling efforts like this one is, have important linkages between the organism and altered environmental conditions been excluded? For example, elevated temperature can be associated with greater secondary production of lotic insects (Morin and Dumont 1994), which might alleviate to some extent the increased energetic demand of higher temperatures on fish. We did not include this possibility in the simulations. For a second example, *inSTREAM* includes the well-quantified effects of turbidity on the ability of trout to feed on drift (Sweka and Hartman 2001), but ignores the possibility that benthic prey may be more available during high-flow events that elevate turbidity.

The reach-scale model used here does not address larger spatial scales that must be incorporated in cumulative effects analyses focused on entire animal populations or metapopulations. Clearly, persistence is affected by a variety of landscape-scale processes (Dunning et al. 1992). Larger scales can be addressed with *inSTREAM*: it can simulate reaches of any size, and even networks of reaches connected by movement corridors. However, the usefulness of complex IBMs is limited by requirements for input and computing power. Given such limitations, another possible approach to cumulative effects analyses would use reach-scale individual-based models to inform less detailed models formulated for larger scales (e.g., Rieman et al. 2001).

From our perspective, the uncertainties and limitations of this approach are offset by the fact that explicit simulation of interactions between individuals and physical habitat that varies realistically in space and time can offer unique insights into the responses of populations to environmental changes, and the mechanisms responsible. Given the potential for alteration of multiple environmental factors to influence animal populations in complex ways, it may often be useful to apply an approach that explicitly incorporates such complexities. ☞

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