Exploring the Persistence of Stream-Dwelling Trout Populations under Alternative Real-World Turbidity Regimes with an Individual-Based Model

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Abstract.—We explored the effects of elevated turbidity on stream-resident populations of coastal cutthroat trout *Oncorhynchus clarkii clarkii* using a spatially explicit individual-based model. Turbidity regimes were contrasted by means of 15-year simulations in a third-order stream in northwestern California. The alternative regimes were based on multiple-year, continuous monitoring in two streams. Turbidity affected model fish by reducing both their risk of predation and their reactive distance to drifting prey. It did not affect their ability to locate nondrifting food, such as invertebrates on the stream bottom. Under a calibration scenario that assumed trout predominantly consume drifting prey, the less-turbid real-world regime produced relatively stable abundance across years (similar to field observations) whereas the more-turbid regime (under otherwise identical physical conditions) resulted in extinction within the 15-year simulation period. Additional simulations revealed sensitivity to the relative amounts of prey available via drift versus search feeding and showed that seasonal variation in food availability or strong positive relationships between streamflow and food concentration would not prevent extinction in the high-turbidity regime under a drift-feeding-based food calibration. Extinction of predominantly drift-feeding trout populations in our simulations contrasts with field observations of salmonid populations that have persisted in moderately turbid regimes. The results highlight the need for better understanding of patterns in the availability of food under turbid conditions and the capability of stream salmonids to use nonvisual cues in feeding.

Logging, road building, and other human activities can increase the levels of suspended sediment in streams, with direct consequences for individual stream salmonids, including death (Bozek and Young 1994). Observed sublethal effects of elevated suspended sediment on stream salmonids include impaired respiration (Berg and Northcote 1985), increased physiological stress (Redding et al. 1987), lower feeding success because of reduced reactive distance to drifting prey (Barrett et al. 1992; Sweka and Hartman 2001a), and lower growth rates in short-term experiments (Shaw and Richardson 2001; Sweka and Hartman 2001b). For drift-feeding fishes such as salmonids, the effect of turbidity on prey capture success would appear to be of particular concern because it occurs at modest levels of turbidity.

In contrast to some well-established effects of elevated turbidity on individual fish, the population-level effects of elevated but sublethal suspended sediment concentrations are less certain (but see Rowe et al. 2000). Addressing this issue for salmonid

populations is challenging because (1) many factors other than suspended sediment influence their abundance; (2) significant spatiotemporal variation in suspended sediment characterizes most natural streams; (3) turbidity can have positive effects on fish by reducing predation risk (Gregory and Levings 1998); and (4) our knowledge of the dependence of overall feeding success on turbidity remains incomplete. We are unaware of any empirical observations on stream fish that quantify population-level consequences of elevated suspended sediment where fish cannot avoid elevated suspended sediment by way of habitat selection.

Given the scarcity of empirical information on the population-level effects of elevated suspended sediment per se and two opposing effects on individuals that occur with only modest increases in turbidity (reduced drift-feeding success and reduced predation risk), we explored the potential population-level consequences of these effects, using an individual-based model with a daily time step. The model used was formulated specifically to estimate the population-level consequences of habitat alterations from the traits of individuals and their interactions with the environment (Railsback and Harvey 2001). Because strong

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temporal variation in turbidity characterizes most ecosystems in which turbidity appears to be an important factor, we explicitly incorporated this variability by using turbidity data collected in natural streams. Recognizing the uncertainty in the relation between drift-feeding success and overall feeding success for salmonids in natural channels, our objectives were to estimate the effect of real-world turbidity regimes on stream trout populations under different assumptions about the extent to which sight feeding on invertebrate drift dominates food acquisition, and to explore the potential for different patterns in food availability to influence population-level outcomes. Given the current state of knowledge, we sought to gain insight into population-level processes and identify key uncertainties rather than predict specific outcomes.

Methods

Model Description

To simulate the effects of different turbidity regimes, we used a reach-scale trout model developed for Little Jones Creek, northwestern California (Railsback and Harvey 2001, 2002). Little Jones Creek drains a 2,700-ha catchment of old-growth and 25–35-year-old second-growth coniferous forest underlaid by marine sedimentary and metasedimentary rocks of the Galice Formation, which are dominated by slate, phyllite, and sandstone. Coastal cutthroat trout *Oncorhynchus clarkii clarkii* is the only fish species present. Railsback and Harvey (2001) provide a complete description of the model; here we summarize the model and provide details relevant to this application. The model has successfully reproduced both individual behaviors (e.g., changes in habitat selection in response to high discharge, predators, and altered food availability; Railsback and Harvey 2002) and population-level patterns (e.g., density-dependent mortality of young of the year and density-dependent growth; Railsback et al. 2002) commonly observed in empirical studies.

The model simulates the complete trout life cycle using a daily time step, with daily mean values of stream discharge, temperature, and turbidity as the driving variables. The model simulates available habitat as an irregular grid of cells with mean depths and velocities that are functions of stream discharge. We delineated habitat cells in the study reach with the goals of capturing the full range of hydraulic variation and complexity in the reach while minimizing habitat variation within each cell. The model incorporates information for each cell on the availability of habitat that provides velocity shelter for drift-feeding fish and the mean distance to hiding cover. Velocity shelters reduce swimming costs. Hiding cover can reduce the risk of predation. We made the simplifying assumption that, for individual habitat cells, these cover and shelter characteristics do not vary with stream discharge. The model of physical habitat included 174 cells along 21 transects in a 186-m reach. To reduce the sensitivity of the results to limited numbers of fish, we doubled the length of the reach by linking two identical sets of transects. Habitat cells averaged 17 m^2 (SD = 12). The stream in the modeled reach is 8–12 m wide at base flow during the dry season.

Habitat selection.—Fish in the model can move daily between cells. Adult fish select cells that maximize their expected probability of surviving over a 90-d time horizon (assuming constant physical conditions over that time period), while habitat selection by juvenile fish also incorporates motivation to reach adult size (Railsback et al. 1999). The expected probability of survival over the time horizon includes both the influence of net energy intake on the probability of starvation and more immediate sources of mortality such as predation. The model assumes fish have explored and selected the best of the cells within a distance that increases with their fork length (FL [cm]), that is,

$$\text{maximum movement distance (cm)} = 20\,(\text{FL})^2.$$

The equation above is based in part on radiotelemetry data for coastal cutthroat trout in Little Jones Creek (Harvey et al. 1999). Territoriality is not included explicitly, but the model simulates competition as a size-based dominance hierarchy (e.g., Hughes 1992), in that fish select habitat in the order of decreasing body size, the food and velocity shelters used by larger individuals being rendered unavailable to smaller fish.

Energetics.—The availability of food, the ability to capture food, the energetic costs of swimming and basal metabolism, and competition among individuals determine the growth and condition of individual fish in the model. The model relies on established methods for simulating fish energetics (Hanson et al. 1997), in which temperature, food intake, and swimming costs are key variables. Fish with positive net energy intake grow in length if they have already achieved the expected mass for a fish of their current length, the expected mass being based on a length–mass relationship for fish from the study site. Fish may use a search strategy intended to reflect feeding on the benthos and on terrestrial invertebrates in low water velocity or may feed on drifting prey. We did not include piscivory by trout in this model because relatively large trout and piscivory are rare in many of the populations of interest. For example, at Little Jones Creek, about 0.1%

of the fish exceed 25 cm FL (with none larger than 30 cm), and only 1 fish has been found in diet samples from more than 270 adult fish. Fish evaluate the net energy intake provided by both search feeding and drift feeding in all the habitat cells accessible to them.

Fish using the search-feeding strategy swim at the water velocity in the cell they occupy; drift-feeding fish either swim at the water velocity of their cell or occupy velocity shelters (30% of cell water velocity). The availability of food for fish using the search strategy is assumed to be independent of stream discharge, turbidity, and fish size, but feeding success under this strategy decreases as water velocity approaches a fish's maximum sustainable swimming speed. Following data and models available in the literature, drift feeding is influenced by fish size, water velocity, turbidity, and temperature. We neglect prey size as a factor affecting drift intake because its variability is very difficult to measure or predict and its effects cannot be easily distinguished from those of other variables. Drift-feeding trout are assumed to capture some of the prey that pass within a "capture area" (A_{cap} [cm^2]), a rectangular area perpendicular to the current, the dimensions of which increase with fish size and decrease with turbidity. The fraction of food items passing through the capture area that are actually caught ("capture success," S) decreases with water velocity, relative to the trout's swimming ability. A fish's intake rate (I [g/h]) is calculated as

$$I = A_{cap} \cdot S \cdot C_d \cdot V \cdot 3,600$$

where C_d is the concentration of drift prey (g/cm^3), V is velocity (cm/s), and the factor 3,600 converts seconds to hours. The variable A_{cap} depends on detection distance and cell depth. Detection distance (D [cm]) is defined as the distance over which fish can see and pursue prey. Fish are assumed to be able to detect all of the drift that comes within D to their left and right as they face into the current. The height of the capture area is the minimum of D and water depth, as fish are assumed more likely to be near the stream bottom than at middepth when feeding.

The ability of salmonids to detect prey depends primarily on the size of the fish and the size of the prey (Schmidt and O'Brien 1982). Hughes (1992) and Hughes et al. (2003) formulated successful models of drift feeding, using data from Schmidt and O'Brien (1982) for arctic grayling *Thymallus arcticus*. We model D using a linear equation fit to data from Schmidt and O'Brien (1982) for fish of 3–13 cm FL feeding on 0.2-cm-long prey; the results indicate that D increases at a decreasing rate with fish length. A logarithmic equation fits these data more closely but
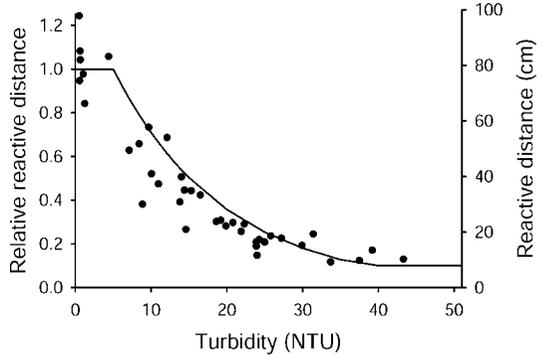

FIGURE 1.—Effect of turbidity on the relative reactive distance of fish in an individual-based model (line), together with data (circles) on the absolute reactive distance of brook trout from Sweka and Hartman (2001a).

predicts D to be negative for fish with FLs less than 2 cm and does not reproduce more recent observations that D continues to increase with size for very large trout (Hughes et al. 2003). The value of D is then adjusted for turbidity; the primary effect of turbidity on drift feeding appears to be reduction in the ability of fish to detect prey (Sweka and Hartman 2001a). We transformed the negative relationship between reactive distance and turbidity quantified by Sweka and Hartman (2001a) for brook trout *Salvelinus fontinalis* into a negative exponential curve for relative detection distance. We modified the Sweka and Hartman curve by setting a minimum relative reactive distance of 0.1, to take a conservative approach to the effect of turbidity on reactive distance above the range of empirical observations. Also, because Sweka and Hartman (2001a) observed considerable variability in reactive distance in the range of 0 to 5 nephelometric turbidity units (NTU), only turbidity above 5 NTU was assumed to affect the reactive distance of fish (Figure 1). We used the reactive distance–turbidity relationship in Sweka and Hartman (2001a) rather than the one for rainbow trout *O. mykiss* in Barrett et al. (1992), in part because the former used prey sizes that better reflect the diet of fish at our Little Jones Creek study site. Although alternative measures of water clarity may in some ways be preferable to nephelometric turbidity (Davies-Colley and Smith 2001), we use this measure in the model to take advantage of available information linking fish feeding success, water clarity, and long-term environmental monitoring data. We assume any bias or loss of precision from the use of nephelometric turbidity is modest in the context of other uncertainties and the magnitude of the population-level responses to alternative turbidity regimes produced by the model.

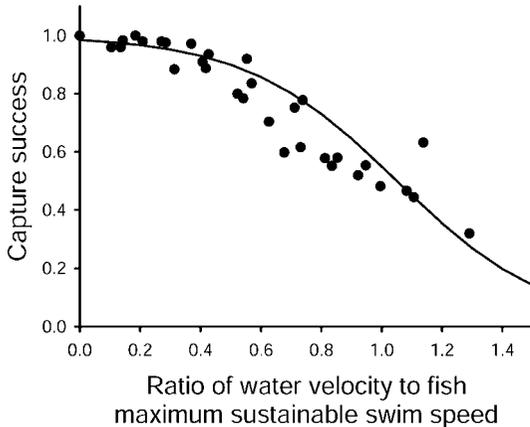We evaluate capture success (S) as the fraction of

FIGURE 2.—Capture success function used in the individual-based model (line) and the laboratory observations (Hill and Grossman 1993) on which the function was based (circles).

prey within the fish's detection distance that are actually caught. We model S as a function of water velocity relative to fish swimming ability, in part because at higher velocities, maneuvering quickly enough to capture prey is more difficult and fish must swim further back upstream to return to their feeding station (Hughes et al. 2003). Hill and Grossman (1993), measuring S for rainbow trout feeding on 0.2-cm prey, assessed capture success within each of three ranges: the inner 20% of D, 20–60% of D, and 60–100% of D. We averaged their results to evaluate S over the entire capture distance. For 35 combinations of fish size (3–13 cm FL), temperature (5–15°C), and water velocity (0–40 cm/s), S fit a logistic function of the ratio of water velocity to maximum sustainable swimming speed (U_{max} [cm/s], defined below) of the fish (Figure 2). The variable U_{max} appears to be useful for modeling capture success for two reasons: (1) it scales capture success by both fish length and temperature and (2) it takes into account the observations of Hughes et al. (2003) that large brown trout *Salmon trutta* actually swim at their sustainable (or even lower) speeds during the pursuit and capture of prey; U_{max} is intended to be a speed that healthy trout can maintain for hours. Because trout begin to use fast-twitch muscle fibers at 90–95% of "critical swimming speed" (U_{crit}; Wilson and Egginton 1994), we model U_{max} as 90% of U_{crit}. Our equation for U_{max} was developed from measurements of U_{crit} at several temperatures and fish lengths, for brown trout (Butler et al. 1992), cutthroat trout (Hawkins and Quinn 1996), and rainbow trout (Taylor et al. 1996; Alsop and Wood 1997; Myrick and Cech 2000). The results of these studies vary substantially, probably because of differences in experimental

techniques and the physiological condition of the fish. However, this literature indicates that U_{crit} increases approximately linearly with FL and nonlinearly with temperature, peaking at temperatures (T) around 10–15°C. We used the following polynomial regression to generate this model of sustainable swimming speed:

$$U_{max} = (2.8\text{FL} + 21) \cdot (-0.0029T^2 + 0.084T + 0.37).$$

Mortality risks.—Fish in the model face a variety of mortality risks, including predation and poor condition. Although the probability of surviving each source of mortality is a deterministic function of fish size and condition and habitat conditions, survival of each risk is determined daily for each fish by comparing its survival probability to a random number between 0 and 1. The survival probabilities for specific risk factors may be influenced by features of individual fish and the habitats they occupy. For the risks of predation from terrestrial and aquatic predators, these influences take the form of potential survival increase factors. For example,

daily probability of surviving terrestrial predators
= minimum probability of surviving
   terrestrial predators
   +[(1 − minimum survival probability)
     · (maximum survival increase factor)],

where the minimum probability of surviving terrestrial predators is a calibration constant that reflects the probability of surviving terrestrial predators under conditions in which fish are most vulnerable; survival increase factors for this risk include water depth, water velocity, fish size, the distance to hiding cover, and turbidity. Because this formulation utilizes the maximum survival increase factor, only one factor affects predation risk within a habitat cell under a specific set of conditions. We commonly model relationships between these factors and relative survival as logistic curves, to reflect that survival is probably relatively insensitive to these factors near their extremes. For example, to reflect greater risk from terrestrial predators for fish in shallow water (Harvey and Stewart 1991), the survival increase factor for habitat depth is an increasing logistic curve with a value of 0.1 in habitats 5 cm deep and 0.9 in habitats 100 cm deep. Following a variety of empirical observations (Cézilly 1992; Abrahams and Kattenfeld 1997; Johnson and Hines 1999), fish in the model can also experience lower predation risk under turbid conditions. Although few data address the turbidity dependence of interactions between salmonids and piscivorous fish (but see Gregory and Levings 1998), we assumed that turbidity of 50 NTU reduced the relative risk for trout from larger fish by about 60% compared with that in clear water (Figure 3; for
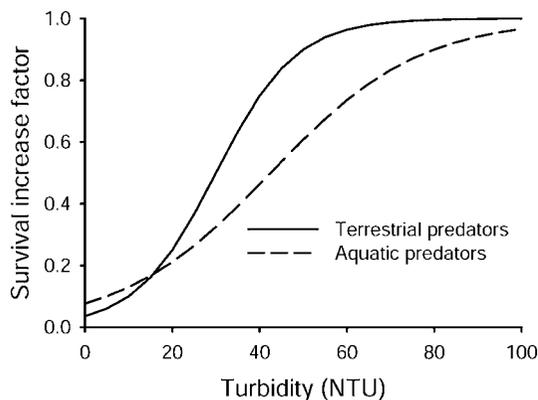
FIGURE 3.—Relationship between turbidity and survival increase factors for fish (see text) with respect to predation by terrestrial and aquatic predators.

example, the daily probability of surviving aquatic predators might increase from 0.95 in clear water to 0.98 in water of 50 NTU). We further assumed that predation risk from terrestrial predators decreases more rapidly with increasing turbidity than does risk from aquatic predators; turbidity of 50 NTU almost completely reduced the risk from terrestrial predators (Figure 3). Because predation risk influences habitat selection in the model, the model reproduces the observation that salmonids exhibit reduced predator avoidance in turbid water (Gregory 1993).

We assume that poor condition, expressed as the weight of a fish as a proportion of a standard weight for its length, increases the risk of mortality from starvation and disease. The daily probability of surviving starvation and disease can increase with condition factor, such that a fish at 60% of the standard weight for its length has a 4% probability of surviving 30 d, a fish at 70% of the standard weight has a 50% probability of surviving 30 d, and a fish at 90% of the standard weight has a 96% probability of surviving 30 d.

The additional mortality risks in the model are unlikely to vary significantly across the simulations presented here. Stranding mortality occurs when fish are unable to avoid very low or zero water depths when stream discharge decreases. The daily probability of surviving stranding is expressed as a function of the ratio of water depth in a habitat cell to fish length. High water velocity is included as a mortality risk because real fish must avoid habitat where extreme velocities would exhaust them. Temperature affects survival in the model only when it is well above 22°C, so it did not influence the simulations presented here, where temperature did not exceed 16°C. The energetic stress of spawning is represented by reducing an individual's mass by 20% when it spawns (similar to results from

Lien 1978), increasing its risk of poor-condition mortality.

Reproduction.—The model does not simulate the energetics of reproduction, but fish must meet size, age, and condition thresholds during a particular period (April and May in these simulations) to spawn. Fish meeting these thresholds are given a daily probability of spawning to produce a realistic temporal distribution. Depth, water velocity, and the amount of spawning gravel influence the usefulness of habitat cells for spawning. The survival of eggs in redds is influenced by discharge-dependent streambed scour and dewatering, temperature extremes, and superimposition of redds. The effects of fine sediment on eggs and embryos are not included in the model.

Calibration.—We calibrated the availability of food to produce a density and a size distribution similar to those of the coastal cutthroat trout at the Little Jones Creek study site. In an initial calibration we adjusted the availability of drifting prey to approximately match observed size distributions of age-1 and older fish, then adjusted benthic prey availability to match size distributions of age-0 fish. This approach to food calibration generally corresponds to observations that age-1 and older salmonids rarely obtain food via the search strategy only and where both strategies are available, drift feeding appears to be preferred (Fausch et al. 1997; Nislow et al. 1998). The calibrated drift concentration used in these simulations (4×10^{-10} g/cm^3 wet weight) falls within the range established with extensive, year-round measures of drift concentration from one salmonid-bearing river (Shearer et al. 2002). In simulations using this drift-based food calibration, the daily percentage of age-1 and older fish using the drift-feeding strategy averaged 86% under the baseline conditions in Little Jones Creek (the low-turbidity regime). To produce an alternative food calibration that assumed the primary source of food for age-1 and older fish was unaffected by turbidity, we calibrated the availability of search food to the observed size distributions of older fish and calibrated the availability of drift food to the size distributions of age-0 fish. In simulations using this search-based food calibration, the percentage of age-1 and older fish using the drift-feeding strategy averaged 16% under baseline (low-turbidity) conditions.

Simulations to Explore Turbidity Effects

To incorporate temporal variability in physical conditions, the model requires input files with daily values for turbidity, stream discharge, and temperature. Recall that turbidity influences drift-feeding success and predation risk, stream discharge determines water depth and velocity in habitat cells, and temperature

affects metabolism and egg development. Turbidity monitoring of Little Jones Creek and a more turbid stream in northwestern California, Freshwater Creek, provided the bases for the turbidity regimes we analyzed. Freshwater Creek is a coastal stream in the Franciscan Formation, which is characterized by graywacke, sandstone, shale, minor conglomerate, chert, and greenstone. Turbidity and discharge data were available from a station on Freshwater Creek that drains about 3,300 ha. Backscatter turbidity probes (Model OBS-3; D & A Instruments) were used at both Little Jones and Freshwater creeks. Turbidity and river stage were recorded 4–6 times per hour. Data from additional turbidity monitoring stations suggest these two sites capture the regional range of turbidity regimes in watersheds influenced by timber harvest and road building (Klein 2003).

The simulations included the period 1 October 1990 through 30 September 2005. We used measured values of discharge and turbidity at the Little Jones Creek study site for the period 1 July 1999 through 30 September 2005. We estimated stream discharge for the period before on-site data were available by using a relationship between discharge at the study site and a U.S. Geological Survey gauging station downstream on the Smith River ($r^2 = 0.96$ with a 1-h lag between sites). We then used 2–3 years of data from both Little Jones and Freshwater creeks to estimate the following relationships between daily mean turbidity and discharge:

Little Jones Creek scenario:

$$\text{turbidity (NTU)} = 2.5 \cdot \text{discharge (m}^3\text{/s)}$$
$$(r^2 = 0.68)$$

Freshwater Creek scenario:

$$\text{turbidity (NTU)} = 18.8 \cdot \text{discharge (m}^3\text{/s)}$$
$$(r^2 = 0.89).$$

We chose not to use power functions to describe the relationships between turbidity and stream discharge because of their tendency to overestimate turbidity at low discharge. We used the Little Jones Creek relationship to estimate turbidity before our field measurements began on 1 July 1999; we used the Freshwater Creek relationship to generate an alternative, high-turbidity regime for the entire 15-year simulation period using the Little Jones Creek discharge record. For these alternative scenarios, maximum turbidity reached 1170 NTU under the high-turbidity scenario and 155 NTU under the low-turbidity scenario. These maximum turbidity values correspond to suspended sediment of 3,370 mg/L for the high-turbidity scenario and 268 mg/L for the low-

turbidity scenario, based on relationships established for the two sites (Freshwater Creek: $r^2 = 0.96$, $n = 370$; Little Jones Creek: $r^2 = 0.98$, $n = 41$) through laboratory analysis of water samples from automated pumping samplers governed by turbidity (Lewis and Eads 2001). Reflecting natural variation, the high-turbidity scenario included extended periods of low turbidity during the dry season. For the 15-year period, median turbidity was 7 NTU for the high-turbidity scenario and 1 NTU for the low-turbidity scenario.

We measured water temperature at the Little Jones Creek study site from 12 December 1998 to 30 September 2005 using a temperature logger set to record data every 1.5 h. To estimate water temperature before the period of record, we developed separate regressions for each month, using daily mean air temperatures at Cave Junction, Oregon, to predict the water temperatures at the study site. The coefficients of determination (r^2) ranged from 0.5 to 0.8 for these regressions. The combination of measured and estimated physical data yielded predictably large temporal variation in discharge and turbidity and a benign thermal regime for cutthroat trout at Little Jones Creek (Figure 4). The consistency in the temperature regimes for estimated and measured periods (before and after 12 December 1998) indicates that the strength of the relationships used to estimate water temperature did not have important consequences for the simulations.

We explored the effects of turbidity and food availability in the individual-based trout model by completing 10 replicate simulations of various scenarios. In constructing scenarios of interest, the two key factors were turbidity level and the extent of food available in the drift versus search food categories. Turbidity scenarios included the two extreme turbidity regimes derived from field data and three intermediate-turbidity regimes, reflecting 10, 25, and 50% of the difference in the slopes of the low- versus high-turbidity regimes established from field data. Drift versus search food scenarios included the alternative calibration scenarios described above and three intermediate levels of drift versus search food availability. To explore the potential for temporal variation in food availability to affect population dynamics under high turbidity, we created scenarios in which food availability was greater than the drift-based calibration values according to season or streamflow. These scenarios were designed to generally illustrate how populations might respond to variation in food availability, not to closely reflect any documented real-world patterns. A seasonal pattern for drift consisted of the drift-based calibration level of food in summer and fall, with 2× this level in winter and 1.5× in spring. In a scenario where drift food varied

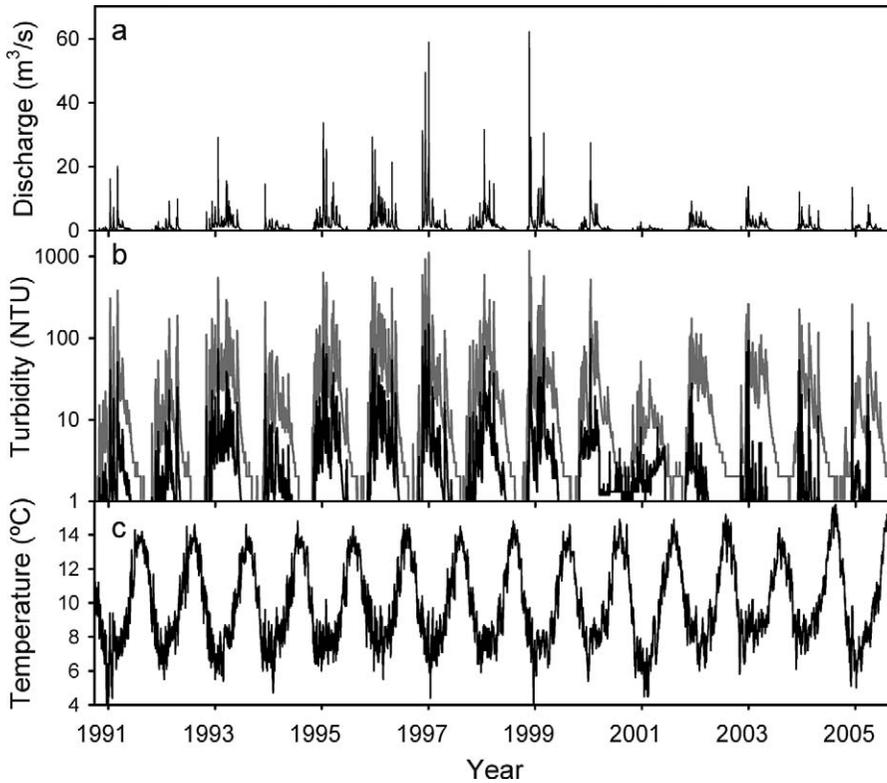FIGURE 4.—Daily mean (**a**) discharge, (**b**) turbidity, and (**c**) water temperature used in 15-year simulations of a coastal cutthroat trout population in Little Jones Creek. In panel (b), the black line indicates turbidity in Little Jones Creek (the low-turbidity scenario in the simulations) and the gray line depicts the high-turbidity scenario.

with streamflow, availability increased linearly from the calibration value at the mean annual minimum streamflow up to 5× the calibration value at the mean annual maximum streamflow. We also created a parallel scenario in which search food increased linearly from its drift-based calibration value at the mean annual minimum streamflow up to 5× the calibration value at the mean annual maximum streamflow. These two scenarios with food concentration linked to streamflow yielded mean values for food availability 20% higher than their drift-based calibration values. Finally, to evaluate the sensitivity of the results to our estimate of the effects of turbidity on predation risk, we created scenarios where turbidity extremely reduced risk. In the most extreme scenario, turbidity offered a survival increase factor for terrestrial predation of 0.9 at 10 NTU rather than at 50 NTU and a survival increase factor for aquatic predation of 0.9 at 10 NTU rather than at 80 NTU. All simulations used the same model of habitat at the Little Jones Creek study reach and the same input data for daily streamflow (Figure 4a) and temperature (Figure 4c). The initial populations for all the simulations had the same

density and age distribution characteristic of the Little Jones Creek study site. The initial lengths of individuals were randomly selected from age-specific distributions. The initial mass of all fish was determined by the overall length–weight relationship for cutthroat trout at the study site. Fish were initially randomly placed in habitat cells.

In evaluating the results, we first inspected habitat selection, feeding strategies, and sources of mortality of individual fish during the simulations to evaluate the credibility of any differences among turbidity regimes in population-level results. We then examined the patterns in population biomass over the 15-year simulation period under the various turbidity and food scenarios simulated.

Results

Inspection of habitat use, feeding strategies, and sources of mortality in the simulations suggested that individual fish responded realistically to changes in turbidity. Under baseline values for food availability that assumed the predominance of drift food, fish occupied shallower, slower water under high turbidity
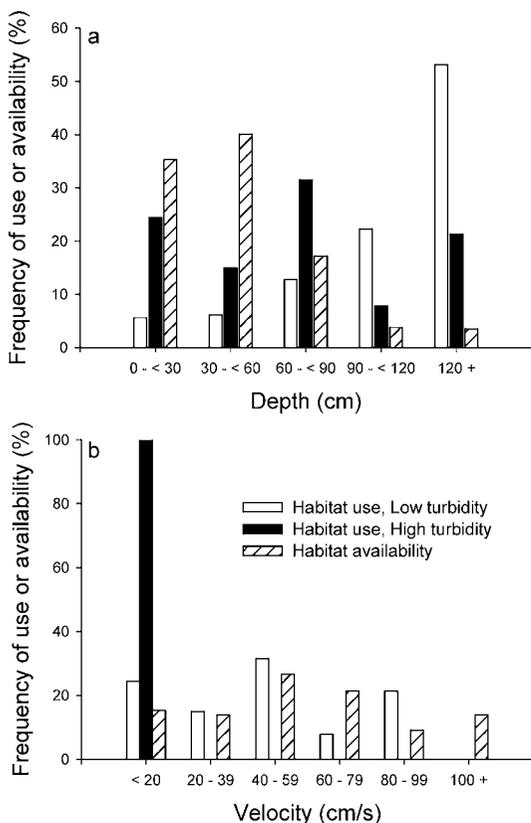
FIGURE 5.—Habitat use by adult coastal cutthroat trout in an individual-based model, along with the availability of simulated habitat, under two different levels of turbidity but otherwise identical physical conditions. Availability data for water velocity in (**b**) reflect mean water velocity in habitat cells. Turbidity in this example was 6 NTU in the low-turbidity scenario and 53 NTU in the high-turbidity scenario. Note that some habitat cells contain velocity shelters; fish occupying these shelters are assumed to swim at 30% of the mean water velocity in that cell.
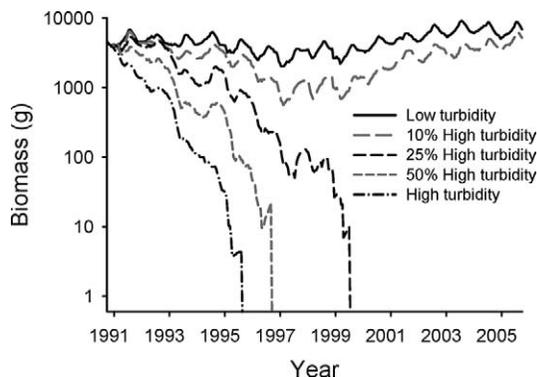

FIGURE 6.—Individual-based model results for total fish biomass of a simulated coastal cutthroat trout population under a drift-based food calibration and five different turbidity regimes. Values represent the median of 10 simulations under each turbidity regime.

(Figure 5) when predation risk at such locations would be relatively low and the benefits of drift feeding elsewhere would be reduced because of lower reactive distances to drifting prey. Under the same conditions (including the predominance of drift food), fish also consistently used the active search strategy more frequently in higher turbidity. For example, on one simulated day with turbidity at 53 NTU in the high-turbidity regime, all fish age 1 and older used the search-feeding strategy but fewer than 25% of these fish experienced net energy gain. On the same simulated day under the low-turbidity regime, with turbidity at 6 NTU, more than 95% of fish age 1 and older fed on drift, about 85% of these experiencing net energy gain. The low- and high-turbidity scenarios

yielded similar patterns in the sources of mortality, although terrestrial predators consumed a slightly higher proportion of fish in simulations of the lower-turbidity regime. This minor difference is reasonable, given that the fish in the model incorporate both food acquisition and short-term mortality risks in habitat selection. Fish that lost condition during periods of prolonged high turbidity would occupy habitats with relatively high predation risk during subsequent periods of clear water, if those habitats offered high net energy intake.

Turbidity regime strongly influenced the population-level outcomes of our simulations in which drift food predominated. The low-turbidity regime produced modest variation in biomass over time within individual simulations, parallel to our 1999–2005 censuses at the study site. In contrast, fish abundance under the high-turbidity regime invariably fell to zero (Figure 6). Results for intermediate-turbidity scenarios with the drift-based food calibration suggested significant effects on fish in modest increases in turbidity. For example, although populations persisted under the 10% high-turbidity regime, median biomass was substantially lower than under the low-turbidity regime (Figure 6), particularly during years with high streamflow around the middle of the 15-year simulation period. Years without successful spawning were common in the higher-turbidity regimes. This pattern is linked to seasonality in the condition of older fish in the alternative scenarios. Fish under more turbid regimes were commonly in very poor condition during late winter and were unable to equal the condition of fish in the low-turbidity scenario before the spring spawning period (Figure 7). Field data from Little Jones Creek on 15 dates from 10 March 1998 through 22 April 1999 (*n*
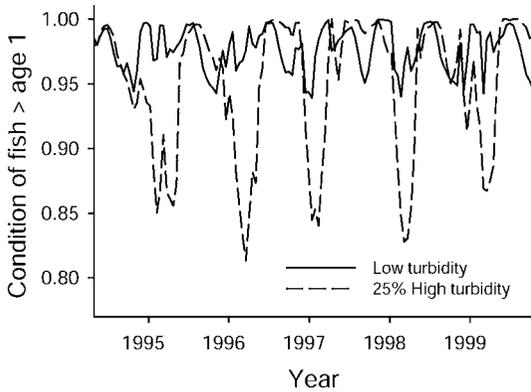
FIGURE 7.—Mean condition for fish older than age 1 in two sets of simulations that varied only in turbidity regime. Condition is defined as the ratio of actual fish mass to the expected mass of a fish of that length based on data from the Little Jones Creek study site.

= 12–28 fish per sampling date) provide support for the low-turbidity simulation results for fish condition: condition was highest in summer, followed by steadily decreasing condition into the late dry season, with occasional decreases in the wet season; minimal mean condition for fish older than age 1 was 0.95 (B.C. Harvey, unpublished data.), parallel to the simulation results (Figure 7).

Because the capture success of model fish using the search strategy is not influenced by turbidity, high-turbidity simulations with a search-based food calibration yielded consistently high biomass throughout the simulation period, similar to the low-turbidity, drift-based food calibration results (Figure 8). However, only the intermediate-food-availability scenario most similar to the search-based food calibration also maintained the population for 15 years under the high- (Figure 8), 50%-high-, and 25%-high-turbidity regimes. In contrast, all combinations of drift and search food availability maintained populations in the low-turbidity regime (Figure 8).

Scenarios based on drift food calibration values but with variable, elevated food concentrations yielded less severe but still dramatic effects of turbidity on population persistence. The seasonal drift food scenario with high values for drift in both the winter ($2\times$ the calibration value) and spring ($1.5\times$ the calibration value) allowed the population to persist under the 25%-high-turbidity regime but not under higher-turbidity regimes. Increasing drift- or search-food concentration with streamflow also yielded persistence under the 25%-high-turbidity regime (Figure 9).

The results appeared to be insensitive to the effect of turbidity on predation risk. For example, all high-
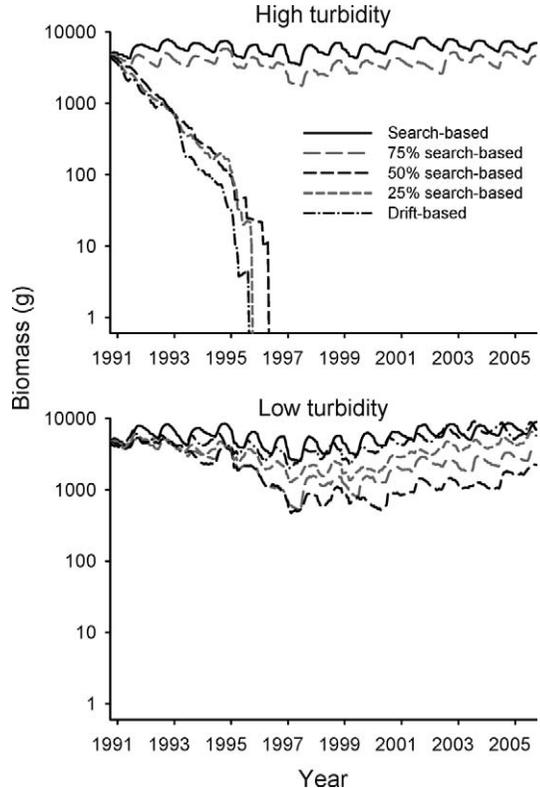

FIGURE 8.—Total biomass of coastal cutthroat trout in an individual-based model under the high- and low-turbidity regimes with various levels of search food versus drift food. The capture success of fish consuming search food was assumed to be insensitive to turbidity.

turbidity and 50%-high-turbidity simulations under the drift-based food calibration, in which a turbidity of 10 NTU provided almost complete protection from predation, still resulted in rapid extinction.

Discussion

Previous research has documented that the behavior of individuals in the model used here parallels a variety of behaviors exhibited by real fish occupying clear water (Railsback and Harvey 2001). Patterns in the behavior and performance of individuals under elevated turbidity in the simulations herein also corresponds with a variety of empirical observations. For example, adult coastal cutthroat trout in the model occupied stream margins during high streamflow and turbidity, which parallels real-world observations in Little Jones Creek (Harvey et al. 1999). An increase in the use of search feeding under turbid conditions paralleled results for brook trout in an artificial stream (Sweka and Hartman 2001b). The patterns in the condition of the fish in the model correspond with slower growth by
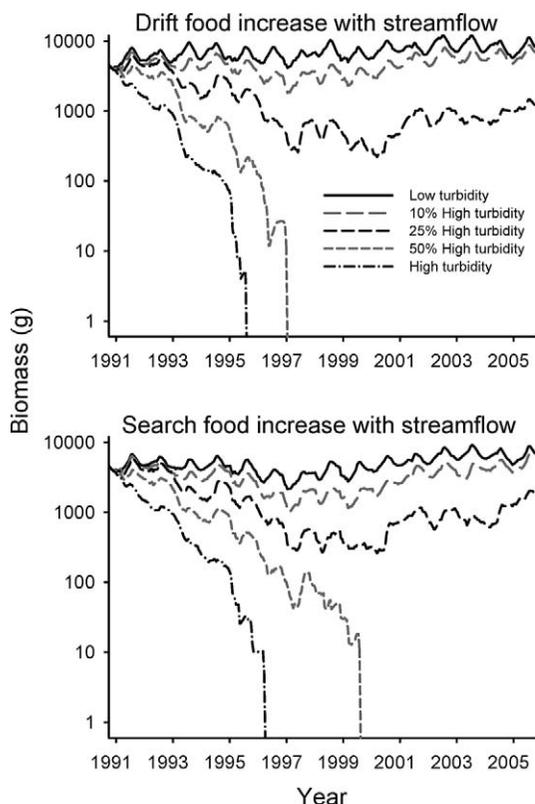
FIGURE 9.—Total biomass of coastal cutthroat trout in an individual-based model under alternative turbidity regimes in which either drift food or search food increases linearly with streamflow relative to drift-based food calibration values.

steelhead (anadromous rainbow trout) and coho salmon *O. kisutch* in artificial channels characterized by chronic elevated turbidity (Sigler et al. 1984) and with the results for rainbow trout subjected to pulses of turbidity in streamside channels (Shaw and Richardson 2001).

Under various food availability scenarios and low-turbidity conditions, the population-level results also paralleled empirical observations, specifically, our observations of modest variation in coastal cutthroat trout abundance over 8 years in Little Jones Creek. However, some population-level results for simulations of elevated-turbidity regimes appear to conflict with field observations. In particular, the simulations under scenarios in which drifting prey dominate the food supply suggest that salmonid populations are not sustainable in some natural settings that do, in fact, support fish. For example, a reach on upper Freshwater Creek containing a resident trout population has a turbidity regime between the 25%- and 50%-high-turbidity scenarios used here (in terms of NTU-days

per year). Similarly, another nearby stream, Jacoby Creek, has both a resident rainbow trout population and a turbidity regime very similar to the 50%-high-turbidity scenario used here. What might explain this apparent conflict between simulation results and field observations?

One explanation, illustrated by our simulation results with relatively high levels of search food, could be the ability of fish to acquire food even when turbidity yields short reactive distances to drifting prey. In fact, adult stream-dwelling trout can feed on the benthos in turbid conditions (Tippets and Moyle 1978), and in standing water the feeding rate of salmonids can be relatively insensitive to turbidity in the range 20–160 NTU (Gregory 1994; Rowe et al. 2003). Diet samples from rainbow trout in Jacoby and Little Jones creeks also indicate successful feeding during high-turbidity, high-streamflow conditions (White and Harvey 2007), suggesting both that salmonids can use nonvisual cues for feeding and that food remains available during high streamflow and turbidity under some field conditions.

As illustrated by several simulations presented here, greater food availability during elevated turbidity might partially offset the effect of turbidity on feeding success. However, empirical observations do not provide broad support for the scenarios we tested with elevated concentrations of drifting invertebrates in winter or with streamflow. For example, extensive drift sampling in the Maruia River of New Zealand yielded the highest concentrations of drift in midsummer, followed by early summer and then winter (Shearer et al. 2002). Strong increases in total drift were documented during rainstorm-elevated streamflows in a small Oregon stream (Anderson and Lehmkuhl 1968), but these were apparently the result of relatively constant concentrations of individuals (number/m^3) across streamflows. The pattern of increasing search food with streamflow that we tested may more closely approach reality than do the elevated drift food scenarios. Although the abundance of benthic prey in flashy gravel-bed streams such as Little Jones Creek probably does not peak in the winter or early spring (Suren and Jowett 2006), the possibility remains that the availability of prey potentially subject to capture across a broad range of turbidity may be greater during high streamflows. Given that greater streambed mobility may enhance the displacement of benthic invertebrates, the potential for elevated food availability during high streamflows may be greatest in streams with elevated loads of fine sediment.

Another possible explanation for the contrast between model results with drift food calibrations and field observations is that the model used here did not include behavioral or physiological flexibility of real

fish that might ameliorate the effects of elevated turbidity on feeding success and population dynamics. For example, the fish in the model were limited to feeding during the day, but salmonid behavior can include feeding and hiding during both day and night, with significant consequences for energetics and predation risk. Model fish also could not store energy as lipids. However, the severity of population declines in high-turbidity simulations with drift-based food calibration suggests these mechanisms are unlikely to fully explain persistence under elevated turbidity, if fish rely mostly on sight feeding.

Where turbidity varies significantly within stream networks, avoidance of elevated turbidity could reduce its population-level effects. This hypothesis is supported by the avoidance of elevated turbidity by salmonids and other stream fishes on small spatial scales (Bisson and Bilby 1982; Sigler et al. 1984); salmonids also are clearly capable of large-scale seasonal movements (e.g., Peterson 1982). However, this mechanism is unlikely to operate in broadly disturbed watersheds pervaded by elevated turbidity, such as our Jacoby Creek study area. Under these conditions, avoidance of high turbidity might lead to population-level losses through emigration, particularly in watersheds with barriers to upstream movement.

Although the simulations presented here incorporated only two linkages between suspended sediment and the performance of individual fish, the individual-based model approach is clearly capable of including additional linkages, such as the effect of elevated suspended sediment on the survival of salmonid eggs and embryos (Reynolds et al. 1988) and sublethal physiological effects on juveniles and adults (Newcombe and MacDonald 1991). More generally, the approach can also be used to address indirect effects of elevated sediment inputs on stream fish. For example, elevated sediment loads may (1) reduce the abundance of the invertebrate prey of stream fishes (Suttle et al. 2004; Cover et al. 2008), (2) lower habitat diversity and winter cover for fish (Hartman et al. 1996), (3) reduce the availability of substrate suitable for spawning by salmonids (Magee et al. 1996), (4) increase the probability of redd scour by decreasing substratum particle size (Montgomery et al. 1996), and (5) increase the probability of habitat loss in summer by elevating the stream channel above bedrock, thereby reducing surface water (May and Lee 2004). Finally, elevated sediment loads can be accompanied by additional alterations of the physical environment such as changes in thermal and hydrologic regimes, and interactions among the effects of these changes can have important consequences for stream fish (Hartman

et al. 1996). Incorporating more of these processes into fish population models may be critical in some settings.

The conflict between our simulation results that predict local extinction for drift-feeding fish and the persistence of resident salmonid populations in streams with relatively high turbidity, however, suggests that modeling efforts incorporating additional effects of sediment on fish may not be the most profitable next step in the effort to estimate the effects of elevated sediment loads on salmonid populations. A better understanding of the effects of elevated suspended sediment and streamflow on food availability and the capabilities of stream salmonids to capture prey using nonvisual cues seems to be critical.

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