

Assessing Population-Level Effects of Zinc Exposure to Brown Trout (*Salmo trutta*) in the Arkansas River at Leadville, Colorado

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ABSTRACT

We assessed population-level risk to upper Arkansas River brown trout (*Salmo trutta* L.) due to juvenile exposure to Zn. During spring, individuals in the sensitive young-of-the-year life stage are exposed to elevated Zn concentrations from acid mine drainage. We built and used a simple life-history population model for the risk assessment, with survival and fecundity parameter values drawn from published data on brown trout populations located in the United States and Europe. From experimental data, we derived a toxicity model to predict mortality in brown trout fry after chronic exposure to Zn. We tested sensitivity of risk estimates to uncertainties in the life-history parameters. We reached 5 conclusions. First, population projections are highly uncertain. A wide range of estimates for brown trout population growth is consistent with the scientific literature. The low end of this range corresponds to an unsustainable population, a physically unrealistic condition due to combining minimum parameter values from several studies. The upper end of the range corresponds to an annual population growth rate of 281%. Second, excess mortality from Zn exposure is relatively more predictable. Using our exposure-response model for excess mortality to brown trout fry due to Zn exposure in the upper Arkansas River at the mouth of California Gulch in the years 2000 to 2005, we derived a mean estimate of 6.1% excess mortality (90% confidence interval = 1.6%–14.1%). Third, population projections are sensitive to all the parameters that contribute to the onset of reproduction. The weight of evidence suggests that young-of-the-year survival is most important; it is inconclusive about the ranking of other parameters. Fourth, population-level risk from Zn exposure is sensitive to young-of-the-year survival. If young-of-the-year survival exceeds 20% to 25%, then the marginal effect of excess juvenile mortality on population growth is low. The potential effect increases if young-of-the-year survival is less than 20%. Fifth, the effect of Zn on population growth is predictable despite high uncertainty in population projections. The estimate was insensitive to model uncertainties. This work could be useful to ecological risk assessors and managers interested in using population-level endpoints in other risk assessments. *Integr Environ Assess Manag* 2013;9:50–62. © 2012 SETAC

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INTRODUCTION

This article presents a population-level ecological risk assessment (ERA) for brown trout (*Salmo trutta* L.). Brown trout are salmonids native to Europe that were introduced to rivers of the United States as game fish. The population of interest is located in the upper Arkansas River, just downstream of the 16.5-square-mile California Gulch mining district of Leadville, Colorado. Historical mining in this area has led to acid mine drainage that contributes Zn to the Arkansas River during spring snowmelt. The California Gulch is of interest for this ERA because Zn concentrations in the river during spring snowmelt, attributable to acid mine drainage from historical mining operations, are high enough to possibly kill some of the brown trout fry that might be present near the mouth of California Gulch (USEPA 2011).

This ERA combines exposure, toxicity, and life-history information to estimate population-level risk. The general approach involves 4 steps:

1. Projecting the brown trout population's vital rates with the life-history model, focusing on $\lambda_1 = \exp(r)$, where r is the per capita rate of increase for an unrestricted population, commonly known as the intrinsic growth rate (Lotka 1925). This first step is intended to establish a "baseline" projection of the population dynamics wherein it is assumed that the population is not exposed to Zn.
2. Integrating Zn exposure and toxicity data to estimate the "excess" mortality to brown trout fry.
3. Modifying parameters of the life-history model to account for organism-level effects from Zn exposures.
4. Examining the effect of these modifications on the brown trout population's vital rates. The change in the brown trout population's intrinsic growth rate (Δr) due to exposure of fry to elevated Zn concentrations during spring snowmelt is the ERA's population-level measurement endpoint. The measurement endpoint is used, with other less readily quantified information, to semiquantitatively characterize effects on the brown trout population

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in the upper Arkansas River at the mouth of California Gulch caused by Zn toxicity to young-of-the-year fish.

Taken individually, the elements of this ERA are not new, but the use of results of a conventional organism-level ERA as input into a population-level ERA is still relatively unconventional and untested. Also relatively new is the use of Δr as the measurement endpoint in an ERA. The synthesis of elements presented here draws attention to emerging ideas in ERA.

The article heavily emphasizes methods of analysis and interpretation. An unusually great deal of critical discussion about the methods of analysis and interpretation is presented in the methods section of the article. The article particularly focuses on uncertainties in the life-history model and their implications for risk management decisions. It demonstrates the feasibility of combining exposure, toxicity, and life-history models to estimate population-level risk. It demonstrates that useful conclusions about the population-level risk posed by a toxicant are possible, even when the life history of a population of interest is highly uncertain. Connecting a life-history model to statistical information about organism-level effects from exposure to a toxicant can reduce uncertainty about the ecological relevance of the organism-level ecotoxicological endpoints (Spromberg and Meador 2005) and aid understanding of specific risks to populations (Dearfield et al. 2005).

METHODS

In a life-history model for brown trout, model parameters were estimated from the scientific literature, and vital statistics, including λ_1 , were projected. Both a probabilistic exposure estimate based on measured Zn concentrations in surface water during spring runoff, and an exposure-response model for brown trout fry based on mortality in laboratory Zn toxicity tests were developed. By combining the exposure and effects models, excess mortality to brown trout fry from Zn exposure was estimated. The life-history model's estimated survival rate for young-of-the-year was adjusted to account for the excess mortality, and vital statistics were then recomputed to examine the effect of Zn exposure on the population.

Because the life-history parameter values used were not specific to the upper Arkansas River and their uncertainties were high, sensitivity analyses were performed to identify the parameter uncertainties with the greatest influence on vital statistics. The risk management implications of those uncertainties were also examined.

Life-history model

The life-history model for brown trout is comprised of a projection matrix A , which contains survival (S) estimates, fecundity (F) estimates, and a population vector n . The projection interval is 1 year. The population in projection interval $t + 1$ is calculated as the product of the projection matrix and the population vector for the previous projection interval

$$n(t + 1) = A * n(t), \quad (1)$$

where $n(t)$ represents the population vector at projection interval t , and A represents the projection matrix.

The life-history model was built as a life-stage model using all age classes up to maturity as individual life stages, and

grouping all mature life stage fish aged 5 years or older. The model is female only; as described below, fecundity varies over an order of magnitude and is not precise enough to warrant specifying the sex ratio of the hatch. Similarly, survival estimates, although not sex-specific, are assumed to apply to females. These assumptions are reasonable for the purpose of this analysis, which is to examine the sensitivity of population-level risk from juvenile exposure to Zn to uncertainties in the life-history parameters. Life stages preceding maturity were defined by age class to be consistent with the way in which survival estimates, typically based on annual stream surveys, are presented in the scientific literature. The 0+ age class begins at "swim-up" (the end of the alevin life stage, which comprises hatched fish with yolk sacs that feed entirely on yolk and live in the gravel nest [redd]); egg and alevin survival are thus included in fecundity (defined here as the product of eggs per spawning female and proportion of spawners in the age class) estimates. Survival estimates represent the proportion of individuals surviving from one projection interval (year) to the next. Because the model's projection interval equals the duration of membership in an age class, survival represents the probability of passing from one life stage (age class) to the next, up until maturity, at which point all surviving fish remain in the same life stage. Regarding fecundity, the model assumed that fish would begin to reproduce at the 3+ age class; however, not all fish in the 3+ and 4+ age classes reproduced. All fish were assumed to be reproducing in the mature life stage. The projection matrix for this model is

$$A = \begin{pmatrix} 0 & F_1 & F_2 & F_3 & F_4 & F_m \\ S_0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_2 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_3 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_4 & S_m \end{pmatrix}, \quad (2)$$

where A represents the projection matrix, S_i represents the survival of age class i , and F_i represents fecundity of age class i .

The data required for the life-history model include survival and fecundity, by age class and projection interval, for all age classes in the model. The projection matrix was populated with survival and fecundity range estimates for populations of brown trout from waters of the United States and Europe. These estimates were used to define ranges for the survival and fecundity parameters assumed to be relevant to the population of brown trout inhabiting the Arkansas River. The literature estimates and parameter values selected for the model for each age class are summarized below. Detailed results are presented as supplemental material (Supplemental Data Tables S1–S3).

Recognizing that there is likely to be additional information not included in the life-history model, including specific knowledge of the upper Arkansas River brown trout population and knowledge of other relevant work, reasonable confidence in parameter estimate accuracy may be held based on 3 considerations. First, in some cases the authors asserted that their data were similar to data previously obtained by other investigators. Second, the estimates obtained were imprecise, which made them more likely to be accurate (albeit less informative). Third, the variability in survival and fecundity in the literature reflected phenomena that could be

identified, such as absence of winter habitat from a site and dispersal associated with high-flow conditions. Conditions affecting the site-specific estimates for the upper Arkansas River at the mouth of California Gulch are likely to yield values that fall within the ranges found in the literature. Were new information to become available, the model parameterization would be expected to evolve, with changes expressed as a tightening rather than shifting of parameter ranges.

Survival

Young-of-the-year (0+ age class, S_0). S_0 values vary greatly from site to site, with an estimated range of 0.001 to 0.64 (0.1%–64% apparent survival to 1 year post-emergence). However, with the exception of the upper end of the S_0 range from Crisp (1993) (see also Table S1), these are apparent survival estimates, reflecting both losses due to dispersal from the study site and losses due to mortality. Therefore, the estimates are biased by unknown and varying degrees to underestimate S_0 . Lund et al. (2003), for example, studied 3 sites in southeastern Norway and obtained data that yielded S_0 estimates of 0.64, 0.29, and 0.05. They attributed the lowest value to emigration from a site with little or no suitable winter habitat, stating that “the high estimated survival rate of brown trout in Osa suggested that permanent emigration from the study site was low.” Thus, the contribution of dispersal to apparent survival estimates seems to be an important source of uncertainty in S_0 estimates. The $S_0=0.05$ estimate from Lund et al. (2003) is comparable to many of the S_0 estimates derived from the literature, suggesting the possibility that dispersal losses during the first year of life may be an important factor in the apparent survival estimates, and that true mortality may be closer to 50% than to 95% to 99%. Beyond this insight, the Lund et al. (2003) article is useful because it begins to answer the question of how to design sampling programs and build models to separate dispersal losses and mortality.

The objective was to understand effects on the brown trout population in the upper Arkansas River at the mouth of California Gulch caused by Zn toxicity to young-of-the-year fish. Given the absence of site-specific data and the central role of 0+ age class survival (S_0) in the model, the analysis must reflect the full range of values for S_0 suggested by the literature (see Table S1). The decision was to vary S_0 over 2 orders of magnitude ($S_0=0.005$, 0.05, and 0.5) to represent its entire estimated range. Although it is suspected that values at the low end of the range (perhaps S_0 values <0.05) are attributable to habitat effects that drive up losses due to dispersal and/or to high egg densities (that could increase dispersal losses, mortality, or both), the possibility of high baseline mortality (i.e., in the absence of elevated Zn exposure) cannot be ruled out. For this reason, the low end of the S_0 range has been retained.

A second possible source of variability in S_0 is density dependence. Elliott (1994), for example, has shown that the brown trout population of Black Brows Beck, in the Lake District of England, exhibited density-dependent survival during the critical period (the first 1–2 months post-emergence). Survival as a function of age (up to 120 days post-emergence) was density-dependent above egg densities of 20 to 40 eggs/m². S_0 would be independent of egg density for egg densities below approximately 20 eggs/m².

One of the 2 very low survival probabilities ($S_0=0.003$, Black Brows Beck) (Elliott 1987) was attributed by the author to density-dependent mortality at high egg density (100 eggs/m²), with survival 10 times as high ($S_0=0.03$) at egg densities less than approximately 17 eggs/m². In the second case ($S_0=0.001$) (Crisp 1993), low survival probability was attributed not to density-dependent mortality, but to differences across 5 streams in winter survival of the 0+ age class. Based on Lund et al. (2003), one possible explanation for the low apparent survival is that lack of winter habitat in the streams with the lowest apparent survival could be causing emigration to the downstream reservoir or other feeder streams.

1+ Age class (S_1). Literature-based survival estimates for the 1+ age class (S_1) are given in Table S2. Two interrelated studies from France (one of which investigated a coastal river on the English Channel and rivers in the Alps and Pyrenees; Table 1 of Gouraud et al. [2004] and Table 2 of Baglinière and Maise [2002]) found consistent S_1 values of approximately 0.4. A study of streams in southeastern Norway (Olsen and Vøllestad 2001a) yielded S_1 estimates closer to 0.3, and a study of Wilfin Beck in the English Lake District (Elliott 1987) yielded S_1 estimates closer to 0.6. A study of a Wisconsin river (Avery et al. 2001) yielded S_1 estimates in 2 consecutive cohorts of 0.22 and 0.34. An S_1 range of 0.3 to 0.6 in was used in this analysis.

2+ Age class (S_2). The data for estimating survival for the 2+ age class (S_2), given in Table S3, are from the same sources as the S_1 data, except that the Norwegian study (Olsen and Vøllestad 2001a) did not provide survival data for this age class. The Wisconsin study's 2+ age class data (Avery et al. 2001), which are from a different river than the 1+ age class data, yielded an S_2 estimate of 0.52. The French and English studies found that 1+ and 2+ age class survival rates are similar. The S_2 range of 0.3 to 0.6 in this analysis is the same as the S_1 range.

Table 1. Parameter values selected for the population projection matrix

Parameter	Minimum	Midrange	Maximum
S_0	0.005	0.05	0.5
S_1	0.3	0.45	0.6
S_2	0.3	0.45	0.6
S_3	0.2	0.35	0.5
S_4	0.2	0.35	0.5
S_m	0.2	0.3	0.4
F	200	1000	2000
m_1	—	0	—
m_2	—	0	—
m_3	—	0.5	—
m_4	—	0.5	—
m_m	—	1	—

3+ Age class (S_3). All survival data for the 3+ age class (S_3), given in Table S3, are from the French studies that were also used for estimating S_1 and S_2 . The data suggest that survival declines somewhat at the 3+ age class. An S_3 range of 0.2 to 0.5 was used in this analysis.

4+ Age class (S_4). The survival data for the 4+ age class (S_4), given in Table S3, are again from the French studies and are indistinguishable from the S_3 data. The S_4 range in this analysis (0.2–0.5) is the same as the S_3 range.

Mature life stage (S_m). The survival data for mature fish cover 5+ to 9+ age classes (Table S3) and come from 2 sources: the French studies (Gourard et al. 2004; Maisse and Baglinière 1990; Baglinière and Maisse 2002), which found no survival beyond the 5+ age class, and a study of a lake in central Norway (Berg et al. 1998), which found survival to age 9+. On the basis of these data, an S_m range of 0.2 to 0.4 was chosen.

Fecundity

Literature values for European and US brown trout populations were used to define ranges for the fecundity parameters in the projection matrix (Table S4). With 1 exception (Taube 1976), the literature did not report fecundity by age class; instead studies related fecundity to size (Elliott 1984; Garcia and Brana 1988; McFadden et al. 1965; Taube 1976). Fecundity estimates ranged from 93 eggs/female in Kernec Creek (Brittany, France) to 4895 eggs/female in Lake Michigan. Most estimates of eggs per female were in the hundreds, with a few in the low thousands. For this analysis fecundity was varied by an order of magnitude, from 200 to 2000 eggs/female. As noted previously, egg and alevin survival should be factored into the fecundity estimates for the model. Based on the literature (e.g., Olsen and Vøllestad 2001b), egg and alevin survival (combined) is estimated to be approximately 0.95. Because this fecundity estimate is too imprecise to justify multiplying the range by 0.95, the round values of $F = 200$ and 2000 eggs/female were used.

An additional factor that enters into the fecundity estimates for the model is the fraction of females in the age class that have reached maturity (i.e., spawners). Brown trout have been documented as reaching maturity from ages 1+ to 5+ (McFadden et al. 1965; Garcia and Brana 1988; Crisp and Beaumont 1995; Olsen and Vøllestad 2005), with individual variation depending on the population. McFadden et al. (1965) and Garcia and Brana (1988) observed females reaching maturity in their first year, with the majority reaching maturity within the second year. Others indicate that the majority of females reach maturity from ages 2 to less than 5 years (Crisp and Beaumont 1995; Olsen and Vøllestad 2005). Because it is assumed that true fecundity is age independent, average fecundity in an age-class cohort can be estimated as

$$F_i = F \times m_i, \quad (3)$$

where F_i represents fecundity in age class i , F represents fecundity at maturity, and m_i represents fraction of mature females in age class i .

By definition, $m_m = 1$. For preliminary modeling purposes it was assumed that all age 1+ and 2+ fish are immature

($m_1 = m_2 = 0$) and that half of the age 3+ and 4+ fish are mature ($m_3 = m_4 = 0.5$). The modified projection matrix, incorporating these fecundity modeling assumptions, is

$$A = \begin{pmatrix} 0 & 0 & 0 & 0.5 \times F & 0.5 \times F & F \\ S_0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_2 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_3 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_4 & S_m \end{pmatrix}, \quad (4)$$

where A represents the projection matrix, and S_i represents survival of age class i .

Excess mortality model

Hardness-dependent chronic Zn toxicity reference values were obtained for nonacclimated brown trout using the equation

$$TRV_H = \exp[0.9805 \times \ln(H) + 1.402], \quad (5)$$

where TRV_H represents hardness-dependent chronic Zn toxicity reference value, and H represents hardness (mg/L).

Equation 5 was derived using data from several 90-day studies by the Colorado Department of Wildlife (CDOW) on the effects of water hardness on Zn toxicity to nonacclimated early life stage and juvenile brown trout (Hoff et al. 2005). Hazard quotients (HQs) were then calculated for the laboratory data by dividing dissolved surface water concentration C ($\mu\text{g/L}$) by TRV_H . Regressing fraction mortality against HQ produced the exposure-response model presented in Figure 1.

This model was used to estimate excess mortality in 0+ age class brown trout from exposure to Zn at station AR-3A on the upper Arkansas River, at the mouth of California Gulch. Samples of surface water were collected annually from spring runoff (typically \approx March 15–June 15) as part of EPA's ongoing remedial investigation at the site. The spring runoff was the main focus of the investigation, because this is where Zn concentrations tend to be highest, and spring is the time of year when brown trout fry are likely to be exposed. Water samples were filtered and analyzed for the concentration of dissolved Zn (Figure 2). Because Zn concentrations tended to decline between 1997 and 2000, estimated excess mortality was used from only the spring 2000 through spring 2005 data. Distributions were fit to the sample data using BestFit (Palisade Corporation 2004). The best-fitting model was a 4-parameter beta distribution ($\chi^2 = 5.18$, $p = 0.82$).

The data and fitted distribution are shown in Figure 3. The mean as well as the 5th and 95th percentiles of the fitted distribution were used as a range of estimates of the excess mortality to 0+ age class brown trout ($mort_{Zn}$) at the mouth of California Gulch.

Baseline projections

Table 1 presents the parameter ranges selected for the projection matrix. Once survivals and fecundities were estimated, MATLAB 7.1 (MathWorks 2005) was used to project λ_1 and w_1 for 9 scenarios of the projection matrix. Equations 6 through 8 each represent 3 scenarios, defined by substituting $S_0 = 0.005$, $S_0 = 0.05$, and $S_0 = 0.5$.

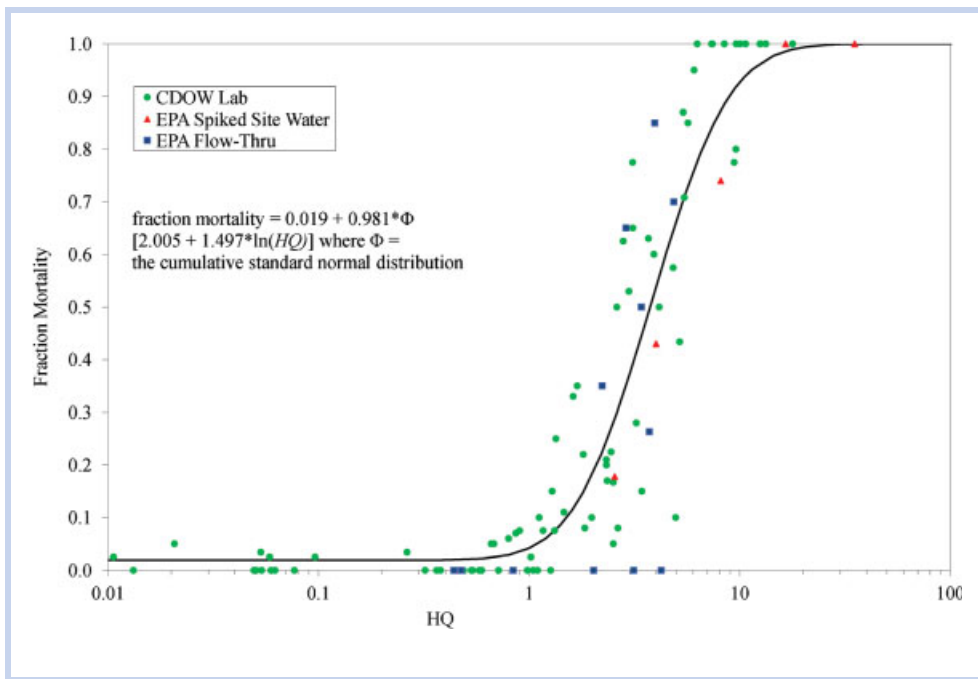


Figure 1. Hardness-adjusted exposure-response model for 0+ age class nonacclimated brown trout.

Minimum values scenario:

$$A = \begin{pmatrix} 0 & 0 & 0 & 100 & 100 & 200 \\ S_0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.30 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.30 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.20 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.20 & 0.20 \end{pmatrix} \quad (6)$$

Midrange values scenario:

$$A = \begin{pmatrix} 0 & 0 & 0 & 500 & 500 & 1000 \\ S_0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.45 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.45 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.35 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.35 & 0.30 \end{pmatrix} \quad (7)$$

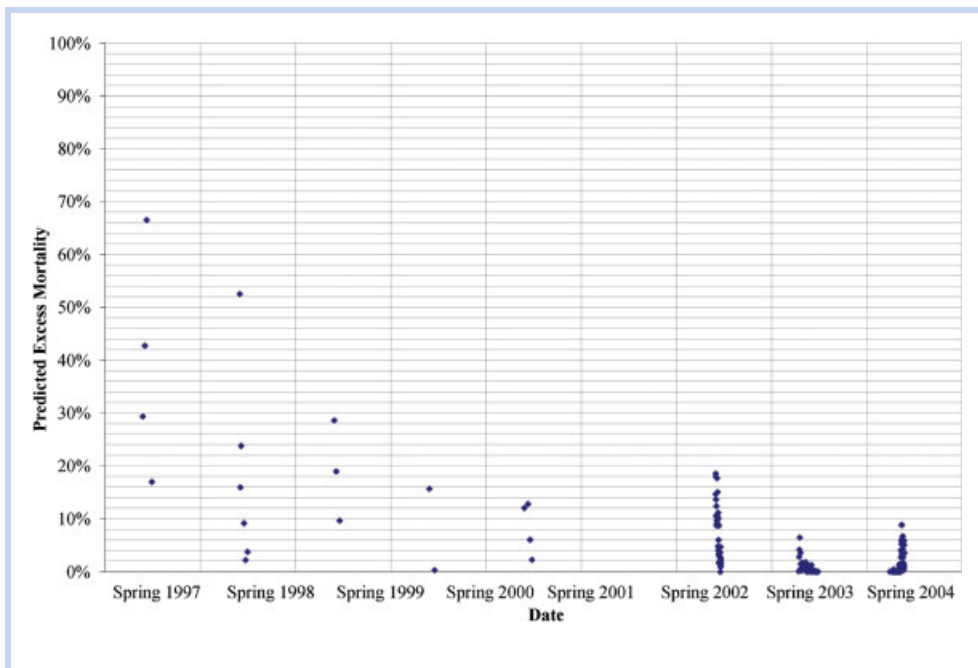


Figure 2. Predicted excess mortality of brown trout fry from exposure to Zn at station AR-3A on the upper Arkansas River, 1997 to 2005.

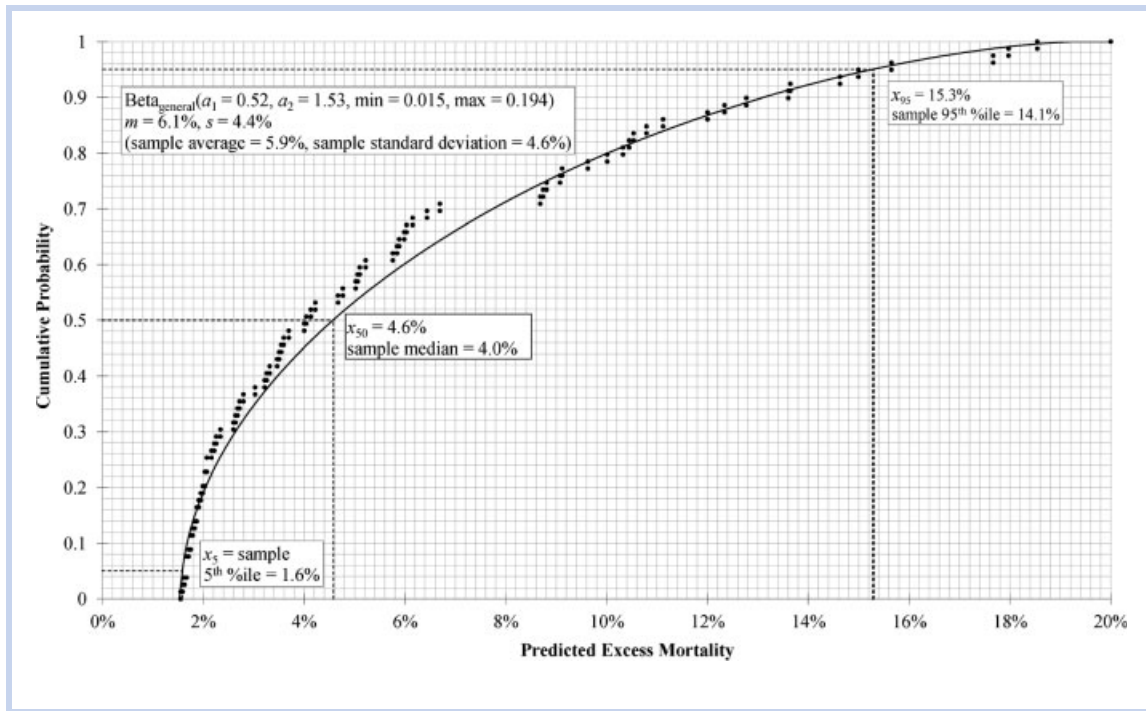


Figure 3. Cumulative probability distribution fit to predicted excess brown trout fry mortality data at station AR-3A, on the upper Arkansas River, 1997 to 2005.

Maximum values scenario:

$$A = \begin{pmatrix} 0 & 0 & 0 & 1000 & 1000 & 2000 \\ S_0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.60 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.60 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.50 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.50 & 0.40 \end{pmatrix}. \quad (8)$$

The model was also run for intermediate values of S_0 to the extent that this was useful for defining baseline model behavior.

The dominant eigenvalue of the projection matrix equals λ_1 and the right eigenvector equals w_1 . The model satisfies the conditions for ergodicity: it has a steady-state population growth rate and a stable population growth structure independent of the assumed initial stage class populations. The conditions necessary for ergodicity are not necessarily met in the upper Arkansas River. For example, spatial structure in the brown trout population, with 1-way dispersal into the reach at the mouth of California Gulch, would violate the irreducibility condition necessary for ergodicity. Nonetheless, the model provides a useful tool for examining the population-level effects of excess mortality in juvenile brown trout. One could draw an analogy to experimental systems used for toxicity testing. Both are useful simplifications in that they provide a means to study potential effects in the absence of confounding environmental factors.

Sensitivity and uncertainty analysis

Sensitivity and elasticity are 2 closely related metrics commonly used for uncertainty analyses (Morgan and Henrion 1990). Sensitivity and elasticity of λ_1 were calculated to each of the parameters in the projection matrix for each of the 9 scenarios described by Equations 6 through 8.

A nominal range sensitivity analysis was also run. Starting with the midrange scenario, with $S_0 = 0.05$, each model parameter (i.e., the nonzero elements a_{ij} of the projection matrix A) was changed one at a time, first to its minimum value, solving for λ_1^- , then to its maximum value, solving for λ_1^+ . The difference between λ_1^+ and λ_1^- was calculated, and repeated for the next model parameter.

The sensitivity (U_s) of model output λ_1 to parameter a_{ij} is given by

$$U_s(a_{ij}, \lambda_1) = \left[\frac{\partial \lambda_1}{\partial a_{ij}} \right]_{A_0}. \quad (9)$$

Higher sensitivity indicates greater influence of a_{ij} on λ_1 (at A_0). One problem with this metric is that it is scale dependent, which can be a problem when comparing sensitivities across models or model runs. For example, if fecundities are expressed as numbers of progeny per female, sensitivities to fecundities would be greater—by a factor of 2 if the sex ratio is 1:1—than if fecundities were expressed as numbers of progeny per individual.

Elasticity, or normalized sensitivity (U_E), has the advantage of being scale independent. It represents the proportional change in a model output relative to the proportional change in a model parameter. Adding elasticities around loops in the life cycle graph gives the relative importance of those loops as contributors to changes in λ_1 . Elasticity is given by

$$U_E(a_{ij}, \lambda_1) = \left[\frac{\partial \lambda_1}{\partial a_{ij}} \right]_{A_0} \times \frac{a_{ij}^0}{\lambda_1^0}. \quad (10)$$

Aside from scale dependence, the main difference between sensitivity and elasticity is in how they represent the importance of parameters that take on large or small numerical values (Caswell 2001). Depending on one’s perspective, it could be said that sensitivity “exaggerates”

the importance of parameters that take on smaller numerical values, or that elasticity exaggerates the importance of parameters that take on larger numerical values. This scale dependence is of particular concern in life-history modeling because survivals are proportions (i.e., they take on values between 0 and 1), whereas fecundities are nonnegative real numbers that, for some populations' life history strategies, are orders of magnitude greater than 1. As such, the sensitivities and elasticities calculated for a life-history model can be quite different from one another.

Both sensitivity and elasticity ignore the actual level of uncertainty about the value of each model parameter. A parameter with low sensitivity (the term sensitivity being used generically to represent either of the 2 sensitivity metrics: sensitivity and elasticity) but high uncertainty may be just as important as a parameter with high sensitivity but low uncertainty. Nominal range sensitivity (U_R) addresses this limitation by calculating the model output (λ_1) at high and low values of each parameter (a_{ij}) in turn, holding all other parameters at their nominal values

$$U_R(a_{ij}, \lambda_1) = \lambda_{a_{ij}^+} - \lambda_{a_{ij}^-}. \quad (11)$$

The limitations of nominal range sensitivity analysis are 2-fold. First, in varying parameters 1 at a time, nominal range sensitivity analysis provides no information about the importance of parameter dependencies. Second, it requires consistency in defining parameter ranges to draw valid conclusions about the relative importance of parameter uncertainties. For example, if for 1 parameter a_{ij}^- and a_{ij}^+ correspond to the 1st and 99th percentiles of the parameter's uncertainty distribution, and for another parameter a_{ij}^- and a_{ij}^+ correspond to the 10th and 90th percentiles of the parameter's uncertainty distribution, the analysis will over-emphasize the importance of the first parameter's uncertainty.

Sensitivity, elasticity, and nominal range sensitivity of λ_1 were calculated to each of the parameters in the projection matrix. Sensitivity and elasticity were calculated for each of the 9 scenarios described by Equations 6 through 8. For the nominal range sensitivity analysis, parameters were varied one at a time from minimum to maximum value, holding all other parameters constant at the midrange value (using $S_0 = 0.05$). Sensitivity results are presented as supplemental information (Supplemental Data Tables S5–S8).

Risk analysis

The purpose of this ERA was to better understand how reducing young-of-the-year survival would affect population growth rate, and then to compare the mortality that would reduce population growth rate below a sustainable level to predicted young-of-the-year mortality from Zn exposure in the upper Arkansas River. This comparison provides insight into whether baseline and proposed water quality conditions are protective of the brown trout population of the upper Arkansas River. Other life stages could be exposed to Zn in spring runoff as well, but the focus here was on young-of-the-year Zn exposure, and how it might affect the population.

The method of analysis is to find the value of S_0 for which the projection matrices given by Equations 6 through 8 have a dominant eigenvalue of 1.0, the threshold at which the brown trout population would theoretically become unsustainable

(S_0^*). The estimated Zn mortality ($mort_{Zn}$) is then added to young-of-the-year brown trout on the upper Arkansas River at the mouth of California Gulch, yielding a critical value for S_0 (S_0^{critical}) for each of the 3 modeled scenarios (minimum, midrange, and maximum)

$$S_0^{\text{critical}} = S_0^* + mort_{Zn}. \quad (12)$$

The 3 S_0^{critical} values are then compared to the range estimate for S_0 to get a sense of whether and to what degree, based on current information as codified by the model, sustainability of the brown trout population is projected to be threatened by Zn toxicity.

This method of analysis uses several simplifying assumptions:

- It is not based on site-specific vital rates (survival and fecundity). Site-specific data could, for example, be used to quantify the following:
 - the influence of dispersal on apparent survival estimates (that is suspected to be an important factor in the nonsite-specific range estimate used for S_0 in this analysis); and
 - the influence of size and age on fecundity.
- The model does not account for potentially important metapopulation processes, in particular:
 - movements of individuals between locations (on fast or slow time scales relative to demographic processes) (Charles et al. 1998a, 1998b, 2000); and
 - spatial variation in vital rates (e.g., due to food supply, population density, water temperature differences).

A size class model with an empirically derived size/fecundity relationship would be more useful than the model presented in this article for making management decisions regarding fisheries (e.g., fishing regulations aimed at preserving the most effective spawners). That added complexity was not warranted given the purpose of the analysis, however, which was to examine the sensitivity of population-level risk from juvenile exposure to Zn to uncertainties in the life-history parameters.

Not quantifying the influence of dispersal on apparent survival estimates is suspected to impart a conservative bias (margin of safety) to the analysis by causing S_0 to be significantly underestimated. Site-specific fecundity data would narrow the range of fecundity estimates, making “worst-case” projections less bad and “best-case” projections less good. Considered at the organism level, incorporating metapopulation processes might reduce Zn exposure estimates, thereby reducing the population-level effects.

RESULTS

Baseline projections

Population growth rate projections for the midrange, minimum, and maximum values models are presented in Figure 4. Any value of r less than 0 represents an unrealistic scenario, which means that the hypothetical populations represented by those scenarios (i.e., by the combinations of survivals, fecundities, and modeling assumptions used to define the scenario) are projected to be unable to sustain themselves.

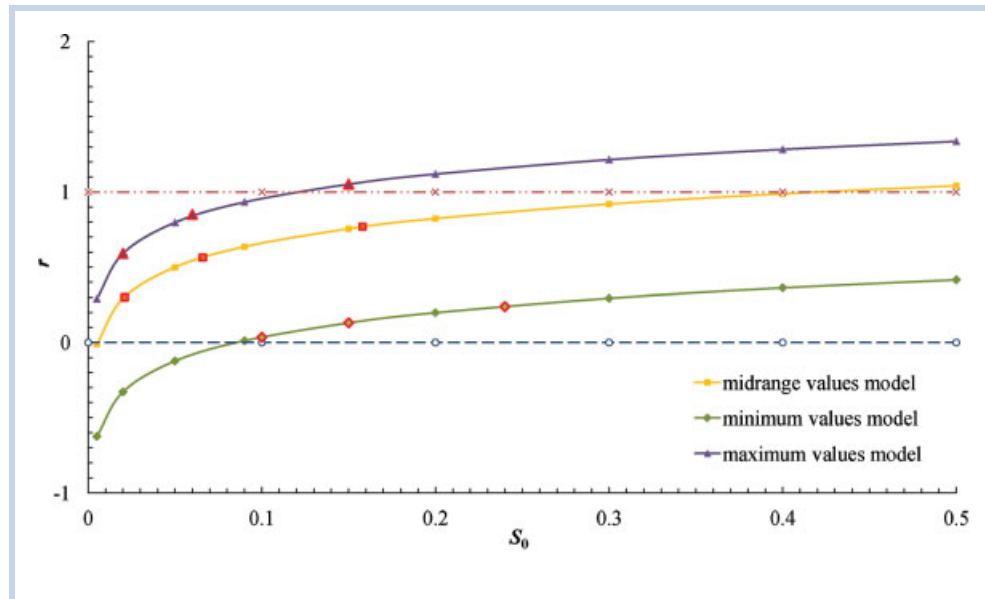


Figure 4. Intrinsic annual per capita rate of increase (r) as a function of young-of-year survival (S_0) for midrange, minimum, and maximum values model. Note: $r = 1$ indicates annual doubling under conditions that permit unrestricted population growth; $r = 0$ indicates zero growth. Red-bordered markers indicate the 90% CI on critical 0+ age class survival ($S_0^{\text{critical}} = S_0 + \text{mort}_{\text{Zn}}$) for each of the 3 models, assuming no acclimation to Zn exposure and no population-level processes compensating for individual mortality.

The minimum values scenario curve in Figure 4 shows how r is projected to change with S_0 when all other varied model parameters (i.e., F , S_1 , S_2 , S_3 , S_4 , and S_m) are set equal to their minimum values. It can be seen that the minimum values scenarios with $S_0 = 0.005$ ($r = -0.63$) and $S_0 = 0.05$ ($r = -0.12$) are unrealistic, and that r is less than 0 when $S_0 < 0.086$. In other words, first-year survival would have to be at least 8.6% for a hypothetical brown trout population represented by the minimum values model to be sustainable; thus, S_0 less than 0.086 is unrealistic. The midrange scenario with $S_0 = 0.005$ falls just below the sustainability threshold $r = -0.01$, but the midrange and maximum scenarios are theoretically sustainable for virtually all values of S_0 in the prescribed range of 0.005 to 0.5.

As shown in Figure 4, the population growth rates are fairly flat above S_0 values of approximately 0.20 to 0.25 for all 3 sets of scenarios. This observation suggests that if first-year survival is above 20% to 25%, then removing stressors contributing to 0+ age class mortality (including Zn exposure) will have little beneficial effect on population growth rate, regardless of the other model parameter values.

The unrealistic scenarios for low S_0 values are not surprising; the literature suggests that systems with such low first-year survivals are suitable as spawning habitat, but that they do not provide sufficient rearing habitat (Elliott 1987; Crisp 1993; Lund et al. 2003). Such sites should not be considered in isolation when studying population dynamics, because they are not suited for sustaining a population.

The systems with the low S_0 values that caused us to extend the range of S_0 to 0.005 for the baseline analysis were Black Brows Beck in the English Lake District, and feeder streams to a reservoir on the River Tees in northeastern England. It was previously noted that the $S_0 = 0.003$ value from Black Brows Beck is attributed to density-dependent mortality at high egg density (100 eggs/m²), and that apparent survival is a factor of 10 higher ($S_0 = 0.03$) at egg densities less than approximately 17 eggs/m² (Elliott

1987). The $S_0 = 0.001$ value from the River Tees system (Crisp 1993) might be due to absence of suitable rearing habitat in reservoir feeder streams, which are pieces of a larger system that would be expected to have ample rearing habitat.

Excluding the low values obtained from Black Brows Beck and the River Tees system would suggest 0.02 as a revised lower limit on the range of S_0 values. That still would leave some unrealistic scenarios when the other varied model parameters are set equal to their minimum values, suggesting that the minimum parameter values for m_i (fractions of mature females in stage i , $i = 1, 2, 3, 4, m$) or the modeling assumptions (e.g., low migration effects) are incorrect.

Sensitivity analysis

The model's projections were found to be sensitive to all parameters that contribute to the onset of reproduction: S_0 , S_1 , S_2 , and F_3 . Although the weight of evidence suggests that S_0 is most important—both in terms of sensitivity of and uncertainty about λ_1 —model projections also are sensitive to assumptions about the onset of reproduction and survival of later prereproductive life stages.

The sensitivity analysis of the baseline matrix places the greatest influence on λ_1 with 0+ class survival at $S_0 = 0.005$ and $S_0 = 0.05$. As S_0 increases to 0.5, its influence on λ_1 decreases to the point where it becomes similar to that of S_1 and S_2 . In fact, for the minimum and midrange value models, S_1 and S_2 have somewhat more influence on λ_1 than does S_0 when S_0 is high ($S_0 = 0.5$). In other words, the population might be as sensitive to losses of older fish as it is to losses of young-of-the-year if S_0 is high and other parameters are low to midrange (in terms of the ranges defined for the model).

The elasticity analysis of the baseline matrix revealed that changes to the first-, second-, and third-year survival rates (S_0 , S_1 , and S_2) will have the greatest per unit effect on λ_1 , followed by fecundity of 3+ age class fish. The importance of

F_3 suggests further analysis of the modeling assumptions about m_i , the fraction of mature females in stage i .

Loop analysis indicates that changes affecting reproductive output of 3+, 4+, and 5+ age class fish will have similar per unit effects on λ_1 under baseline conditions, across the range of S_0 values examined. This finding is as expected, given the relative importance of S_0 , S_1 , and S_2 , which contribute to all 3 reproductive loops in the model.

Nominal range sensitivity analysis results generally are consistent with the earlier findings, except that they place somewhat more importance on F_3 given its relatively higher uncertainty than S_1 and S_2 . The nominal range sensitivity analysis suggests that uncertainty about S_0 is the most important contributor to uncertainty about λ_1 , followed by F_3 and then by S_1 and S_2 (that are of equal importance). The preeminence of S_0 holds even if the minimum S_0 value is raised from 0.005 to 0.02 (as suggested by the baseline projection results). Increasing the minimum S_0 value from 0.005 to 0.02 reduces its nominal range sensitivity from 1.85 to 0.50. In comparison, the next highest nominal range sensitivities are 0.50 for F_3 and 0.26 for S_1 and S_2 .

The overall findings of the sensitivity analysis suggest that the model's projections are sensitive to all parameters contributing to the onset of reproduction, and that although the weight of evidence suggests that S_0 is most important, both in terms of sensitivity of and uncertainty about λ_1 , model projections are also sensitive to assumptions about the onset of reproduction and survival of later prereproductive life stages.

Risk analysis

The baseline projections identified 0.086 as S_0^* for the minimum values model (Eqn. 6), where S_0^* is the value of S_0 at which the model projects zero population growth (Figure 4). An S_0 less than S_0^* would indicate an unsustainable population. For the midrange values model (Eqn. 7),

$S_0^* = 0.0053$, and for the maximum values model (Eqn. 8), $S_0^* = 0.0012$.

Adding the excess mortality estimates to S_0^* (Eqn. 12) gave a range of estimates for S_0^{critical} . The midrange values model projects that sustainability of the brown trout population requires 0+ age class survival to be at least 7% (90% confidence interval = 2%–16%). Comparable survival rates for the minimum and maximum values models are 15% (10%–24%) and 6% (2%–15%), respectively.

Graphically, the effect of excess mortality on the population appears as a shift of the population growth rate curves of Figure 4 to the right, by Zn mortality ($mort_{Zn}$) units (Figure 5). Although the data represented by the curves in Figure 5 are not directly observable, the curves help show how much better off a population would be (as measured by the intrinsic growth rate, r , of the population) if excess fry mortality were reduced or eliminated (i.e., by reducing Zn exposure). S_0 plotted on the x-axis of Figure 5 is 0+ age class survival in the absence of Zn exposure.

To illustrate, Figure 6 focuses on the midrange curves from Figures 4 and 5. Both Figures 4 and 5 depict S_0 in the absence of excess mortality but differ in that the y-axis of Figure 4 shows r in the absence of excess mortality, where z the y-axis in Figure 5 shows r in the presence of excess mortality. The excess mortality shown on the curve from Figure 5 is 6.1%—the predicted excess brown trout fry mortality data for the period 2000 to 2005 at station AR-3A, as presented in Figure 3. Figure 6 shows that a population with $S_0 = 0.20$ in the absence of excess mortality would have an intrinsic growth rate of 0.74 in the presence of excess mortality and of 0.82 in the absence of excess mortality.

Figure 6 may be used to answer the question of how much better off the population would be in the absence of excess mortality, given a baseline estimate of S_0 . Project up from the x-axis to the upper curve and then right to the lower curve to determine S_0 in the absence of excess mortality. Projecting back left to the y-axis (gray line) would give the value of r in

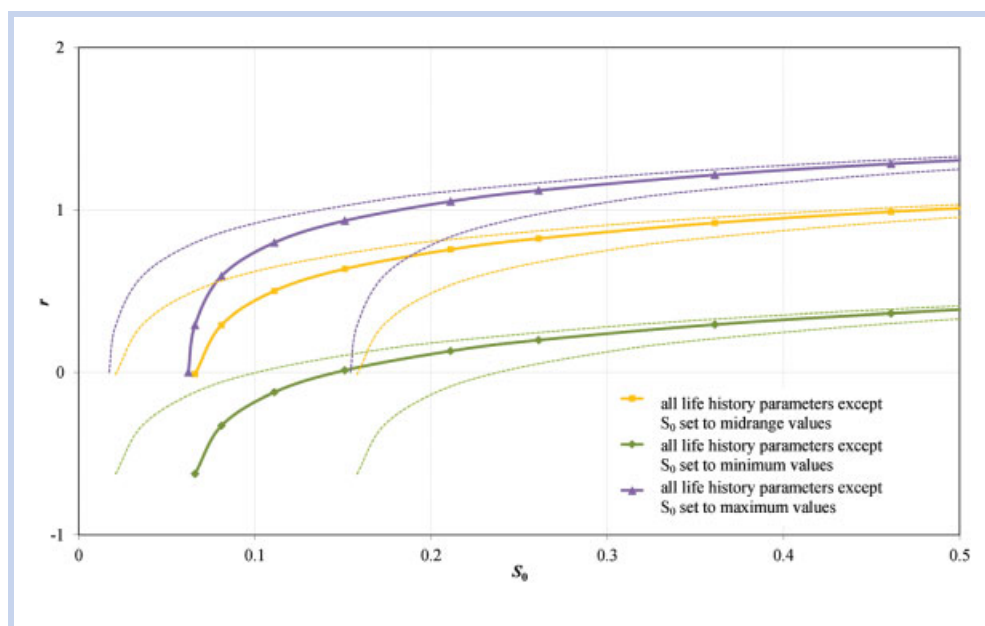


Figure 5. Intrinsic annual per capita rate of increase (r) as a function of young-of-the-year survival (S_0) after adjust for excess mortality of brown trout fry from zinc expose. Note: The solid lines correspond to mean (6.1%) excess mortality from Zn expose; dashed lines represent the 90% confidence interval accounting for uncertainty about excess mortality.

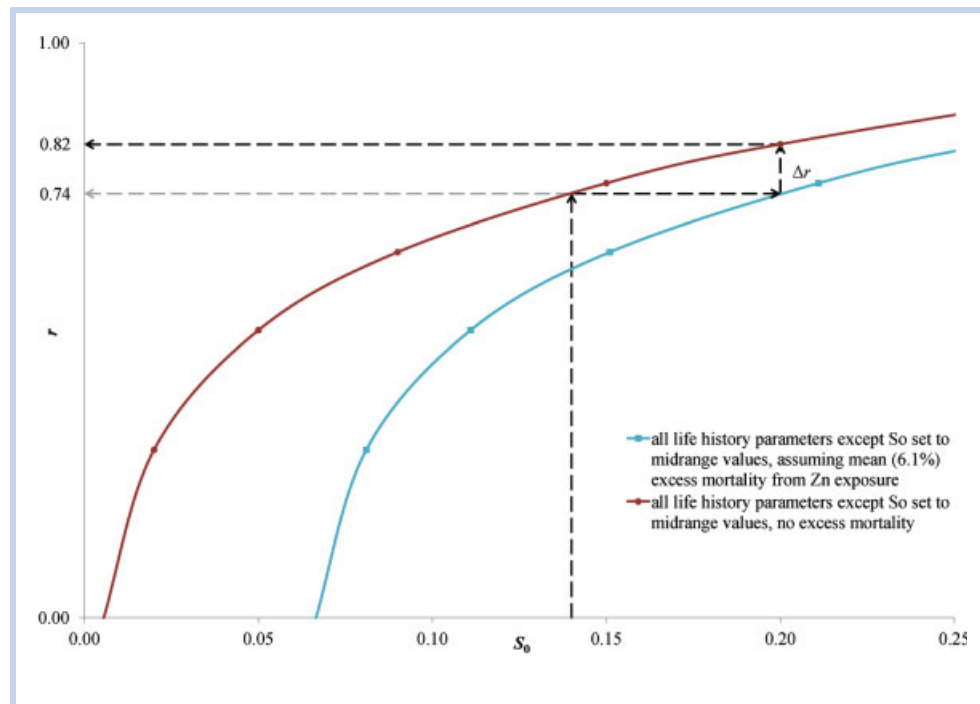


Figure 6. Example of the use of r vs. S_0 curves to assess population-level risk of excess mortality to the 0+ age class.

the presence of excess mortality, and projecting up to the upper curve then across to the y-axis gives the value of r in the absence of excess mortality. The difference between these 2 r values (Δr) is a measure of how much better off the population would be in the absence of excess mortality.

For example, if a mark-recapture survey found that the baseline $S_0 = 14\%$, the specific situation depicted on Figure 6 would apply: the population's intrinsic per capita annual rate of increase, currently 0.74, would increase by 0.08 to 0.82 in the absence of the excess Zn mortality. To put this into more practical terms, over a 5-year span, the population would have the intrinsic capacity to increase approximately 16-fold (1.74^5) under current conditions versus approximately 20-fold (1.82^5) without the excess mortality from the exposure of fry to Zn.

As noted previously, the effect of reducing Zn exposure on population growth appears to be low if first-year survival is greater than approximately 20% to 25%. Figure 6 makes this easier to see. As the slope of the growth rate curve flattens out, the Δr associated with any particular ΔS_0 declines. For example, if the mark-recapture survey in the previous example had found $S_0 = 0.25$, the Δr would have been $(0.93 - 0.88) = 0.05$. Over a 5-year span the population would have the intrinsic capacity to increase approximately 23-fold under current conditions versus approximately 26-fold without the excess mortality from the exposure of fry to Zn.

DISCUSSION

Although the site-specific relationship between S_0 and r —the (S_0, r) curve—for the upper Arkansas River at the mouth of California Gulch is unknown, the existence of such a curve is known; it probably looks something like one of those plotted on Figure 4. From the example of Figure 6, it is also known how to examine the population-level impact of Zn toxicity. It involves shifting the (S_0, r) curve to the right by

an amount corresponding to the excess mortality caused by fry exposure to Zn and then making certain projections to find the impact on r , which represents the intrinsic capacity of the population to grow.

The importance of the different sources of uncertainty in this risk analysis depends on the question being asked. If the question is whether r falls above or below some defined threshold, then the uncertainties about survival and fecundity parameters become most important because, as can be seen in Figure 4, they have the effect of shifting the (S_0, r) curve up and down. If on the other hand, the question is the change in r (Δr) when a stressor is removed, then the (S_0, r) curve's shift to the right becomes most important; this shift is a function of the magnitude of the excess mortality and its associated uncertainty.

Regardless of the specific (S_0, r) curve, the relevant observation is the vertical distance between 2 points on that curve. Uncertainty about excess mortality determines the distance projected from left to right in the risk analysis, and therefore the identity of the second point in the vertical distance comparison. Uncertainty about survival and fecundity parameters tends to shift the curve up and down, with relatively little effect on the vertical distance between 2 points on the curve. In practical terms, this means that even though the uncertainties about survival and fecundity values may be large, they might be relatively unimportant for predicting population-level risk. If impact is measured in terms of Δr , then the uncertainty about site-specific excess mortality, even if low, can be more important than all of the uncertainties in the life-history model, even if those are high. This is of practical importance because uncertainty about site-specific excess mortality is more readily reduced than is uncertainty about site-specific life history of the brown trout population.

With that said, several notable uncertainties in the life-history model could be decreased with further refinements.

Generally, these issues relate to site-specific conditions that could influence survival and fecundity characteristics of brown trout populations. To estimate realistic survival and fecundity parameter values, range estimates were compiled from literature describing research on European and US brown trout populations. Although these range estimates are species specific, they do not precisely describe any particular population. Differences in survival and fecundity among populations can be attributed to differences in environmental conditions, genetic conditions, or both. Site-specific data would be needed to address these uncertainties, if warranted based on risk management considerations.

Given the importance of S_0 , one type of model refinement that might be warranted is modification to account for metapopulation processes. This would be feasible; Baldwin et al. (2009), for example, used a projection matrix model developed in MATLAB and incorporated metapopulation processes into an analysis that investigated how the effect of pesticides on acetylcholinesterase (AChE) activity might reduce survival of outmigrating juvenile chinook salmon. For the California Gulch model, a logical next step would be to break out the 0+ age class into at least 2 life stages, the first of which would be the critical period for juvenile mortality. Significantly higher mortality rates have been recorded in the first 3 months postemergence than in the remaining 9 months of the first year postemergence (Elliott 1993; LeCren 1973; Mortensen 1977). This difference matters because population size would drop relatively quickly in the critical period, affecting movements of individuals between locations and vital rates within a location (e.g., growth rates and onset of maturation might be accelerated because high mortality early in the first year increases per capita food supply).

The importance of the early fecundity parameter (F_3) identified by the elasticity analysis suggests that time to maturity of female brown trout is an important source of uncertainty, but it was given relatively cursory treatment in this ERA. Another factor that might merit further analysis is the correlation (Elliott 1984; Garcia and Brana 1988; McFadden et al. 1965; Taube 1976) between fecundity and size (or age). Any future refinements of the model should consider incorporating age- or size-dependence into age-class fecundity estimates, either by making F age-class-specific or by incorporating it into m_i (that currently represents the fraction of mature females in stage i , but could be extended to include a correction factor based on average fish length in the age class).

The survival, fecundity, and excess mortality estimates in the model as it stands are static (time invariant). Clearly all these parameters can vary from year to year within a population (e.g., Elliott 1987). It might be helpful in future refinements of the model to add an element of stochasticity to examine how it affects population projections. This modification would be especially relevant for depicting effects of severe events, such as large snowmelts, large fluxes of Zn, drought, and severe temperature.

Several researchers have identified influences on brown trout survival and fecundity of abiotic environmental factors, such as temperature (Jensen et al. 2000), water velocity (Daufresne et al. 2005), and stream fertility (McFadden et al. 1965; Pender and Kwak 2002). Consideration of such environmental influences on population dynamics would allow for a more realistic assessment of Zn effects on brown trout (2001, 2004). As a local example that could influence

site-specific survival estimates, Norris et al. (1999) reported that brown trout chronically stressed by exposure to metals in Colorado's Eagle River responded abnormally to acute stresses. Thus, individual fish and populations may be unable to cope with additional stresses.

The survival and fecundity values incorporated into the model originated from descriptions of field studies of brown trout populations, making environmental factors (abiotic and biotic) implicit in the parameter estimates. These influences are not specific to the upper Arkansas River, the Front Range, or even western North America; as the broad parameter range estimates suggest, they mean little. Nonetheless, it is thought that site-specific environmental factors will tighten estimates within the established parameter ranges, rather than shifting parameters outside their current ranges.

A final uncertainty is that the model does not explicitly incorporate biotic environmental influences caused by intra- and interspecific competition. Several researchers have observed density-dependent effects on survival of young-of-the-year fish (LeCren 1973; Mortensen 1977; Crisp 1993; Elliott 1994; Charles et al. 1998b), as well as changes of brown trout survival and fecundity in competition with other fish (Olsen and Vøllestad 2001a). Some biotic influences would be incorporated into a future site-specific model implicitly through parameters estimated from site-specific field data. Others, for example, density-dependent effects, are less likely to be captured (at least in the short run) by site-specific data, but might be considered for inclusion.

By explicitly accounting for how populations will respond to stressors affecting organisms, life-history models add realism, relevance, credibility, and efficiency to commonly used ERA methods. Nonetheless, at least in their basic form, they do not attempt to describe many relevant processes and factors that would influence the effects of stressors on populations, including, for example, inter-species interactions (Olsen and Vøllestad 2001a, 2000b; Holmen et al. 2003), migratory processes (Charles et al. 1998a, 2000; Lund et al. 2003), density-dependence (Charles et al. 1998b; Jenkins et al. 1999; Vøllestad et al. 2002), environmental stochasticity (Carroll 2002), unmodeled stressor-response relationships (Marschall and Crowder 1996; Olsen and Vøllestad 2005), and parameter correlations (e.g., negative correlation between adult fecundity and juvenile survival rate) (Crisp 1993).

One can draw an analogy to laboratory toxicity tests that are used to project the effects of toxicants on organisms. As with laboratory toxicity tests, life-history models in their basic form control many of the factors that could affect the experimental response variable, allowing the effect of a stressor of concern to be measured under controlled conditions. Controlled experimental methods such as the laboratory toxicity test, or the basic life-history model, sacrifice some environmental realism to eliminate confounding factors from the experiment.

Are the projections made by these methods more or less ecologically relevant than projections for less tightly controlled (and presumably more realistic) conditions? There is no good generic answer to this question; the appropriate level of control will depend on one's ability to interpret the data produced, which will vary depending on the questions asked of the data, and on one's prior knowledge of the experimental system and the ecological system it is meant to represent. The only generalization one can safely make is that experimental

systems (including models) should evolve toward more realistic conditions over time, as understanding improves.

The model and uncertainty analysis presented in this article were developed to provide quick answers (i.e., within weeks) to important, practical questions about the relative protectiveness of different levels of Zn in California Gulch. The model and analysis that were developed and presented in this article proved to be timely and effective for answering those questions. The demonstration that a simple, quickly developed population model has use as a risk management tool is an important message, one that hopefully will help encourage others to apply population models in their own environmental risk assessment projects.

CONCLUSIONS

The projections of this population model are sensitive to all the population-level parameters that contribute to the onset of reproduction (i.e., S_0 , S_1 , S_2 , and F_3). The weight of evidence suggests that S_0 is most important, but is inconclusive about the rankings of S_1 , S_2 , and F_3 . The wide range of brown trout population growth estimates ($r = -0.63$ to 1.34) is consistent with the scientific literature. The low end of this range (any $r < 0$) corresponds to an unsustainable population, a physically unrealistic artifact of combining minimum parameter values from several studies. The upper end of the range ($r = 1.34$) corresponds to an annual population growth rate of 281%.

Creating and using a probabilistic model of excess mortality to brown trout fry from Zn exposure in the upper Arkansas River at the mouth of California Gulch in the years 2000 to 2005, a mean value of 6.1% excess mortality (90% confidence interval of 1.6%–14.1%) was estimated. If young-of-the-year survival (S_0) is higher than approximately 20% to 25%, then the marginal effect of excess mortality (e.g., from Zn toxicity) on population growth is low. The potential risk increases as S_0 declines below approximately 20%.

The relative importance of parameter uncertainties depends on the way the risk management question is posed. If the risk management question is posed in terms of a threshold population growth rate (i.e., an r value), then population-level parameter uncertainties are most important. If the question is posed in terms of how severely Zn exposure changes the population growth rate (i.e., a Δr value), then uncertainty about excess mortality is more important than uncertainty about population-level parameters.

Simple life-history models can help bridge the gap between organism-level measurement endpoints (survival, growth, and reproduction) and population-level assessment endpoints. Given the current state of the practice of ERA, they are useful for examining the effects of ecological stressors on populations, even in the face of limited and uncertain life-history data.

SUPPLEMENTAL DATA

- Table S1.
- Table S2.
- Table S3.
- Table S4.
- Table S5.
- Table S6.
- Table S7.
- Table S8.

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