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Extrapolating Growth Reductions in Fish to Changes in Population Extinction Risks: Copper and Chinook Salmon

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ABSTRACT

Fish commonly respond to stress, including stress from chemical exposures, with reduced growth. However, the relevance to wild populations of subtle and sometimes transitory growth reductions may not be obvious. At low-level, sustained exposures, Cu is one substance that commonly causes reduced growth but little mortality in laboratory toxicity tests with fish. To explore the relevance of growth reductions under laboratory conditions to wild populations, we (1) estimated growth effects of low-level Cu exposures to juvenile Chinook salmon (*Oncorhynchus tshawytscha*), (2) related growth effects to reduced survival in downriver Chinook salmon migrations, (3) estimated population demographics, (4) constructed a demographically structured matrix population model, and (5) projected the influence of Cu-reduced growth on population size, extinction risks, and recovery chances. Reduced juvenile growth from Cu in the range of chronic criteria concentrations was projected to cause disproportionate reductions in survival of migrating juveniles, with a 7.5% length reduction predicting about a 23% to 52% reduction in survival from a headwaters trap to the next census point located 640 km downstream. Projecting reduced juvenile growth out through six generations (∼30 years) resulted in little increased extinction risk; however, population recovery times were delayed under scenarios where Cu-reduced growth was imposed.

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INTRODUCTION

Reduced growth is a common stress response in fish. A variety of causes can lead to stress responses and reduced growth in fish, including suboptimal nutrition or temperatures, low ion content of water (soft water), crowding, subordinate social status, and either the direct effects of chemical exposures or the energy costs of detoxifying chemicals (Wendelaar Bonga 1997). In ecotoxicological bioassays that run long enough, growth effects are a readily and routinely measured endpoint. In water-quality criteria derivation in the United States, the only sublethal effects that *a priori* are considered biologically important are growth or reproductive impairment, although on a case-by-case basis, data on a variety of other sublethal effects of chemicals to fish could also be important, such as swimming performance, disease resistance, or behaviors related to chemoreception (Stephan *et al.* 1985; Stephan 1986). However, laboratory bioassays seldom are a means unto themselves, but probably are at least indirectly conducted because of some societally significant values such as protecting the abundance and persistence of populations, biodiversity, conservation of threatened species, and recreational aesthetics (Stephan 1986; Barnthouse *et al.* 1989).

This motivation implies some consideration of population-level effects when interpreting toxicity bioassays. Yet, from a population biology perspective, the only endpoints that matter for a closed population are birth and death rates. Growth and any other sublethal endpoints are irrelevant unless they can be related to birth or death rates. The reproductive consequences of profound growth effects are self-evident; an organism that fails to grow will doubtfully reproduce. However, the consequences of transitory or subtle growth reductions are less obvious. For instance, in lifecycle testing with brook trout (*Salvelinus fontinalis*) and Cu, McKim and Benoit (1971) reported that, for their first several months of life, fish that were exposed to low, sublethal Cu concentrations lagged behind control fish in their growth. However, after about six months of Cu exposure, fish experienced compensatory growth rates and largely caught up with control fish by the end of the tests (McKim and Benoit 1971). Because the differences were no longer statistically different at the end of their tests, the growth delays were discounted as adverse effects. Similar instances of transitory or subtle growth reductions have been noted for rainbow trout (*Oncorhynchus mykiss*) exposed to Cu (Marr *et al.* 1996; Hansen *et al.* 2002).

However, delayed growth may not necessarily be a discountable effect in the wild because, if juvenile fish encounter a size-dependent bottleneck in early life, smaller fish may not survive long enough to benefit from compensatory growth. Traits and costs that have been associated with reduced growth in juvenile fish include acquisition of feeding territory or shelter, predation risk, body size at key times, energy reserves at key times, increased thermoregulatory costs, and cold mortality (Sogard 1997; Metcalfe and Monaghan 2001; Harwood *et al.* 2002; Coleman and Fausch 2007). The magnitudes of size differences that have been important in outcomes of challenges with juvenile fish can be small. For example, torrent sculpin

(*Cottus rhotheus*) are a predator of juvenile salmon in streams. Torrent sculpin that were about 60 mm long were no threat to coho salmon (*O. kisutch)* that were also about 60 mm long. However, the 60 mm sculpin could successfully ambush, subdue, and eat 50 mm coho salmon (Patten 1977). Abbott *et al.* (1985) found that bigger fish tend to dominate smaller fish in contests for territory, and a size disparity of only 5% in body weight confers significant advantage. However, subtle growth reductions may be discounted as "effects" in toxicity tests if they are not statistically different from controls in null hypothesis significance testing with less than a 5% likelihood of making a Type I error. These purely statistical definitions of significant effects are at best incomplete and at worst misleading, in part because the probability that a given reduction is statistically significant is inversely related to the quality and quantity of the data (*e.g.*, Barnthouse *et al.* 1989).

In this article, through a case study of growth effects from Cu and a threatened Chinook salmon (*O. tshawytscha)* population, we explore how subtle growth reductions in juvenile fish might affect the abundance and persistence of natural populations of migratory fish. Our specific study objectives include:

1. estimating the magnitude of growth reductions likely for Chinook salmon resulting from prolonged laboratory test exposure to Cu at chronic criteria concentrations that had been estimated to be safe for most aquatic ecosystems;
2. estimating potential consequences of reduced growth for the survival of juvenile Chinook salmon during rearing and migration; and
3. quantifying the potential consequences of reduced survival in migrating juvenile salmon as changes in the long-term extinction risk and recovery potential of the salmon populations.

These three objectives lead to evaluating the congruence of water-quality criteria that were developed to protect most aquatic species, and the provision of the U.S. Endangered Species Act to not "jeopardize the continued existence of listed species" or "result in the destruction or adverse modification" of critical habitat of threatened or endangered species (http://www.nmfs.noaa.gov/pr/laws/esa/). Because in jeopardy analyses, the questions of interest relate to effects on the abundance, production, and persistence of distinct populations of listed species, organism-level effects need to be related to these "higher" levels of organization. Organism-level effects to members of listed populations or species usually would be considered to be incidental take, which includes the killing of, or indirect or sublethal harm to members of threatened or endangered species. Under the Endangered Species Act in the United States and similar species protection policies in Canada and the European Union, incidental take of listed species may be permitted so long it as it is not of an extent that could "jeopardize" the persistence of the species in the wild and that the take was incidental to some otherwise lawful activity (McGowan and Ryan 2009). While estimating effects of potential stressors to listed species is often done qualitatively using checklist assessments or subjective judgments (Good *et al.* 2003), organism-level effects can be extrapolated to these higher levels of organization through mathematical simulations that integrate laboratory-population toxicity testing results with ecological theory.

Here population-level effects of Cu at its chronic criterion concentration to a threatened, wild Chinook salmon population were evaluated using demographic structured matrix projection models, also known as Leslie matrix models. Cu was chosen for modeling because we were interested in the potential consequences of low-level, sublethal contaminant effects, and low-level Cu exposures often cause subtle growth effects without being directly lethal to fish (McKim and Benoit 1971; Sauter *et al*. 1976; Marr *et al*. 1996; Hansen *et al*. 2002; Hecht *et al*. 2007). The model uses a matrix of survival and reproduction rates (vital rates) of the different life stages, and it projects them in time using matrix algebra. The technique is a cross between ecology and mathematics that brings together species characteristics and environmental variability to forecast population health and extinction risk (Akçakaya *et al.* 1999; Akçakaya 2000; Caswell 2001).

Conservation biologists and ecotoxicologists alike have called for better integration of these fields. Hansen and Johnson (1999a, 1999b) argued that conservation biologists should consider explicitly including contaminant effects in conservation modeling and research efforts, including chronic toxicity impacts on life-history parameters. Likewise, environmental toxicologists should specifically consider species that may be at risk of decline as a result of exposure to contaminants. Here we try to consider some of these issues at the population level, assuming that these inferences have relevance to other scales of ecological organization that are too complex to directly consider in this analysis, such as metapopulations or ecosystems (Ferson and Ginzburg 1996). Some previous uses of demographic population models to estimate risk from contaminants to aquatic organisms include striped bass with several chemicals (Barnthouse *et al*. 1989), larval estuarine fish, crustaceans, and hypoxia (USEPA 2000), brook trout and fathead minnow populations with endocrine disrupting chemicals (Brown *et al.* 2003), contaminant effects on swimming speed and predator evasion behaviors in a juvenile marine fish (Rose *et al.* 2003; Murphy *et al.* 2008), coastal salmon populations with an ocean-type life history of limited freshwater residency exposed to a generic contaminant causing 10% reduction in mortality and reproduction (Spromberg and Meador 2005, 2006), cutthroat trout populations and selenium (Van Kirk and Hill 2007), and benthic crustacean populations and cadmium (Mebane 2010).

CASE STUDY AREA

For this exercise, we selected the Marsh Creek Chinook salmon population, located at the headwaters of the Middle Fork of the Salmon River, Idaho, USA (44° 27′N, 115°14′W at its mouth). Marsh Creek is an oligotrophic, forested watershed, with few pollution or human attributable disturbances other than potentially decreased freshwater productivity and correspondingly diminished carrying capacities from the decline of marine derived nutrients (Kohler *et al.* 2008). The lack of pollution sources greatly simplifies predicting the potential effects of a chemical stressor. Furthermore, by using a headwaters population for this modeling exercise, the baseline model accounts for a myriad of other factors affecting Chinook salmon populations besides the potential stress of Cu pollution considered here. For example, Marsh Creek Chinook salmon must survive long river migrations including a gauntlet of eight reservoirs and dams, predation and fishing in the estuary and the open ocean, and return upstream to successfully spawn.

The Marsh Creek Chinook salmon population, along with most other Chinook salmon populations in the Snake River basin, has been well characterized, which improves the realism of population modeling scenarios. The Idaho Department of Fish and Game (IDFG) has conducted standardized censuses of juvenile and spawning Chinook salmon in this stream for more than 12 years. Juvenile salmon have been trapped as they begin their downstream migration toward the ocean within around 15 months of age, fork lengths measured, and some implanted with passive-integrated-transponder (PIT) tags. Tagged fish were released upstream of the trap and recapture rates were used to estimate trap efficiency and then expand catch to population estimates. The trap is located about 8 km upstream of the mouth of Marsh Creek at about 1950 m above mean sea level, and downstream of annually-surveyed index spawning reaches. It is operated from April to November most years. The underlying raw data sources (*e.g.*, redd counts, juvenile and adult tag detections, dam passage counts) are similar to those used in several previous articles and reports (*e.g.*, Schaller *et al.* 1999; Kareiva *et al.* 2000; Petrosky *et al.* 2001; Isaak *et al.* 2003; McClure *et al.* 2003). Much of the raw data underlying this and previous analyses are available from online databases (*e.g.* the Passive Integrated Transponder Tag Information System (www.ptagis.org/) and the Columbia River Data Access in Real Time (http://www.cbr.washington.edu/dart/dart.html).

PIT tags are interrogated as the fish pass counting stations in downstream dams, and again when the fish migrate back upstream after spending about two to three years in the ocean. This system tracks the fish's movements, and provides means to estimate sample and population survival at different times and locations (Gibbons and Andrews 2004). The IDFG also conducts annual surveys of spawning adult salmon. Thus, accurate estimates of demographics needed in population modeling can be developed (*e.g.*, population size, variability, and survival by life stage).

MODELING

Projections of potential population-level effects of reduced growth from Cu were made in five steps:

Step 1. Evaluating the effects of chronic Cu toxicity on salmon in laboratory tests;
Step 2. Extrapolating reduced growth in toxicity test results to survival of juvenile migrants;
Step 3. Analyzing population demographics;
Step 4. Developing a baseline population model; and
Step 5. Linking changed population vital rates from Cu-influenced scenarios to population size and extinction risks.

Step 1. Effects of Chronic Copper Exposures to Salmon in Laboratory Tests

We know of only one study (Chapman 1982) that tested the long-term effects of Cu exposures on growth and survival of Chinook salmon early-life stages (ELS) under conditions relevant to the conditions in natal headwater streams in the United States' Pacific northwest (*e.g.*, soft water, low dissolved organic matter). Some toxicity test endpoints can be applied directly to population analyses, such as changes in fecundity or survival at different life stages. Other endpoints such as growth, behavioral changes, immune changes, chemosensory function, and swimming performance are only meaningful at the population level if they can somehow be related to birth or death rates. With migratory fish, some of these endpoints have obvious implications for an organism to reproduce and replace itself in a population. For instance, fish that use chemosensation to avoid predators, to find spawning areas, or to find mates will be at a disadvantage if this capability is diminished (Hecht *et al.* 2007). Likewise, swimming performance is fundamental for fish to pursue prey, avoid predators, and make long migrations. While the importance of test endpoints relating to these critical functions is self-evident, such endpoints are not directly useful in numerical population simulations without some quantitative way of relating them to changes in birth or death rates. Growth, as length differences of fish, was the sole effects endpoint used here to extrapolate potential effects from laboratory bioassays to population size.

The Chinook salmon and Cu chronic toxicity test by Chapman (1982) met U.S. Environmental Protection Agency (USEPA) data-quality requirements for criteria derivation (Stephan *et al.* 1985), and the data have been used in national criteria derivation (USEPA 1985, 2007). However, since the study was never published and these data are not widely available, we summarize the results in Table 1. For the hardness of the test (25 mg/l), the corresponding National Toxic Rule (NTR) chronic Cu criteria (CCC) for total Cu is 3.6 μg/l (USEPA 1992) (henceforth, the "1992 criteria").

An obvious problem for estimating effects at the chronic criterion concentration is that growth reductions occurred at the lowest concentration tested, which was twice as high as the CCC (7.4 *vs.* 3.6 μg/l, Table 1). Nonlinear regression was used to interpolate between effects at the control concentration and the lowest effect concentration to estimate effects at the 1992 criteria concentration. Because of this uncertainty, we also examined a chronic test of rainbow trout in soft water that tested lower Cu concentrations and required less interpolation (Marr *et al.* 1996). Chinook

Table 1. Chinook salmon, *Oncorhynchus tshawytscha,* mortality and growth effects from Cu, 120-day early-life stage test (Chapman 1982).

Copper (μg/l)	1.2 (Control)	7.4	9.4	11.7	15.5	20.2
Mortality (%)	8.95	10.00	9.55	20.30	48.50*	94.15*
Mean length (mm)	47.9	43.0*	40.6*	40.2*	36.5*	—
Mean wet weight (g)	0.990	0.624*	0.493*	0.518*	0.341*	—

*Significantly different from control, $p = .05$, Dunnett's Procedure. Water chemistry estimates: hardness (mg/l CaCO3) 25.4 ± 3.9, alkalinity (mg/l $CaCO_3$) 23.9 ± 2.3, pH 7.32 ± 0.07, T 12.2°C; dissolved organic carbon 1.2 mg/l, Ca 6.8 mg/l, Mg 1.8 mg/l, Na 5 mg/l, K 0.6 mg/l, sulfate 4.2 mg/l, chloride 6 mg/l (Chapman 1978, 1982; USEPA 2007).

salmon and rainbow/steelhead trout are closely related, and other tests have shown similar sensitivity to Cu and other metals (Chapman 1978).

Logistic regression described the relation between length and Cu concentrations well, and it provided an estimated length reduction from controls of 7.5% and a weight reduction of 20% at 3.6 μg/l, the hardness-adjusted 1992 CCC. The estimated length reductions at 3.6 μg/l ranged from 4% to 18%, obtained using different statistical distributions and curve fits (*e.g.* linear, piecewise linear, logistic). For weight reductions, the corresponding reductions were greater, 12 to 20%, depending on the model used. The rainbow trout growth reductions were very similar to those estimated at similar concentrations with Chinook salmon using the same statistical models, suggesting that the needed interpolations of the Chinook toxicity data were reasonable (Figure 1).

The selection of a regression model to fit these Chinook salmon data involves fundamental, implicit assumptions of the ecotoxicology of chronic Cu and fish. The logistic regression curves slope smoothly downward to interpolate from the control concentration to the first treatment. Thus, an implicit assumption of the model shape is that slight increases in Cu result in corresponding slight growth reductions, with no threshold of response. In contrast, the piecewise linear regressions implicitly assume a threshold of response, below which Cu concentrations have no effect on growth. It may be unrealistic to assume that no threshold exists for Cu exposure and the onset of growth effects (but see Cairns 1992). Likewise, the abrupt bend in the corners of the piecewise linear regression that indicate the threshold concentration may also be arbitrary and unrealistic (Figure 1). Because neither model had an obviously better theoretical basis and because both models fit the data well, the effects estimates with each are carried forward through the population modeling using both 7.5% and 4% length reductions at 3.6 μg/l Cu from the logistic and piecewise models, respectively. This provided a range of estimates of growth effects of Cu to Chinook salmon at the 1992 CCC of 3.6 μg/l.

This analysis focuses on USEPA's (1992) Cu criteria. Updates have been published (USEPA 2006, 2007), although at the time of writing, the 1992 values remained effective in some states, including Idaho. USEPA's 2006 recommended criteria were based on the same approach as the 1992 version with minor dataset revisions. In contrast, the 2007 values were derived from a fundamentally different approach that predicted Cu bioavailability through geochemical modeling to estimate Cu accumulation on gills and subsequent toxicity. For the water chemistry conditions of Chapman's (1982) test, the 2006 and 2007 chronic Cu criteria values would be about 2.7 and 2.1 μg/l, respectively. The interpolated length reductions with Chapman's (1982) Chinook salmon test at the 2006 criterion value of 2.7 μg/l ranged from about 6% to zero using logistic regression and piecewise regression models, respectively. For the 2007 criterion value of about 2.1 μg/l, the corresponding length reduction estimates ranged from about 4.5% to zero. Thus the modeled scenarios are also relevant to the more recent Cu chronic criteria updates. For the 2006 version, the upper effects estimate (6% length reduction) would be intermediate to the 7.5% and 4% length reduction scenarios modeled here. For the 2007 version, the upper effects estimate (4.5% length reduction) is close to the lower effects scenario modeled here (4% length reduction).

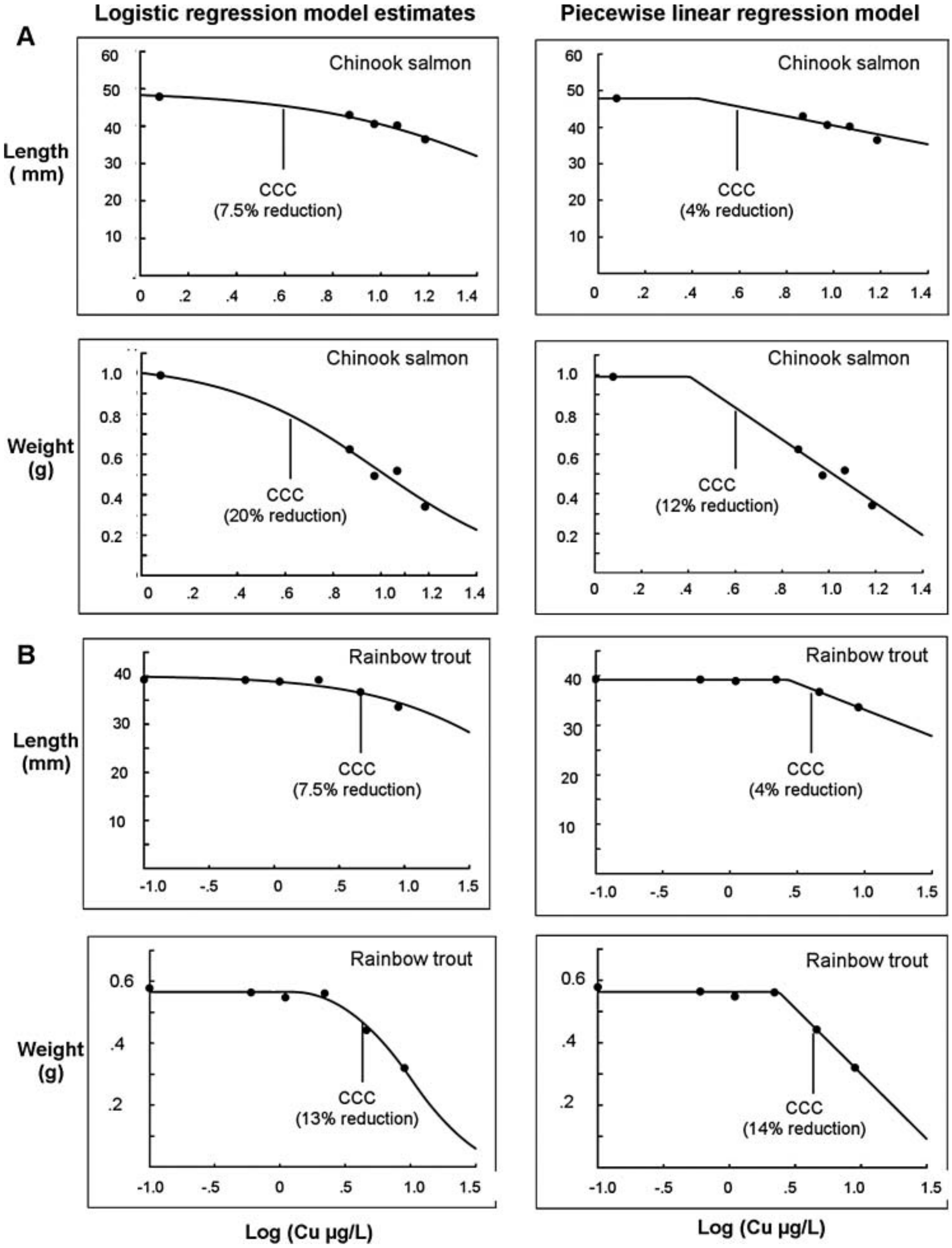


Figure 1. Chinook salmon and rainbow trout length and weight reductions caused by Cu at its 1992 chronic criterion (CCC) at hardness 25 mg/l as $CaCO_3$. Curves in the plots on the left were fitted using logistic regression, the plots on the right used piecewise linear regression. Data from Table 1 and Marr *et al.* (1996), respectively.

Step 2. Linking Toxicity Test Results to Changed Survival Rates

To extrapolate effects observed at the organism level in laboratory tests to potential effects in wild populations, the toxicity test endpoints must be linked to population vital rates (*i.e.*, births and deaths). Relationships between the size of migrating juvenile Chinook salmon and their survival rates through the initial part of their downstream migration from their natal stream to the first dam encountered were determined. This was done by calculating average sizes of migrants by group and year class from fish traps near their natal streams and then by regressing them against the average survival rates to Lower Granite Dam, the first dam encountered on the Snake River. Juvenile Chinook salmon begin their downstream migration in three or more groups or pulses each year. Subyearlings (60–120 mm) migrate downstream during their first year either in late spring or early summer (early subyearlings) or in autumn (late subyearlings), and yearlings (80–130 mm) begin their migration in the spring of their second year (Bjornn 1971, 1978).

Reduced growth in juvenile salmonids has elsewhere been linked to age or size-dependent survival rates, age at reproductive maturity, fecundity, and spawning success (Sogard 1997; Spromberg and Meador 2006; Coleman and Fausch 2007). Growth is commonly measured in toxicity tests as differences in either lengths or weights of test animals in comparison to controls. Weight has been recommended as a primary test endpoint for growth reductions because weight tends to be a more sensitive response than length reductions in toxicity testing (Meador *et al.* 2004). This was the case with the two tests analyzed here (Figure 1). However, the PIT tag monitoring provided much more data on survival *vs.* fork lengths rather than weights. Thus we only considered length data in our analyses.

Generalized relations between size and survival or reproductive successes could be confounded by other factors such as season and temperature because different emigration groups tend to migrate at different times. Thus, we examined relations between the annual average length of each juvenile fish migration group and their survival rates between their first two census points on their outmigration while still in freshwater (Marsh Creek and Lower Granite Dam). Correlations within migration groups were strong and had steeper slopes than when the relations were pooled across groups (Figure 2a). Populations from two other locations in the upper Salmon River basin, the Lemhi River and the upper Salmon River at the Sawtooth Hatchery near Stanley, Idaho, were also examined for comparison. For all emigration groups and populations, survival rates of PIT-tagged, migrating juvenile Chinook salmon were strongly correlated with their size as they left their natal stream (Figure 2b). When all migrating groups (early subyearlings, late subyearlings, and yearlings) were pooled into a single, simple linear regression for each population, mean length of the fish as they left their natal stream accounted for 50–63% of the survival variability in the regressions for the three populations.

Pooling the length–survival relations across the Marsh Creek emigration groups greatly simplified the modeling. This is because matrix-based, demographically structured models assume all individuals within a stage are identical, can be treated in aggregate using statistical distributions, and individuals sequentially transition from one stage to the next or else die (Akçakaya 2000). However, the migrant groups are not sequential stages, but different developmental and behavioral responses by

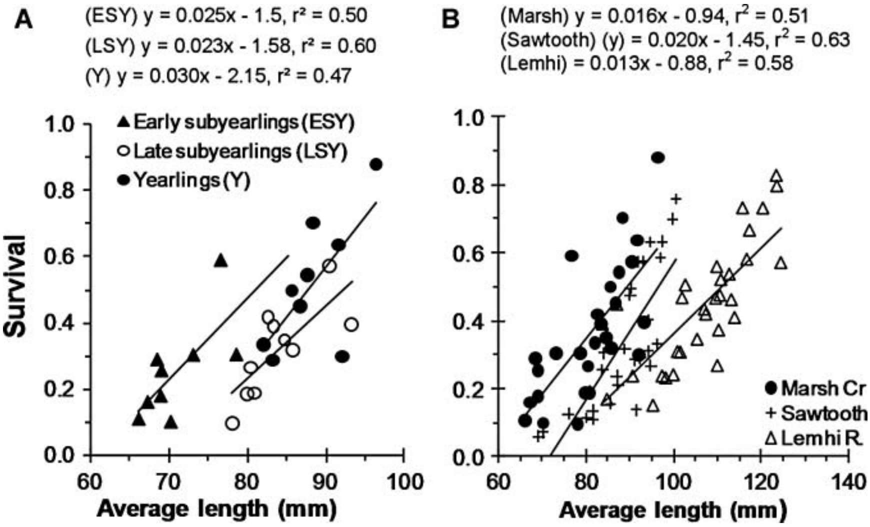


Figure 2. Relations between the size of migrating juvenile Chinook and their survival rates from their natal stream to the first downstream dam encountered, Lower Granite Dam, (LGD), about 640 km downstream; (A) Marsh Creek, grouped by emigration groups and (B) relations from Marsh Creek fish compared to two other populations from the upper Salmon River basin (Lemhi River and the Salmon River above the Sawtooth Hatchery). Each symbol represents the annual average for an emigration group, numbers of fish in each group ranged from 25 to 5317.

individual fish. To model individual fish through time for a population in which the numbers of individuals approach 1 million (Table 2) would have been labor intensive, beyond our objectives, and would have required very specific simplifying assumptions to make individual-based modeling feasible (*e.g.*, Miller and Lacy 2005; Munns *et al.* 2007). Such an approach would further have greatly limited the generality of our model and results.

Still, our solution of pooling of length–survival relations was likely nonconservative because pooling data resulted in a shallower length–survival slope than that observed when emigration groups were treated separately (Figure 2a). Using the shallower, pooled slopes probably underestimated survival reductions associated with length reductions. For the largest-sized yearling migrants (average lengths of 88 mm), length reductions of 7.5% would result in average reductions in survival of about 39 versus 23% when treating the migrant group separately versus using the pooled regression with its shallower slope, respectively. For the intermediate-sized late-subyearlings (average 84 mm), the differences were about 45 versus 25%, respectively, and for the smallest-sized early-subyearling migrants (average 71 mm), the differences were about 52 versus 44%. When calculated for a 10% reduction in length (EC10) the estimates for downriver survival using the regressions from separate migrant groups or the pooled regressions were 52 versus 30%, 60 versus

Table 2. Marsh Creek Chinook salmon census summaries from the period 1992–2003.

Brood year	Index reach redds	Index reach estimated number of eggs	Adult returns from brood year[c]	Population estimate of migrants at Marsh Creek trap	Egg-to-trap migrant survival	Trap-to-trap smolt-to-adult ratio (SAR)
1992	43	218,655	9	19,583	0.09[a]	0.0005
1993	41	208,485	168	24,370	0.11[a]	0.0069
1994	4	20,340	—	1419	—	—
1995	0	0	0[b]	—	—	0[b]
1996	4	20,340	48	3715	0.1826	0.0129
1997	38	193,230	368	22,204	0.1149	0.0152
1998	35	177,975	518	33,247	0.1868	0.0156
1999	0	0	0[b]	—	—	0[b]
2000	26	132,210	40	15,882	0.1201	0.0025
2001	94	477,990	17	114,157	0.2388	0.0002
2002	114	579,690	138	148,436	0.2561	0.00093
2003	172	874,620	0	213,872	0.2445	0.0000
Average,	48	241,961	145	59,689	0.1920	0.00497
Standard Deviation	53	270,610	182	73,047	0.0581	0.00651

[a] Values not used because trap was operated for shorter periods than other years.

[b] Because no redds were detected by air or ground in the index reach, SAR must have been close to zero, although it could not be estimated in the same manner as years with detections.

[c] Adult returns from brood year are offset to correspond with their brood year. For example, for brood year 2002, the 138 adults that ultimately returned to spawn began life as eggs deposited in redds in fall 2002, were trapped, measured, and PIT-tagged as juveniles leaving March Creek in either 2003 and 2004 (their 1st or 2nd year of life), and returned upriver as 4- or 5-year-old adults in 2006 or 2007.

"—" could not be calculated.

33%, and 70 versus 58% for the yearlings, late sub-yearlings, or early sub-yearlings, respectively (Figure 2a).

These length–survival relations are stronger than those estimated for 15 Salmon River, Idaho tributary populations of Chinook salmon in analyses by Zabel and Achord (2004) that were not separated by migrant group. Still, they also found strong relations between relative lengths of individuals within populations and survival to downstream recapture sites. Most fish in their analyses from Marsh Creek were likely ESY, based on the average lengths of 68 and 70 mm for the 2 years studied. On the average across all 15 populations, a fish with a 10% shorter length would have a 20% lower survival rate to downstream sites (Zabel and Achord 2004). Similar rates were observed for small (30 mm) cutthroat trout in high elevation, cold streams in Colorado, where fish that were 10% shorter in length also experienced a 20% lower overwinter survival rate (Coleman and Fausch 2007). In contrast, the length–survival relations we found for the Marsh Creek population may have been somewhat weaker than those for steelhead smolts from Waddell Creek, California, in the marine environment where length reductions of 5 to 20% would reduce survival to adulthood by 20 to 85%, respectively (Quinn 2005:255).

Step 3. Population Demographics

To build a life stage structured population model, population vital-rate characteristics are needed. These characteristics include birth rates, survival rates from one life stage to another, and relative initial population sizes. Vital rates were estimated by evaluating demographic characteristics of the Marsh Creek Chinook salmon population over the 12-year period of record with nearly complete data. Where additional estimates of vital rates such as fecundity and sex ratios were needed, they were estimated from nearby hatchery populations.

Contained in Tables 2 and 3 are the demographic estimates that were developed from monitoring data over the period of record (1992–2003). During this period, the Marsh Creek population fluctuated wildly; population estimates for adults ranged over a factor of 56, and population estimates for juveniles ranged over a factor of 150. Survival rate (or transition) is the rate at which fish in one life stage graduate to the next life stage. These survival rates are given between census points (traps or PIT tag readers) on the migratory corridor, which approximately capture biological life stages. The extreme fluctuations in the numbers of fish counted during that time are reflected in the standard deviations that exceed the means for all life stage estimates. Our estimates of usual life histories, migrations, and survival rates are summarized in Figure 3.

Step 4. Baseline Population Model

A baseline life-history model was built based on the Marsh Creek Chinook salmon population using life stage structured projection matrix methods. Calculations were made using RAMAS modeling software for the viability analysis of structured populations (Ferson *et al.* 1989; Akçakaya 2005). To simulate the intrinsic unpredictability of natural systems (stochasticity), 1000 Monte Carlo simulations were made based on parameter variability estimates under both density-independent and density-dependent scenarios (Akçakaya 1991).

The average demographics of the Marsh Creek Chinook salmon population (Table 3) were re-expressed in a form used in the Leslie projection matrix (Table 4). While the terminology differs, the table values were calculated from estimates in Table 3, and modeled with the length–survival relationships estimated in Figure 2 to simulate the Cu-influenced scenarios. Maternity, the number of offspring produced per spawning female, is the product of the average number of eggs per redd and the average sex ratio from Table 3. Fecundity is calculated by multiplying maternity diagonally on the matrix with the transition rate from migrants to adults. The potential toxicant effects of Cu on early-life stage Chinook salmon were combined with the baseline population demographics by altering survival rates using the Cu-length relations from Figure 1 and the length–survival relations for Marsh Creek from Figure 2b.

The finite population growth rate (λ, lambda) is a statistic that is often used in population ecology (*e.g.*, Akçakaya 2000; McClure *et al.* 2003). Lambda is the ratio

Table 3. Population attributes derived for the Marsh Creek Chinook salmon population from the period 1992–2003.

Year	Stage	Description	Initial numbers, average (SD; range)	Survival to the next stage (%)	Notes
0	Early-life stage	Egg to trap migrant ("smolt")	241,961 (270,610; 0–864,620)	19.2 (5.81; 11–26)	1
1	Juvenile	Smolt to adult (SAR, (Marsh Cr to Marsh Cr)	59,689 (73,047; 1412–217,832)	0.497 (0.0065; 0–1.6)	
2–5	Adult	Total adults from brood (includes year 4 & 5 fish)	145 (182; 0–518)	0	2
		Age of maturity (spawners)	5- years (71%), 4-years (25%), 3-years (4%)		3
		Female:male sex ratio	0.467		4
		Average eggs per redd	5085 (703; 3688–6389)		5
		Maternity (offspring/spawner, as fecundity X sex ratio	2375 (318)		

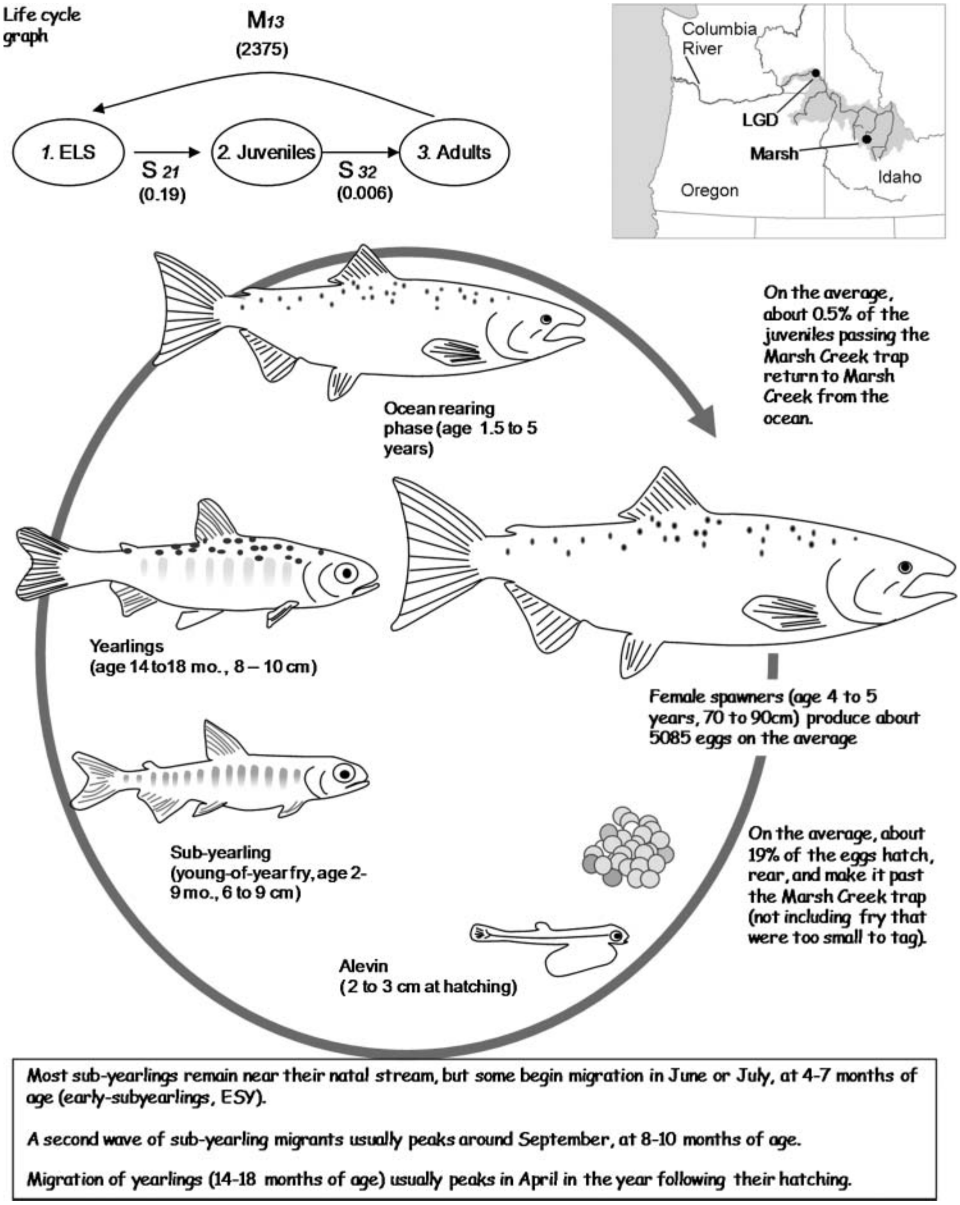
1. Annual juvenile population estimates represent the sum of population estimates for fry, subyearlings, and yearlings, each adjusted for estimated trap efficiency. Annual survival rates are estimated as the product of the counted redds in the index reach and average number of eggs per redd, divided by the juvenile population estimates, the table value represents the grand average.

2. Numbers of adults are the average of index reach redd counts conducted in Marsh Creek form 1992 to 2003, multiplied by 2.3 fish/redd. We considered the index redd counts to represent all total number of redds present in Marsh Creek population and assumed that all juvenile chinook salmon migrating past the screw trap were produced in the counted redds. Smolt-to-adult survival was estimated from departure at the Marsh Creek juvenile trap to adults counted in the index reaches. Reproduction estimate is the average of the products of the number of returning adults, sex ratio, and assumed number of eggs per redd. Estimates of numbers of adults/redd in the Salmon River basin were about 2.2 and 2.3 fish/redd. For the upper Salmon River basin Chinook population, 2.15 fish/redd were estimated based on 9 years of record reported by Kiefer and Lockhart (1997, their Table 4); for the Lemhi River population, 2.3 fish/redd were estimated based on a 10 year record reported by Bjornn (1978, his Table 34).

3. All 3-year-old spawners are males ("jacks"). Stage survival percentages were based on 4- and 5-year-olds only. Values from Waples (2002).

4. Sex ratio is the average of the average female:male ratios estimated by Kiefer and Lockhart (1997), 0.44, from 9 years of data in various streams in the upper Salmon River drainage, and the average ratios estimated by Bjornn (1978, his table 34), 0.49, using 10 years of data from the Lemhi River, Idaho.

5. Fecundity was estimated as 5085 eggs per redd, which was the average number of eggs collected from female Chinook salmon at the Sawtooth Hatchery from 1981–2000 (range of annual averages was 3688–6389, SD ±703). The Sawtooth Hatchery is located near the headwaters of the Salmon River at a similar elevation as Marsh Creek; Fecundity was similar to that determined at the lower elevation Pahsimeroi Hatchery with a 15- year annual average of 5117 (range of annual averages was 4388–6424, SD ± 625 (data from Peter Hassemer, IDFG, personal communication).



On the average, about 0.5% of the juveniles passing the Marsh Creek trap return to Marsh Creek from the ocean.

Female spawners (age 4 to 5 years, 70 to 90cm) produce about 5085 eggs on the average

On the average, about 19% of the eggs hatch, rear, and make it past the Marsh Creek trap (not including fry that were too small to tag).

Most sub-yearlings remain near their natal stream, but some begin migration in June or July, at 4-7 months of age (early-subyearlings, ESY).

A second wave of sub-yearling migrants usually peaks around September, at 8-10 months of age.

Migration of yearlings (14-18 months of age) usually peaks in April in the year following their hatching.

Figure 3. Life history stages and migrations of the Marsh Creek Chinook salmon population. The schematic lifecycle graph in the upper left corresponds with the matrix elements in Table 4 (LGD—Lower Granite Dam).

of population size at the end of one time step (generation) to population size at the end of the previous generation. Under static conditions, using the mean population characteristics and ignoring variability, λ was calculated as 1.31 for the baseline scenario (Table 4). This indicates that on the average the model population was

Table 4. (A) Marsh Creek Chinook salmon model inputs for baseline and Cu-reduced growth scenarios with calculated growth rates, λ, Leslie matrix notation, and (B) the resulting elasticity matrix.

(A) Scenario	Life stage	Initial stage structured numbers	Maternity (M_x)	Survival (S_x)	Fecundity ($M_{x+1}\ S_x$)	Matrices (note 1) $\begin{bmatrix} 0 & 0 & F_{13} \\ S_{21} & 0 & 0 \\ 0 & S_{32} & 0 \end{bmatrix}$
Baseline lambda (λ) ≈ 1.31	1. ELS	241,961	0	0.192	0	$\begin{bmatrix} 0 & 0 & 2375 \\ 0.192 & 0 & 0 \\ 0 & 0.00497 & 0 \end{bmatrix}$
	2. Juvenile	56,689	0	0.00497	11.80	
	3. Adult	145	2375		0	
Cu: 4% length reduction (piecewise) λ ≈ 1.26	1. ELS	(Same as baseline)	(Same as baseline)	0.1646	0	$\begin{bmatrix} 0 & 0 & 2375 \\ 0.165 & 0 & 0 \\ 0 & 0.00426 & 0 \end{bmatrix}$
	2. Juvenile			0.00426	10.1	
	3. Adult			0	0	
Cu: 7.5% length reduction (logistic) λ ≈ 1.07	1. ELS	(Same as baseline)	(Same as baseline)	0.141	0	$\begin{bmatrix} 0 & 0 & 2375 \\ 0.141 & 0 & 0 \\ 0 & 0.00364 & 0 \end{bmatrix}$
	2. Juvenile			0.00364	8.65	
	3. Adult			0	0	

Note 1. F_i and S_i are fecundity (as maternity) and survival between the *i*th life stages. Survival is represented on the subdiagonal and fecundity on the top row.

(B) Elasticity matrix by life stage for the baseline scenario.

Life stage	1	2	3
1	0	0	0.2457
2	0.0009	0	0
3	0	0.4989	0

in a growth phase for the period of study. Under both of the Cu criteria scenarios, λ values were still >1.0 indicating that the population would still be growing, albeit more slowly than under the baseline scenario. However, λ is of limited utility for the present analysis because it is calculated from the matrices and cannot directly be determined from Monte Carlo simulations that simulate natural variability (stochasticity). These estimates of risk under variable conditions are better captured by probabilistic risk statistics and minimum population sizes. As a crude approximation of the effects of environmental fluctuations in the model, constant parameters for the survival rates, fecundities, and carrying capacity were replaced with randomly generated values, drawn from normal distributions defined by measured averages and standard deviations. These parameters were assumed to be positively correlated with each other. That is, if there were a low survival rate for the early-life stage, then it was considered likely that there would be low survival rate for the juvenile stage as well.

Thus, in "bad years" all survivals, fecundities, and carrying capacities are lower than their respective averages, and in "good years" all are higher than average (Akçakaya *et al.* 1999). This assumption is made because for salmonids living in streams, low flow can act as a master variable that influences habitat availability for all freshwater stages and migratory survival (*e.g.*, Dunham and Vinyard 1997; Isaak *et al.* 2003). The simulations used normal distributions for the environmental stochasticity simulations because when plotted as histograms, the distributions of historical data in Table 2 were not highly skewed from normal, and because as discussed later, when lognormal distributions were tried some results appeared unrealistic. For each time step of each replicate simulation, the abundance is calculated and tallied by randomly selecting parameter values using the means and variability observed during the period of record used to estimate the parameters (Akçakaya 2005).

Elasticity indicates the contribution of each life stage in the matrix to the population growth rate (de Kroon *et al.* 1986). Elasticity shows that the trap-to-adult survival rate was far more important to the population growth than was the early-life stage (egg to trap) survival rate. This does not necessarily mean that instantaneous survival rates were lower throughout the trap-to-adult period, but rather that our delineation made it much longer in duration (Table 3), because data were limited during ocean residence.

An important question for applying these relations in the population models is whether the size–survival relations determined for migrating juvenile salmon from the Marsh Creek trap to the next census point at Lower Granite Dam only apply to their early freshwater residency and migration for which there were good data, or whether they influence later survival in the impounded lower river, estuarine, or ocean habitats as well. We assumed that life stages are inter-related and that the advantages that larger size generally conferred on the early-life stage salmon would lead to advantages later in life (*e.g.*, better ability to catch prey and to evade predation, leading to better growth and survival prospects, leading to better fitness for the upriver migration and successful mating.) However, survival rates of the smolt-adult stages (downstream from Lower Granite Dam) were not allowed compensatory or additive effects in the Cu simulation scenarios and thus lifecycle rates remained at the same proportion as those affecting only the egg-to-trap and trap-to-Lower Granite Dam stages.

Others have argued for the interdependency of life stages, although we did not locate any direct quantitative values that could be used directly in the stage-structured projection matrix model. For example, Quinn (2005:255) noted that length differences in juvenile Chinook salmon of around 7% above average as they entered an estuary were more likely to survive to adulthood, and much smaller size differences can affect survival at sea. Zabel and Achord (2004) found that the largest parr survive to the smolt stage at nearly twice the rate of smaller parr, and Zabel and Williams (2002) reported that larger smolts consistently return as adults at greater rates than do smaller ones. During their first year in the ocean, juvenile coho and Chinook salmon appear to need a growth trajectory that lets them reach critical sizes in order to survive their first winter (Beamish and Mahnken 2001; Beamish *et al*. 2004).

Density dependence

The probability of extinction is highly sensitive to the presence and character of density dependence controlling the dynamics of a population. When habitats are overcrowded, competition for food and space intensifies. Individuals expend increased energy foraging or defending territories, which in turn may result in lower growth or the displacement to suboptimal habitats, reducing chances of overwinter survival and increasing the risk of being captured and eaten. In a declining population, as densities thin, these overcrowding effects are relaxed, resulting in compensatory increases in growth, survival, and the overall chance of reproductive success. Self-thinning, the interplay between early growth, mortality, and movement, can vary greatly by year within and among populations (Dunham and Vinyard 1997; Keeley 2001, 2003). Dunham and Vinyard (1997) observed that low water levels and reduced habitat volume may cause intraspecific competitive crunches and self-thinning in stream-living cutthroat trout during a drought year, but not during a year with average stream flows. Thus, density compensation for overcrowding effects will tend to stabilize populations and to lessen extinction risks as populations decline (Ginzburg *et al.* 1990). For example, in a trout population that was strongly constrained by the availability of overwintering stream habitat, Van Kirk and Hill (2007) suggested that that population-level effects would be lower than organism-level effects until juvenile mortality rates exceed 80%.

In contrast to the general ecological principle that increasing densities drive a negative feedback on populations through resource limitation, there may be a positive feedback with increases in numbers of anadromous salmon returning to natal streams to die. When salmon spawners are abundant, streams are more productive because the spawners disturb substrates and provide nutrients via their carcasses, which tend to increase benthic biofilms, macroinvertebrates, and growth and condition factor of juvenile salmonids (Wipfli *et al.* 2003; Kohler *et al.* 2008). When migrants are abundant they may emulate schools that can reduce mortalities through predator saturation. These factors have led to theories of a downward salmon “spiral” when runs decline and enrichment is insufficient to sustain juveniles (Janetski *et al.* 2009). As the undercrowding of habitats worsens, population declines may lead to further declines in population growth, which have been referred to as depensatory, Allee, or simply undercrowding effects (Akçakaya *et al.* 1999). When spawning adults

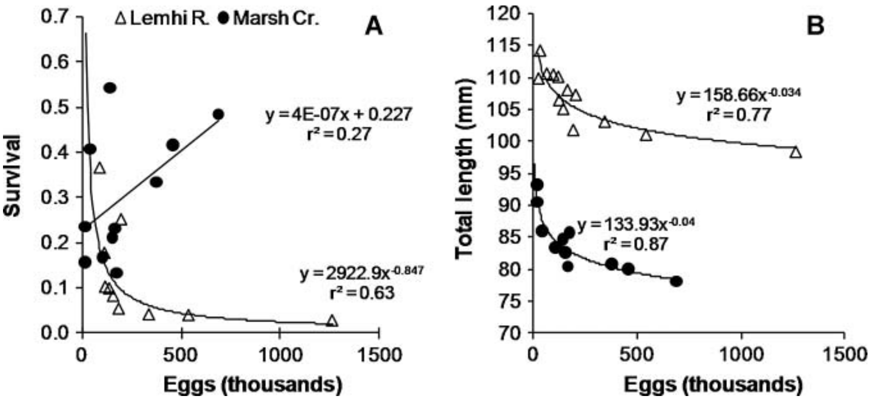


Figure 4. Density dependence of early survival (A) and first year growth (B) of juvenile Chinook salmon migrants estimated from redd density to capture of juveniles at the Marsh Creek trap. Similar data from the Lemhi River population are included for comparison.

are scarce, they may not find each other or may expend more energy finding each other, thereby reducing the probability of reproducing. (Liermann and Hilborn 2001; Rose *et al.* 2001; Barrowman *et al.* 2003). Further, when a population gets very small inbreeding can cause genetic problems (Allendorf *et al.* 1997; McElhany *et al.* 2000). If a population declines to a critical level these undercrowding effects can further pull it down, increasing the risk of a final decline.

We evaluated the Marsh Creek Chinook salmon counts for evidence of density dependence. Regression of survival of all migrant Marsh Creek juvenile fish against the number of eggs (estimated from index redd counts) shows a positive relationship between abundance and survival rates (Figure 4a). The Marsh Creek trap is located only a short distance downstream from spawning habitats and at higher densities, more smaller fish (early-subyearlings) were likely displaced earlier and therefore moved downstream below the trap where they probably continued to rear. Thus, average survival of the population at the trap was not a true survival rate but rather a transition rate past the only census point during early life. Whether upstream or downstream of the trap, all groups likely reared in the headwaters area until smoltifying and migrating seaward as yearlings. Our group specific survival rates from trap to Lower Granite Dam along with our population averaged egg to Lower Granite Dam survival rates represent transitions of "true" survival.

Juvenile salmonids are territorial and when competing for territory or food, larger fish tend to win out, displacing smaller fish (Chapman 1966; Abbott *et al.* 1985; Dunham and Vinyard 1997; Harwood *et al.* 2002; Keeley 2003). In salmonid populations, these displacements have been shown to vary by age of subyearling fish, with reversals in positive or negative relations between density and survival (Elliott 1989) similar to apparent differences in patterns with early-subyearling or late-subyearling fishes in our analysis (Figure 4a). These patterns have also been observed in controlled experiments. In tests of interactions between Chinook salmon and minnows in experimental stream channels under warm and cold temperature regimes, migrant Chinook were smaller than fish that remained in the channel (Hillman 1991).

These examples are consistent with our interpretation that increased numbers of sub-yearling fish surviving to be counted at the Marsh Creek trap likely just reflected counts of smaller fish getting displaced to suboptimal habitats.

Risk estimations of extinction or population decline can be sensitive to the form and strength of density dependence in the population model. This is a serious problem because density dependence is often difficult to measure from limited population census data. In Ginzburg *et al.*'s (1990) reconstruction of density dependence from a 40-year record of a well-studied, exploited species (cod, *Gaddus morhuha*) they found that different but plausible density-dependence functions led to completely different risk estimates. Depending solely on the mathematical density dependence function used in their models, the risk estimates that the fish population would drop below 50% of its carrying capacity ranged from zero to about 70%. From this, Ginzburg *et al.* (1990) cautioned that "by choosing the model of density dependence carefully, one can achieve any quasiextinction risk desired." (p. 69)

While a confusing surplus of at least 29 different density-dependence functions have been published (Henle *et al.* 2004), two models, the "scramble" competition and the "contest" competition, are widely used with fish populations, using the Ricker or the Beverton-Holt functions, respectively. In the scramble competition model, the sharing of resources is roughly equal so when habitats are overcrowded no individual gets enough resources and all suffer equally. By contrast, in the contest competition model, the sharing of resources is unequal, so when habitats are overcrowded suffering is unequal, with contest winners getting enough resources and the rest getting fewer or no resources (Akçakaya *et al.* 1999).

The relevance of these patterns is that previous analyses have estimated or assumed different density relations for the Marsh Creek population. While *a priori* the territorial nature of salmonids in streams may suggest contest models, there has been no consensus among previous studies which relation might be assumed in lieu of using population-specific density-dependence relations. Previous models have variously considered salmon populations in the Snake River and other Pacific northwestern rivers to be density independent (Botsford and Brittnacher 1998; Kareiva *et al.* 2000; Zabel and Levin 2002; Ellner and Fieberg 2003; McClure *et al.* 2003), or density dependent following scramble Ricker competition models (Emlen 1995; Ratner *et al.* 1997; Nickelson and Lawson 1998; Schaller *et al.* 1999), or density dependent following contest Beverton-Holt competition models (Spromberg and Meador 2005, 2006; Copeland 2007).

A further complication is whether compensatory growth and survival increases would occur under an ongoing chronic toxic stress scenario. Our baseline data that we analyzed for density compensation had apparently stochastic environmental variations (*e.g.*, variable flows, temperature, estuarine and ocean conditions), in which growth and survival vital rates varied in the *absence* of pollutant effects. Similarly, fisheries literature on density-dependence patterns is generally from exploited populations in which the survivors that escaped getting harvested were better off than before the harvest and the compensatory increases in vital rates of the remaining individuals were not compromised by pollutant stress. In contrast, under a chronic toxic stress scenario, the remaining individuals may still be physiologically affected by the chronic stress that could dampen compensatory responses. Density compensation probably does persist under low toxic stress scenarios. Apparent density-dependent patterns have been noted in several toxicity tests in which partial kills lowered fish densities accompanied by increased growths by the survivors (Mebane *et al.* 2008). However, it is unclear how to quantitatively model dampened compensation.

Nonetheless, it is inescapable that stream habitats do have limits that in turn limit exponential population growth, regardless of our incomplete understanding of the mechanisms and our inability to mimic the mechanisms mathematically. As a compromise between completely ignoring density dependence or making speculative adjustments to vital rates, we also modeled the scenarios using a "ceiling" type of density dependence. In a ceiling model (as with the density independent model), the population grows exponentially until it reaches a habitat saturation ceiling. A population that reaches the ceiling remains at that ceiling until a population decline from random fluctuation takes it below the ceiling (Akçakaya *et al.* 1999). A key distinction between the ceiling model and the scramble or contest competition models is that the ceiling model does not assume that the population would recover from low densities (*i.e.,* no compensatory increases in survival or fecundity at low densities). The simple ceiling model thus avoids unrealistic unbounded population increases without requiring unsupported assumptions about what vital rate increases would be under the toxic-stress scenarios. However, assuming no vital rate increases at low densities might also be unrealistic. At least for the baseline condition the data were sufficient for a simplified contest density dependent model, and we also compared abundance projections among the contest and ceiling density dependent and the density independent exponential growth models.

To define a ceiling in the model, we used the maximum adult abundance occurring during the period of years 1992–2003 as an approximation of the contemporary carrying capacity of the habitat (Table 2). Abundances during this period were much lower than those occurring during 1957–1975, which is the period when systematic, standardized surveys of index reaches were used but prior to the subsequent severe declines that led to the ESU being classified as "threatened" with endangerment of extinction. The average number of adults returning to the Marsh Creek index reaches redds during the 1957–1975 period was about 869, ranging from about 202 to 1631 (Emlen 1995) compared to an average of 145 ranging from 0–518 during 1992 to 2003 brood years (Table 2). The imposition of a population ceiling that is lower than the historic ceiling seemed reasonable because the present stream habitat is likely less productive than it was before the declines in salmon runs and fewer carcasses resulted in declines of marine-derived nutrients, productivity, and carrying capacity (Achord *et al.* 2003; Thomas *et al.* 2003; Kohler *et al.* 2008; Janetski *et al.* 2009).

Density dependence in stream salmonids commonly occurs in the survival of juveniles through their first winter (*e.g.*, Cunjak 1996), which would be reflected by basing the ceiling on the numbers of eggs deposited. However, because both the numbers of eggs and adults were estimated from redd counts, densities of early-life stages (eggs and fry) can be captured through basing the population ceiling on the number of adults. This also allowed defining a population floor to incorporate undercrowding effects based on the reduced chance of successful mating when densities are extremely low.

The assumed habitat saturation for the ceiling model was 518 adults (s.d. 182). The undercrowding threshold was 10 adults, which was near the low range of observed non-zero returns to the Marsh Creek spawning grounds (Table 2), and is close to the 1 fish/km threshold for undercrowding observed with coho salmon (Barrowman *et al.* 2003). In the stochastic simulations, the assumption that mating is more difficult at very low densities is approximated by reducing the fecundity by half of what it would have been without the undercrowding effect when the number of adults fell below 10. Reducing the fecundity by half is admittedly arbitrary, but it seemed more reasonable than other easily modeled alternatives such as assuming that reproduction falls to zero or ignoring undercrowding and assuming that fecundity rates are maintained at very low densities.

The contest density dependence model for the baseline scenario used the following population growth function equation, $N(t + 1) = N(t) \cdot R_{max} \cdot K/(R_{max} \cdot N(t) - N(t) + K)$ where N is abundance of each life stage, t is time step, R_{max} is the maximum population growth rate, and K is the habitat carrying capacity (Akçakaya *et al.* 1999). We used the same carrying capacity as with the ceiling model. To estimate the maximum population growth rate, we constructed a matrix using the same approach as shown in Tables 2–4, except we only used data from a string of three "good years" from 1996–1998 during which time survival rates were higher than average and abundances grew at higher than average rates (Table 2). For this period, R_{max} (equivalent to λ) was about 1.77. The undercrowding factor was used in combination with the above contest growth function above as $N(t)/(A+N(t))$ where A is the Allee or undercrowding threshold at which the vital rates are reduced by half of what they otherwise would have been. This multiplicative factor is close to 1.0 when abundances are large relative to A.

The interacting effects of the undercrowding and overcrowding density dependent functions on the baseline population growth rate (R) are shown in Figure 5a. In the density independent exponential growth function, R is constant at 1.31. In the contest function R is very low when the number of adults is very low; R peaks at about 100 adults, drops below the average R of 1.31 when the number of returning adults is greater than about 180, and falls into population decline ($R < 1.0$) when the specified carrying capacity of 518 is passed (Figure 5a). The ceiling density dependence function affects R somewhat similarly except it is not allowed to exceed the average growth rate ceiling for the matrix of 1.31, and rather than declining with increasing abundance, the growth rate stays at the ceiling until the carrying capacity is approached, after which it declines more steeply than the contest function (Figure 5a). Both the contest and ceiling density dependent functions were consistent with the growth rate predicted by the stage matrix alone for the initial model abundance of 145 adults (open circle plotted in Figure 5a), suggesting that these Allee-contest or Allee-ceiling density dependence functions are plausible for the Marsh Creek dataset and models.

Step 5. Influence of Reduced Growth Scenarios on Projected Population Size, Extinction Risks, and Recovery Chances

For the Cu-influenced population scenarios, the survival rates of the baseline model of Step 4 were proportionally reduced using the Cu-length relations from

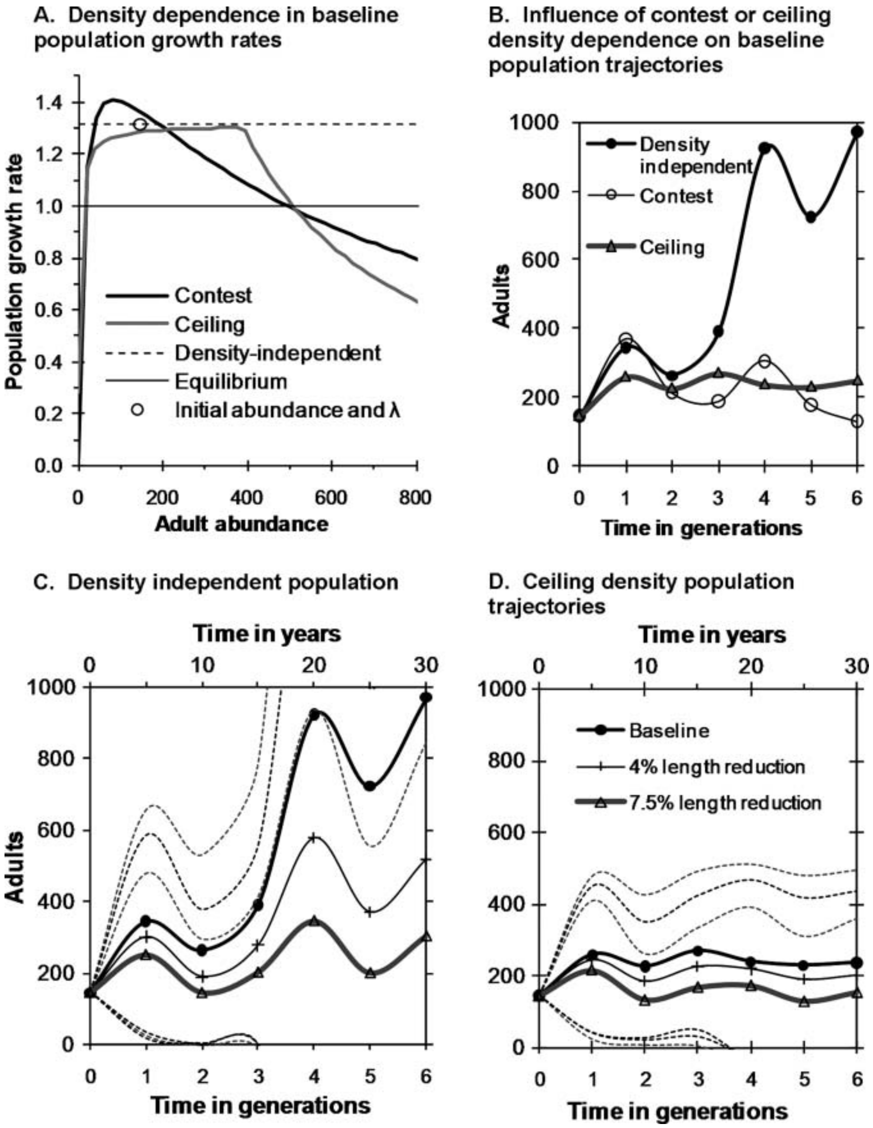


Figure 5. (A) Chinook salmon baseline population model growth rates in relation to adult abundance under density dependent (DD) scenarios versus the constant, exponential growth rate of the density independent (DI) scenario; (B) baseline population trajectories for the DI and contest or ceiling DD scenarios; (C) baseline and low-level Cu exposure DI scenarios; (D) baseline and low-level Cu exposure DD scenarios. Solid lines show the mean of 1000 Monte Carlo population trajectory simulations, dashed lines show ± 1 SD.

Step 1 and the migrant length–survival relations of Step 2. These calculations provide estimates of the reduced growth of ELS fish that could be associated with low-level Cu stress to survival rates of wild juvenile migrants. This assumes that if juvenile fish had reduced sizes because of Cu toxicity, the consequence would be the reduced downstream migration survival associated with smaller-sized fish in a natural population. Finally, once the baseline and Cu-influenced life-stage matrices were assembled, various iterations of the model were run. We compared population abundance projections, risk of severe population decline or extinction, and recovery chances.

Population trajectories

Under baseline conditions, the density-independent model projected that the Marsh Creek Chinook salmon population would fluctuate, but would generally increase. Over the course of six generations or about 30 years, the average of the 1000 population simulations was an increase by a factor of over six. In contrast, the contest and ceiling density-dependent models projected strong growth only for one generation, after which the average adult population trajectories fluctuated between <1 and 2× the initial abundance for the contest model and stayed near 2× the initial abundances for the ceiling model (Figure 5b). The population trajectories from the contest model were more variable than the ceiling model, with average adult abundances dropping below initial numbers by the end of the simulations.

Under the Cu-exposed scenarios, the population was still projected to increase relative to the starting abundances with or without density dependence. Under the density-independent scenarios, end of projection abundances for our high and low estimates of Cu effects on growth, 7.5% length reduction by logistic regression and 4% length reduction by piecewise regression, were about 70 to 50% lower than baseline, respectively (Figure 5c). Under the density-dependent simulations, differences between scenarios were less with the abundances for the Cu-exposed scenarios of about 58 and 26% lower than baseline, respectively (Figure 5d).

Quasi-extinction thresholds

Quantitative projections of extinction probabilities requires a specific definition of extinction. While an obvious definition of extinction is zero, for mathematical and biological reasons we use a quasi-extinction approach (Ginzburg *et al.* 1982). Quasi-extinction occurs when a population falls below a specified level. Biologically, a quasi-extinction approach makes sense because it can reflect undercrowding mechanisms in which recruitment drops to near zero before spawner abundance declines to zero. Further, simulations should be stopped when the population reaches some very small number such as around 25–50 animals or around 5% of initial values (Beissinger and Westphal 1998; Akçakaya *et al.* 1999; Coulson *et al.* 2001). For making accurate estimates of population extinction or decline, selection of a quasi-extinction threshold could be very important to avoid the destabilizing feedback of undercrowding effects that could accelerate the final decline of a population to extinction. Instances in which accurate risks of decline predictions would be important include Red List classifications of species as vulnerable to extinction (DeMaster *et al.* 2004; IUCN 2006) or setting harvest quotas for exploited populations. However, for our purposes, we are not trying to predict absolute risks of population declines or extinction, but rather relative probabilities of an adverse change under different water-quality scenarios. While we tried to select realistic thresholds, in this approach picking the quasi-extinction value is not of critical importance so long as the risk curves are similar.

Quasi-extinction risks were estimated by considering the population to consist of five temporal subpopulations made up of five annual spawning runs (Botsford and Brittnacher 1998; Lindley and Mohr 2003). Reproduction in Pacific salmon is unusual compared to most animals in that adults die immediately after spawning (*i.e.*, semelparous). Most spawners in Marsh Creek are 5-year old fish (Table 3). If, for simplicity, all spawners were considered to be 5-year olds, then the population can be thought of as five distinct, independent subpopulations. Thus, the population can be assumed to persist until all of these temporal subpopulations reach a quasi-extinction threshold.

If a salmon population is considered to be made up of temporal subpopulations, one cannot use a typical quasi-extinction approach of the population dropping below some low number. Instead, quasi-extinction would be considered to have occurred only if all consecutive temporal subpopulations drop below a threshold. For example, in population viability models for the Sacramento River winter-run Chinook salmon, a population that mostly has a 3-year lifecycle, quasi-extinction was defined as three consecutive spawning runs of fewer than 200 adults within 50 years (Botsford and Brittnacher 1998). This threshold was about 1% of the historical abundance of this population.

For the present simulations with the Marsh Creek population, we defined quasi-extinction as five consecutive spawning runs that each were depressed to fewer than 25 adults. This quasi-extinction threshold is equivalent to about 3% of the historical number of spawners prior to the declines that started around 1975 and that led to the population's threatened status (from "Density dependence" section). It also is about 15% of the contemporary number of spawners (Table 2). Genetic evidence further indicates that populations with effective populations below 50 per generation would be at very high risk of extinction in the short term, and below 500 genetic diversity may not be able to cope with environmental change (Shaffer 1981; Allendorf *et al.* 1997). In Marsh Creek, an "effective population" of 50, as used in population genetics, would be about 82 total breeding adults (Waples 2002). However, the index reach used for the standardized population estimates does not include the entire watershed, so presumably additional uncounted fish would be present.

This quasi-extinction definition was too complex to easily use directly with the Monte Carlo simulations, because the RAMAS modeling software provides no way of directly tallying consecutive events within a simulation. However, if the annual spawning runs were assumed to be independent of one another, the risk of N consecutive low returns may be approximated by the risk of a single low return raised to the Nth power. This assumption is doubtfully always true because conditions and abundances may be correlated in time as a result of climate patterns (*e.g.*, Isaak *et al.* 2003). Good years tend to follow good years, and bad years tend to follow bad years. Considering the annual runs to be independent of one another probably lowers the estimate of consecutive extinction risks because, for vulnerable populations, temporal synchrony tends to increase extinction risk (Lev Ginsburg, personal communication, December 4, 2007). With these cautions against interpreting the results too literally, quasi-extinction seemed a reasonable way to capture the idea that, in a population comprised of overlapping temporal subpopulations, extinction occurs when all subpopulations are lost. For example, if there were a 0.8 chance that the number of adults in the population dropped to less than 25 for any single spawning run during the entire simulation, then if runs were independent of one another, the chance that five consecutive runs would have fewer than 25 adults would be 0.8^5 or a 0.33 (33%) chance (Table 5).

Risks of quasi-extinction or declines

Risk probability statistics may provide more relevant assessments of the population's relative risks of declines or extinction than do the population trajectory projections (Ferson *et al.* 1989). Rather than plotting abundance predictions over time as was done with adult salmon in Figure 5, abundance projections can be expressed as the risk that the population will be less than a given number or that it will decline by more than a given amount from the initial conditions.

Risk curves for the probability of population declines as a function of the amount of decline are shown in Figures 6a and 6b. For example, following the thick, black line in Figure 6b of the baseline projections with density dependence, the curves show that, even though the baseline population may be in a general growth phase, it is highly likely (0.88 probability) that at some period during the simulations a run of spawning adults will drop to or below its initial numbers, (*i.e.,* > 0% decline). Also, there is about a 78% risk of a 100% decline (*i.e.*, the complete failure of a spawning run) during the projection period (Figure 6b).

If the risks are instead expressed as the probabilities that the projected numbers would drop below a given number of fish (quasi-extinction), then the risk curves have a similar, but mirrored shape (Figures 6c and 6d). The probabilities of five consecutive severe declines are much lower than the risk of a single, very low spawning run. For example, under the baseline scenario with density dependence, there is about a 50% risk that the population drops below its initial numbers (145 adults) and stays below that value for five years, and there is about a 32% risk that the population similarly drops and stays below our assumed quasi-extinction threshold of 25 adults. In contrast to population trajectory projections wherein by the third generation, the density independent or dependent projections differed markedly (Figure 5), when the baseline versus Cu-growth reduction scenarios are compared as relative risks of decline or quasi-extinction, the risk values were mostly similar but slightly higher under the density dependent than independent model either assumptions of density independence or dependence (Figure 6).

Projections that show the population generally increasing in abundance while concurrently having a high risk of severely declining or becoming extinct may seem counterintuitive. However, these projections are a consequence of the extreme variability in the population's abundance and demographic rates (Tables 2 and 3), and they are consistent with the ecological theory that increased variability in population demographics results in increased extinction risk (Pimm *et al.* 1988; Vucetich *et al.* 2000).

Table 5. Risks of severe population decline or quasi-extinction, probabilities of recovery greater than a given threshold for different Cu effects scenarios, using both density dependent and density independent simulation models.

	Density independent projections			Density dependent projections		
Scenario	Baseline	4% length reduction scenario	7.5% length reduction scenario	Baseline	4% length reduction scenario	7.5% length reduction scenario
Expected minimum adult abundances (individuals)	46	34	22	36	28	19
Risk of a single severe (90%) decline of adult spawners (CI)	78% (76–81%)	80% (77–83%)	82% (79–85)	79% (76–82%)	80% (77–82%)	82% (79–85%)
Risk of quasi-extinction (<25 adults per year for 5 consecutive years)	30% (25–36%)	35% (30–42%)	40% (34–48%)	33% (27–39)	35% (29–42%)	42% (35–49%)
Probability of recovery to >500 adults for 5 consecutive years	41% (35–49)	14% (11–17%)	4% (3–5%)	6% (5–9%)	3% (2–4%)	0.2% (0.1–0.3%)
Probability of ending abundances >500 adults (CI)[1]	44% (41–46%)	30% (27–33)	21% (18–24%)	21% (18–24%)	15% (12–18%)	8% (5–11%)
Ending abundance, 50% probability of exceeding (CI)[2]	274 (179–357)	112 (74–167)	62 (43–88)	146 (103–190)	83 (59–133)	41 (23–64)

Table notes: Results of 1000 Monte Carlo simulations, simulations were run through 6 generations. CI- 95% Kolmogorov-Smirnov confidence intervals; [1]Probability that the adult abundance will end up greater than the recovery threshold of 500 after six generations; [2]After 6-generations, there are 50% probabilities that the adult abundances will end up greater than these numbers.

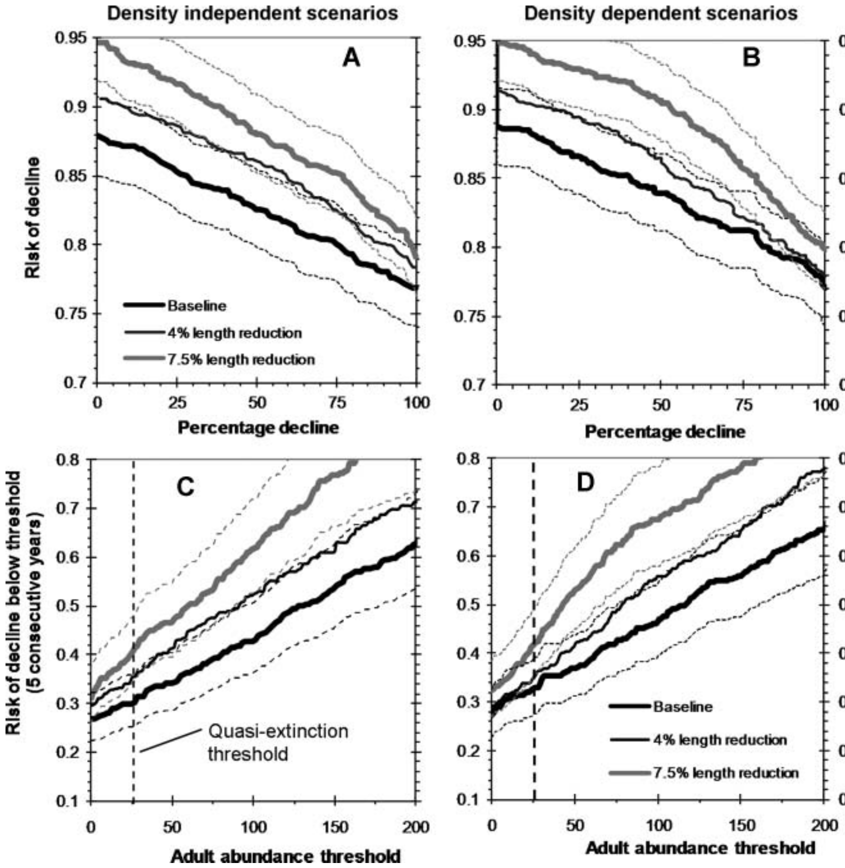


Figure 6. Risks of decline for a single spawning run (A, B) or quasi-extinction of the entire Chinook salmon population (C, D), under density independent or ceiling density dependent scenarios. Risks of decline are plotted as a function of the magnitude of decline; for a given percentage decline in the number of spawning adults (horizontal axis), the relative risk for each scenario is read from the vertical axis. Solid lines are mean risk estimates from 1000 replicate model runs; dashed lines in A and B are 95% CI for the baseline and 7.5% length reduction scenarios. Quasi-extinction "CIs" plotted in C and D are CIs for the decline of a single run raised to the 5th power.

The risk of decline plots in Figure 6a and 6b show Kolmogorov-Smirnov (KS) 95th percentile confidence intervals (CIs). The term "confidence interval" can be misleading because the width of the CIs are a function of the number of replications, thus the CIs cannot indicate anything about the accuracy of the model. Rather, assuming the model is a reasonable representation of our population of interest, the CIs do suggest whether the risks of declines for the different scenarios are similar. If the simulations were to be re-run, the new risk curves would likely plot within the CIs. Thus if the CI bands encompass the mean curves for the different scenarios, the mean risks projected for the different scenarios are within the precision of the risk estimates. The CIs for the baseline and Cu higher effects (7.5% length reduction, logistic regression model) scenarios do not encompass one another's means, except for the parts of the curves with extreme declines (>~90%), indicating that these two average decline risks projections are mostly distinct from each other. The risk of decline curve for the Cu low effects (4% length reduction, piecewise regression model) scenario mostly lies within the CI for the baseline scenario, indicating that the risk of severe population declines did not differ using the KS test. The CI for the Cu low effects scenario was omitted from the plots to reduce clutter (Figure 6a,b). With the quasi-extinction risk curves, KS CIs could not be directly calculated. Instead "confidence intervals" were generated in a parallel way as were the risk curves for *N* consecutive low returns: the KS CIs for the risk of a single low return were raised to the *N*th power. These "*N*th power CIs" for quasi-extinction show similar overlap in the risk of quasi-extinction for the baseline and the lower Cu effects scenario as the risk of decline curves for a single spawning run (Figure 6b,c).

Risk estimates of population decline or extinction are intuitively attractive indices for estimating species vulnerability, but have the disadvantage of changing abruptly over a relativity narrow range of parameters. Small errors or uncertainties in model parameter estimates can lead to large errors in predicted extinction risks (McCarthy and Thompson 2001). This was the case with our model as well. For simulating environmental stochasticity, a lognormal distribution was initially assumed because lognormal distributions are nearly ubiquitous in environmental and ecological data (*e.g.*, Limpert *et al.* 2001). Using otherwise the same models presented, but simply specifying a lognormal distribution instead of a normal distribution to simulate environmental variation, the risk estimates for population declines or quasi-extinction were much lower than when run with normal distributions. For example, with the density independent baseline scenario, the average projected risk of a severe (90%) decline in a single spawning run over six generations (~30 years) using a lognormal distribution was 0.10 compared to 0.78 using a normal distribution. Because severe declines to zero actually occurred in 3 of the 12 years of record used to develop the model parameters (Table 2), the probability of a single occurrence at some point during a 30-year projection should be much closer to 1.0 than zero. While relative risk rankings of the scenarios did not change, this cautions against placing too much reliance on whether projected risks of decline or quasi-extinction are "high" or "low."

McCarthy and Thompson (2001) argue that the expected minimum population size may be a more reliable statistic for the likelihood of a population to decline than is risk of extinction or quasi-extinction because the former is less prone to large errors. The expected minimum population size is obtained by recording the smallest population size observed in each iteration of a stochastic model and taking the average of these minimums. Our results seem to support their arguments, as the differences in expected minimum population size differed by less than a factor of two using normal or lognormal distributions, whereas risk of decline statistics varied by a factor of eight or more. The expected minimum abundances under the Cu higher effects (7.5% length reduction) scenarios were about half those of the baseline scenarios. For the lower Cu effects (4% length reduction scenarios), the expected minimum abundances were about 20 to 25% lower than baseline (Table 5).

CHANCES OF RECOVERY

A corollary to evaluating extinction risks is the probability that a threatened population will recover from previous declines. How to interpret population recovery probabilities is less obvious than extinction risks. Without recolonization, a population that goes extinct stays extinct. However, for a threatened population to recover from a previous decline, population growth that exceeds a recovery target is not much of a recovery if an initial increase is followed by a crash. To approximate the relative probabilities of a durable recovery, the concept that quasi-extinction only occurred when all temporal subpopulations were lost was extended to the chances that recovery would exceed a given threshold for five consecutive annual runs. This required selecting a threshold for "recovery." Using a similar rationale as with the quasi-extinction threshold, we used a recovery threshold of 500 adults for the population projections. To maintain long-term adaptive potential, Allendorf *et al.* (1997) proposed that salmon populations needed effective sizes greater than 500 per generation to reduce risk of chronic decline or depression from inbreeding.

We interpreted the population recovery chances in three ways. First, the most lenient and optimistic statistic was the probability that the population would exceed the recovery threshold of 500 adults at any one time interval during the simulations. When these probabilities are plotted as a cumulative probability distribution, the cumulative distribution of recovery times increases monotonically. Each point on this cumulative curve can be interpreted as there is a Y% probability that the population abundance will exceed the 500 adult threshold in or before the year 30. Focusing on the medians of the distributions, the relative times to reaching the recovery abundance threshold can be compared between the scenarios. When the population growth was unconstrained by carrying capacity limitations, median times for the population to reach 500 adults were about 12, 17, and 27 years for the baseline, 4% length reduction from Cu, and 7.5% length reduction from Cu scenarios, respectively. When the population was constrained below a carrying capacity ceiling of 518 adults in the density dependent model, this nearly precluded the population from reaching a recovery target that was only slightly lower; median times projected for the population to reach 500 adults ranged from 22 years for the baseline to >30 years for the Cu-lower and higher effects scenarios (Figure 7a,b).

Second, when considering recovery as a more persistent increase in adult abundances over for five consecutive years, under the density independent scenarios, there were 50% probabilities that at least for one period of five-consecutive years at some time during the 30-year simulations, the adult abundances would reach about 420, 260, and 175 for the baseline, Cu-lower effects (4% length reduction), and Cu-higher effect (7.5% length reduction) scenarios, respectively (Figure 7c). Under the ceiling density dependent scenarios, the adult abundances were similarly projected, with 50% probabilities, to reach about 290, 225, and 150 for the baseline and Cu-lower or higher effects scenarios, respectively (Figure 7d, Table 5). When the threshold for recovery was defined as exceeding 500 adults for any one five-year period, attaining this recovery threshold within 30-years was unlikely for any modeled scenario, with chances of reaching that threshold ranging from 41% to nearly 0% across the scenarios (Table 5).

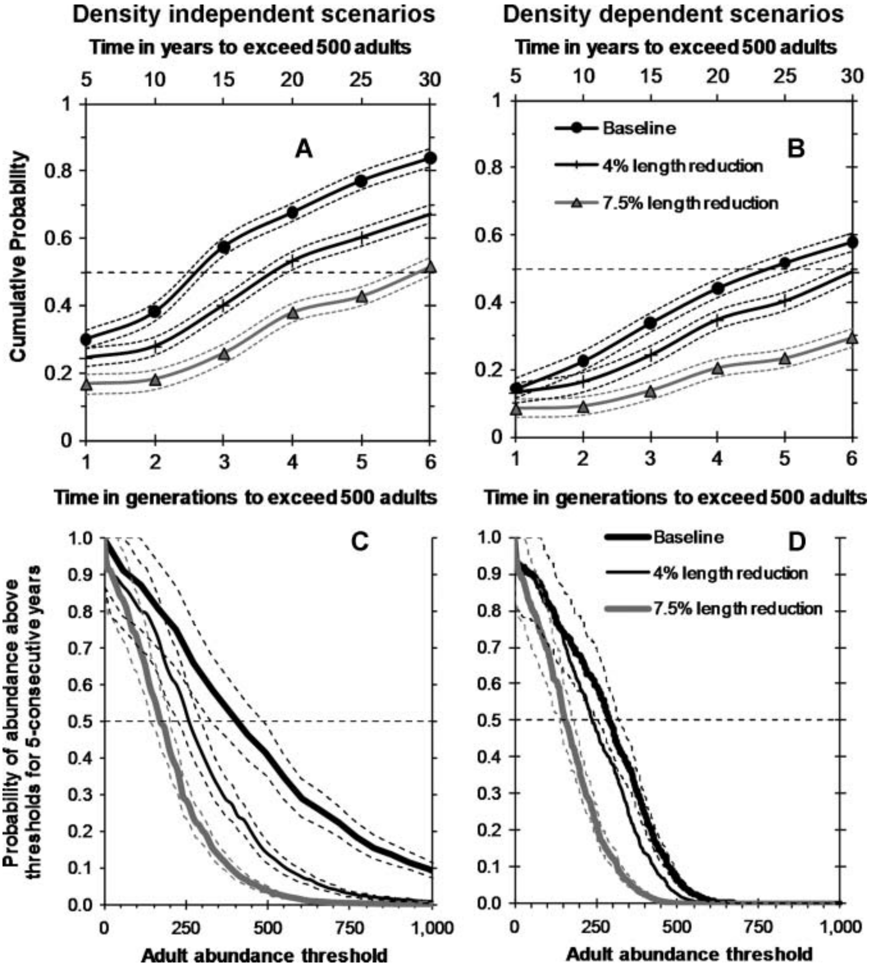


Figure 7. Chinook population recovery probabilities as median times for the cumulative probability of exceeding a recovery threshold at any time through six generations under density independent or ceiling density dependent scenarios (A, B); and probabilities of increases in adult abundances that persist for five consecutive years (C, D).

Third, if recovery were interpreted as the chances that after the 6-generation (30-year) simulations, terminal abundances would end up greater than the recovery threshold of 500 adults, then that would still be an unlikely outcome under all scenarios. The projected chances of the adult terminal abundances ending up greater than 500 ranged from about 44% to 8% across the scenarios (Table 5). There would be about a 50% chance that, in year 30, the population abundances will end up greater than 274 to 146 for the baseline scenarios under density independence or dependence, respectively. For the Cu-higher effects (7.5% length reduction) scenarios, the similar projected abundances in year 30 would be about 62 to 40 (Table 5).

These projected median abundances in year 30 are lower than the average abundances in year 30 (Figure 5), which was an influence of the high variability in the population matrix.

These projections imply that if the processes that governed the Marsh Creek population for the brood years 1992 to 2003 operated in a way that was simulated by our baseline models, and if these processes continued into the future, then our recovery threshold of 500 adults was too ambitious for the next 30 years. This is because even under the most optimistic scenarios, chances of exceeding this threshold at after 6-generations were <50%. However, this does not affect our interpretation of relative chances of recovery among the scenarios, or that for a given chance of recovery, 50%, the population was projected to recover to lower abundances under scenarios that imposed growth reductions than under baseline projections.

DISCUSSION

These exercises illustrate how reductions in growth of juvenile Chinook salmon could result in disproportionately larger reduction in survival. If growth were reduced on the order of 4 to 7.5% by low-level water-quality stressors such as Cu at its highest allowable long-term criteria concentrations, proportionally greater reductions in survival during freshwater rearing and migration life stage are expected. The magnitudes of the survival reductions were dependent on both the body size and migratory behavior of the juvenile Chinook salmon. For instance, from the length–survival regressions, a 5% length reduction could result in survival reductions ranging from about 35 to 26% for the smallest migrant group (early-subyearlings, 71 mm average length) and for the largest migrant group (yearlings, 88 mm average length), respectively. Length reductions of 10% for those two groups could similarly result in migrant survival reductions on the order of about 70 to 52%, respectively.

One implication of the length–survival patterns is that when interpreting aquatic toxicity testing, applying a fixed effect concentration percentile (ECp) across different measures of effect could result in serious misjudgments about what represents a negligible or substantial adverse effect. In the previous example, a 10% reduction in length (EC10) could result in up to a 70% reduction in survival of migratory juvenile salmon, yet under strong density dependence, reductions on the order of 10 to 20% in fecundity or first year survival of stream resident trout might not cause any population reductions (Elliott 1989; Van Kirk and Hill 2007).

Utility of the Modeling

We were able to use extensive field data to parameterize the model, which we think may have improved the realism of our model over approaches that have used generic species life history parameters (*e.g.*, Mebane 2010). However, this realism for a specific population leads to questions about how germane this or other models that were parameterized to one system are to other aquatic systems. Are such models only of narrow interest to those interested in the specific system for which it was developed? Although it depends on the question, we think not. Much as demographic studies of a stream brook trout population can be useful far beyond the purpose of the original study, setting angling regulations in Wisconsin, USA (*e.g.*, McFadden 1961; Brook *et al.* 2000; Brown *et al.* 2003), we think the demographic information compiled here on the Marsh Creek Chinook population could be useful for others. For fisheries managers who make stock assessments in order to set harvest limits for exploited species or to make other specific population forecasts, the absolute accuracy of the model projections matter a great deal. In contrast, in ecological risk assessment or environmental planning the relative risks of different alternatives may be sufficient, and models such as ours can be more broadly useful. For purposes such as those, our modeled population of Chinook salmon from a headwaters tributary of the Snake River in Idaho, could be generalized to a model "stream-type" anadromous salmonid population, complementary to "ocean-type" salmon population models (*e.g.*, Ratner *et al.* 1997; Spromberg and Meador 2006). In "ocean-type" salmon populations, fish migrate downstream to estuaries and the ocean within a few months of hatching in their natal streams, whereas for "stream-type" salmon populations, juveniles overwinter in freshwater before migrating to the ocean (Healey 1991; Quinn 2005). Our stream-type model population probably has some similar dynamics to stream-type migratory salmonids that occur in the inland portions of the large Pacific river systems of western Canada and the United States. Some Atlantic salmon and sea-run brown trout populations in Canada and Europe also share stream-type life histories (Elliott 1989; Cunjak *et al.* 1998) and we surmise that stressors that reduce early growth could also reduce migratory survival in these types of populations. More generally, stressors causing growth reductions in juvenile fish can often be expected to result in decreased survival chances relative to less affected members of the same or sympatric species. This is because winter mortality can be an important limiting factor for freshwater, temperate fish populations. In general, winter mortality is size-selective and selects against the smaller members of cohorts and populations (Sogard 1997; Hurst 2007). Thus we think the demographics of the Marsh Creek Chinook salmon population compiled here may have utility beyond the present article. At least qualitatively, growth reductions in juvenile fish can be extrapolated to reduced first-year survival of many fishes in the wild, although the population impacts may be tempered by density dependence.

Risk Interpretation and Communication

The Chinook salmon length reductions estimated for the 1992 Cu criterion concentration of about 4 to 7.5% were projected to result in 2 to 10% additional risk of quasi-extinction sometime in the next 6-generations, depending on the model. The corresponding estimated length reductions for the 2007 updated Cu criterion concentration would range from about 0 to 4% and would be projected to result in 0 to 5% additional risk of quasi-extinction sometime in the next 6-generations. The risk of decline curves for the 4% length reduction scenarios largely fell within the KS confidence intervals for the baseline scenarios, whereas the risk of decline curves for the 7.5% length scenarios were largely outside the baseline intervals (Figure 6). Metrics for chances of recovery differed more between the baseline and Cu exposed scenarios in the density independent model than in the ceiling density dependence model. For instance, there were about 40 to 60% reductions, attributable to length reductions of 4 to 7.5%, respectively, of the highest population adult abundances projected with 50% likelihood of being reached and maintained for 5-years running in the next 6-generations. With the ceiling density dependent model, the reductions were projected to be about 20 to 50% from baseline (Figure 7).

Our modeling included both conservative and non-conservative biases that could make the specific population and risk estimates unreliable. The use of the ceiling density dependence function with no compensatory increase in stage survival would lean toward producing conservative estimates of risk. In contrast, our use of length–survival relations that were pooled across migrant groups resulted in lower reductions in survival for the Cu influenced reduced growth scenarios and would lean toward producing non-conservative risk estimates. Likewise our treatment of the Marsh Creek Chinook population as five independent temporal subpopulations that all had to be lost before the population as a whole could go extinct would lean toward non-conservative risk estimates. Thus we have emphasized relative projections and risks for the different scenarios rather than specific values. We share the conclusion of Pastorok *et al.* (2003) that even though we do not know if our projections have any accuracy in an absolute sense, the relative risk estimates provided far more insight than could have been obtained from simple risk-quotient type approaches or subjective analyses. Although we focused on Cu as a model stressor, any stressor that caused similar growth reductions would result in similar projections for the population.

Using demographically structured models, the growth reductions in the Cu-exposed scenarios were extrapolated through regressions to reduced survival in the migration from the natal stream to the impounded lower river segments. The reduced survivals were in turn projected to ripple through the salmon life history, with reduced survival rates leading to reduced reproduction and population growth rates, and increasing risks of population declines, quasi-extinction, and lower chances of recovery. These projections of increased population extinction risk and reduced chances of recovery lead back to one of the original reasons for the modeling: if water pollution controls allowed critical habitats of threatened or endangered species to be at the authorized Cu criterion concentrations, would the increased risks to a population of a listed species be too great and jeopardize their chances of long-term survival? In the United States, the Endangered Species Act provides little guidance on that point. Implementing regulations define "jeopardize the continued existence of" to mean "to engage in an action that reasonably would be expected, directly or indirectly, to reduce appreciably the likelihood of both the survival and recovery of a listed species in the wild by reducing the reproduction, numbers or distribution of that species" (USFWS and NMFS 2004). This definition of "jeopardy" lacks precise biological definition; instead, it is defined in a legal context that introduces secondary terms that do not have precise biological definitions either, such as survival "into the future" (McElhany *et al.* 2000). Likewise "reduce appreciably" is undefined. Definitions of "appreciable" such as "possible to estimate, measure, or perceive; perceptible" (*American Heritage Dictionary of the English Language,* 3rd edit, Houghton Mifflin), leave room for debate because prospective extinction risks cannot be measured, yet with population model outputs, very small differences can be estimated and be perceptible in graphs and tables.

The "appreciable" standard for acceptable additional risks has implications for how to most appropriately communicate modeled results of risks of extinction or chances of recovery. The different scenarios that can be modeled and the resulting metrics are limited only by the modelers' imaginations and for a given scenario, very different implications of risk can be presented. For instance, if advised only that the risk of a complete run failure in any single year was projected to be very high for either the baseline or Cu-exposed scenarios (77 to 79%, Figure 6a), one might conclude that the Cu-exposed scenarios present little additional risk of decline. Yet, if the results were presented to emphasize that the population was projected to recover to numbers 2× to 4× higher in the baseline than Cu-exposed scenarios, or that chances of a durable population recovery could be more than 10× lower for the Cu-exposed scenarios (Table 5, rows 4 and 5), the implications would likely be perceived as more alarming. As with many aspects of risk assessment, this presents a challenge how to most appropriately communicate risk estimates. We suggest that the more vulnerable the population of interest is (*e.g.*, ranging from populations of least concern to those critically endangered), the more conservative estimates of risk should be emphasized.

In a broad sense, the United States' Endangered Species Act involves a process of risk assessment and risk management. Assessing risks of extinction or chances of recovery are purely risk assessment procedures while determining whether additional risk is allowable involves a degree of subjective risk management (Carroll *et al.* 1996). While this subjectivity may lead to inconsistent interpretations of risk, rigid policy or legal frameworks that, for example, set blanket time frames for evaluating extinction risks across species with different life histories are inappropriate (Lubchenco *et al.* 1996). This challenge is shared by field studies where statistical tests for differences or lack thereof are dependent on the choice of a threshold for a meaningful effect size to test for. These choices are often subjective (McGarvey 2007; Brosi and Bilber 2009; Munkittrick *et al.* 2009). The benefit for risk management of quantitative modeling is that metrics such as projected population trajectories, expected minimum abundances, risks of quasi-extinction and chances of recovery are in a currency that more closely relates to narrative policy requirements such as to "not appreciably reduce the likelihood of the survival and recovery of the species in the wild" than either the original effects, such as reduced juvenile growth measured in a laboratory, or exceedences of criteria or effects benchmarks. While the results of population modeling and viability analyses cannot directly answer whether the future effects of some proposal such as revising water quality criteria could lead to unreasonably increased risks to the long-term survival of vulnerable populations, the results can inform the debates and provide a structure for evaluating measures expected to mitigate potential harm.

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