Modeling the effect of striped bass (*Morone saxatilis*) on the population viability of Sacramento River winter-run chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract—We estimated the impact of striped bass (*Morone saxatilis*) predation on winter-run chinook salmon (*Oncorhynchus tshawytscha*) with a Bayesian population dynamics model using striped bass and winter-run chinook salmon population abundance data. Winter-run chinook salmon extinction and recovery probabilities under different future striped bass abundance levels were estimated by simulating from the posterior distribution of model parameters. The model predicts that if the striped bass population declines to 512,000 adults as expected in the absence of stocking, winter-run chinook salmon will have about a 28% chance of quasi-extinction (defined as three consecutive spawning runs of fewer than 200 adults) within 50 years. If stocking stabilizes the striped bass population at 700,000 adults, the predicted quasi-extinction probability is 30%. A more ambitious stocking program that maintains a population of 3 million adult striped bass would increase the predicted quasi-extinction probability to 55%. Extinction probability, but not recovery probability, was fairly insensitive to assumptions about density dependence. We conclude that winter-run chinook salmon face a serious extinction risk without augmentation of the striped bass population and that substantial increases in striped bass abundance could significantly increase the threat to winter-run chinook salmon if not mitigated by increasing winter chinook salmon survival in some other way.

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Predation is a factor in the decline of many Pacific salmon populations (Nehlsen et al., 1991), and fisheries managers may need to evaluate the potential benefits of predator control or the possible impacts of predator augmentation. Such evaluations require estimates of the current predation rate, how the predation rate would change with changes in predator abundance, and how changes in predation rate affect the prey population viability. Predation rate can be estimated in at least three ways. Coordinated studies of predator and prey distribution and abundance, combined with predator diet studies, can provide direct estimates of predation rate (e.g. Rieman et al., 1991). This approach, however, is time-consuming, labor-intensive, and difficult because of the typically patchy distribution of predators and prey in space and time. Another approach is to build highly detailed, spatially explicit simulation models of predator and prey populations (e.g. Jager et al., 1997; Petersen and DeAngelis, 2000). Such models, although biologically realistic, are data-intensive, have many parameters, and have outputs that can be sensitive to parameter values that are not well constrained by data. An alternative modeling approach is to use simple models of predator and prey population dynamics and estimate the unknown parameters from time series of predator and prey abundance within a statistical framework (Walters et al., 1986; Berryman, 1991; Carpenter et al., 1994). This approach is based on readily available data and is relatively quick to implement, making it suitable for initial assessments of predation effects. The model, once its unknown parameters have been estimated, can also be used to assess the impact of predator population size changes on the prey population.

We took this statistical modeling approach to investigate how the proposed augmentation of the Sacramento River striped bass (*Morone saxatilis*) population might increase the risk of extinction faced by the endangered winter-run chinook salmon (*Oncorhynchus tshawytscha*). Striped bass prey on juvenile chinook salmon in the Sacramento River system (Stevens, 1966; Thomas, 1967), as well as in other west-coast rivers (Shapovalov, 1936), and striped bass prey upon juvenile Atlantic salmon in east-coast rivers were they co-occur (Blackwell and Juanes, 1998). Although winter-run chinook salmon juveniles are not the primary prey of striped bass and striped bass predation is only one of many mortality sources affecting winter-run chinook salmon, an increase in striped bass abundance has the potential to negatively impact winter-run chinook salmon. This potential must be assessed before the striped bass population can be augmented because winter-run chinook salmon are listed as endangered under the U. S. Endangered Species Act.

Because few data are available on the details of the interaction between winter-run chinook salmon and striped bass (e.g. functional response, role of alternate prey), we explored the simplest models that can capture the predation effect to assess the effect of striped bass population manipulations.

The ultimate goal is to assess whether the proposed plan might pose a significant increase in risk of extinction. We took a Bayesian approach in order that uncertainty in parameter estimates could be incorporated into extinction risk predictions (Ludwig, 1996). If significant risk cannot be ruled out, managers might reduce the scope of proposed striped bass stocking and collect data to better constrain the predation rate so that appropriate mitigation can be implemented. Although not the primary focus of this paper, our results also serve as a population viability assessment (PVA) for winter-run chinook salmon that can be compared to the recent winter-run chinook salmon PVA reported by Botsford and Brittnacher (1998).

Methods

Background and data

Winter-run chinook salmon Sacramento River winter-run chinook salmon are genetically distinct from other chinook salmon populations (Kim et al., 1999; Banks et al., 2000) and have a unique life history pattern that is a blend of the stream- and ocean-type life histories. Spawning fish leave the ocean in winter, mature in freshwater, and spawn in headwater areas from April through September (Healey, 1991). Juveniles enter the ocean the following spring. Up to 200,000 winter-run chinook salmon may have once spawned in the Sacramento River headwaters (Fisher, 1994). The completion of Shasta Dam in 1944 blocked access to the entire historic winter-run chinook salmon spawning range but created suitable spawning conditions for some distance (≈100 km) downstream of the dam (Moffett, 1949) (Fig. 1). In 1967, Red Bluff Diversion Dam (RBDD) was installed about 110 km downstream from Shasta Dam. Installation of RBDD apparently created passage problems for both adult and juvenile chinook salmon and the winter-run chinook salmon population has declined dramatically since completion of RBDD; fewer than 100 adults returned to spawn in 1980 (Fig. 2). Additional factors contributing to the decline of winter-run chinook salmon include high summer water temperatures, water diversions, habitat modification and degradation, fishing, hydropower operations, toxic spills, and predation by native and introduced animals, including striped bass (NMFS[1]). Winter-run chinook salmon were listed as threatened under the U.S. Endangered Species Act (ESA) in 1989 and as endangered in 1994.

The California Department of Fish and Game counts returning winter-run chinook salmon as they pass over fish ladders on RBDD; counts have been reported by Myers et al. (1998). Fish are determined to be adult (age 3 or 4) or "jack" (age 2, usually male), but are not otherwise routinely aged or sexed. From 1967 to 1985, nearly complete counts of winter-run chinook salmon were made. Since 1985, the dam flashboards have been removed for much of the year to improve passage of juvenile and adult winter-run chinook salmon. During this period, winter-run chinook salmon spawning escapement (spawning population size) has been estimated by expanding fish ladder counts made when the flashboards are in place. It is estimated that about 15% of the run is now counted, but the actual fraction observed in any given year is unknown. Population estimates made since 1985 therefore contain measurement error.

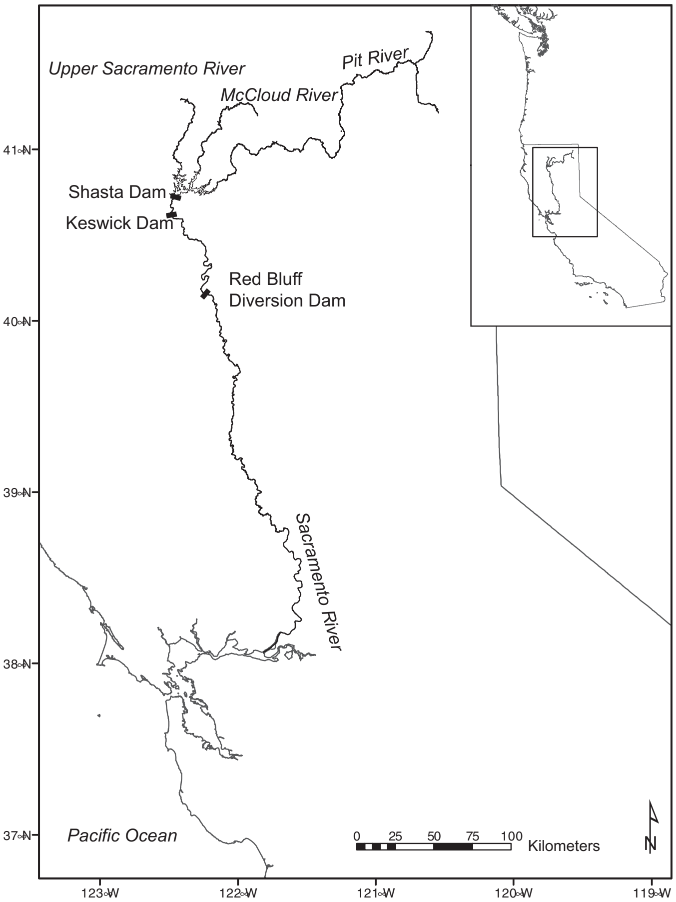

Figure 1

Sacramento River, tributaries, and dams. Current spawning range of winter chinook salmon spawning is between Keswick Dam and Red Bluff Diversion Dam.

Striped bass Striped bass were intentionally introduced to the Sacramento River in 1879, supported a commercial fishery in the early twentieth century, and now support a popular sport fishery (Kohlhorst, 1999). Over the last 30 years, the striped bass population has declined from around 2.2 million adults to fewer than 1 million adults (Fig. 3). The striped bass decline has been attributed to entrainment of striped bass larvae by the large State and Federal water diversion facilities in the Sacramento River delta (Stevens et al., 1985) and ecosystem changes that have reduced the carrying capacity for subyearling striped bass (Kimmerer et al., 2000). The State of California has a legal obligation to mitigate the negative effects of State water diversions on striped bass, but striped bass

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[1] NMFS (National Marine Fisheries Service). 1997. NMFS proposed recovery plan for the Sacramento River winter-run chinook. Southwest Region, 501 West Ocean Blvd, Long Beach, CA 90802-4213.

augmentation is constrained by the ESA because of the potential impact on winter-run chinook salmon. Striped bass prey upon a wide variety of invertebrates and fish and are predominately piscivorous from age 2. In the Sacramento River system, juvenile chinook salmon compose a variable portion of the diet depending on season and location (Stevens, 1966; Thomas, 1967). By rearing juvenile striped bass captured at the water diversion fish screens in net pens and releasing them after one or two years, it is thought that the adult striped bass population could be stabilized at 3 million adults. Without augmentation, the population is expected to decline to about 500,000 adults. For a striped bass augmentation program to be in compliance with the ESA, the level of mortality on winter-run chinook salmon must be specified and the impact of this mortality must not appreciably reduce the likelihood of winter-run chinook salmon survival and recovery.

The California Department of Fish and Game estimates annually the abundance of striped bass; estimates have been reported by Kohlhorst (1999). Adult striped bass are captured with gill and fyke nets during the spring spawning migration and tagged with disc tags. Tags are recovered in summer and fall creel surveys and in subsequent springtime tagging operations. The field methods and estimation procedure, based on the Peterson estimator, are described by Stevens (1977). The estimate includes animals that are 3 or more years old, although striped bass begin feeding on juvenile salmon during their second year of life. We assume that the adult striped bass abundance estimate is a reasonable index of the total striped bass population capable of preying on juvenile chinook salmon. Note that an abundance index is sufficient because the predation parameter estimate will scale accordingly, i.e. the product of the striped bass abundance index and the predation rate parameter is unitless, as explained below.

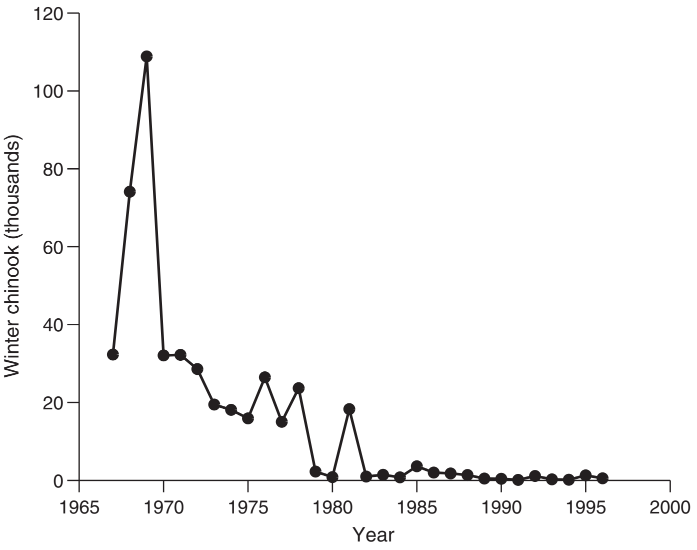

Figure 2

Estimated number of winter-run adult spawning chinook salmon passing the Red Bluff Diversion Dam.

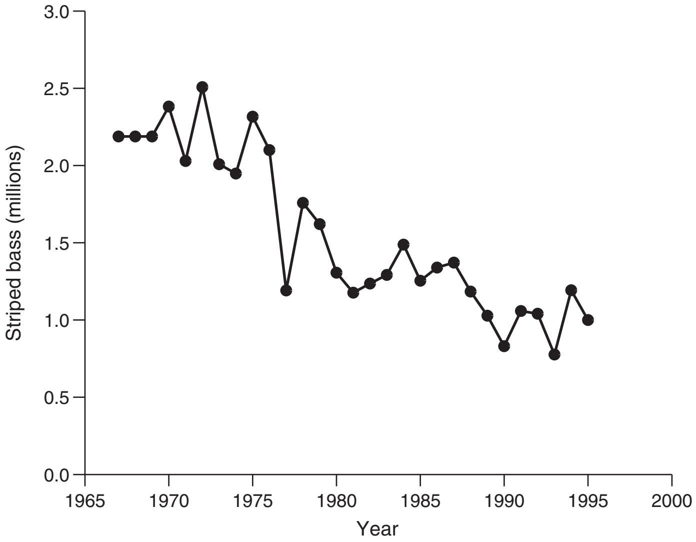

Figure 3

Peterson mark-recapture estimates of adult striped bass population size in the Sacramento-San Joaquin rivers and estuary.

Winter-run chinook salmon population model

In this section, we develop a probability model for winter-run chinook salmon spawning escapement. The model includes several potentially important factors influencing winter-run chinook salmon population growth: predation by striped bass, initiation of conservation measures in 1989, possibly density-dependent reproduction, and lognormal variability in reproduction (so-called process variation). Because winter-run chinook salmon juveniles are a minor prey item in the striped bass diet, owing to the rarity of winter-run chinook salmon in relation to other chinook populations, we do not model the striped bass population dynamics but rather treat the striped bass population-size observations as an input to the winter-run chinook salmon population model.

Winter-run chinook salmon adults spawn mostly at age 3 and to a lesser extent at age 4 (some males return at age 2, but we did not include them in the analysis on the presumption that 2-year-old males contribute little to population growth). The number of adult spawning fish in year *t* is the sum of 3- and 4-year-old spawning fish:

$$W_t = W_{t,3} + W_{t,4}. \qquad (1)$$

The number of age a spawning fish in year t depends on the number of spawning fish a years before, the productivity (g) of these fish, and the propensity to spawn at age a (π_a) given survival to spawning:

$$W_{t,a} = W_{t-a} g_{t-a} \pi_a. \qquad (2)$$

For winter-run chinook salmon, $a \in \{3,4\}$ and we set $\pi_3 = 1-\pi_4 = 0.89$ (Botsford and Brittnacher, 1998), assuming that the maturation rate of age-3 fish and the annual mortality rate of age-4 fish is constant across years. We modeled $\log(g_t)$ as the sum of several effects,

$$\log(g_t) = \mu + \Delta I_t - \alpha S_{t+1} - \beta W_t + \varepsilon_t,\ \varepsilon_t \sim \text{Normal}(0,\sigma^2), \qquad (3)$$

including a mean population growth rate in the absence of striped bass and density dependence (μ); a possible change (Δ) in the mean population growth rate resulting from conservation measures initiated in 1989 (Williams and Williams, 1991) ($I_t=0$ for $t<1989$; $I_t=1$ for $t\geq 1989$); an effect due to variations in the abundance of striped bass (αS_{t+1}, where S_{t+1} is the abundance of adult striped bass in year $t+1$ and α is the per-bass predation rate); a density dependence effect (βW_t); and a normally distributed process error (ε_t) having mean = 0 and variance = σ^2. We ignored the measurement error in $\{W_t, t>1985\}$ for simplicity; the main effect of including measurement error would be to increase the uncertainty in Δ. Together, Equations 2 and 3 imply that $W_{t,a}$ is a lognormal random variable, and that W_t (see Eq. 1) is distributed as the sum of two lognormal random variables.

Density dependence in this formulation is equivalent to the Ricker model of stock-recruitment (Ricker, 1954): as stock size increases to infinity, per-capita productivity declines exponentially to zero. Because population viability analysis (PVA) model predictions can be sensitive to density dependence, we also considered Equation 3 with β set to zero.

Equation 3 states that predation by an individual striped bass is a linear function of winter-run chinook salmon abundance, ignoring the possibility of satiation or a minimum prey abundance to initiate feeding. Although the actual functional response of striped bass to winter-run chinook salmon is probably more complex, it is unlikely that satiation is a major issue for a rare prey species such as winter-run chinook salmon. We use S_{t+1} rather than S_t because striped bass population size is estimated in the spring, and the juvenile winter-run chinook salmon born in year t are vulnerable to striped bass predation as they develop and migrate to sea the following winter and spring (year $t+1$).

Parameter estimation

In this section, we couple the time series data and the winter-run chinook salmon population dynamics model with a prior distribution of the model's parameters to yield a Bayes posterior distribution for those parameters. For convenience, we denote the vector of model parameters as $\theta = (\mu, \Delta, \alpha, \beta, \sigma)$, and the data vectors as $W = (W_{1967}, W_{1968}, \ldots)$, $S = (S_{1967}, S_{1968}, \ldots)$, and $I = (I_{1967}, I_{1968}, \ldots)$. We denote a probability density as $p(\cdot)$ and a conditional probability density as $p(\cdot\,|\,\cdot)$. The unnormalized Bayes posterior distribution of the model parameters is given by

$$p(\theta\,|\,W, I, S) \propto p(\theta)p(W\,|\,I, S, \theta), \qquad (4)$$

where $p(\theta)$ is the prior distribution of θ, and $p(W\,|\,I,S,\theta)$ is the model probability density function of W conditional on I, S, and θ, given by

$$p(W\,|\,I,S,\theta) = \prod_t P(W_t\,|\,W_{t-3}, W_{t-4}, I_{t-3}, I_{t-4}, S_{t-2}, S_{t-3}, \theta). \qquad (5)$$

From the previous subsection, $p(W_t\,|\,\cdot)$ on the right hand side of Equation 5 is the probability density for a sum of two lognormal random variables. We evaluated $p(W_t\,|\,\cdot)$ using the analytic expression provided in Johnson et al. (1994, Eq. 14.20), solving the integral contained therein by adaptive quadrature.

The prior density $p(\theta)$ is the joint probability of the components of θ: $p(\theta) = \prod_i p(\theta_i)$. Because we have little information about θ that is independent of the data used in our analysis, we desired a prior that would have little influence on the posterior. There are many ways such a noninformative prior could be specified. In the results presented here, we set $p(\mu, \Delta, \alpha, \beta) \propto 1$ over the range of the parameters (α and β are restricted to positive values) and $p(\sigma) \propto \sigma^{-1}$, following the recommendations of Lee (1989) and Gelman et al. (1995) based on the work of Jeffreys (1961). We also examined the effects of using other reference priors, such as normal and exponential distributions with very large variances, and found there to be little difference in the results (not shown).

We did not attempt to derive a closed-form analytical expression for the posterior distribution of θ. Instead, we used the Metropolis-Hastings algorithm (Metropolis et al., 1953; Hastings, 1970; Gilks et al., 1996), a Markov chain Monte Carlo method. The Metropolis-Hastings algorithm produces a Markov chain with a stationary distribution equivalent to the posterior of θ. Estimates of parameter means, medians, and credible intervals were obtained from samples of the stationary Markov chain. We used a multivariate normal distribution centered on the current value of θ for the algorithm's proposal distribution. The variance-covariance matrix of the proposal distribution was adjusted by trial and error until the resulting Markov chain was well-mixed and the probability of accepting candidates fell in the range of (0.15, 0.50) (Gilks et al., 1996). Note that the proposal distribution form does not presume anything about the distribution of the unknown parameters, and as long as certain criteria are met (see Gilks et al. [1996]), only the convergence speed and mixing are affected, not the stationary distribution of the chain. To assess convergence, we initiated chains from many widely varying starting places and observed convergence to the same distribution. We found that 50,000 iterations following an initialization of 10,000 iterations provided stable parameter estimates. For an additional convergence check, we compared the modes of θ to maximum likelihood estimates of θ obtained using a quasi-Newton method for minimization of a multivariate function with simple bounds (IMSL Fortran Numeric Library subroutine BCONF, Visual Numerics, Inc., Houston, TX).

Extinction and recovery probabilities

Given our winter-run chinook salmon population dynamics model, alternative striped bass population levels, and the posterior distribution of θ, we used Monte Carlo methods to determine the probability distribution of winter-run chinook salmon abundance in each of the next 100 years. From these distributions, the probability (P) that winter-run chinook salmon abundance is below a quasi-extinction threshold or above a recovery benchmark can be estimated directly. It was assumed, for simplicity, that striped bass abundance over the next 100 years will be held constant (S_t=S) at a level depending on the intensity of striped bass stocking. We considered three levels of striped bass abundance of interest to fishery managers, corresponding to no stocking (S=512,000 adults), moderate stocking (S=700,000 adults), and heavy stocking (S=3,000,000 adults). For comparative purposes, we also examined the effect of removing all striped bass (S=0 adults). Of particular interest is the increase in extinction probability due to striped bass stocking in relation to the no-stocking alternative. We denote this increase in extinction risk as δ. We generated the distribution of extinction and recovery probabilities and δ under the four striped bass population levels as follows:

1. Initialize the model by setting $\{W_t, t=-3, -2, -1, 0\}$ equal to the four most recent observations of spawning escapement.
2. Randomly select a value for θ according to its posterior density using the Metropolis algorithm.
3. For each striped bass abundance level S, $\{W_t, t=-3, -2, -1, 0\}$, and the particular value of θ, simulate 1000 100-year trajectories of winter-run chinook salmon spawning escapement according to Equations 1, 2, and 3.
4. For year t, the fraction of simulations in which spawning escapement was below the quasi-extinction threshold or above the recovery benchmark (levels specified below) approximates P_t(quasi-extinction | S,θ) and P_t(recovery | S,θ), respectively, for t=1,2,...,100.
5. For year t=50 and each level of striped bass abundance S, the increase in extinction probability in relation to that for the no-stocking level is approximated by $\delta(S, \theta) = P_{t=50}$(quasi-extinction | S,θ) – $P_{t=50}$(quasi-extinction | S=512,000, θ).
6. Repeat steps 2–5 10,000 times. For each year t and striped bass abundance level S, the average values of P_t(quasi-extinction | S,θ) and P_t(recovery | S,θ) over these repetitions approximates their expected values with respect to θ given S. For brevity, in the "Results" and "Discussion" sections, we refer to these values as simply the probabilities of quasi-extinction and recovery in year t given striped bass abundance S.

We focused on quasi-extinction to avoid the problems of modeling depensatory effects, such as demographic stochasticity, inbreeding depression, and Allee effects (Allee, 1931). Estimates of absolute extinction risk are very sensitive to how these processes are modeled and parameterized, and relevant data are lacking. Quasi-extinction is less sensitive to these processes and is more likely to occur over short time horizons; therefore it is a more useful management benchmark than absolute extinction (Beissinger and Westphal, 1998). The draft recovery plan for winter-run chinook salmon (NMFS[1]) defines the quasi-extinction level as 100 females and the recovery level as 10,000 adult females; therefore we set the quasi-extinction threshold at 200 adults and the recovery threshold at 20,000 adults on the working assumption that the sex ratio is approximately 1.

Results

Parameter estimates and model fit

Table 1 lists summary statistics for parameter estimates for both the density-dependent and density-independent models; Figure 4 shows posterior marginal distributions and pairwise bivariate density contour plots for the winter-run chinook salmon density-dependent population dynamics model. The posterior median of μ was –0.69 per generation and the 0.90 credible interval (CI lower and upper endpoints of the posterior distribution equal to the 0.05 and 0.95 percentiles, respectively) for μ was (–1.2, –0.046), which indicates that the decline of winter-run chinook salmon most probably reflects a real trend rather than solely a series of random events. The median of the posterior distribution of the listing effect parameter Δ was positive, which suggests that the winter-run chinook salmon population growth rate has increased since initiation of conservation measures in 1989. The present-day realized growth rate, log(g), as determined from the joint posterior distribution and current winter-run chinook salmon and striped bass abundance according to Equation 3, has a median of –0.19 (0.90 CI=(–1.08, 0.66)), which indicates that the winter-run chinook salmon population may still be in decline in spite of the conservation measures and the decline in striped bass abundance.

At current striped bass abundance, the median estimate of α translates into about a 9% chance of an individual juvenile chinook salmon being consumed by a striped bass. Because log(g_t) is highly variable (median of σ estimate was 1.18), only fairly large values of α are inconsistent with the data. Furthermore, there was positive correlation between the estimates of α and μ (correlation coefficient=0.77), meaning that fairly high predation rates are consistent with the data if the underlying population growth rate was also high. The negative correlation of Δ with μ and α indicates that the potential improvement in winter-run chinook salmon population growth rate could have been due to either conservation measures or reduced predation.

At recent population sizes, there is little reduction in winter-run chinook salmon population growth due to density-dependent effects: the median of β translates into a

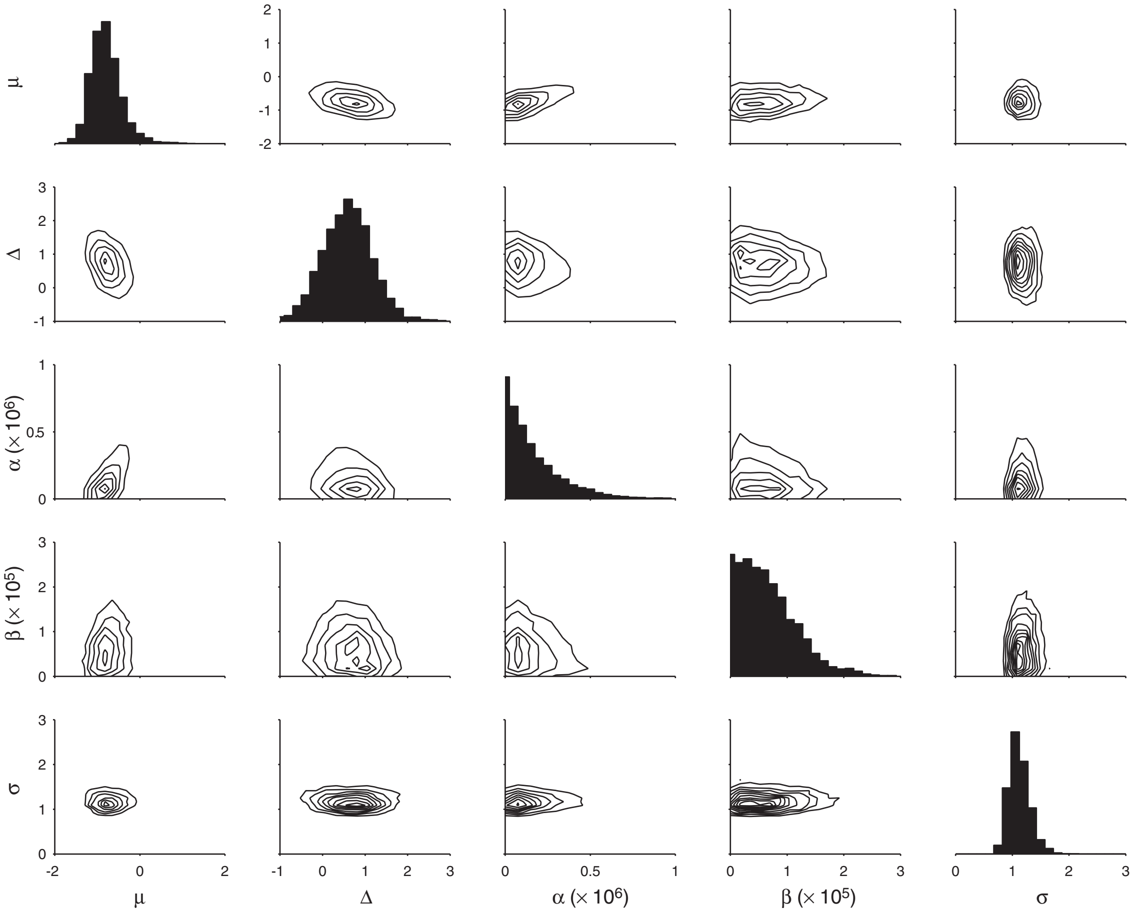

Figure 4

Posterior marginal distributions (histograms along the diagonal) and bivariate densities (off-diagonal contour plots) for the density-dependent winter chinook salmon population dynamics model parameters.

Table 1

Summary of posterior distributions under alternative model formulations. DD refers to density-dependent model, DI refers to density-independent model.

Model	Parameter	Mean	Median	0.90 CI
DD	μ (growth rate)	–0.694	–0.735	(–1.20, –0.046)
	Δ (growth rate change)	0.683	0.692	(–0.275, 1.64)
	α[1] (predation rate)	1.86	1.29	(0.100, 5.44)
	β[2] (density dependence)	7.16	6.26	(0.507, 16.9)
	σ (process error SD)	1.20	1.18	(0.936, 1.53)
DI	μ (growth rate)	–0.777	–0.825	(–1.34, –0.051)
	δ (growth rate change)	0.823	0.829	(–0.118, 1.77)
	α[1] (predation rate)	2.19	1.63	(0.116, 6.29)
	β (process error SD)	1.18	1.16	(0.921, 1.50)

[1] Values multiplied by 10^6 to increase legibility.

[2] Values multiplied by 10^5 to increase legibility.

$\log(g_t)$ of only 2.6×10^{-3} per generation less than that at a stock size near zero. At the recovery target population size of 20,000 adult winter-run chinook salmon, in contrast, the median estimate of β corresponds to a population growth rate reduction of 0.13 per generation.

The fit of the model was assessed by comparing the observed spawning escapement data series to the posterior predictive distribution of W (Gelman et al., 1995), which was estimated by drawing 10,000 samples from $p(\theta\,|\cdot)$ and a normal$(0,\sigma^2)$ and applying Equations 1–3. Figure 5 shows the observed data and boxplots of the posterior predictive distributions for the data points. Observed escapement in 1980 and 1991 was below the fifth percentile of the distribution for predicted escapement for those years. Winter-run chinook salmon returning in 1980 and 1991 were born during the drought years of 1976–77 and 1987–88. The 1976–77 drought was particularly severe; there were very low river flows and water temperatures exceeded 21°C during the winter-run chinook salmon egg incubation period, well above the 50% mortality temperature of 16°C reported for chinook salmon (Alderice and Velsen, 1978). The association between these outliers and droughts suggests that the model does not accurately handle an important source of risk. The estimate of σ was influenced by the 1980 and 1991 escapements, but because critically dry years appear to reduce survival more than wet years increase it (as suggested by the lack of large positive deviations in Fig. 5), estimates of absolute extinction risk may be optimistic. Our focus, however, is on the relative risk of extinction under different management scenarios.

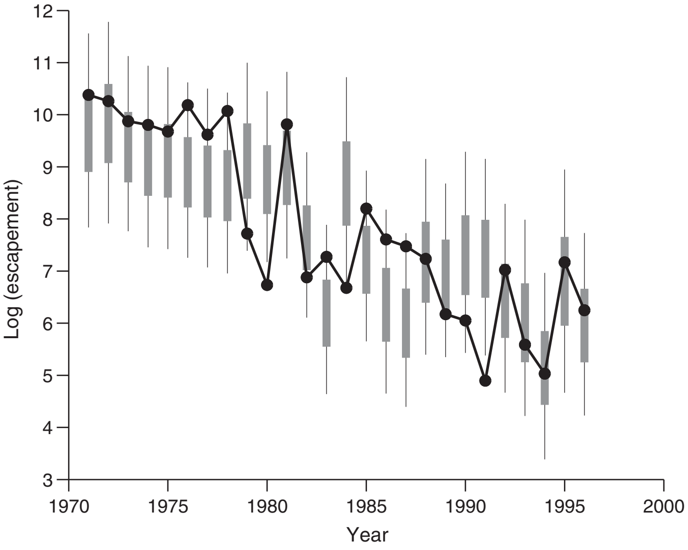

Figure 5

Posterior predictive distributions (gray boxes and whiskers) and observed winter chinook salmon spawning escapement (circles). Gray boxes cover the middle 0.50 percentile interval, and whiskers represent the middle 0.90 percentile interval.

Table 2

Expected probabilities of quasi-extinction and recovery within 50 years under alternative model formulations. DD refers to density-dependent model, DI refers to density-independent model.

Probability	Striped bass abundance	Model DD	 DI
Extinction	0	0.231	0.198
	512,000	0.276	0.246
	700,000	0.295	0.268
	3,000,000	0.554	0.582
Recovery	0	0.135	0.405
	512,000	0.107	0.328
	700,000	0.097	0.302
	3,000,000	0.038	0.116

Extinction risk estimation and stocking plan analysis

Figure 6 shows the cumulative distributions of quasi-extinction and recovery probabilities under the three striped bass stocking levels predicted by the density-dependent model. Winter-run chinook salmon have a 28% chance of becoming quasi-extinct and a 11% chance of recovering to more than 20,000 adults in 50 years, if no striped bass stocking were to occur (Table 2). If a striped bass stocking program were to stabilize the striped bass population at 700,000 adults, the probability of quasi-extinction in 50 years would rise from 28% to 30% (δ=1.9%, 0.9 CI=[1.2%, 2.6%]), and the probability of recovery would decline from 11% to 10%. A future adult bass population of 3.0×10^6 would raise the chance of winter-run chinook salmon quasi-extinction to 55% (δ= 27.7%, 0.9 CI=[25.4%, 30.1%]) and lower the recovery probability to 3.8%. If, on the other hand, striped bass predation could be eliminated completely, the probability of quasi-extinction would decline to 23% (δ=–4.5%, 0.9 CI=[–5.6%, –3.4%]) and the probability of recovery within 50 years would rise to 14%.

The probability of quasi-extinction according to the density-independent model is quite similar to that of the density-dependent model, but the predicted probability of recovery is substantially higher with density independence (Table 2). Extinction probability is somewhat more sensitive to striped bass predation in the density-independent model. This greater sensitivity to striped bass abundance results from the higher estimate for the bass predation rate parameter and the lack of compensation in the density-independent model.

The density-dependent model indicates that without further population growth rate increases, winter-run chinook salmon are unlikely to reach the recovery benchmark: recovery will not occur within 20 years, and there is less than an 11% chance of reaching the 20,000 adult

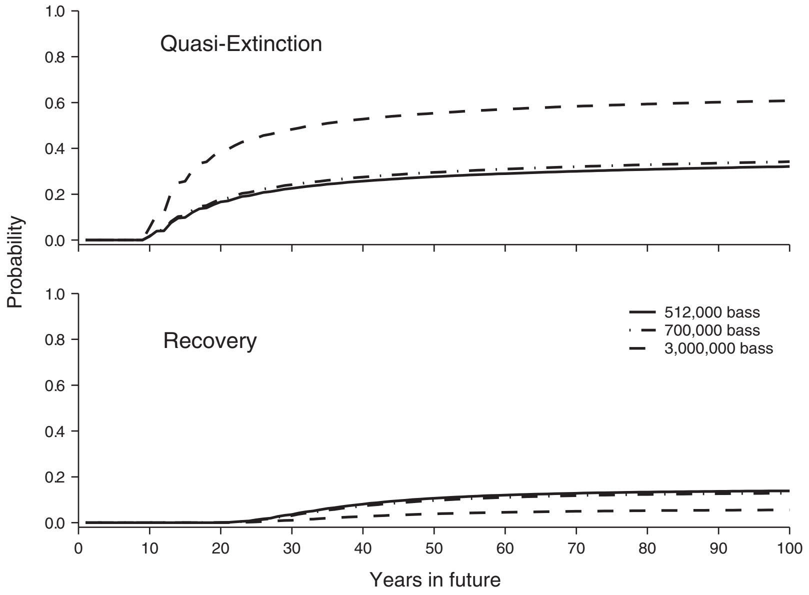

Figure 6

Probabilities of winter chinook salmon quasi-extinction and recovery under different adult striped bass population sizes.

winter-run chinook salmon level within 50 years. The low probability of recovery predicted by the density-dependent model is due in part to reductions in productivity at moderate population sizes. The median equilibrium winter-run chinook salmon population size, given by $(\mu+\Delta-\alpha S)/\beta$ with S = 512,000, is 18,100, which is below the recovery target of 20000.

Discussion

Predation by striped bass and effect of stocking

The results presented here indicate that striped bass predation may be a nontrivial source of mortality for winter-run chinook salmon. According to our analysis, the current striped bass population of roughly 1×10^6 adults consumes about 9% of winter-run chinook salmon outmigrants. By comparison, 85,000 northern squawfish consume about 11% of juvenile salmonids passing through the John Day Reservoir on the Columbia River (Rieman et al., 1991), based on prey consumption rates and predator and prey abundances. Jager et al. (1997), using a spatially explicit individual based model, estimated that between 13% and 57% of fall-run chinook fry were consumed by piscivorous fish in the Tuolumne River, California. The predation rate by striped bass on winter-run chinook salmon juveniles inferred from the time series of their abundances appears plausible in light of these comparisons. If striped bass predation is truly in this range, a significant increase in striped bass abundance could substantially increase the risk of winter-run chinook salmon extinction and reduce the likelihood of recovery. A limited program aimed at stabilizing the striped bass population at its recent size might pose an acceptably small risk: the model indicates with 95% certainty that the stabilization program would add less than 3.1% to the baseline extinction risk of 28%. Although this analysis suggests that striped bass predation may be a significant risk factor for winter-run chinook salmon, striped bass eradication would not be enough to ensure recovery of winter-run chinook salmon. In the following two subsections, we discuss how data limitations and model uncertainty influence the results and our interpretation of them.

Model uncertainty

Model uncertainty arises from our ignorance of the exact processes driving population dynamics. Although there is a well-developed statistical basis for model identification and selection (Burnham and Anderson, 1998), different models may fit the data equally well yet make quite different predictions (Pascual et al., 1996). In such cases, one should consider a variety of models and ensure that important conclusions are upheld by all of them (Beissinger and Westphal, 1998).

Population dynamics and PVA models can be very sensitive to the presence and form of density dependence in the model. Because the work presented here was concerned primarily with the change in extinction risk posed by a change in striped bass abundance, it is encouraging that the probability of quasi-extinction was not sensitive to assumptions about density dependence. We presented results of both a Ricker-type density dependent model and a density-independent model; we also analyzed a Beverton-Holt type model (where per-capita productivity reaches an asymptote instead of declining to zero as population size increases to infinity) and found that it gave similar predictions to the Ricker model (results not shown). The insensitivity of extinction risk to the form of density dependence is perhaps not surprising because density dependence is considered to have little influence on the extinction process if populations are well below carrying capacity (Emlen, 1995), although it has the potential to create both compensatory population growth that can increase population persistence and oscillatory or chaotic dynamics that can reduce population persistence (Ginzburg et al., 1990; Mills et al., 1996; Belovsky et al., 1999). The probability of recovery, however, was strongly dependent on whether density dependence was included: regardless of striped bass stocking level, the recovery probability predicted by the density-independent model was about threefold higher than that predicted by the density-dependent model. Although the density dependence parameter was not well-identified by the data, winter-run chinook salmon are currently restricted to a limited portion of the Sacramento River and it is certainly possible that there is not enough habitat to support a spawning run of 20000 adults. Further study of the Sacramento River's carrying capacity for winter-run chinook salmon is warranted.

The dynamics of food web and predator-prey models can also be sensitive to the form of the predator's functional response to prey abundance (Overholtz et al., 1991; Berryman, 1992). The models presented here assumed that the predation-related per-capita mortality of winter-run chinook salmon is a linear function of striped bass abundance only. It is possible, however, that this mortality rate depends on winter-run chinook salmon abundance as well, through the feeding response of individual striped bass to winter-run chinook salmon abundance. In deterministic models, the form of the functional response (as well as predator abundance and prey productivity) determines the equilibrium prey population size. In particular, whether a prey population can persist may depend on whether the predator's functional response is sigmoidal or increases monotonically to an asymptote with increasing prey abundance (Sinclair et al., 1998). In cases where the prey is the major food source of the predator, it can be possible to detect a nonlinear functional response from the time series themselves (Jost and Arditi, 2000), especially if the system is perturbed (Carpenter et al., 1994). Winter-run chinook salmon are not the main prey of striped bass, and any possible depensatory effect of predation may be reduced by alternate prey, including juvenile chinook salmon of other races. Juvenile fall chinook salmon, in particular, are abundant, and often co-occur with winter-run chinook salmon (Healey, 1991). If the abundance of fall chinook salmon is uncorrelated with, and high in relation to, winter-run chinook salmon, then the striped bass predation rate may be related to fall chinook salmon abundance and unrelated to winter-run chinook salmon abundance. In the absence of relevant data, further consideration of nonlinear feeding responses and effects of alternate prey (e.g. Spencer and Collie, 1995), is beyond the scope of this paper.

Another aspect of model uncertainty is the assumption that the future will be like the present. The future will probably include increased conservation efforts, changing ocean productivity, and perhaps further habitat degradation. Although the level of absolute risk would change substantially if these processes were included in the simulations, the relative risks posed by the different striped bass stocking schemes would change much less. The main goal of this work was to compare these relative risks; a secondary goal was to predict what would happen if things continued in the future as they are now. We therefore feel confident in stating that a large striped bass stocking program would be risky and that further winter-run chinook salmon restoration actions are needed.

Data uncertainties

Imprecise estimates of predator and prey abundance limit the precision of parameter estimates and can bias parameter estimates if not accounted for (Seber and Wild, 1989; Carpenter et al., 1994). For the bulk of the winter-run chinook salmon series, observation error is probably quite low because all fish were counted directly; the CV for the striped bass population estimates is thought to be about 25% (Stevens, 1977). We ignored measurement error in both the striped bass and winter-run chinook salmon population abundance data. Further work is required to assess how much of an influence these errors might have on parameter estimates for the model presented here.

Informative priors

A major advantage of the Bayesian approach is the ability to include informative prior probability distributions for model parameters. Informative priors can greatly improve the precision of posterior parameter estimates and model predictions. In the example presented here, the estimate of the striped bass predation rate could be improved, and uncertainty in stocking impacts reduced, by incorporating direct information on the rate of striped bass predation on winter-run chinook salmon into an informative prior on α. Such information would include estimates of the number of salmon that striped bass eat per day (obtainable from food habits and metabolic studies), and the number of juvenile salmon that are vulnerable to striped bass predation. Some information on these quantities is available for the Sacramento system (Stevens, 1966; Thomas, 1967).

A Bayesian meta-analysis of the available food habits data was performed to estimate the number of salmon that striped bass eat per day, and the number of juvenile salmon passing through the Sacramento River system was estimated from ocean catches, spawning escapements, and considerations of smolt-to-adult survival rates. Unfortunately, including the informative prior did not substantially improve the precision of the posterior distribution of α, nor did it significantly alter the central tendency. Given the number of necessary assumptions, the complexity of the meta-analysis, and the minimal impact of including the informative prior on the posterior distribution of α, we opted to retain a noninformative prior on α. Should better data become available, it could be worthwhile to include them in the prior for α, although there is no practical value in including the data currently available.

Status of winter-run chinook salmon

Although not the primary purpose of this study, our model does provide an assessment of the present status of winter-run chinook salmon: the quasi-extinction probability of 28% within 50 years indicates that winter-run chinook salmon face a substantial extinction risk, in spite of the probable improved survival since the ESA listing. The ESA does not specify quantitative risk levels corresponding to threatened or endangered status, but under the World Conservation Union's Red List extinction risk criteria (IUCN, 1994), winter-run chinook salmon would be classified as "vulnerable" (>10% extinction probability in 100 years). Winter-run chinook salmon extinction risk is higher than the 10% probability of extinction in 50 years specified as "safe" by Botsford and Brittnacher (1998). Furthermore, the true quasi-extinction risk is probably higher than indicated by our analysis because we have neglected some sources of risk that could be significant at population levels in excess of the quasi-extinction threshold, such as catastrophic events.

Botsford and Brittnacher (1998) developed a somewhat similar model of winter-run chinook salmon spawning escapement that predicts almost certain extinction for winter-run chinook salmon in the absence of increased survival. The differences between the results presented here and those of Botsford and Brittnacher (1998) illustrate the importance of including parameter uncertainty and allowing for time-varying population growth rate. Their model assumed constant mean population growth rate, whereas ours allowed for a change (Δ) in the population growth rate following the conservation measures initiated in 1989. The more optimistic prediction in this paper derives mostly from the substantial probability that population growth rate increased following implementation of conservation measures. This can be illustrated by setting Δ to zero and refitting our model. The quasi-extinction probability with $\Delta = 0$ is 69%. Much of the remaining discrepancy between our results and those of Botsford and Brittnacher (1998) arises from including parameter uncertainty, which allows for the possibility that population growth might be higher than its maximum likelihood estimate. The predicted decline of the adult striped bass population from 700,000 to 512,000 contributes a smaller effect to increased survival probability than does the effect of conservation measures. Both analyses are similar, however, in that they indicate winter-run chinook salmon face significant extinction risk and require further conservation action.

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