

Article

## Estimating critical abundance thresholds in exploited populations: a simulation approach based on species resilience to disturbance

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### Abstract

Managers of exploited species too often assume that populations can be maintained at equilibrium abundances that will provide maximum yield. Most evidence to date suggests that populations seldom adhere to equilibria, but rather fluctuate stochastically between bounds. The last decade has revealed the consequences of not incorporating uncertainty around point estimates of equilibria, which has led to the decline of several fisheries. We used the sample importance re-sampling (SIR) algorithm to exhibit the uncertainties in point estimates generated by models for management of two Chinook salmon *Oncorhynchus tshawytscha* stocks and a bowhead whale *Balaena mysticetus* population. We then incorporated the cumulative uncertainties of each system into a simulation technique similar to population viability analyses (PVA) to provide decision support for establishing threshold abundances of each exploited population. The simulation presented was based upon the resilience (time to recover from perturbations to abundance) of each population, which was found to be relatively high for the Chinook stocks and low for bowhead whale. Various thresholds could be chosen depending on: (1) how much time should be allowed for the population to recover from a perturbation, (2) when should the stock be considered recovered (i.e., within 1%, 5%, 10%, and so on of what abundance would be had there been no perturbation), and (3) the maximum allowable risk that a threshold is too low. Reasonable thresholds for the Chinook stocks were 60% to 80% of abundances that provide maximum sustained yield ( $S_{MSY}$ ). Due to their low productivity, no clear threshold below the biomass point estimate was apparent for bowhead whale.

**Keywords** population; threshold; exploitation Chinook; resilience; disturbance; simulation; stochastic; salmon; bowhead whale; recovery; risk.

### 1 Introduction

There remains a conceptual commitment (*sensu* Khun, 1996) among some fisheries and wildlife managers to the idea that nature is in balance even though ecologists have been questioning this perception for several decades (Egerton, 1973; DeAngelis and Waterhouse, 1987). Balance or stability has been defined in many ways following a disturbing force including presence/absence of species (persistence), distance from which populations or communities can recover to equilibria (amplitude), and time for this recovery to take place (resilience) (Connell and Sousa, 1983; Grimm and Wissel, 1997). Stability has been searched for in metrics ranging from the collective biomass of communities to species densities or relative abundances. Individual

populations seldom adhere to or even cycle regularly around equilibrium abundances (Connell and Sousa, 1983; Tilman, 1996). Although, population stability may increase when ample resources are available to younger life stages but are limited to adults (in theory; Mueller and Huynh, 1994), persistence of species may stabilize at large spatial scales due to several hypothesized steadying mechanisms (DeAngelis and Waterhouse, 1987), and in some studies the collective biomass of the community was shown to be more or less constant (Rodriguez, 1994; Tilman, 1996; Doak et al., 1998). Regardless, most research suggests that it may be more reasonable to conceptualize individual populations as fluctuating stochastically within bounds (Connell and Sousa, 1983). The density-dependence we observe with respect to mortality and natality in some species (e.g., Beverton and Holt, 1957; Ricker, 1975) implies there is a carrying capacity, which defines the upper bound. Researchers studying exploited populations have recently shifted their attention to identifying the lower bound or threshold abundance below which a population cannot return within a reasonable amount of time. Setting thresholds too low limits future production and yield and can expose populations to greater risk of extinction; setting thresholds too high unduly limits harvest. Understanding how long it takes for populations to recover from low abundances and that recovery cannot be defined as adherence to equilibrium will help managers and resource stakeholders set limits on the extent to which populations can be exploited.

Since the early 1920's when innovative technologies were developed to harvest natural resources at unsustainable levels, numerous species of fish and other aquatic resources vanished altogether or were reduced dramatically (Smith, 1994). As these natural resources were exploited at high rates, a wealth of harvest and abundance data became available, and population parameters for management were estimated based on population growth and density-dependent models (Schaefer, 1954; Beverton and Holt, 1957; Ricker, 1975). However, most managers have ignored the underlying noise and uncertainty in parameter estimates. The last decade has pointed out the flaws with point estimates for sustainable management of aquatic, terrestrial, and avian populations (Hilborn and Mangel, 1997). The New England cod-fishery for example shows how target biomass estimates were misleading due to uncertainty as the biomass remained constant, but year class strength was mostly from younger fish in the population (Myers and Cadigan, 1994). The consequence of not acknowledging this uncertainty was a complete stock collapse in the late 1980's and early 1990's. Even for populations with short life cycles (such as salmon), which should allow greater resilience to stochastic abundance reductions (see Discussion), the lack of attention to parameter uncertainty in management models has caused severe stock declines (e.g., Snake River Chinook salmon (Emlen, 1995)).

Management based on point estimates invokes the implicit assumption that if exploited at optimum rates, a population will settle upon an equilibrium that will yield maximum production. Most all evidence from field surveys and experiments are either equivocal or do not support the presence of equilibria with respect to population abundances, but rather stochastic boundedness (Connell and Sousa, 1983). Not surprisingly, managers often fall short of point estimate benchmarks because of stochastic population fluctuations that are beyond their control. A better approach is to establish a lower bound that represents the threshold abundance above which recovery occurs during an acceptable length of time. Managers would then have a broader target between this threshold and optimum abundance.

Establishing this threshold can be determined based on the resilience of the population. The key question becomes how to observe the recovery of a population from abundance reductions in the presence of substantial random fluctuation. Time to recovery could be observed directly if the same population with the same random fluctuations could be observed over the same time period once with the perturbation and once without. An impossibility of course, but then simulation-based approaches are not limited to real world logistics. We offer such an approach that compares the modeled responses of populations that have been perturbed (reduced abundances) to an undisturbed control; resilience was measured as the rate of convergence between the two.

We examined threshold points below which time to recovery was protracted. First, the uncertainty in the parameter estimates generated by the models for management purposes was examined using Rubin's (1988) sample importance resample (SIR) algorithm. Then, using these uncertainties in model parameters and incorporating natural variation, we illustrated the degree to which several exploited populations were resilient to reductions in abundance. We used measurements of resilience to decide upon a lower threshold abundance based on probabilities obtained from our simulations. Our approach is similar to population viability analyses (PVA's) used in conservation biology for determining risk of extinction (e.g., Ellner and Fieberg (2003)); we illustrate the broader utility of PVA type analyses in establishing optimum abundances for sustained harvest of exploited populations.

These modeled populations included two stocks of Chinook salmon, *Oncorhynchus tshawytscha* and one population of bowhead whale, *Balaena mysticetus*. Among exploited vertebrate populations in the ocean, Chinook salmon and bowhead represent taxa with disparate life history strategies (opposite ends of the  $r$ - $K$  spectrum) and serve as good test populations with respect to the versatility of our approach in finding threshold population sizes.

## 2 Methods

### 2.1 Data sources

We used stock-recruitment data from Chinook salmon stocks found in the Queets, Stikine, Siletz, and Siuslaw Rivers on the west coast of North America (Table 1). Stocks were partitioned into escapement (spawners) and the mature adults (recruits) they produced. Data for the Queets stock was collected by the Quinault Indian Nation and for the Siletz and Siuslaw stocks by the Oregon Department of Fish and Wildlife via area under the curve methods described by Hilborn et al. (1999). Stikine data was collected by Alaska Department of Fish and Game using mark-recapture methods as per Seber (1982). The Queets and Stikine stocks were used during the modeling exercises; the Siletz and Siuslaw stocks were used to pseudo-validate predictions from the Chinook models. Census data for bowhead whales were taken from Raftery et al. (1995), but were collected by Breiwick et al. (1984) and Zeh et al. (1995).

### 2.2 Population dynamics models

Chinook salmon tend to exhibit over-compensatory mechanisms of recruitment; thus, we modeled these recruitment processes using the log-normal form of the Ricker curve (Hilborn and Walters, 1992):

$$R_{y_i} = \alpha S_{y_{i-1}} e^{-\frac{S_{y_{i-1}}}{\beta}} \quad (1)$$

where  $R$ =recruitment in year  $i$  and is a function of  $S$  (escapement or spawners) in year  $i-1$ , and

$$\hat{S}_{y_i} = (\hat{R}_{y_{i-2}} + \hat{R}_{y_{i-3}} + \hat{R}_{y_{i-4}} + \hat{R}_{y_{i-5}} + \hat{R}_{y_{i-6}}) \times (1 - \hat{\mu}) \quad (2)$$

where  $S$  in year  $i$  is a function of  $R$  from the previous 6 year classes (excluding jacks [year  $i-1$ ]), and  $\hat{\mu}$  is the proportion harvested.

Optimum escapement,  $S_{MSY}$ , was estimated as a function of  $\alpha$  and  $\beta$  using the Hilborn and Walters (1992) approximation:

$$\hat{S}_{MSY} = \frac{\ln(\hat{\alpha})}{\frac{1}{\hat{\beta}}} (0.5 - 0.07 \ln(\hat{\alpha})) \quad (3)$$

For the bowhead population, we used a logistic model of population growth as per Hilborn and Walters (1992):

$$N_{t+1} = \left( N_t + rN_t \left( 1 - \frac{N_t}{K} \right) \right) \times (1 - \mu) \quad (4)$$

where  $N$  = population size at a particular time  $t$ ,  $r$  = intrinsic growth rate of the population,  $K$  = carrying capacity or population size at virgin biomass, and  $\mu$  = harvest rate during a particular year.

**Table 1** Abundance data for 4 Chinook salmon stocks in rivers emptying into the Pacific coast of North America. Stocks are partitioned into escapement (spawners—S) and the mature adults (recruits—R) they produced.

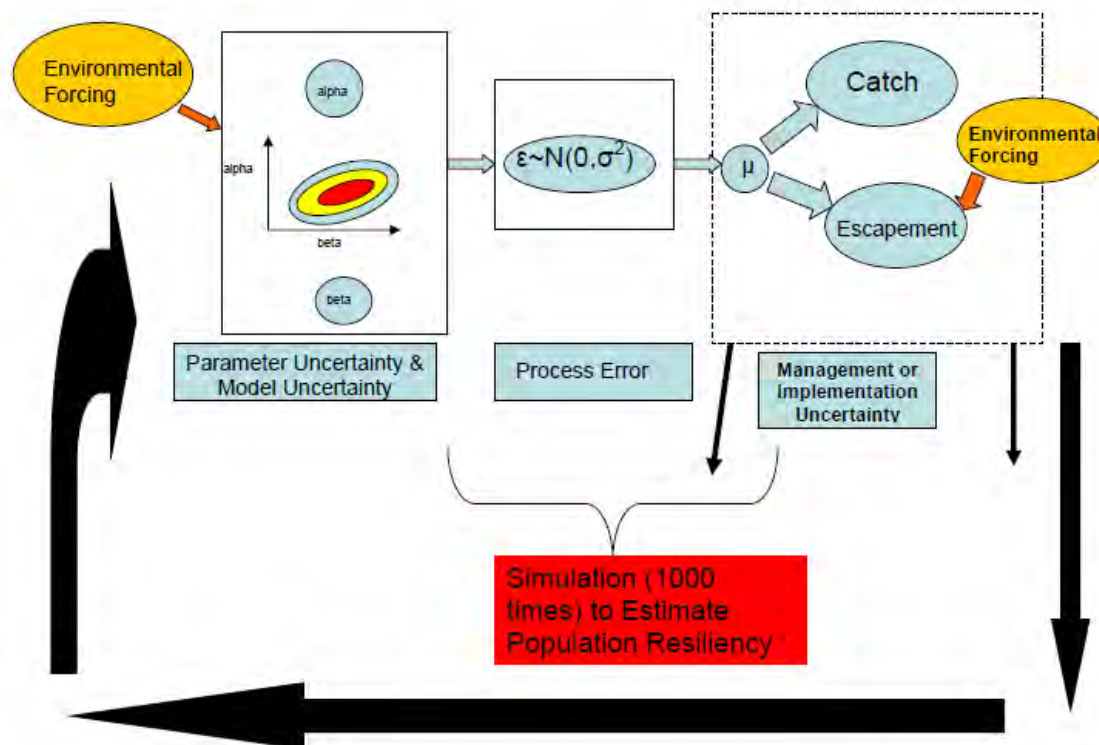
Year	Siuslaw		Siletz		Queets		Stikine	
	S	R	S	R	S	R	S	R
1965	3,816	19,758						
1966	9,497	15,044						
1967	5,395	11,374	2,712	6,366				
1968	3,151	9,544	1,233	6,653				
1969	7,337	7,734	780	5,855				
1970	13,028	10,116	3,810	5,956				
1971	3,141	11,452	2,547	4,388				
1972	3,539	18,577	2,464	6,702				
1973	879	18,551	3,019	10,694				
1974	6,015	19,243	2,564	16,777				
1975	4,427	18,965	2,062	13,635				
1976	7,999	17,474	1,326	14,132	1,200	14,043		
1977	9,492	25,555	3,314	12,233	3,600	13,852	11,445	15,223
1978	5,872	26,301	2,062	14,066	2,200	6,396	6,835	7,520
1979	8,040	22,031	7,217	11,231	3,799	11,481	12,610	35,107
1980	10,630	30,249	3,680	15,439	3,126	9,965	30,573	19,438
1981	8,724	41,320	4,435	16,584	4,256	18,215	36,057	29,245
1982	10,870	17,250	3,415	12,714	4,160	11,391	40,488	51,568
1983	4,186	53,599	2,136	13,860	2,487	20,602	6,424	20,575
1984	11,168	75,928	3,461	17,109	3,927	29,154	13,995	38,284
1985	14,822	41,966	6,628	7,110	4,220	14,410	16,037	20,000
1986	14,844	68,924	6,748	14,822	7,902	10,912	14,889	47,132
1987	17,603	51,937	4,577	18,739	6,392	12,654	24,632	71,951
1988	41,746	51,888	7,805	12,906	9,386	6,220	37,554	39,733
1989	28,279	27,557	4,401	26,206	9,259	18,086	24,282	17,947
1990	26,799	65,712	4,313	18,411	10,504	6,604	22,619	14,659
1991	26,100	26,649	5,633	19,235	4,786	3,438	23,206	54,824

### 2.3 Sample importance resampling

Sample importance resampling techniques (Rubin, 1988) were used to estimate distributions around the model and management parameters. We ran simulations that picked 100,000 pairs of randomly selected values of  $\alpha$  and  $\beta$  or  $r$  and  $K$  from non-informative prior distributions to estimate posteriors. The prior distributions were uniformly distributed as  $\alpha \sim U[0,15]$ ,  $\beta \sim U[0,250000]$ ,  $r \sim U[0,0.05]$ , and  $K \sim [1000,31000]$ . For simulation purposes, we estimated joint probability distributions to generate stochastic values for sets of parameters ( $\alpha$  and  $\beta$  or  $r$  and  $K$ ) and their associated error.

### 2.4 Simulating perturbations

Chinook salmon.—Simulations were used to estimate the probabilities of various return outcomes given different perturbations to escapements. These perturbations involved spawning escapements ranging from 0% to 90% (10% increments) of  $S_{MSY}$  for 1 to 4 consecutive years (total scenarios=40). Two simulations were performed simultaneously for each scenario—a simulation with spawning escapements perturbed and a standard simulation without perturbations (Fig. 1). The figure represents a scenario with (or without perturbations). A similar structure is followed for bowhead whales, though the model formulation used is a little different.



**Fig. 1** Schematic of the simulation process for Chinook salmon, showing model uncertainty through parameter uncertainty and environmental uncertainty as the forcing function for escapements, and recruitment. Process error is modeled as random variable,  $N(0, \sigma^2)$  and  $\mu$  is the harvest rate on the population of concern.

There were 1,000 iterations per scenario. For each iteration, we projected spawning escapements for 50 years beyond the last perturbed year ( $yr_i$ ) based on randomly selected parameters and error rates (simulated from the joint distributions described above). For  $yr_{i-6}$  to  $yr_{i-4}$  escapements were held constant at  $S_{MSY}$ . During  $yr_{i-3}$  to  $yr_i$  escapements were assigned according to each scenario for the perturbed simulation, but were held constant at  $S_{MSY}$  for the standard simulation. From  $yr_{i+1}$  to  $yr_{i+50}$  escapements were allowed to fluctuate between iterations by using the Ricker model to predict recruits based on randomly selected values of the parameters  $\underline{\alpha}$ ,  $\underline{\beta}$ , and  $\hat{\sigma}_1$  generated from their joint distribution (Equations 5 and 6 below).

$$\hat{R}_{yr_i} = \hat{\alpha} \cdot \hat{S}_{yr_{i-1}} e^{-\frac{\hat{S}_{yr_{i-1}}}{\hat{\beta}}} \times \exp(\varepsilon) \tag{5}$$

$$\varepsilon \sim (N(0, \hat{\sigma}_1^2)) \tag{6}$$

We used randomly selected return rates (selected by bootstrapping values observed in the data set) and exploitation rates  $\underline{\mu}$  (which fluctuated uniformly between 50% and 150% of the mean annual exploitation rate) to estimate calendar year returns of ages-1.2-1.5 (Equation 2).

The same randomly selected parameters and error rates were used for the standard simulation as were used for the perturbed simulation during each iteration. The response variable was a set of values recorded for the projected 50 years. For each projected year, we observed the difference between the perturbed simulation's escapement and the standard simulation's escapement and recorded this difference as the percent below standard escapement. In other words, we recorded the percent below the escapements that would have occurred had there been no perturbation.

**Bowhead**—A similar methodology as shown in equations 5 and 6 was used for the Bowhead simulations (Equations 7 and 8 below).

$$\hat{N}_{t+1} = \left( \hat{N}_t + \hat{r}\hat{N}_t \left( 1 - \frac{\hat{N}_t}{\hat{K}} \right) \times \exp(\varepsilon_2) \right) \times (1 - \hat{\mu}) \quad (7)$$

$$\varepsilon_2 \sim N(0, \hat{\sigma}_2^2) \quad (8)$$

Perturbations for bowhead were 0-90% of the biomass estimate in 1988 (total scenarios=10). Population biomass was projected (Equation 7) for 100 years beyond the 1988 population based on randomly selected values of the parameters  $\underline{r}$ ,  $\underline{K}$  and  $\sigma_2$  generated from their joint distribution;  $\underline{\mu}$  was again allowed to fluctuate uniformly between 50% and 150% of the mean annual exploitation rate. The same simulation technique was applied to bowhead as for Chinook salmon, and we recorded the percent below the standard biomass estimate in each of the 100 years.

### 2.5 Probabilities of unlikely fluctuations

For us to rely upon the predictions of the simulations described above we must assume that distributions for model parameters are stationary; in other words, past relationships between abundance and recruitment are indicative of the future. However, if productivity parameters ( $\underline{r}$  or  $\underline{r}$ ) are declining over time for whatever reason (e.g., habitat destruction), our simulations will yield overly optimistic predictions about population resilience. Given no perturbations, population abundance will still vary over time, and the range of this varying will depend upon stochastic events coupled with biological limitations of the system. We must be able to distinguish between low abundances that are not unreasonable given the cumulative uncertainties in the system from low abundances that result from unknown forces attenuating productivity. We assigned probabilities to the scenarios described above by allowing the populations to fluctuate randomly (within the bounds of the distributions for model parameters) over the course of 10,000 years and observing the frequency with which the scenarios occurred. We allowed 100 years of burn in before recording frequency (i.e., frequencies of scenarios were recorded from year 100 to year 10,100). If the probability of a scenario was less than 0.05, then we would use caution when relying on our models to predict resilience under this scenario because there would be an increased chance that the low abundances were due to productivity declining. During such events harvest may need to be further restricted.

## 3 Results

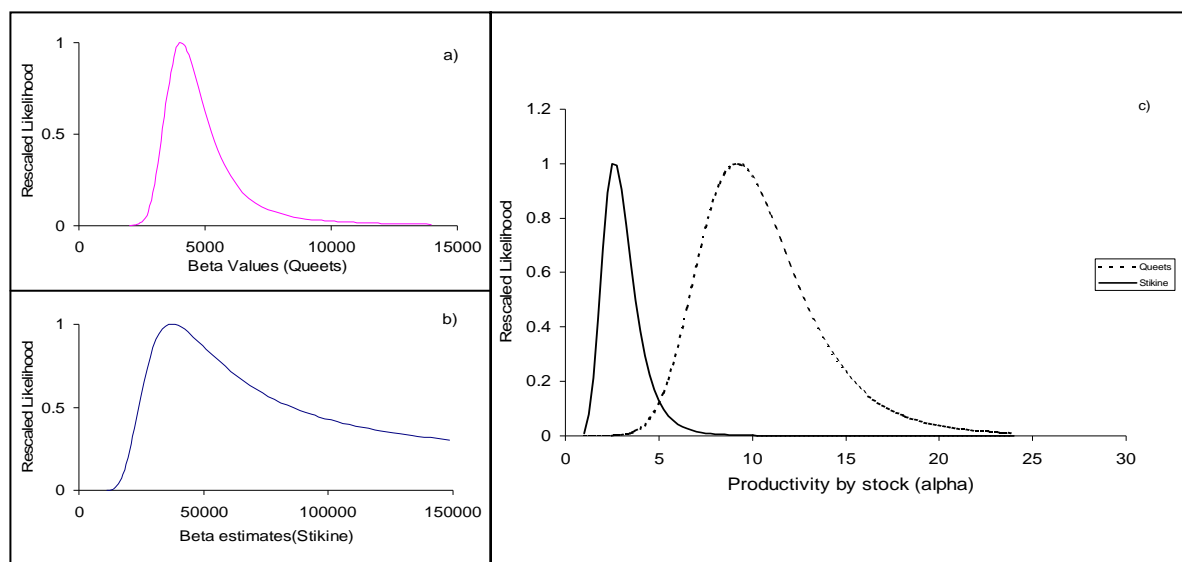
### 3.1 Model fits and parameter uncertainty

Parameter estimates for the Ricker spawner-recruit models are given in Table 2 and describe model fits that had the greatest probability of being true (Fig. 2). The Queets stock exhibited greater productivity per spawner, while the Stikine stock maintained greater carrying capacity. Alternate model fits resulted in a range of

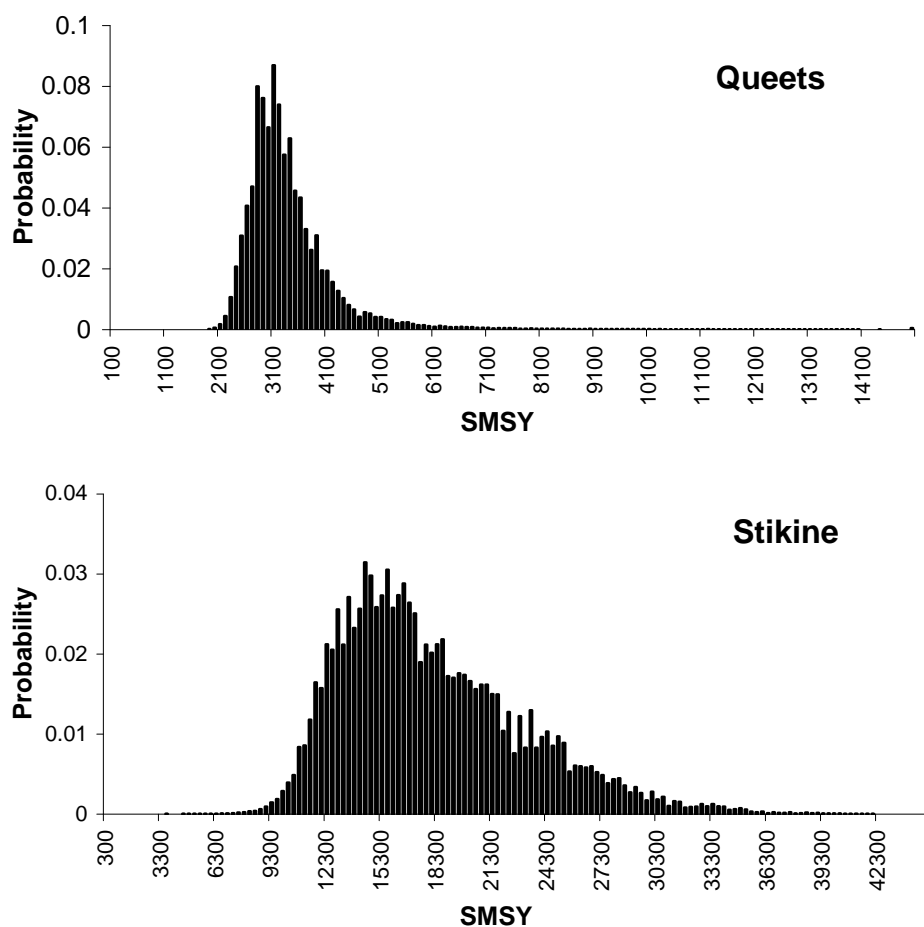
possible values for  $\underline{S}_{MSY}$  with upper estimates of approximately 1.5 to 2 times the modal values for each stock (Fig. 3); thus, true spawning abundances may deviate substantially from what point estimates indicated. The bowhead data yielded low estimates of  $\underline{r}$ , which ranged about 0.5 to 2 times the modal estimate (Fig. 4).

**Table 2** Life history information for 4 Chinook salmon stocks in rivers emptying into the Pacific coast of North America. Parameter estimates describe models having the highest probability of being true. Life history type refers to the number of years spent in the stream after hatching and before migrating to the ocean—ocean=0 and stream=1.

	Queets	Stikine	Siletz	Siuslaw
Life history type	ocean	stream	ocean	Ocean
Ricker curve parameter				
$\ln(\hat{\alpha})$	2.22	0.96	2.5	1.57
$\hat{\beta}$	4,048	37,370	3,633	22,727
$\hat{\sigma}$	0.51	0.51	0.49	0.62
$\hat{S}_{MSY}$	3,095	15,515	2,944	12,925
$\hat{U}_{MSY}$	0.77	0.42	0.8	0.57
Average return rates after X number of years spent in the ocean (%)				
2	12	6	14	10
3	26	27	30	33
4	51	63	47	49
5	11	4	9	8



**Fig. 2** Parameter uncertainty in Ricker models describing spawner-recruit data for Chinook salmon in the Queets and Stikine Rivers.



**Fig. 3** Posterior distributions on target management goals ( $\underline{S}_{MSY}$ ) for Chinook salmon in the Queets and Stikine Rivers.

### 3.2 Resilience

Our modeling indicated that Chinook salmon should be resilient to random abundance perturbations (Figures 5 and 6). Even if no spawning occurred in a single year due to some random catastrophe, the stocks included in this study recovered within 30 to 50 years. When harvest was suspended, recovery occurred after 6 years (Fig. 5). Reduced percentages of  $\underline{S}_{MSY}$  spawned resulted in longer time to recovery. Because most Chinook salmon return to spawn after spending 4 years in the ocean (Table 2), the effects of perturbations to spawning abundances were most pronounced 6 years later and then subsequently diminished. Recovery took longer when perturbations occurred in two or more consecutive years (Fig. 6).

Bowhead whales were not resilient to population perturbations (Fig. 7). When the population was reduced to only 90% of the 1988 abundance estimate, bowhead did not recover completely within 100 years (Fig. 7).

Suspending harvest, which was already low ( $\hat{\mu} = 0.015$ ), did little to improve resilience.



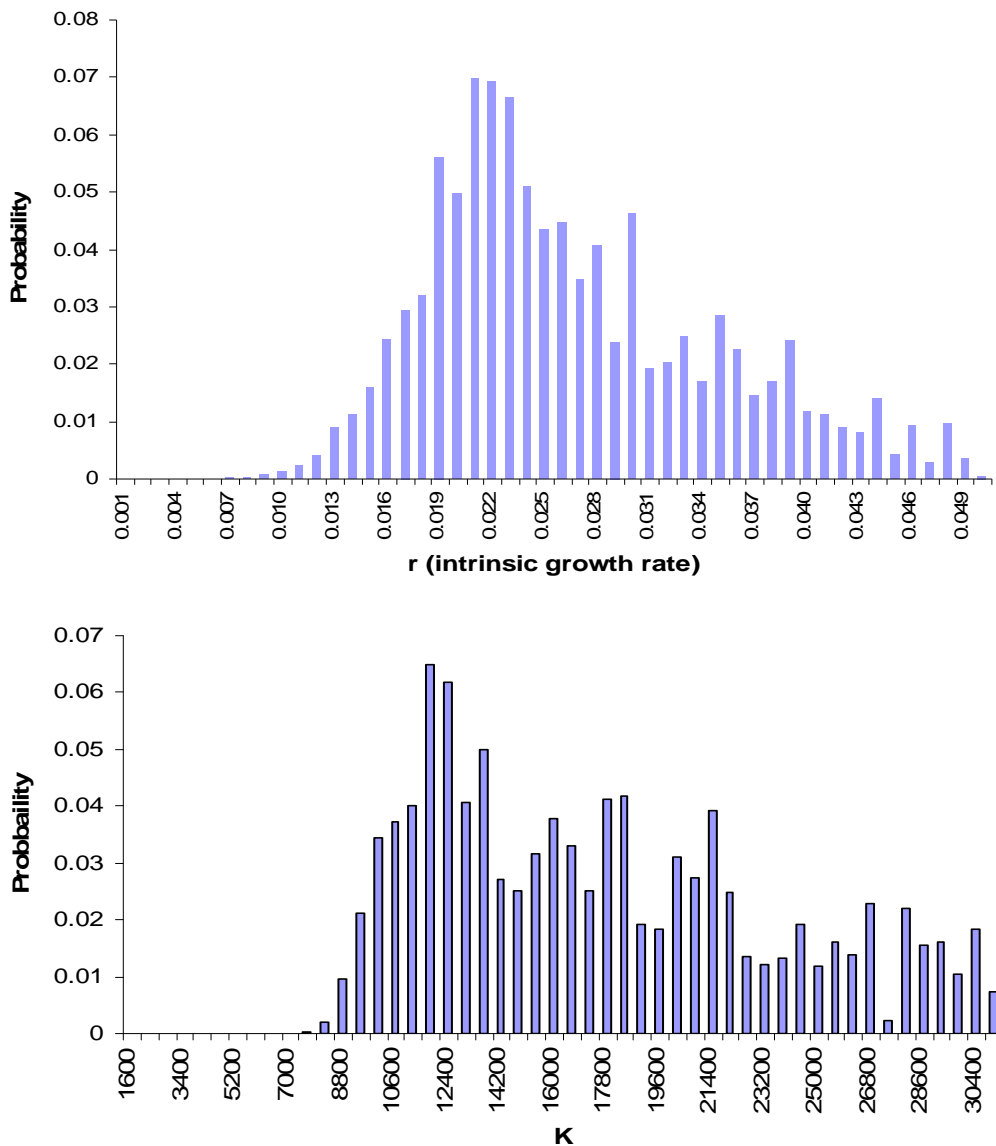
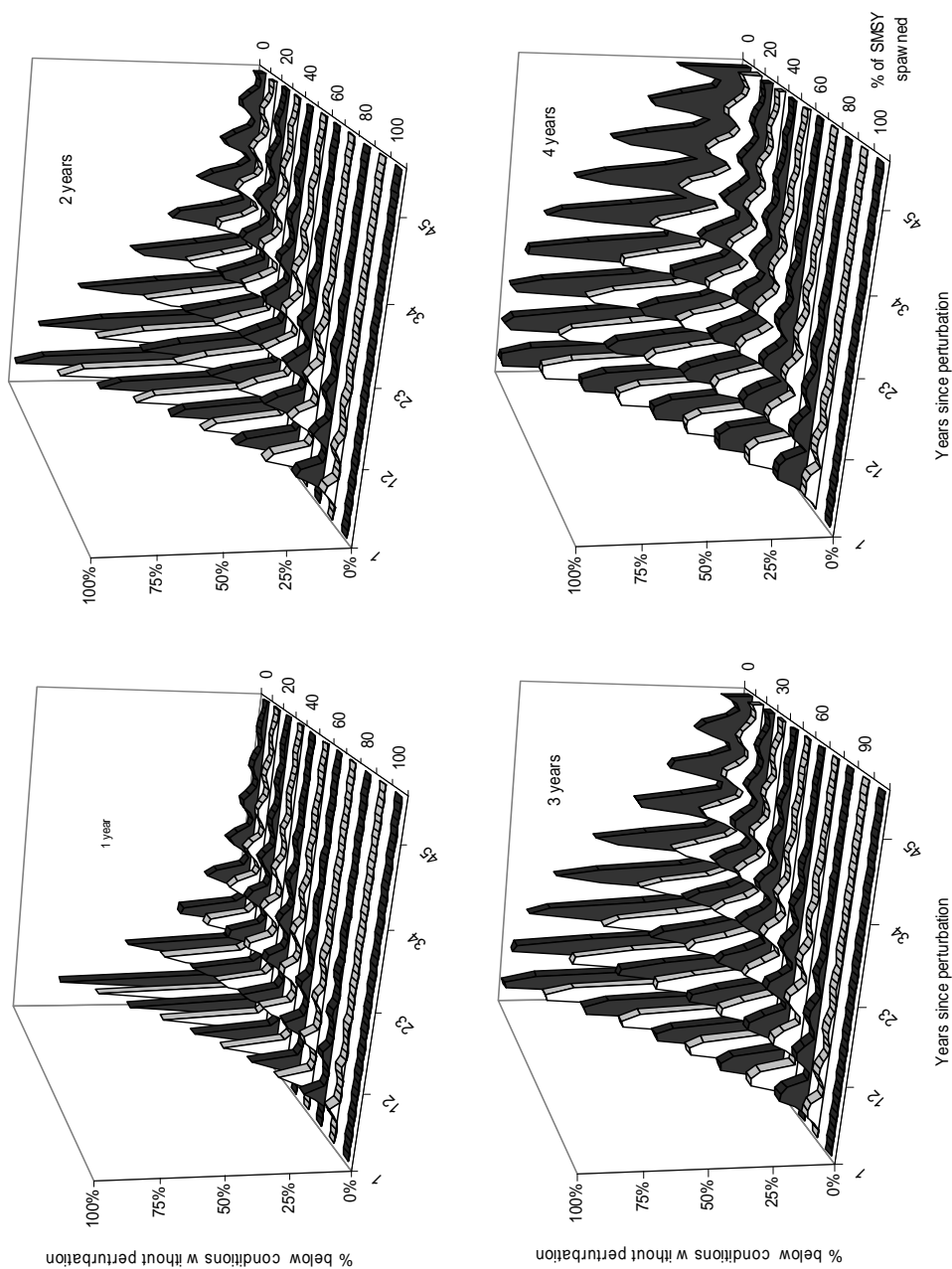
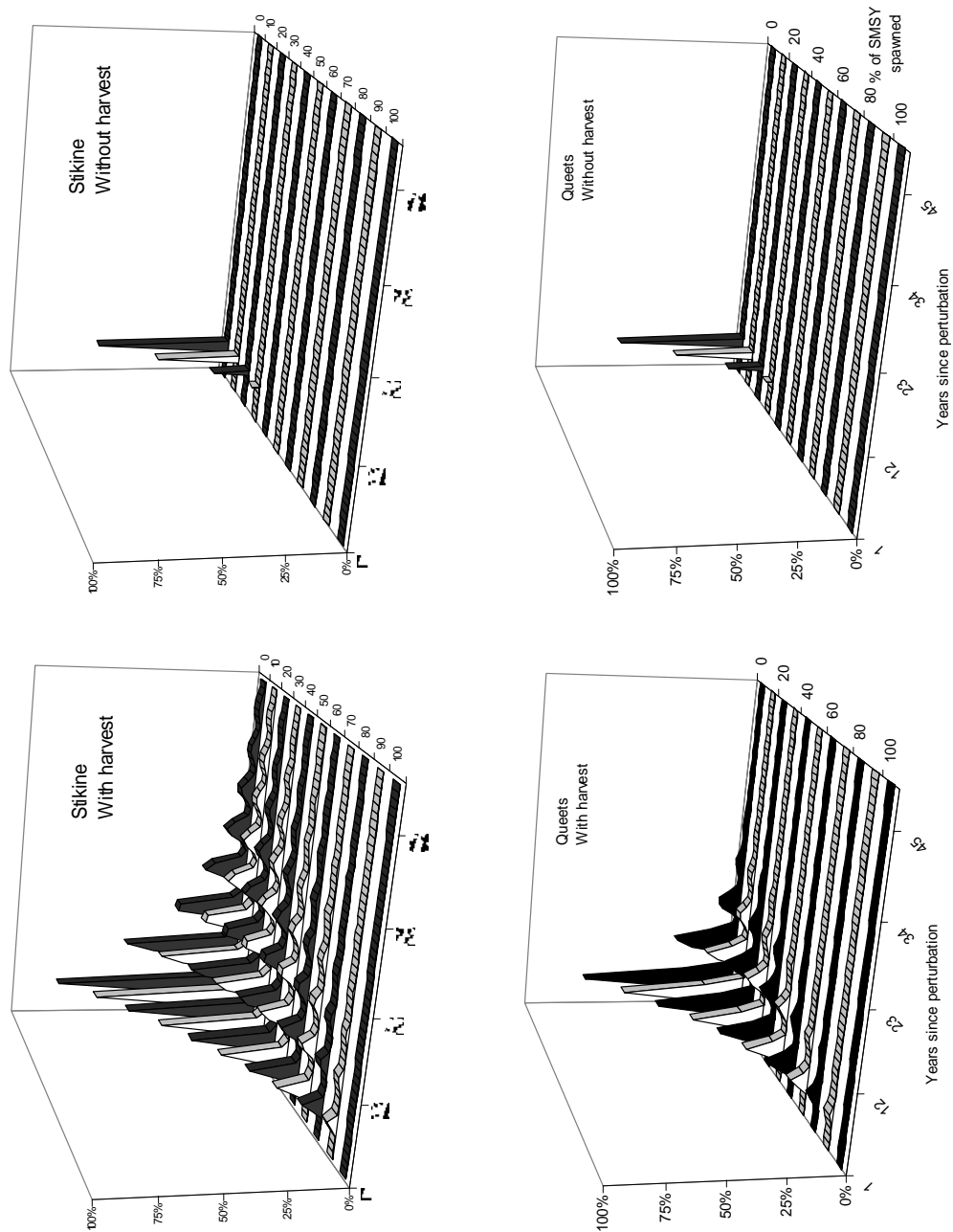


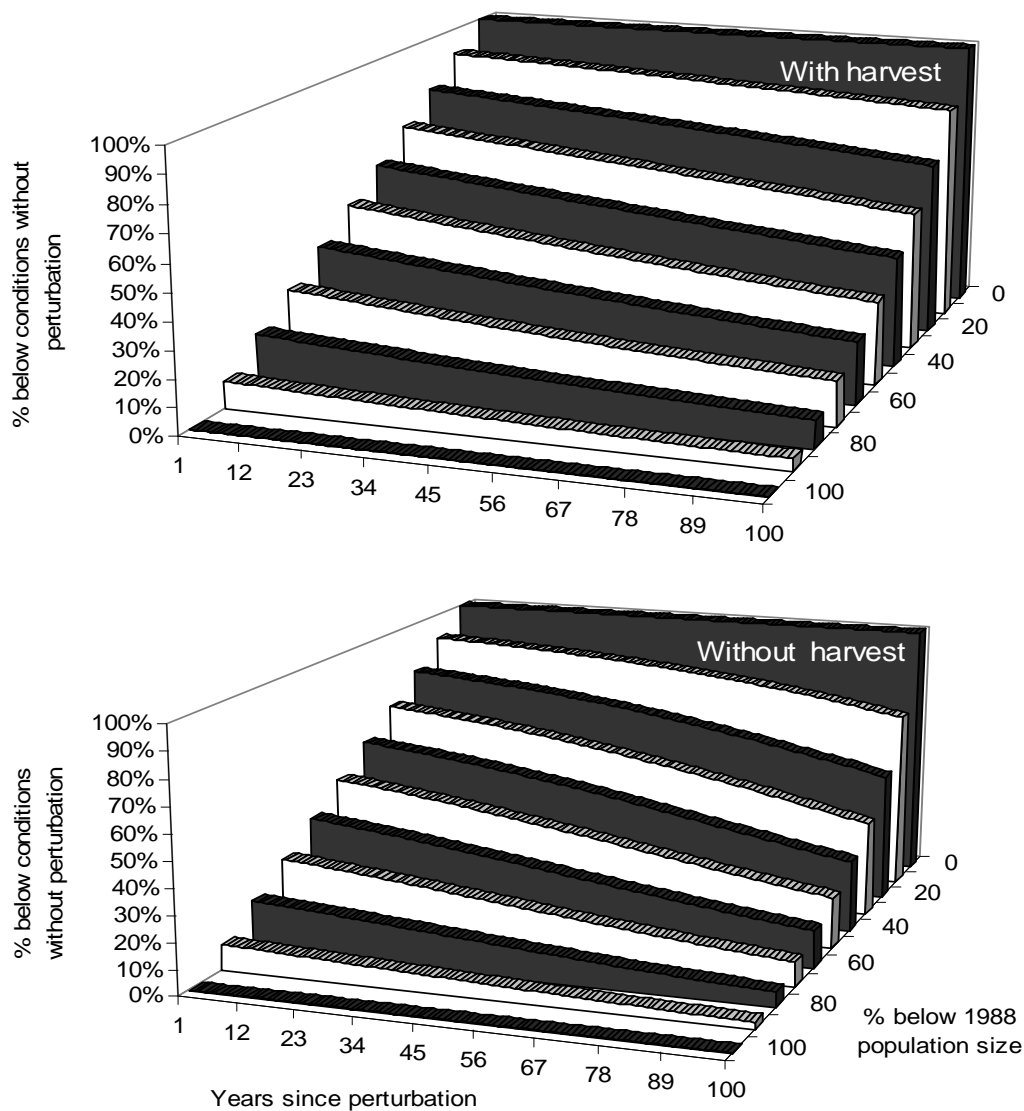
Fig. 4 Posterior distributions on  $r$  (inset a) and  $K$  (inset b) for the bowhead whale data.



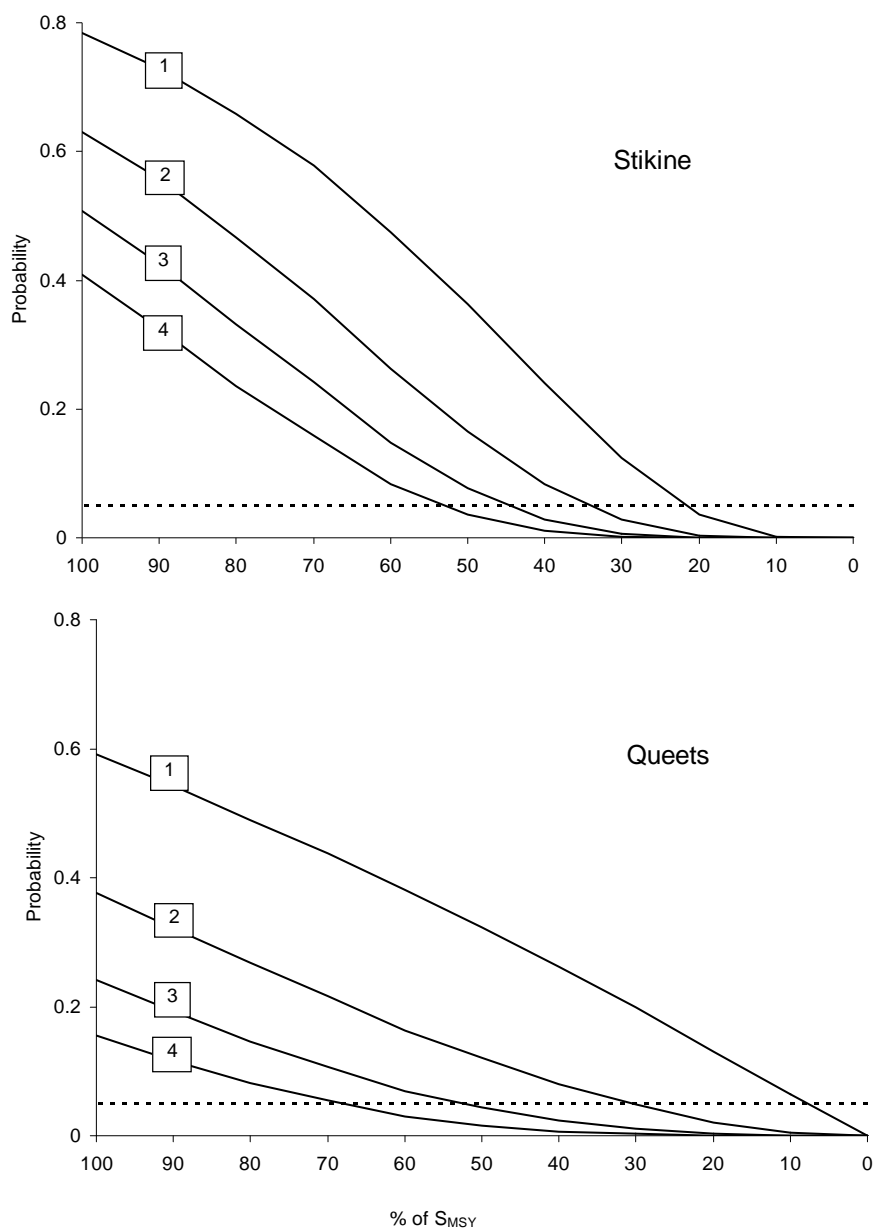
**Fig. 5** Population resilience of Chinook salmon from the Queets and Stikine Rivers with and without harvest. Various perturbations (% of  $S_{MSY}$ ) are modeled to have occurred in only one year (the graph begins with the first year after the perturbation). Values reported are from the 75<sup>th</sup> quartile (i.e., there is a 25% risk that recovery will take longer than what is depicted). The Z axis represents the percent below the escapements that would have occurred had there been no perturbation (i.e., if 100% of  $S_{MSY}$  had been spawned).



**Fig. 6** Population resilience of Chinook salmon from the Stikine River. Various perturbations (% of  $S_{MSY}$ ) are modeled for one, two, three and four consecutive years (the graph begins with the first year after the last perturbation). Values reported are from the 75<sup>th</sup> quartile (i.e., there is a 25% risk that recovery will take longer than what is depicted). The Z axis represents the percent below the escapements that would have occurred had there been no perturbation (i.e., if 100% of  $S_{MSY}$  had been spawned).



**Fig. 7** Population resilience of bowhead whales in the Pacific Ocean with and without harvest. Various perturbations (% of 1988 abundance estimate) are modeled to have occurred in only one year (the graph begins with the first year after the perturbation). Values reported are from the 75<sup>th</sup> quartile (i.e., there is a 25% risk that recovery will take longer than what is depicted). The Z axis represents the percent below the abundances that would have occurred had there been no perturbation (i.e., if 100% of 1988 abundance estimate began each iteration).



**Fig. 8** Probability of Chinook salmon escapements from the Queets and Stikine Rivers being below various levels of  $S_{MSY}$  for 1-4 consecutive years. The dotted line indicates 0.05 probability.

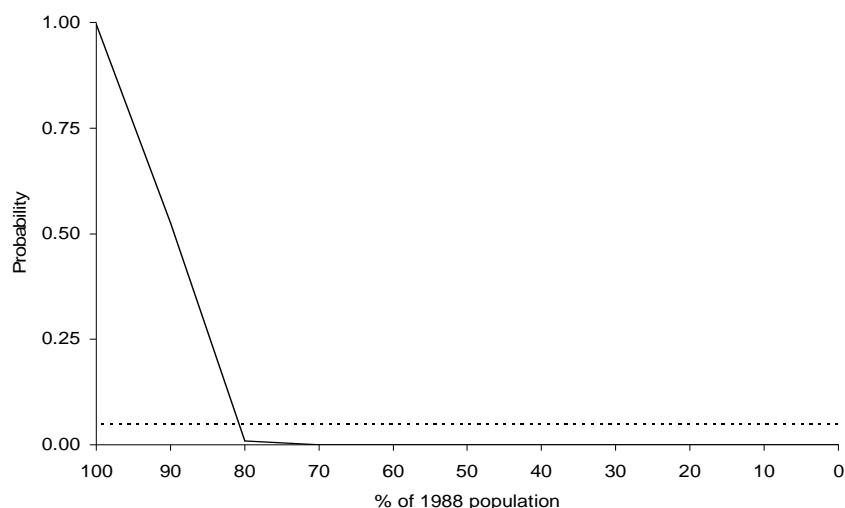
### 3.3 Probabilities of perturbations

We estimated the probabilities of abundance fluctuations given the cumulative variability of the system to help identify situations where abundances were below the normal range. There was at least a 0.05 probability that the Queets stock could fall to 10% of  $S_{MSY}$  in any one year (Fig. 8). However, the probability of the Stikine stock falling to 10% of  $S_{MSY}$  was less than 0.05. The probability that perturbations of abundance below  $S_{MSY}$  could occur in two, three, and four consecutive years diminished with each additional year. There was less than a 0.05 probability that bowhead could decline to  $\leq 80\%$  of the 1988 population estimate (Fig. 9).

## 4 Discussion

### 4.1 Scale and model validation

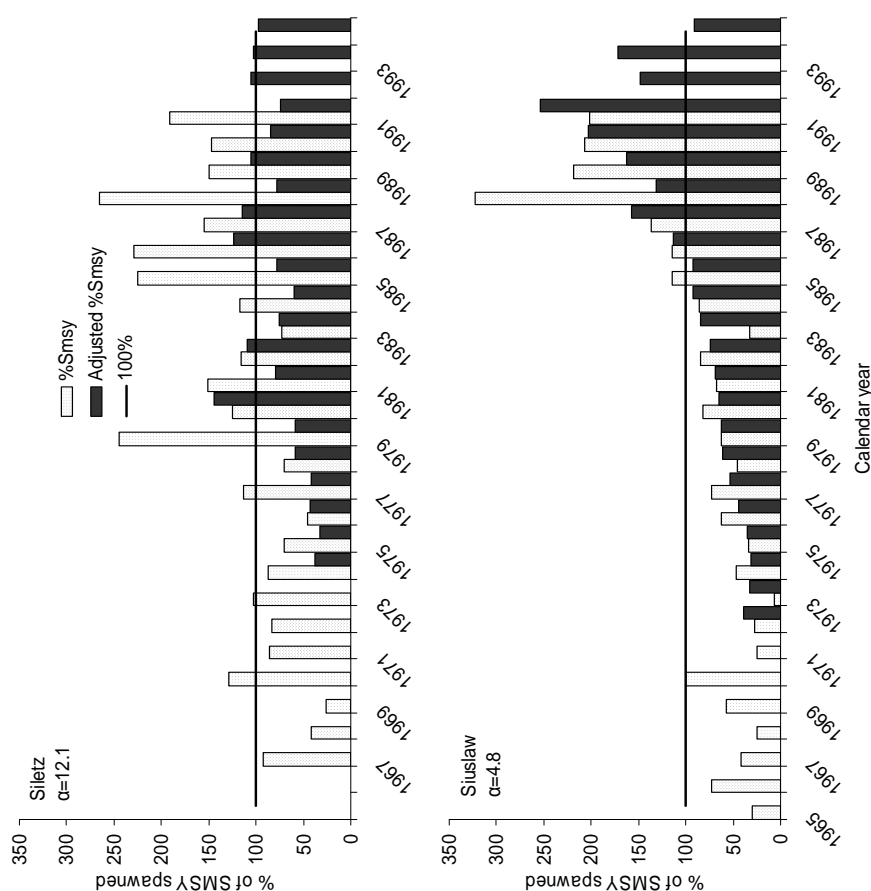
Resilience defines the rate at which a population or community metric responds to a disturbing force. An assessment of resilience is useless without understanding the severity and frequency of disturbance, as well as the temporal and spatial scale of observation (Grimm and Wissell, 1997; Syms and Jones, 1999). The objective of our analysis was to determine the threshold disturbance (maximum allowable frequency and severity of reductions in abundance) that a population could recover from within a reasonable amount of time while allowing sustainable harvest. Connell and Sousa (1983) reasoned that the minimum temporal scale for observing population responses to disturbances was one complete turnover of all individuals in the population. Estimates of escapement spanned 2-4 turnovers for the Chinook stocks included in this study (Table 1), and we projected escapements for seven turnovers beyond the simulated perturbations. Minimum spatial scale for measuring population responses depends upon the life history of the species, and finding the minimum area that allows for population stability should be the focus of studies seeking to find equilibria (Connell and Sousa, 1983). Our goal was not to document equilibria, but rather to identify thresholds given inherent random fluctuations in abundance. Also, our estimates of escapements represented Chinook abundances for entire river systems; thus, we captured the dynamics of the total population for each stock (as opposed to indexing abundance for only a segment of each river). Overall, we feel the scale of measurement for Chinook salmon was adequate for assessing resilience. Our approach allowed for the measurement of resilience (recovery to what would have happened in absence of perturbation) in the context of stochastic boundedness. However, without prescience or time travel our approach cannot be validated in an absolute sense. Predictions about the resilience of the two modeled stocks may be supported by following the pattern of escapements for other stocks not used during simulation construction. Modeling indicated there was a 75% chance that recovery to within 10% of unperturbed conditions from being reduced to half of  $S_{MSY}$  would take about 12 years or two



**Fig. 9** Probability of bowhead whales in the North Pacific Ocean being below various percentages of the 1988 abundance estimate. The dotted line indicates 0.05 probability.

generations (Fig. 5). Having population parameters similar to the modeled stocks (Table 2), we would expect the Siuslaw and Siletz stocks to have similar responses to low abundances as well. That is, following a perturbation, abundance levels will begin to fluctuate around  $S_{MSY}$  after the necessary time for recovery. The Siletz stock was reduced to 50% of  $S_{MSY}$  in 1976, but recovered to 100% of  $S_{MSY}$  6 years later (Fig. 10). The

effects of protracted perturbations ( $<50\% S_{MSY}$ ) to the Siuslaw stock from 1971 to 1975 were mitigated within 12 years. The high potential for resilience in both the Siletz and Siuslaw is evident as we would expect given our simulated results from the modeled stocks.



**Fig. 10** Escapement estimates (relative to  $S_{MSY}$ ) for Chinook salmon from the Siletz and Siuslaw Rivers. The solid line indicates 100% of  $S_{MSY}$ . Dark bars represent escapements projected to have occurred had harvest been constant at the optimum rate.

Logistic problems arise when measuring aspects of resilience among long lived species (Connell and Sousa, 1983) such as bowhead, which are also difficult to census. Admittedly, the data were limited with respect to accurately judging the resilience of bowhead. We relied on two estimates (1978 and 1988) of abundance and 141 years (from 1848 to 1988) of harvest data to build our model. The average age to maturity of bowhead is between 18-20 years (Schell et al., 1989), and though our projections covered 5 generations of mature adults, the empirical data afforded us limited resolution with respect to temporal scale of observation. Nevertheless, managers must often make do with available data and our approach is more useful in deciding between management decisions than in predicting population dynamics of bowhead (as is the case with PVA analyses; Ellner and Fieberg, 2003).

#### 4.2 Reasons for resilience

Factors contributing to the resilience we find in Chinook salmon include short generation time, high individual productivity, and multiple brood years comprising escapements. Short generation time and high individual productivity have long been recognized as life history characteristics of species adapted to environments with increased frequency of disturbance (i.e.,  $r$  selected species). Complete turnover of individuals occurs every 7 years for Chinook salmon and most reproduce after 6 years. Productivity is relatively high for Chinook salmon,

and was probably the single greatest determinant of resilience. The Stikine stock possessed the least potential for resilience and also exhibited the lowest  $\alpha$ . If recruitment depensation (reduced productivity at low spawning abundances) is not important for Chinook salmon, then the potential for high recruitment from low escapements will promote resilience. Myers et al. (1995) found only 3 of 128 fish stocks exhibited evidence for depensatory mechanisms, which suggests that depensation is of little concern for most fish stocks. Chinook salmon are semelparous species, but rely on multiple broodyears comprising annual escapements to mitigate the risk of low or failed reproductive effort in any one year. Chinook salmon return to natal streams after spending 2 to 5 years in the ocean, but most returns occur after 3 and 4 years (Table 2). Strong escapements in years adjacent to poor escapements provide buffers against population decline. If perturbations occur in two or more consecutive years, this buffering is lost and recovery can be substantially prolonged (Fig. 6; but note the Siuslaw stock in Fig. 10). Failed reproductive effort would have to occur for 7 consecutive years for local extirpation of a stock.

Bowhead are K-selected species having a prolonged generation time and low intrinsic rate of growth, which renders them less able to respond to perturbations. In the event that abundance is reduced, recovery will take longer, as was observed from our simulations.

### 4.3 Estimating thresholds

Efforts in the past have been made to estimate critical thresholds for different fish species, but uncertainty around those estimates has too often been ignored (Myers et al., 1994). In recent years, more focus has shifted to ideas of risk and the uncertainties associated with management parameters (Punt and Butterworth, 1993; Hilborn, 2001; Walters and Korman, 2001). Simulation techniques are routinely used to estimate critical population thresholds and extinction probabilities (Bessinger and Westphal, 1998; Fieberg and Ellner, 2000; Ellner and Fieberg, 2003). A thorough investigation of the model and parameter choices is recommended (Gerber and VanBlaricom, 2001), but is not always implemented in all species. Furthermore, most approaches that incorporate uncertainty in the parameter estimates fail to consider how much fluctuation can be attributed to natural variation and not just measurement error (Hilborn and Walters, 1992; Hilborn, 2001).

Spawner-recruit or biomass assessment data are often messy, and ambiguous answers to specific management questions are often the best science has to offer. By estimating probabilities to various outcomes, we offer an approach to establishing abundance thresholds in the face of uncertainty. When low abundances occur that are below that which can be expected under normal random fluctuation and harvest, researchers must question whether these occurrences were due to one-time-only perturbations or declining system productivity. Declining productivity can be guarded against by recognizing unreasonably low abundances using Figures 8 and 9, and when they occur, suspending or scaling back harvest below the previously estimated optimum rate in order to expedite recovery.

Once managers are aware of which critical abundance levels may indicate problems with productivity, higher thresholds can be established based on the resilience of the population. Managers and stakeholders must then agree upon the answers to three questions concerning recovery and allowable risk. First, how much time should be allowed for the stock to recover from a perturbation? The answer to this question can be given in years or number of generations. Second, when is a stock considered to be recovered? In other words, do abundances have to be within 1%, 5%, 10%, and so on of what they would be had there been no perturbation? Third, what is the maximum allowable risk that a threshold is too low? Answering this question necessitates an understanding of how much chance there is that recovery will take longer than predicted—something that management decisions based on point estimates do not do.

Possible thresholds given varying levels of risk can be presented in a decision table (Table 3). Thresholds were modeled in 10% increments, but greater resolution could be added as desired. A conservative approach



would seek to achieve recovery to within 1% of unperturbed conditions after 1 generation with no more than a 5% risk that recovery will take longer than what was projected. Neither of the Chinook populations modeled in this study were resilient enough to achieve these specifications; therefore, the lowest threshold under these conditions would have to be 100% of  $S_{MSY}$ . For Chinook salmon, a more reasonable approach might be recovery to within 5% after 2 generations with 10% risk of longer recovery; these criteria yield thresholds of 80% of  $S_{MSY}$  for the Stikine stock and 60% for the Queets stock. Due to their low productivity, no clear threshold below the point estimate was apparent for bowhead, and harvest may need to be suspended to maintain the population at the observed levels of abundance.

**Table 3** Decision table for estimating the lower threshold abundances for various Chinook salmon stocks and bowhead whales of the North Pacific Ocean. Table values represent percentages of  $S_{MSY}$  for Chinook and the 1988 abundance estimate for bowhead. One generation represents 6 years for Chinook and 20 years for bowhead. For each generation increment, thresholds necessary for recovery to within 1, 5, and 10% of unperturbed conditions are reported. Shaded values represent thresholds defining abundances that have less than a 5% chance of occurring from random fluctuations alone (Figures 7 and 8); hence, if such abundances occur then productivity may be declining and recovery time may be overly optimistic.

Stock	% risk of longer recovery	Recovery (within 1, 5, and 10%) after								
		1 generation			2 generations			3 generations		
		1%	5%	10%	1%	5%	10%	1%	5%	10%
Stikine River Chinook	5	100	90	90	100	90	70	90	60	40
	10	100	90	90	100	80	70	90	50	30
	25	100	90	80	100	80	60	80	40	10
Queets River Chinook	5	100	90	70	90	70	50	60	20	0
	10	100	80	70	90	60	50	50	10	0
	25	100	80	70	80	50	30	20	0	0
Bowhead	5	100	100	90	100	100	90	100	100	90
	10	100	100	90	100	100	90	100	100	90
	25	100	100	80	100	100	70	100	100	70

The relatively short recovery time observed for Chinook salmon has the potential to be misleading. The shaded areas in Table 3 indicate abundance levels that have little chance of occurring under normal circumstances (Fig. 8). The estimates of recovery from these abundances should not be trusted for reasons discussed above. For example, the most liberal approach presented—recovery to within 10% after 3 generations and a 25% risk of longer recovery—yielded unreasonably low thresholds according to Fig. 8. Thus, shaded thresholds are obviously too low, but are reported for purpose of illustration.

Management of exploited populations should be based on the most sound and up to date ecological theory. Techniques used in fisheries management to establish abundance thresholds have lagged behind peer reviewed literature on population ecology and conservation. Management decisions based on point estimates are antiquated and should be based on new analytical techniques that allow for the inclusion of uncertainty and the assessment of risk. The approach presented in this paper incorporates the cumulative uncertainties in the data, provides stakeholders with more options, and necessitates that they understand the risk involved with each. Using this approach, managers would be better able to maintain abundance levels necessary to achieve maximum sustainable yield, and stakeholders may be more satisfied with the management of their resources.

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