

**A BAYESIAN BENEFIT-COST ANALYSIS OF AN EXPERIMENTAL  
FERTILIZATION PROJECT FOR SOCKEYE SALMON  
(*Oncorhynchus nerka*) IN CHILKO LAKE, BRITISH COLUMBIA**

by

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## **Abstract**

Lake fertilization has been used for decades by fisheries management agencies to enhance Pacific salmon productivity. However, few studies have examined how many additional adult recruits are made available to the fishery through lake fertilization projects, and in particular, how much the harvest from these additional recruits is worth. Estimating the economic value resulting directly from fertilization is necessary to evaluate the project's economic efficiency, which allows fisheries managers to assess the economic merits of fertilization relative to other enhancement projects. To address this issue, I developed and applied a framework for estimating the changes in economic value of a sockeye salmon stock following lake fertilization, using data from the Chilko Lake fertilization project. I used Bayesian statistics and various modifications to the Ricker model to take into account uncertainties in the shape of the stock-recruitment relationship, and the effect of fertilization on that relationship. Two of the models used incorporated a time series of average annual productivity data from other Fraser River stocks (the Fraser Index), to account for environmental variation common to all stocks in this river system. Results indicated a strong probability that lake fertilization had increased the number of adult recruits produced per spawner, and also that this increase was sufficient to yield a large net economic benefit. This finding was robust to a range of conditions, including the shape of the prior probability distributions placed on the model parameters, the model form, and the discount rate used. Formal model comparison using Akaike's Information Criterion indicated that models incorporating the Fraser Index provided the best representation of the information contained in the data. However, limited contrast in the data at high spawner abundances restricted the ability to properly estimate the effect of fertilization, regardless of whether best-fit or Bayesian methods were applied.

*To Marg and Free,  
whose love, patience, and financial subsidies  
were integral to the completion of this little blue book.*

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## Introduction

In recent decades, fertilization has become a popular enhancement technique for lakes and streams throughout British Columbia (BC) and Alaska (Hilborn and Winton 1993; Stockner and MacIsaac 1996). One common objective of fertilization has been to increase the number of adult sockeye salmon (*Oncorhynchus nerka*) returning to nutrient-poor lakes, thereby increasing the potential harvest from these stocks (LeBrasseur et al 1978; LeBrasseur et al 1979; Stockner 1981; Kyle 1994b). Specifically, fisheries managers expect that adding nutrients to oligotrophic lakes will improve rearing conditions for juveniles, and will ultimately translate into increased stock productivity (defined as the number of recruits produced per spawner at a given spawner abundance) (Foerster 1968; LeBrasseur et al 1978; Hyatt and Stockner 1985; Kyle 1994b).

Indeed, in nutrient-poor lakes, supplementing existing nutrient inputs with chemical fertilizer can substantially increase zooplankton abundance (LeBrasseur et al 1978; Kyle 1994b; Budy et al. 1998). Depending on the zooplankton composition within the lake, this may lead to improved food availability to juvenile sockeye, resulting in greater juvenile survival and/or growth rates (Foerster 1968; Hyatt and Stockner 1985; Stockner 1987; Kyle 1994b). Proponents of fertilization believe that increasing the juvenile survival rate at a given spawner abundance will also improve the number of adult recruits per spawner, assuming that ocean survival rate is independent of density. Similarly, proponents hypothesize that increasing the growth rate of juveniles will also increase life-time sockeye survival rates, assuming that survival rate in the ocean and juvenile body size are positively related (Foerster 1954; Ricker 1962; Henderson and Cass 1991; Koenings et al. 1993). If either of these proposed mechanisms is valid, the result will be an increase in productivity for fertilized stocks, with an associated rise in

sustainable harvest level and economic value (LeBrasseur et al. 1978; LeBrasseur et al. 1979; Hyatt and Stockner 1985; Kyle 1994b).

Managers in the Canada Department of Fisheries and Oceans (DFO) are interested in estimating the magnitude of change in economic value for fertilized stocks, in part because they are required to evaluate the economic efficiency (e.g. benefit-cost ratio) of all enhancement projects (G. Steer, Department of Fisheries and Oceans, Vancouver, B.C., personal communication; Hilborn and Winton 1993; Pearse 1994). However, due to variability in stock-recruitment data and the short duration of most fertilization experiments, any change in harvestable value of fertilized stocks has been difficult to assess. My purpose here is to develop and apply a framework for estimating changes in the economic value of a sockeye salmon stock following fertilization. This framework takes into account uncertainties in the shapes of the pre- and post-fertilization stock-recruitment relationships that were not considered in previous examinations of lake fertilization, and calculates the resulting uncertainty in economic value.

To evaluate whether a particular enhancement project is meeting accepted standards for economic efficiency (i.e. achieving a minimum benefit-cost ratio of 1), DFO managers must estimate both the costs and benefits resulting from enhancement. This can be difficult to do, however, because the *indirect* costs (e.g. increased probability of algal blooms, disruption to recreationists) and benefits (e.g. increased long-term abundance of a weak stock line) associated with lake fertilization are not easily quantified. It is therefore reasonable to perform an initial economic evaluation of fertilization projects based on *direct* financial costs and benefits. The direct financial costs of fertilization include expenditures for the purchase and application of fertilizer. These are reasonably straightforward to estimate because they are usually recorded by the

accountant or project manager. However, it is more complicated to estimate the direct financial benefits of fertilization, specifically, the monetary value of *additional* fish harvested as a result of fertilization. Estimating this quantity requires an understanding of the effect of lake fertilization on the production of adults, which few researchers have attempted.

Instead, most studies of fertilization of salmon-rearing lakes have considered the effect of fertilization on smolts, not on adult recruits. This is likely because their purpose was to describe biological effects of nutrient additions on a lake's food web rather than to estimate the economic value of enhancement (Hyatt and Stockner 1985; Stockner and Shortreed 1985; Kyle 1994a; Kyle 1994b). Typically, experiments that have examined smolt populations pre- and post-fertilization have found that fertilization: (1) increases average smolt abundance (Kyle 1994a; Edmundson et al. 1997), (2) increases average smolt body size (LeBrasseur et al. 1978; Kyle 1994a; Bradford et al. in press), and (3) reduces the proportion of 2-winter and older smolts (Kyle 1994a; Kyle 1994b; Edmundson et al. 1997; Bradford et al. in press). As well, sockeye smolts in treated (i.e. fertilized) coastal lakes were on average larger than smolts in untreated lakes (Hyatt and Stockner 1985). However, few results from these studies have been statistically significant because of the problems of high variability and limited availability of fertilized year classes in stock-recruitment data.

The problems of variable data have been further compounded in most research on fertilization by fluctuations in juvenile abundance during the experiment. In many studies (LeBrasseur et al. 1978; Hyatt and Stockner 1985; Kyle 1994b; Edmundson et al. 1997), yearly variation in the number of juveniles may have caused changes in survival and growth rates independent of fertilization effects, producing higher growth and survival

rates at low juvenile densities, and vice versa. In some studies, changes in juvenile abundance resulted from variable spawner abundance (LeBrasseur et al. 1978; Hyatt and Stockner 1985; Kyle 1994b), while in others, changes were caused by yearly variation in juvenile stocking rates (Kyle 1994b; Edmundson et al. 1997). In any case, failure to account for the variable number of juveniles could have confounded conclusions from these experiments. Observed increases in smolt growth or survival rates that were attributed by those studies to nutrient additions may have resulted, at least in part, from decreased competition due to lower juvenile densities.

Despite the shortcomings of such studies, similar findings were reported in two analyses that did account for juvenile abundance. Kyle (1994a) found that fertilization increased the average fingerling-to-smolt survival rate of coho salmon (*Oncorhynchus kisutch*) in Bear Lake, Alaska, by 13%, with no significant difference detected between the number of stocked fingerlings before and during fertilization. In a second study, Luecke et al. (1996) compared growth rates of juvenile kokanee (*Oncorhynchus nerka*) in fertilized and unfertilized experimental limnocorrals in Redfish Lake, Idaho. When the same number of individuals was stocked in treatment and control corrals, the average juvenile growth rate was 20% greater in the fertilized corrals. These studies clearly support the potential of fertilization to increase growth or survival rates in juvenile salmon, independent of juvenile density. However, they provide no information on the effect of fertilization over the entire life span of a salmon, particularly on the potential of fertilization to increase the number of adult recruits.

Although some authors have hypothesized that increased smolt size or abundance following fertilization will translate into greater adult returns (Hyatt and Stockner 1985; Stockner 1987; Budy et al. 1998), this hypothesis must be treated with caution. Research

has shown that an increase in the survival rate of salmon eggs to some juvenile life stage will not necessarily translate into the same increase in survival rate to adult recruitment. This can occur because density-dependent survival rates can exist in the marine life stage, in addition to the freshwater life stage, thereby compensating for increases in juvenile abundance (reviewed by Peterman 1991). Ignoring this effect can produce overly optimistic forecasts of the benefits of enhancement by exaggerating estimates of adult recruits that will be produced (Peterman 1991).

In the specific context of lake fertilization, it is therefore critical to examine whether fertilization increases survival rates over the entire life of a salmon, rather than assuming that increases seen in the juvenile life stage will persist through to adult recruitment. To my knowledge, only two studies have attempted to measure this effect. First, LeBrasseur et al. (1978) found that the average number of sockeye salmon recruits per spawner to Great Central Lake, British Columbia, was four times greater in fertilized than unfertilized years, while the recruits per spawner to the adjacent, unfertilized Sproat Lake increased only two-fold over the same period. Unfortunately, the observed changes in recruits per spawner were calculated using only two pre-fertilization brood years and three fertilized broods. Although the selected pre- and post-fertilization years did have similar spawner abundances, the limited years of data in this analysis restrict inferences that can be made concerning the contribution of fertilization to this change in recruits per spawner relative to other potential sources.

Recently, in a more comprehensive study, Bradford et al. (in press) examined changes in pre- and post-fertilization productivity estimates for the Chilko Lake sockeye stock. The authors accounted for the effect of variable spawner abundance by fitting a modified Ricker stock-recruitment model. Their analysis also incorporated a time series

of average annual productivity data from other Fraser River sockeye stocks, which was included to account for environmental variation common to all stocks in this river system. Results showed that best-fit estimates of the Ricker 'a' parameter increased in fertilized years, indicating that fertilization had a positive effect on the number of adult recruits produced per spawner at a given spawner abundance. However, variability of data around the stock-recruitment relationship created considerable uncertainty in the magnitude of this increase.

For any sockeye stock, the natural variability and measurement error inherent in stock-recruitment data make it impossible for researchers to determine the shape of the "true" underlying stock-recruitment relationship, assuming that such a relationship exists. It is therefore insufficient to simply use changes in "best-fit" parameters of stock-recruitment relationships to estimate changes in productivity in fertilized years, because there is some non-zero probability that the "true" relationship is described by a set of parameters other than the best-fit values. If models described by the best-fit parameters do not reflect reality, the results they yield may lead to erroneous management decisions. In the case of lake fertilization, the use of inappropriate models could lead to inaccurate estimates of the effect of fertilization on stock productivity. This, in turn, may result in either over-spending on fertilization projects that do not provide a sufficient return on investment, or under-spending on cost-effective fertilization projects and instead investing in less economically efficient enhancement measures.

Uncertainty and measurement error are also pervasive in estimates of economic parameters in benefit-cost analyses. Most introductory textbooks in this area discuss the importance of accounting for uncertainty in inputs to an analysis, including the discount rate, shadow prices (i.e. corrections made to market prices if that price does not

accurately reflect a commodity's true value to society), and the project lifespan (Hanley and Spash 1993; Brent 1996; Zerbe and Dively 1994). It is usually advocated that uncertainty be taken into account either through sensitivity analyses on uncertain parameters, or through assigning probabilities to uncertain events, and calculating expected (weighted average) values of the project outcome. To more accurately reflect the benefit to society of a particular project, it is often recommended to use expected utilities as performance measures, rather than expected dollar values, to reflect the diminishing marginal utility of increasing income to society (Abelson 1996; Brent 1996).

Despite this recognition and understanding of the need to account for uncertainty, the economic literature contains few case-studies of such an approach applied to benefit-cost analysis. Nonetheless, the limited examples available display a range of methods for dealing with uncertainty, including sensitivity analyses (Anderson et al. 1993), Bayesian decision theory (Costello et al. 1998), analytical generation of a probability distribution of benefit-cost ratios (Goicoechea et al 1982) and the assignment of probabilities to a small number of values for one input parameter (Raffiee et al 1997). However, only one of these studies estimated both benefits and costs of a project (Goicoechea et al 1982), while the others focussed either on the benefit or the cost component of the analysis. The current literature focuses instead on methodologies, as reflected by the abundant literature on how to account for uncertainty in welfare measures (i.e. indicators of net benefits to society generated by a policy or project) (Graham-Tomas 1995; Smith 1987; Ready 1995; Freeman 1993), and in non-market valuation (Ekstrand and Loomis 1998). There is also considerable research devoted to the methods for assessing how various welfare measures (Reed and Ye 1994; Graham 1981) and uncertainty in parameters (Andersen 1982;



Bockstael and Opaluch 1983; Anderson 1986) would affect government policies under particular conditions.

Therefore, the purpose of my research was to develop a framework that takes uncertainty into account while estimating the effect of lake fertilization on productivity of adult sockeye salmon. This framework explicitly accounts for uncertainty in the shape of the stock-recruitment relationship by using Bayesian statistics, which assign a probability of occurrence to various possible parameter combinations for a stock-recruitment model (Ianneli and Heifetz 1995; Robb and Peterman 1998). I applied this approach using data from Chilko Lake, a large sockeye-rearing lake in the Fraser River basin that was the site of a DFO experimental fertilization program in the early 1990s. The results of this research will be reported in terms of probability distributions for numbers of additional recruits, benefit-cost ratio, and net present value (NPV) produced from this project, to reflect both the biological and economic impacts of lake fertilization and uncertainties in them.

Finally, I emphasize that the purpose of this study is *not* to make general recommendations on the effectiveness of fertilization as an enhancement technique, but rather to illustrate a specific quantitative framework for evaluating net benefits of lake fertilization. The following analysis of the Chilko Lake fertilization project is merely an example of applying this framework. While the Bayesian approach used here should be useful for evaluating other enhancement projects, results from this experiment should not be considered representative of future fertilization projects, either at Chilko Lake or in other systems. The findings of this study represent only one sample of a range of outcomes that depend on highly variable factors, such as spawner abundance and ocean survival rates in the particular years covered. Furthermore, managers must take into

account broader issues when assessing the value of fertilization projects, recognizing the varied and potentially conflicting objectives of numerous stakeholders that may be affected by enhancement measures.

## **Methods**

### **Study area and data sources**

#### **Chilko Lake**

Chilko Lake (70 km long, 200 km<sup>2</sup>) is home to one of the largest sockeye populations in the Fraser River watershed. It is located within Ts'yl-os Provincial Park, on the eastern side of the Coast Mountain range in British Columbia. Chilko Lake is drained at the north end by the Chilko River, which flows east into the Fraser River. Migrating sockeye travel 180 km along the Chilko River to its confluence with the Fraser, and then 350 km to the ocean.

Chilko Lake was fertilized by the DFO for the last six weeks of summer in 1988, and for twelve weeks through each summer from 1990 through 1993. Fertilizer was applied weekly at a rate of 4 mg P m<sup>-2</sup> wk<sup>-1</sup>, at a N:P ratio of 25:1. This rate was decreased somewhat in 1993 (Stockner and Shortreed 1994).

#### **Data sources**

I used spawner-recruit data for Chilko Lake for 1949 through 1992 brood years (Fig. 1) (Al Cass, Department of Fisheries and Oceans, Nanaimo, B.C., personal communication). Because most juveniles from this stock spend only one winter in freshwater, I included only these sub-2 age-classes (that migrated to sea in their second year) in the recruit data. Historically, sub-2 recruits represent 94% of total returns for

1949 through 1992 brood years, and 98% of total returns for the fertilized broods. I used effective female spawners (EFS) rather than total spawners because this measure takes into account the retention of some portion of eggs (Al Cass, personal communication). Harvest rates on the Chilko Lake stock for calendar years in which fertilized broods returned were calculated using the spawner-recruit data (1991, 76%; 1992, 85%; 1993, 80%; 1994, 82%; 1995, 56%; 1996, 52%; 1997, 74%). Average weights for age 4<sub>2</sub> and 5<sub>2</sub> sockeye were estimated from Chilko body length data for 1988 through 1992 brood years (Mike Lapointe, Pacific Salmon Commission, Vancouver, B.C., personal communication). All fertilization costs were provided by Erland MacIsaac (Department of Fisheries and Oceans, Burnaby, B.C., personal communication), and commercial benefits for net, troll, and First Nations sockeye fisheries were supplied by Chris Sporer (Department of Fisheries and Oceans, Vancouver, B.C., personal communication). The time series of average productivities for Fraser River stocks (the “Fraser Index”) was provided by Michael Bradford (Department of Fisheries and Oceans, Burnaby, B.C., personal communication).

## **Estimating the effect of fertilization on sockeye productivity**

### **General description of the procedure**

To estimate the effect of fertilization on Chilko Lake sockeye productivity in a Bayesian framework, I calculated the number of additional recruits produced due to fertilization for a large number of hypothesized shapes of a modified Ricker stock-recruitment relationship. Each hypothesized shape and associated change in the number of recruits produced was assigned a probability of occurrence, according to Bayes’ formula (see “Evaluating Bayesian posterior probabilities,” below), to produce a

distribution describing the probability that the fertilization project generated a particular number of additional recruits. To account for various assumptions of how fertilization affected the Ricker relationship, I investigated four different modifications to the Ricker model. A generalized flow chart of this procedure is shown in Figure 2, and the details are described below.

Briefly, the sequence of steps was: (1) A single set of parameter values ( $\theta_i$ ) for a hypothesized stock-recruitment relationship was randomly selected from a joint uniform prior distribution of modified Ricker model parameters. Using Bayes' theorem (Box and Tiao 1973) and historical data on Chilko Lake sockeye spawners and recruits, I calculated the posterior probability (or relative degree of belief) for this parameter set. (2) I then estimated, using this  $\theta_i$ , the additional recruits and the economic benefits (the value of additional harvest) generated by one year of fertilization, for each year in which fertilization occurred (e.g. 1988 and 1990 through 1993). The yearly economic benefits were discounted to the first year that fertilization took place (i.e. 1988). (3) I then summed the additional recruits and discounted benefits resulting from each year of fertilization over all fertilized years to yield the total additional recruits and the total discounted benefits generated by the project. (4) The yearly fertilization costs were discounted to 1988 (the first year of the project) and summed to yield the total discounted costs of the project. (5) The project's benefit-cost ratio was calculated along with NPV. Steps 1 through 5 were then repeated until a sufficient number of parameter sets had been sampled to produce a stable probability distribution for the number of additional recruits produced due to fertilization. (6) The expected (weighted average) values for benefit-cost ratio, NPV, and total additional recruits from the project were calculated by integrating

across all possible parameter sets ( $\theta_i$ ) for a given stock-recruitment model. I then repeated this procedure for each of the four models investigated.

### Modeling the effect of fertilization on the stock-recruitment relationship

For all calculations, the Ricker stock-recruitment model was the “core” model used to describe the spawner-recruit relationship:

$$(1) \quad R = S \cdot e^{a - bS + \nu}$$

where  $S$  is the abundance of spawners,  $R$  is the number of recruits produced by  $S$  spawners, and  $\nu$  is the stochastic error term. The error term was assumed to be normally distributed with standard deviation  $\sigma$ , which reflects the multiplicative, log-normal error structure common in salmon recruitment data (Peterman 1978). Equation 1 can also be expressed as a linear, normal error model:

$$(2) \quad \log_e (R/S) = a - bS + \nu.$$

The effect of fertilization on the above relationship was modeled as a shift in productivity, in which, for a given spawner abundance, the expected  $\log_e (R/S)$  was different for fertilized brood years than for unfertilized broods. However, uncertainty concerning the mechanism by which this shift occurs necessitated the use of four models to take all reasonable potential effects into account. In the first model (herein referred to as the Density-Independent or DI model), I assumed that fertilization changed  $\log_e (R/S)$  by the same amount, independent of spawner abundance:

$$(3) \quad \log_e (R/S) = a - bS + cF + \nu$$

where  $c$  is the shift in productivity (i.e. the incremental change in  $\log_e (R/S)$ ) for brood years that were fertilized, and  $F$  is a dummy variable equal to 1 for fertilized brood years and 0 for unfertilized brood years.

In the second model (the Density-Dependent or DD model), I assumed that spawner abundance could affect the magnitude and direction of change of  $\log_e (R/S)$  caused by fertilization. This could happen, for example, if the number of juveniles produced at low spawner abundance was insufficient to graze down the forage base within the unfertilized lake. If this occurred, fertilization would only increase  $\log_e (R/S)$  at high spawner densities. This effect is represented by:

$$(4) \quad \log_e (R/S) = a - (b + dF)S + cF + v$$

where  $d$  is the incremental change in the slope of the relationship for brood years affected by fertilization. In this model, the shift in productivity in fertilized years is represented by  $dS + c$ .

Variability in environmental conditions should also be considered when estimating the effects of nutrient treatment on stock productivity. During the Chilko Lake fertilization, it is possible that there were coincident shifts in environmental factors such as ocean productivity that could affect marine survival rate of smolts, thereby masking or exaggerating the true impact of fertilization. To help control for this potential source of variation, I incorporated the 'Fraser Index' into Equations 3 and 4. This index is a time-series of annual average residuals in  $\log_e (R/S)$  from their expected values (based on their best-fit Ricker models) for each of seven other major Fraser River sockeye populations, as reported by Bradford et al (in press):

$$(5) \quad \log_e (R/S) = a - bS + cF + eFI + v$$

$$(6) \quad \log_e (R/S) = a - (b + dF)S + cF + eFI + v$$

where  $FI$  is the Fraser River Index by brood year, and  $e$  is a parameter that describes the incremental change in  $\log_e (R/S)$  for a given change in  $FI$ . I refer to Equations 5 and 6 as

the Density-Independent + Fraser Index (DIFI) and the Density-Dependent + Fraser Index (DDFI) models, respectively. Note that all variables (i.e.  $R$ ,  $S$ ,  $F$ , and  $F'$ ) in Equations 1 through 6 are implicitly subscripted by brood year.

### Comparing candidate models

The use of four candidate models to describe the effect of fertilization on the underlying stock-recruitment relationship for Chilko Lake sockeye provided me with the opportunity to formally compare these models, and to identify the model that best approximates the information available in the stock-recruitment data. To accomplish this, I used a modification of Akaike's Information Criterion (AIC) for small sample sizes ( $AIC_c$ ). The AIC model selection approach is based on information theory, and provides an estimate of the relative Kullback-Liebler (K-L) distance between a candidate model and reality (Burnham and Anderson 1989). The best approximating model of a group of candidate models is identified as the model with the smallest relative K-L distance, and consequently the smallest AIC value. The AIC for a particular model is calculated using the following equation:

$$(7) \quad AIC = -2 \log_e (L(\hat{\theta}|D)) + 2K$$

where  $\hat{\theta}$  is the estimated best-fit parameter vector for a particular model,  $D$  is the observed stock-recruitment data, and  $K$  is the total number of estimated parameters in the model, which includes parameters shown in equations 3 to 6, as well as  $\sigma^2$  of the residuals,  $v$ .

When using least squares estimation with normally distributed errors, as in this analysis, the AIC can be equivalently expressed as:

$$(8) \quad AIC = n \log_e (\hat{\sigma}^2) + 2K$$

where  $n$  is the number of years of stock-recruitment data, and

$$(9) \quad \hat{\sigma}^2 = \frac{\sum d_k^2}{n}$$

where  $d_k$  is the deviation between the observed and estimated value of  $\log_e(R/S)$  for data point  $k$  using  $\hat{\theta}$  for a particular model.

In cases where the ratio  $n/K$  is small ( $< 40$ ), the AIC may perform poorly, and Burnham and Anderson (1998) advocate the use of a modified AIC, the  $AIC_c$  (Hurvich and Tsai 1989), which includes a bias-correction term:

$$(10) \quad AIC_c = n \log_e(\hat{\sigma}^2) + 2K \left( \frac{n}{n-K-1} \right)$$

Because the  $AIC_c$  is a measure of the relative performance of a model, it is the differences between  $AIC_c$  values calculated for different models, rather than the absolute  $AIC_c$  value for a particular model, that is of interest. For this reason,  $AIC_c$  values are typically reported as the difference between the  $AIC_c$  value for a particular model  $m$ , and the lowest  $AIC_c$  value calculated from the set of candidate models (Burnham and Anderson 1998). Accordingly, in this paper, I will report  $AIC_c$  values as:

$$(11) \quad \Delta AIC_c = AIC_{c(m)} - \min AIC_c$$

### Evaluating Bayesian posterior probabilities

While comparing different best-fit cases of the four models is instructive, it does not capture the uncertainty in parameter values of any given model, which is essential for the purposes of this investigation. Specifically, stock-recruitment data are highly variable, and because of this, stock-recruitment parameters are highly uncertain. To account for this uncertainty in the economic analysis, I used a Bayesian approach to describe the possible shape of the Chilko Lake sockeye stock-recruitment relationship for each of



Equations 3 through 6. For all probable combinations of model parameters, I calculated the degree of belief that one specific set of parameters described the stock-recruitment relationship, given the observed data. Each parameter set ( $\theta_i$ , i.e.  $a$ ,  $b$ ,  $c$ ,  $d$ ,  $e$ , and  $\sigma$  for  $v$ ) defined a different shape of stock-recruitment relationship, and consequently, a different shift in productivity in fertilized years. For example, when using the Density-Independent (DI) model, I used Bayes' theorem to calculate the probability that one combination of  $a$ ,  $b$ ,  $c$  and  $\sigma$  parameters ( $\theta_i$ ) fit the model, given the observed stock-recruitment data,  $D$ :

$$(12) \quad P(\theta_i | D) = \frac{L(D | \theta_i)P(\theta_i)}{\sum_j L(D | \theta_j)P(\theta_j)}$$

where  $L(D | \theta_i)$  is the likelihood of the observed stock-recruitment data,  $D$ , given  $\theta_i$ ,  $P(\theta_i)$  is the prior probability assigned to  $\theta_i$  independent of the data, and  $P(\theta_i | D)$  is the posterior probability for  $\theta_i$  given the observed data.

To calculate the likelihood of the stock-recruitment data given  $\theta_i$ , I evaluated the likelihood of each brood year's stock-recruitment data using:

$$(13) \quad L_k(\text{data point}_k | a_i, b_i, c_i, \sigma_i) = \frac{1}{\sigma_i \sqrt{2\pi}} \exp\left(-\frac{d_k^2}{2\sigma_i^2}\right)$$

where  $L_k$  is the likelihood of the data point  $k$  given  $\theta_i$ , and  $d_k$  is the deviation between the observed  $\log_e(R/S)$  and the value of  $\log_e(R/S)$  estimated using  $\theta_i$  for that same brood year.  $\sigma$  is the standard deviation of the distribution of  $d_k$ , which is assumed to be normally distributed with a mean of zero. However, instead of calculating  $L_k$  as above, I transformed Equation 8 using natural logarithms and calculated  $\log_e L_k$ , to prevent errors from extremely small values due to insufficient computer precision:

$$(14) \quad \log_e L_k(\text{data point}_k | a_i, b_i, c_i, \sigma_i) = \log_e\left(\frac{1}{\sigma_i \sqrt{2\pi}}\right) - \left(\frac{d_k^2}{2\sigma_i^2}\right)$$

The joint likelihood of the entire data set of  $k$  points,  $D$ , for a given  $\theta_i$  was then determined by exponentiating the sum of the  $\log_e L_k$  values according to Equation 10:

$$(15) \quad L(D | \theta_i) = \exp\left(\sum_k \log_e L_k\right)$$

I used uniform distributions to describe the prior probabilities of stock-recruitment parameters for all calculations. This means that for any parameter, all reasonable values of that parameter were assigned an equal probability of occurrence. As a result, all parameter sets  $\theta_i$  used in the calculation of posterior probabilities were initially equally probable. By using uniform prior distributions, the posterior probability of  $\theta_i$  is determined primarily by the stock-recruitment data,  $D$ .

For each of the four models used in this analysis, I initially chose the range of the prior distributions based in part on best-fit parameters of the model according to least squares regression. I set the upper and lower bounds of all parameters to +3 standard errors (SE) and -3 SE of the best-fit values except for the  $b$  parameter, whose lower bound was set to zero, and  $\sigma$ , whose prior was taken to be  $1/\sigma$ , based on Press (1989). The posterior probability distribution was then calculated using these priors, and if any resulting marginal posterior appeared truncated, the upper and lower bounds for that prior were increased. Once appropriate priors had been determined for each model, I created a single prior distribution for each parameter that encompassed the entire range of probable values from all models. These new “combined” priors were used in all baseline calculation (Table 1). In a later sensitivity analysis, I explored how results were affected by assuming different prior probability distribution functions.

The large number of uncertain parameters evaluated in this analysis (4 to 6, depending on the model) made it impractical to use a grid search to calculate posterior

probabilities. The grid search approach would require calculating posteriors for each possible set of parameter values ( $\theta_i$ ) in the model. Even if only twenty values were evaluated for each parameter, this would involve  $20^6$ , or 64 million, calculations for certain models. I thus instead used a less time consuming sampling approach, a sampling-importance-resampling (SIR) algorithm (Rubin 1988; Smith 1991). The SIR algorithm estimates the posterior probability distribution function by drawing a sample from the posterior using Monte Carlo methods (see Appendix A for details). It has been used in previous fisheries analyses to reduce the computational demands of complex, multi-parameter models (McAllister et al. 1994; Kinas 1996).

### Estimating benefits and costs

#### *Benefits*

Benefits from the fertilization of Chilko Lake were evaluated as both total number of additional recruits produced by the fertilization project, as well as total economic value of additional recruits harvested in commercial or First Nations fisheries. I estimated the number of additional recruits produced by each fertilized calendar year  $y$  (where  $y = t + 1$  and  $t$  is the year of spawning) for a given parameter set  $\theta_i$ , by calculating the number of recruits produced both with fertilization ( $F = 1$ ), and without fertilization ( $F = 0$ ) given the observed spawner abundance,  $S_t$ . I then took the difference between these values to estimate the additional number of recruits produced due to fertilization for that particular  $\theta_i$  and  $S_t$ . For example, in the Density-Independent model (Equation 3), I used the following equations:

$$(16) \quad \text{Number of recruits with fertilization in year } y = S_t \cdot e^{(a + bS_t + c)}$$

$$(17) \quad \text{Number of recruits without fertilization in year } y = S_t \cdot e^{(a + bS_t)}$$

where  $S_t$  is the abundance of spawners that produced the juveniles affected by fertilization in year  $y$  (e.g. the females that spawned in 1989 produced the brood class that was affected by fertilization in the summer of 1990). Because 94% of all juveniles spend only one summer in Chilko Lake, I therefore assumed that juveniles were only exposed to fertilization for one year. Subtracting Equation 12 from 11 then gave:

$$(18) \quad \text{Additional recruits due to fertilization in year } y = (S_t \cdot e^{(a + bS_t)})(e^c - 1)$$

The estimated additional recruits produced by one year of fertilization were then used to evaluate the resulting increase in harvest. To do this, the number of additional recruits from brood year  $t$  (which were exposed to fertilization in year  $y$ ) were apportioned among return years according to the observed proportional age distribution for that brood year. The recruits were then harvested according to the observed harvest rate in their return year. For example, if using a particular model and set of parameter values,  $\theta_t$ , I calculated that there were 100,000 additional recruits from brood year 1989 produced by the fertilization in 1990, 97% would return in 1993 and be harvested at a rate of 80% (the harvest rate observed in the 1993 fishery), and 3% would return in 1994 and be harvested at a rate of 82% (the harvest rate observed in the 1994 fishery). It was assumed that harvesting was not age- or size-selective; therefore the proportion of each age class represented in the harvest was identical to that observed in adult returns.

The number of harvested fish was then translated into dollars based on an estimate of the average value per sockeye harvested from the Chilko stock. The estimate of \$5.50 per kilogram (in 1997 dollars) was calculated using a weighted average of the values of net commercial benefits received from the net, troll, and First Nations fisheries (Appendix B), assuming that the majority of fish harvested from this stock were caught in the net fishery (estimates of the proportion of the Chilko Lake sockeye stock caught by

each fishery were unavailable). Assumed net benefits received in the First Nations fishery were based on landed value of a net-caught sockeye, and assumed net commercial benefits received in the net and troll fisheries incorporated both processing net benefits and harvesting net benefits (see Appendix B for details). The average weights used for age 4 and 5 Chilko sockeye were 2.3 and 3.2 kg, respectively. This procedure was repeated for each fertilized year  $y$ , and the estimated commercial net benefits received in each year were discounted back to 1988, the first year of the fertilization project, using 0, 5, 10, and 15% discount rates.

The number of additional recruits and the discounted value of additional harvest produced by each fertilized year  $y$  were then summed over all fertilized years to yield the total additional recruits and the total discounted commercial net benefits produced by the fertilization project, respectively. This procedure was repeated for all  $\theta_i$ . Estimates of total additional recruits for each  $\theta_i$  were then weighted by their associated posterior probability and summed to yield expected, or weighted average, additional recruits for the project.

### **Costs**

The costs of lake fertilization included in this analysis were limited to direct costs incurred through the application of fertilizer to Chilko Lake. These costs include fertilizer costs, base costs, flying costs, and administration charges implemented by Supply and Services Canada (Appendix B). All costs were translated to 1997 dollars using the Canadian Consumer Price Index for all economic sectors (see Appendix C). Costs were discounted to the first year of the project (1988) and summed to yield the project's total discounted costs.

### ***Economic performance measures***

I examined the project's benefit-cost ratio and net present value (NPV) to determine whether fertilization was a cost-effective method of increasing sockeye production. For each  $\theta_i$ , I calculated the benefit-cost ratio by taking the ratio of discounted commercial net benefits to discounted costs of the fertilization project, and I calculated the NPV by subtracting the project's discounted costs from discounted commercial net benefits. Each benefit-cost ratio and NPV was then multiplied by the posterior probability associated with the particular parameter set,  $\theta_i$ , and summed over all  $\theta_i$  to yield expected, or weighted average, values for the project's benefit-cost ratio and NPV.

## **Results**

### **Biological performance measures**

Figure 3A displays estimates of the cumulative number of additional recruits that would be produced, on average, if it were possible to repeat the Chilko Lake fertilization experiment a large number of times, *given the same spawner abundance and biological variability that existed during the original experiment*. The expected number of additional recruits that would result from such hypothetical repeated experiments ranged from 3.9 to 6.1 million fish over five years of fertilization, depending on the model used, and making the baseline assumption that the 1987 brood class was affected by the limited fertilization in 1988 (Fig. 3A). This is equivalent to approximately 0.8 to 1.2 million additional recruits per fertilized year, which is biologically plausible given that yearly recruits have exceeded 2 million for numerous brood years. Models that incorporated the

density-dependent term (DD and DDFI) yielded lower estimates than the other two models.

These expected values of additional recruits were calculated from their probability distributions (Fig. 4), which indicate, for a given model, the probability that various numbers of additional recruits would be produced by the fertilization project, given a large number of hypothetical replications of this experiment and uncertainty in the model parameter values. For all four models, most of each distribution fell to the right of zero (81% to 96%, depending on the model), indicating a large probability that there would be additional recruits produced by a given fertilization project. However, there was also a portion of each distribution to the left of zero (4% to 19%, depending on the model), which means that some portion of the hypothetical repeated fertilizations would yield *fewer* recruits than would have been produced if the lake had not been fertilized. The portion of the distribution to the left of zero was greater for the models that include the density-dependent term (DD and DDFI).

### **Economic performance measures**

Expected values for economic performance measures for the five-year fertilization project ranged from 21.1 to 28.1 for the benefit-cost ratio and from \$25.2 to \$33.8 million for net present value, depending on the model, when the 1987 brood year was assumed to have benefited from fertilization (Table 2A). As noted above for expected additional recruits, estimated values for both expected benefit-cost ratio and expected net present value were smallest for the two models that contained the density-dependent term (DD and DDFI). Probability distributions for benefit-cost ratio and net present value (Figs. 5 and 6) also displayed the same trends that were noted for additional recruits, with all models having the majority of the distributions (84% to 95%, depending on the model) to

the right of the break-even point (equal to one for the benefit-cost ratio, and zero for NPV) and only a small portion lying to the left. As well, the portion of the distribution below the break-even point was greater for models that incorporated the density-dependent term (DD and DDFI).

### **Comparison of models**

Results from the model comparison using  $AIC_c$  (Table 3) show that models that incorporate the Fraser Index have much lower  $\Delta AIC_c$  values (DIFI, 0.0; DDFI, 0.92) than equivalent models that did not include this index (DI, 7.48; DD, 5.67), assuming the 1987 brood year benefited from fertilization. Burnham and Anderson (1998) state that differences in AIC of greater than about 4 indicate quite different explanatory power of the models. This means that the DIFI and DDFI models are the best approximating models of those considered in this analysis, and that incorporating the Fraser Index substantially improves the fit of both the DD and DI models to the data. In contrast, incorporating the density-dependent term improves model fit only slightly, and only if the Fraser Index is not already included in the model (Table 3).

### **Sensitivity analyses**

Chilko Lake was only fertilized for half as long (six weeks) in 1988 as in following fertilized years, which created uncertainty about whether the 1987 brood year should be treated as fertilized or unfertilized in my analysis. Accordingly, I examined the sensitivity of my results to the fertilization status of the 1987 brood year. When this brood year was considered *unfertilized*, the values of all performance measures (i.e. the expected number of additional recruits, benefit-cost ratio, and NPV summed over the four years that were considered fertilized, but still discounted back to 1988, the first year of



the project) decreased by between 30 and 70 percent compared to the above results, in which 1987 was considered a fertilized brood (Table 2A, Fig. 3A). Models that incorporated the density-dependent term (DD and DDFI) were more sensitive to changes in the fertilization status of the 1987 brood year than models that did not include this term.

However, changing the fertilization status of this brood year did not affect the overall conclusion about the fertilization project. Regardless of the model used, results suggest that hypothetical repeated fertilization projects would generate additional recruits and a net economic benefit, on average. Furthermore, assumptions about the fertilization status of the 1987 brood year had no effect on the ranking of models according to the AIC model selection approach, and had little effect on the  $AIC_c$  differences among models (Table 3).

Further analyses were performed to test the sensitivity of the results to changes in the baseline discount rate of 10%, using 0, 5, and 15% discount rates. As expected, increasing the discount rate from the baseline 10% to 15% resulted in decreases in the baseline benefit-cost ratio and NPV of up to 20%. When no discount rate was applied, benefit-cost ratio and NPV increased by up to 60% from the baseline case. In all scenarios, however, changes in value of the economic measures were insufficient to affect the overall economic conclusion about of the project. All economic measures still indicated strong evidence for a net economic benefit from fertilization.

Finally, in order to examine whether my choice of prior probability distribution contributed to the large estimates of expected additional recruits that would result from hypothetical replications of this fertilization project, I performed the same analysis using much narrower priors. For each model, I set the upper and lower prior bounds of each

parameter to +1 SE and -1 SE of the best-fit value for that model (Table 4). The prior bounds for a given parameter were therefore different among models, unlike the baseline priors used in the initial calculations, which were the same for all models. Results of all performance measures using these new priors were less than 10% smaller than those calculated with the baseline priors for the DI, DIFI, and DDFI models (Table 2B, Fig. 3B). However, the DD model produced estimates of expected additional recruits that were 13% smaller than those calculated with the baseline priors when the 1987 brood year was considered fertilized, and 40% smaller than the baseline values when the 1987 brood year was considered unfertilized. Analogous changes were noted for benefit-cost ratio and NPV when using the DD model, with both indicators decreasing by 12% and 37% with the new priors, depending on the fertilization status of the 1987 brood year.

## **Discussion**

Results indicate a strong probability that the Chilko Lake fertilization program increased productivity of the sockeye brood years affected by fertilization. Furthermore, this increase in productivity was sufficient to yield a substantial expected net economic benefit under all alternative models and scenarios. There was nonetheless a wide range of outcomes in both biological and economic performance measures, reflecting large uncertainty in the stock-recruitment parameters. This range of outcomes also depended on the model used in the analysis, the assumed fertilization status of the 1987 brood year, and to a lesser extent, the bounds placed on the prior probability distributions of the model parameters.

## Differences among models

### Density-independent vs. density-dependent models

The expected values of all performance measures depended on which model was assumed to reflect the Chilko Lake sockeye salmon situation. Specifically, the estimate of expected additional recruits that would be produced by repeated hypothetical fertilization experiments was substantially lower when using the DD model (Equation 4), which incorporated a density-dependent term in which the effect of fertilization varied with spawner density, compared with results using the DI model (Fig. 3A). The decrease in expected recruits translated into smaller expected economic benefits with the DD model (Table 2A), because harvest was reduced while the costs of the fertilization program remained constant. However, analysis using the DD model still showed an impressive return on investment for this project.

The DI model (Equation 3) assumes that fertilization increases  $\log_e R/S$  by the same amount independent of spawner abundance for all fertilized years. Therefore, all treated brood years show an increase in recruits due to fertilization when using this model. However, when using the DD model (Equation 4), it was hypothesized that introducing the density-dependent term into the model would flatten the slope of the inverse relationship between  $\log_e R/S$  and spawners when compared with the DI model, resulting in a greater increase in  $\log_e R/S$  in years of high spawner abundance than in years of low spawner abundance. Interestingly, analysis using the DD model produced the opposite result. Most of the marginal posterior probability distribution of the  $d$  parameter in Equation 4 fell to the right of zero, as indicated by its 95% credibility interval (Table 1A), which describes the upper and lower limits that contain 95% of the distribution. Therefore, the slope of the stock-recruitment relationship with fertilization

( $F=1$ ) was steeper and more downward sloping, on average, in the DD model than the slope of that relationship without fertilization ( $F = 0$ ). This means that, according to this model, the majority of hypothetical repeated fertilization experiments would produce a greater increase in  $\log_e R/S$  at low spawner abundance than at high spawner abundance.

Although the results using the DD model make little ecological sense in terms of competition for limited resources, they can be easily explained by examining the stock-recruitment data shown in Figure 1. The fertilized 1990 and 1991 brood years represent the two greatest spawner abundances in this data set. Because there are no corresponding unfertilized brood years in this range of spawner abundance, these two data points exert a disproportionate leverage on parameter estimates for the DD model (Equation 4). When using this model, the negative slope of the stock-recruitment relationship with fertilization became steeper to fit to these data points, producing the results described above. The addition of data from unfertilized brood years at spawner abundances greater than 400,000 might reduce this effect, although the extent to which the results would reflect the hypothesized outcome (where the slope of the stock-recruitment relationship becomes flatter with fertilization) would depend on the specific data.

Despite observed reductions in biological and economic performance measures when the density-dependent term was added to the DI model, results from model comparisons using  $AIC_c$  indicated that there was, in fact, little difference in the overall fit of the DI and DD models. Apparently, both models account for a similar amount of variability in the stock-recruitment data, and are therefore equally appropriate representations of the information available. The inferences made using either of these models should thus carry equal weight in further analyses (Burnham and Anderson 1998). However, the fit of both the DI and DD models is relatively poor when compared to the

increased information gained by including the Fraser Index in the DIFI and DDFI models, as discussed in the following section. Accordingly, estimates of performance measures derived from the DIFI and DDFI models should thus receive greatest attention.

### Fraser Index

Incorporating the Fraser Index into the DI model accounted for a substantial portion of the variability in Figure 1 that was shared with other Fraser River sockeye stocks, according to  $AIC_c$  results (DIFI, Table 3). However, this made little difference to estimates of the biological and economic performance measures, producing only a slight decrease in expected additional recruits (< 4%) when compared to the DI model without the index (for the baseline case where the 1987 brood year was considered fertilized) (Table 2A, Fig. 3A). Inclusion of the Fraser Index in Equation 5 caused the marginal distribution of the  $b$  parameter to shift toward lower values (Table 1A), resulting in a flatter line than observed with the DI model and reflecting reduced density dependence in the stock-recruitment relationship. Because of the particular values of Fraser Index residuals that occurred coincident with the fertilization project, analysis using the DIFI model produced fewer expected additional recruits for the 1991 and 1992 brood years and more expected additional recruits for the 1987, 1989 and 1990 brood years than occurred using the DI model, resulting in an overall decrease in expected additional recruits for the project.

Despite the observed reduction in expected additional recruits using the DIFI model, this model nonetheless produced a greater expected net economic benefit than the DI model, with the expected benefit-cost ratio and NPV each increasing by 4%. Although this seems counterintuitive, it can be explained by considering the fact that harvest rates were not constant in all years. This means that increasing the number of recruits in a

brood year subjected to relatively high harvest rates will yield a greater benefit, in terms of harvest, than increasing the number of recruits by the same amount in a brood year exposed to relatively low harvest rates. In this particular instance, the brood years which produced more expected additional recruits under the DI model than the DIFI model (1991 and 1992) were subjected to much lower harvest rates (56% and 52% respectively) than were the remaining three broods that produced more recruits under the DIFI model (1987, 76%; 1989, 80%; 1990, 82%).

Adding the Fraser Index to the DD model produced considerably different results from those described above for the DI model, with expected values for all performance measures increasing when the Fraser Index average residuals were removed from the Chilko stock-recruitment data (Equation 6) (expected additional recruits increased by 25%; NPV by 22%; benefit-cost ratio by 21%). This result occurred because the inclusion of the Fraser Index flattened out the slope of the stock-recruitment relationship with fertilization when compared with the DD model, as seen in a shift of the marginal distribution of the  $d$  parameter to lower values (Table 1A). The net result of this shift was an increase in the number of expected additional recruits produced due to fertilization over the duration of the project, and consequently, an increase in the values of the economic performance measures.

The Fraser Index was included in this analysis because it provides an estimate of sockeye survival rates during the period of downstream migration and ocean residence that determine, in part, the number of adult returns to the Fraser River. Because these survival rates are highly variable, any interpretation of the effect of fertilization on the Chilko stock must be evaluated in conjunction with these rates. Incorporating the Fraser Index into the Ricker model should therefore remove some of the variation in the Chilko

data, leaving a better estimate of the Chilko-specific stock-recruitment parameters, and of particular relevance to this analysis, providing a better estimate of the change in stock-recruitment parameters due to fertilization. Formal comparison of the four models used herein indicated that the Fraser Index did, in fact, improve parameter estimation, as indicated by the  $\Delta AIC_c$  values in Table 3, and therefore the results generated from the two models incorporating this index should receive greater consideration when interpreting results than those that did not include the index. The results show that the DIFI model provides the best representation of the data, and that the DDFI model also merits further consideration, based on the small difference between its  $AIC_c$  value and the minimum value obtained among the models examined (according to Burnham and Anderson (1998), models with  $\Delta AIC$  values  $< 2$  have substantial support, and should be considered when making inferences about the data). Furthermore, the models that did not include the Fraser Index had sufficiently large  $\Delta AIC_c$  scores ( $\Delta AIC_c > 4$ ) that they should receive little consideration in the analysis (Burnham and Anderson 1998).

### Implications of the differences among models

The range of results produced by the four different models used in this analysis highlights the effect of underlying assumptions on model output. In this study, all models indicated substantial expected net economic benefits from this project because the number of expected additional recruits produced was very large under all scenarios. Therefore, any management recommendations based on this particular analysis would be relatively insensitive to the model used. However, the value of the largest expected benefit-cost ratio (from the DIFI model, which, interestingly, was found to be the best approximating model according to  $AIC_c$ ) was 33% larger than the value of the smallest (from the DD model), and the range in NPV was analogous. Given a different set of

stock-recruitment data (from an experiment done on Chilko Lake in different years, or at a different lake), this range in outcomes may be large enough that the choice of model could affect whether an expected net benefit or loss is produced in the benefit-cost analysis.

Managers should therefore be aware of how various assumptions inherent in their models can affect the outcomes of their analyses. Managing according to one model, when in fact another model is a better representation of reality, can produce misleading results and incorrect management decisions. For example, using the DD model in a benefit-cost analysis when the DIFI model is actually the most biologically appropriate model would underestimate expected economic benefits, given the stock-recruitment data observed for Chilko Lake. It is therefore important that researchers carefully test the assumptions in their models, whenever the data are available to do this. In addition, it is recommended that any modeling exercise incorporate a formal model selection process, in which a group of well-considered, scientifically defensible candidate models are rigorously evaluated, according to well-established model selection criteria (see Burnham and Anderson (1998) for a review of the information-theoretic approach, and Draper (1995) for a review of Bayesian methods). Incorporating formal model selection will enable researchers and managers to determine which of several candidate model outcomes is most defensible, based on which model is best supported by the available data. At the very least, it is crucial that researchers explicitly state the assumptions inherent in their models, so that readers can properly interpret results.

This point is particularly relevant for the analysis of future lake fertilization projects. An interesting area for potential research could consider whether fertilization produces larger net benefits over some range of spawner abundance by examining the



effects of fertilization on smolt size or weight over a range of escapements. Results from this research might provide empirical justification for the inclusion of density-dependent fertilization effect in future modeling exercises, and could also indicate certain conditions where fertilization is most cost-effective. This concept is analogous to that investigated by Guthrie and Peterman (1988), who examined the economic benefits of a pulsed fertilization strategy for B.C. sockeye stocks. Based on previous research that indicated the potential for density-dependent marine growth (Peterman and Wong 1984), that study investigated the conditions in which timing the fertilization of B.C. lakes to coincide with years of low smolt production for all other Gulf of Alaska sockeye stocks would maximize net economic benefits from fertilization.

### **Fertilization status of the 1987 brood year**

Values of all performance measures were highly sensitive to the assumed fertilization status of the 1987 brood year, decreasing from 30 to 70% depending on the performance measure and model considered (Fig. 3A, Table 2). In general, this occurred because the 1987 brood year contributed a disproportionate amount (from 25 to 40% instead of the expected 20%) to the expected additional recruits generated by the project relative to the other fertilized brood years, when all five years were considered fertilized. This result was generated because the low spawner abundance observed in the 1987 brood year, in conjunction with the particular parameter values supported by the data for all models, meant that the 1987 brood generated more expected additional recruits than other fertilized years, when it was considered fertilized. Furthermore, the 1987 brood year sustained a relatively high harvest rate compared to other fertilized broods (see Fraser Index section, above). The combination of these two factors meant that the 1987 brood year contributed more than 20% (the expected value for one of five years) to the net

economic benefits generated by the fertilization project, when it was considered fertilized. Based on this observation, the expected value of economic performance measures would be expected to drop by at least 25 – 40% when the contribution of the 1987 brood year was removed.

However, the 1987 brood year had an even greater influence on expected values of performance measures because the data point for this year lies on the upper edge of the scatter of stock-recruitment data, thereby exerting considerable influence on the posterior probabilities assigned to various  $\theta_i$ . In general, when the 1987 brood year was considered unfertilized, the marginal distributions of the  $c$  and  $b$  parameters shifted to lower values, and the marginal distribution of the  $d$  parameter shifted to higher values (Table 1). For all models, this meant that the increase in  $\log_e R/S$  was smaller and there were fewer expected additional recruits produced for the *remaining* fertilized brood years (i.e. 1989, 1990, 1991, and 1992) when the 1987 brood year was considered unfertilized.

There is biological evidence (Kyle 1994a) that food shortages for sockeye smolts occur during late summer, when zooplankton abundance begins to decrease due to predation. Accordingly, lake fertilization should provide the greatest benefit to smolts during this period, which is when the 1987 fertilization occurred. There is thus reason to believe that the abbreviated fertilization in 1987 may have been as effective as longer-duration fertilizations in following summers, and that analyses treating 1987 as fertilized provide a more realistic representation of the true state of nature.

### **Prior probability distributions**

According to this study, the Chilko Lake fertilization project would be expected to produce from 1.1 to 6.1 million expected additional recruits, if the same fertilization experiment could be repeated a large number of times, depending on the model used and

on assumptions of the fertilization status of the 1987 brood year. This represents an increase in expected recruits of between 37 and 110% from the number expected without fertilization, which is similar to results reported by LeBrasseur et al. (1978), who found an increase in recruits of approximately 100% due to fertilization. However, the economic benefits generated by the Chilko Lake fertilization project (from 6.9 to 28.1 for benefit-cost ratio, and from 7.4 to 33.8 million dollars for NPV) are substantially larger than those reported in the literature for other enhancement projects (Pearse 1994), and are considerably greater than the target benefit-cost ratio of 1.5:1 established by the Salmonid Enhancement Program (Hilborn and Winton 1993).

The discrepancy between the economic results of this analysis and those reported in the literature suggested that methodological biases could have contributed to the impressive numbers of expected returns generated in my analysis. In particular, previous studies have indicated that the choice of prior probabilities can have a significant effect on posterior distributions (Walters and Ludwig 1994; Adkison and Peterman 1996). I used uniform priors on all parameters in this analysis to ensure that the shape of the posterior distribution was determined primarily by the stock-recruitment data. However, research has shown that uniform priors can potentially contain considerable information, and can strongly influence the shape of the posterior, particularly when stock-recruitment data contain little information. Specifically, Hill and Pyper (1998) performed Bayesian forward simulations of stock-recruitment dynamics using uniform priors, and found that estimates of expected escapement after five generations were highly sensitive to the lower bound placed on the  $b$  parameter of the Ricker model (as defined in Eqn. 2). When using stock-recruitment data that contained little information at high spawner abundances, and wide uniform priors, the authors found that estimates of expected escapement generated

by Bayesian simulations were up to 60% greater than estimates generated by best-fit stochastic simulations. This is of particular relevance to this study, as Chilko Lake stock-recruitment data are also very limited at high spawner abundance. Such “missing” data can result in extreme parameter values (values at the limits of the prior probability distributions) being assigned a greater posterior probability of describing the stock-recruitment relationship than they would be the case if the data were more informative. This produces diffuse distributions for all parameters.

Based on these findings, I performed further analyses using much narrower prior probability distributions in order to assess how much influence the baseline priors had on the shape of the posterior, and hence on the estimated number of expected recruits. With the exception of one scenario, all performance measures showed only a slight decrease when narrow priors were used (Table 2B, Fig. 3B), suggesting that the use of a wide prior probability distribution had little influence on the shape of the posterior. Rather, it would appear that the scarcity of stock-recruitment data from unfertilized brood years at high spawner abundances was the most important factor contributing to the large estimates of expected additional recruits. This lack of contrast in the unfertilized data confounded the estimation of the stock-recruitment parameters, and created large uncertainty in estimates of the difference in  $\log_e R/S$  between fertilized and unfertilized brood years. This effect was also evident when calculating benefits using best-fit estimates for model parameters (Table 5). For example, the estimated number of additional recruits produced using best-fit values was less than 19% smaller than expected values from Bayesian analysis using the baseline priors, and less than 16% smaller than expected values from the narrow priors for all but one trial (DD model, 1987 unfertilized) (Table 6).

Spawner abundances at Chilko Lake have been quite large in recent years, with estimates of effective female spawners exceeding 400,000 for 1996 to 1999 (Michael Bradford, personal communication). These new data from unfertilized brood years should provide sufficient contrast in the data at high spawner abundance to reduce the uncertainty in parameter estimates in future analyses. However, the process of refining these estimates is necessarily delayed because estimates of the number of adult recruits from these brood years will not be available for several years. Until then, it is recommended that estimates of economic benefits from the Chilko Lake fertilization project presented here be considered speculative.

### **Management implications**

The cost-effectiveness of lake fertilization, in terms of adults produced, has seldom been evaluated, and to my knowledge, Bayesian methods have never been incorporated into existing lake fertilization studies. This analysis demonstrated that Bayesian statistics can be used to account for uncertainties in a sockeye stock-recruitment relationship and in the effect of lake fertilization on this relationship. Using this framework, I showed that there was a strong probability that the Chilko Lake fertilization project realized a net economic benefit. The methods can be easily adapted to other fertilization experiments, particularly because the spawner-recruit data required for the Ricker model are already collected for several Pacific salmon stocks. Using a stock-recruitment model provides the additional advantage of measuring the end result of fertilization - the number of additional recruits - rather than some intermediate life stage, as in most previous studies (Hyatt and Stockner 1985; Kyle 1994a; Kyle 1994b; Luecke et al 1996; Edmundson et al 1997). Furthermore, by using several modifications to the Ricker model, I was able to demonstrate that different assumptions about how

fertilization affects sockeye stocks result in markedly different estimates of the project's economic outcome. However, for the stock-recruitment data presented here, these assumptions did not affect conclusions concerning the economic efficiency of the project.

One notable, although unsurprising, finding of this study is that Bayesian methods cannot compensate for uninformative data. When there is insufficient contrast in stock-recruitment data, the Bayesian framework is just as limited as best-fit approaches in estimating model parameters. Although the Bayesian approach provides a method of taking into account uncertainties in the values of model parameters that is not available using best-fit estimates, the outcome of any analysis ultimately depends on the quality of data input to the model. In this particular instance, the absence of data from unfertilized years at large escapement makes it difficult to properly estimate the effect of fertilization for years of high spawner abundance, and consequently, to evaluate the degree of density dependence in the stock-recruitment relationship.

It is essential to note that the increase in recruits due to fertilization reported in this analysis is representative only of this particular project, and that results presented here should not be generalized in any way. There are many sources of variability that could affect future fertilization programs, such as the abundance of spawners in future fertilized years, that would have to be incorporated in order to extend the findings of this research to future fertilization projects at *Chilko Lake*, let alone fertilization projects in other systems. Similarly, observed effects of fertilization on juvenile life stages should not be extrapolated to adult recruits, because of variability in ocean survival, and possible density-dependent survival in the marine life stage (Peterman 1991).

Finally, I must reiterate that this research considered only the direct costs and benefits of lake fertilization, and that there are many other indirect costs and benefits that

could be incurred from any project of this nature. In particular, I caution that the history of manipulating nutrient cycling by either supplementing or removing nutrient inputs has been demonstrated to cause major ecological changes in both terrestrial and aquatic ecosystems (Likens et al. 1977; Schindler et al. 1978). Furthermore, the practice of enhancing one stock for the sake of augmenting its harvests should be rigorously examined, because it may have indirect negative effects on smaller, threatened stocks. Increased harvesting effort directed at a fertilized run could potentially increase bycatch of less productive stocks, reducing the effectiveness of existing conservation efforts.

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Table 1. Upper and lower bounds of baseline prior probability distributions for model parameters (Equations 3 through 6), and 95% credibility intervals of marginal posterior distributions of model parameters. Models were DI (Density-Independent); DIFI (Density-Independent + Fraser Index); DD (Density-Dependent); DDFI (Density-Dependent + Fraser Index). Part A is for the case where the 1987 brood year was assumed to be fertilized; Part B is where it was assumed unfertilized.

**A) 1987 fertilized**

Parameter	Model				
	DI	DIFI	DD	DDFI	
a	Prior bounds	1.9	1.9	1.9	1.9
		3.2	3.2	3.2	3.2
	Posterior 95% intervals	2.4	2.3	2.2	2.2
		3.0	2.9	2.9	2.8
b	Prior bounds	0	0	0	0
		$6.0 \times 10^{-6}$	$6.0 \times 10^{-6}$	$6.0 \times 10^{-6}$	$6.0 \times 10^{-6}$
	Posterior 95% intervals	$1.5 \times 10^{-6}$	$0.7 \times 10^{-6}$	$0.3 \times 10^{-6}$	$0.3 \times 10^{-6}$
		$5.0 \times 10^{-6}$	$4.0 \times 10^{-6}$	$4.2 \times 10^{-6}$	$3.8 \times 10^{-6}$
c	Prior bounds	-1.0	-1.0	-1.0	-1.0
		4.0	4.0	4.0	4.0
	Posterior 95% intervals	-0.1	-0.2	0.4	0.0
		1.3	1.3	2.9	2.3
d	Prior bounds			$-4.0 \times 10^{-6}$	$-4.0 \times 10^{-6}$
				$10 \times 10^{-6}$	$10 \times 10^{-6}$
	Posterior 95% intervals			$0.2 \times 10^{-6}$	$-1.3 \times 10^{-6}$
				$7.2 \times 10^{-6}$	$5.7 \times 10^{-6}$
e	Prior bounds		-0.1		-0.1
			1.4		1.4
	Posterior 95% intervals		0.3		0.1
			1.0		0.9

**B) 1987 unfertilized**

Parameter	Model					
	DI	DIFI	DD	DDFI		
a	Prior bounds	1.9	1.9	1.9	1.9	
		3.2	3.2	3.2	3.2	
	Posterior 95% intervals	2.4	2.3	2.2	2.2	
		3.0	2.9	2.9	2.8	
b	Prior bounds	0	0	0	0	
		$6.0 \times 10^{-6}$	$6.0 \times 10^{-6}$	$6.0 \times 10^{-6}$	$6.0 \times 10^{-6}$	
	Posterior 95% intervals	$1.2 \times 10^{-6}$	$0.6 \times 10^{-6}$	$0.3 \times 10^{-6}$	$0.3 \times 10^{-6}$	
		$4.8 \times 10^{-6}$	$3.7 \times 10^{-6}$	$3.9 \times 10^{-6}$	$3.5 \times 10^{-6}$	
c	Prior bounds	-1.0	-1.0	-1.0	-1.0	
		4.0	4.0	4.0	4.0	
	Posterior 95% intervals	-0.3	-0.3	0.2	-0.2	
		1.3	1.3	2.9	2.5	
d	Prior bounds			$-4.0 \times 10^{-6}$	$-4.0 \times 10^{-6}$	
				$10 \times 10^{-6}$	$10 \times 10^{-6}$	
	Posterior 95% intervals			$-0.2 \times 10^{-6}$	$-1.3 \times 10^{-6}$	
				$7.3 \times 10^{-6}$	$5.8 \times 10^{-6}$	
e	Prior bounds		-0.1		-0.1	
				1.4		1.4
	Posterior 95% intervals			0.3		0.2
				1.0		1.0

Table 2. Expected economic performance measures over the entire 5 years of Chilko Lake fertilization, using 10% discount rate. Models were DI (Density-Independent); DIFI (Density-Independent + Fraser Index); DD (Density-Dependent); DDFI (Density-Dependent + Fraser Index). For Part A the baseline prior probability distributions were used; for Part B the narrower ( $\pm 1$  SE) priors were used.

Performance measure		Model			
		DI	DIFI	DD	DDFI
Expected benefit-cost ratio	1987 fertilized	27.1	28.1	21.1	25.6
	1987 unfertilized	15.0	16.7	6.9	13.5
Expected net present value (millions \$)	1987 fertilized	32.6	33.8	25.2	30.7
	1987 unfertilized	17.5	19.7	7.4	15.6
<b>A) baseline priors</b>					
Performance measure		Model			
		DI	DIFI	DD	DDFI
Expected benefit-cost ratio	1987 fertilized	27.0	25.7	18.8	24.8
	1987 unfertilized	14.2	15.7	4.7	12.6
Expected net present value (millions \$)	1987 fertilized	32.5	30.9	22.3	29.8
	1987 unfertilized	16.6	18.3	4.6	14.5



Table 3. Relative values of the modified Akaike's Information Criterion for the four models used in this analysis. The  $\Delta AIC_c$  value is the difference between the  $AIC_c$  value for a given model, and the model with the lowest  $AIC_c$  value. The model with the smallest  $\Delta AIC_c$ , in this case the DIFI model, is the model that best approximates the information in the stock-recruitment data. Models were DI (Density-Independent); DIFI (Density-Independent + Fraser Index); DD (Density-Dependent); DDFI (Density-Dependent + Fraser Index).

		Model			
		DI	DIFI	DD	DDFI
$\Delta AIC_c$	1987 fertilized	7.48	0	5.67	0.92
	1987 unfertilized	8.10	0	6.03	0.75

Table 4. Upper and lower bounds of narrow ( $\pm 1$  SE) prior probability distributions for model parameters (Equations 3 through 6), and 95% credibility intervals of marginal posterior distributions of model parameters. Models were DI (Density-Independent); DIFI (Density-Independent + Fraser Index); DD (Density-Dependent); DDFI (Density-Dependent + Fraser Index). Part A is for the case where the 1987 brood year was assumed to be fertilized; Part B is where it was assumed unfertilized.

**A) 1987 fertilized**

Parameter	Model				
	DI	DIFI	DD	DDFI	
a	Prior bounds	2.5	2.4	2.4	2.3
		2.9	2.7	2.7	2.7
	Posterior 95% intervals	2.5	2.4	2.4	2.3
		2.9	2.7	2.7	2.7
b	Prior bounds	$2.4 \times 10^{-6}$	$1.5 \times 10^{-6}$	$1.0 \times 10^{-6}$	$0.8 \times 10^{-6}$
		$4.2 \times 10^{-6}$	$3.3 \times 10^{-6}$	$3.1 \times 10^{-6}$	$3.0 \times 10^{-6}$
	Posterior 95% intervals	$2.5 \times 10^{-6}$	$1.6 \times 10^{-6}$	$1.1 \times 10^{-6}$	$0.9 \times 10^{-6}$
		$4.2 \times 10^{-6}$	$3.1 \times 10^{-6}$	$3.0 \times 10^{-6}$	$2.9 \times 10^{-6}$
c	Prior bounds	0.3	0.2	1.0	0.6
		1.0	0.9	2.3	1.8
	Posterior 95% intervals	0.3	0.2	1.0	0.7
		1.0	0.9	2.3	1.8
d	Prior bounds			$2.0 \times 10^{-6}$	$0.5 \times 10^{-6}$
				$6.0 \times 10^{-6}$	$4.0 \times 10^{-6}$
	Posterior 95% intervals			$2.2 \times 10^{-6}$	$0.7 \times 10^{-6}$
				$5.7 \times 10^{-6}$	$3.8 \times 10^{-6}$
e	Prior bounds		0.4		0.3
				0.8	
	Posterior 95% intervals		0.4		0.3
				0.8	

**B) 1987 unfertilized**

Parameter	Model				
	DI	DIFI	DD	DDFI	
a	Prior bounds	2.5	2.4	2.4	2.3
		2.9	2.7	2.7	2.6
	Posterior 95% intervals	2.5	2.4	2.4	2.3
		2.9	2.7	2.7	2.6
b	Prior bounds	$2.0 \times 10^{-6}$	$1.3 \times 10^{-6}$	$0.8 \times 10^{-6}$	$0.6 \times 10^{-6}$
		$3.0 \times 10^{-6}$	$3.0 \times 10^{-6}$	$2.8 \times 10^{-6}$	$3.0 \times 10^{-6}$
	Posterior 95% intervals	$2.2 \times 10^{-6}$	$1.4 \times 10^{-6}$	$0.9 \times 10^{-6}$	$0.7 \times 10^{-6}$
		$3.9 \times 10^{-6}$	$2.9 \times 10^{-6}$	$2.7 \times 10^{-6}$	$2.7 \times 10^{-6}$
c	Prior bounds	0.0	0.1	0.9	0.6
		0.9	0.9	2.3	1.8
	Posterior 95% intervals	0.0	0.1	1.0	0.7
		0.9	0.9	2.2	1.7
d	Prior bounds			$2.0 \times 10^{-6}$	$0.6 \times 10^{-6}$
				$5.8 \times 10^{-6}$	$4.0 \times 10^{-6}$
	Posterior 95% intervals			$2.2 \times 10^{-6}$	$0.7 \times 10^{-6}$
				$5.6 \times 10^{-6}$	$3.7 \times 10^{-6}$
e	Prior bounds		0.4		0.4
			0.9		0.8
	Posterior 95% intervals		0.4		0.4
			0.9		0.8

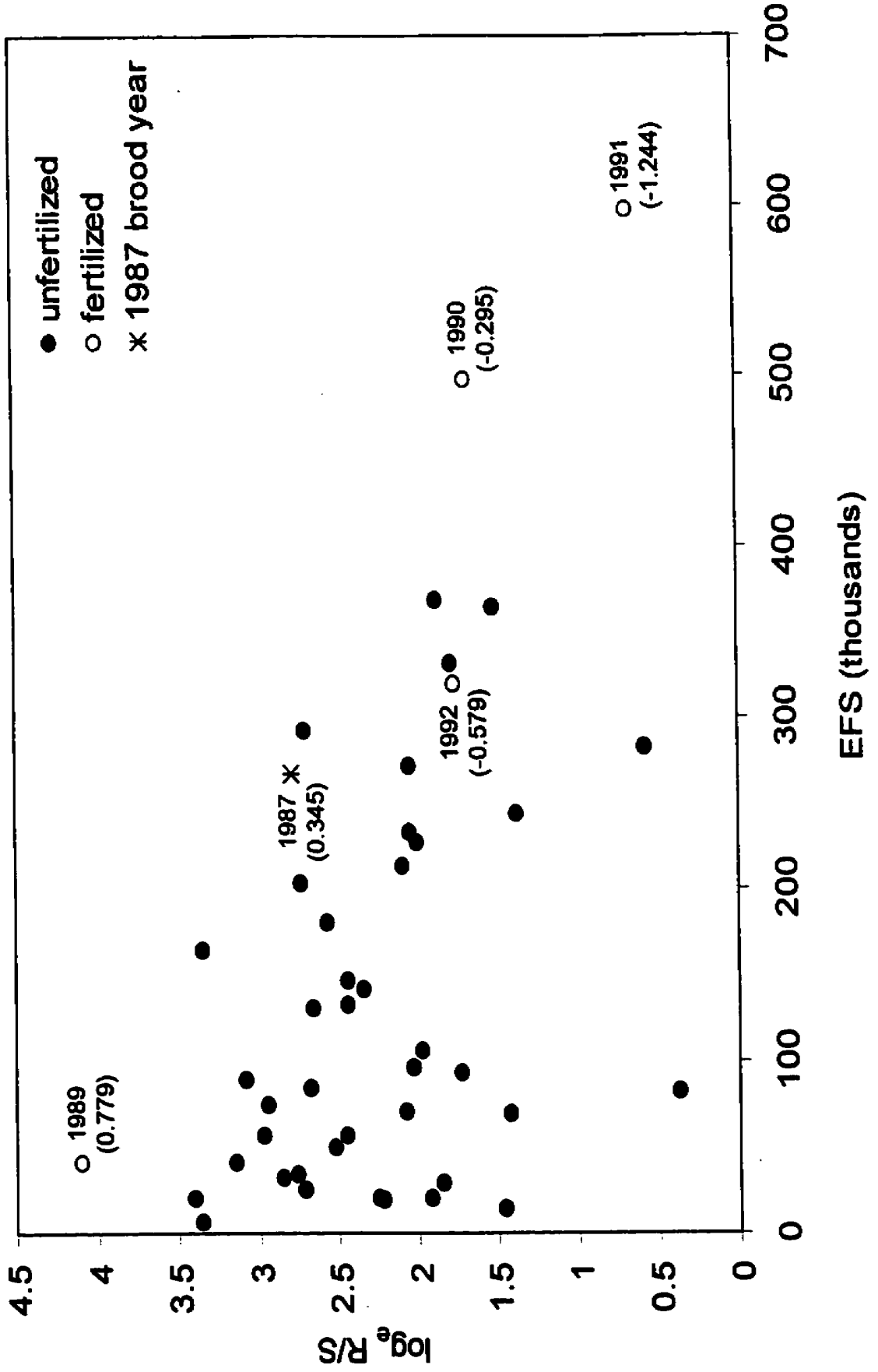
Table 5. Best-fit estimates of model parameters (a through e). Models were DI (Density-Independent); DIFI (Density-Independent + Fraser Index); DD (Density-Dependent); DDFI (Density-Dependent + Fraser Index).

Parameter		Model			
		DI	DIFI	DD	DDFI
a	1987 fertilized	2.71	2.58	2.55	2.50
	1987 unfertilized	2.69	2.57	2.54	2.58
b	1987 fertilized	$3.3 \times 10^{-6}$	$2.4 \times 10^{-6}$	$2.1 \times 10^{-6}$	$1.7 \times 10^{-6}$
	1987 unfertilized	$3.0 \times 10^{-6}$	$2.2 \times 10^{-6}$	$1.8 \times 10^{-6}$	$1.5 \times 10^{-6}$
c	1987 fertilized	0.63	0.57	1.65	1.19
	1987 unfertilized	0.46	0.50	1.60	1.19
d	1987 fertilized			$3.7 \times 10^{-6}$	$2.3 \times 10^{-6}$
	1987 unfertilized			$3.9 \times 10^{-6}$	$2.4 \times 10^{-6}$
e	1987 fertilized		0.63		0.55
	1987 unfertilized		0.66		0.57

Table 6. Estimates of expected additional recruits (in millions of fish) produced over the entire 5 years of Chilko Lake fertilization using the best-fit estimates of model parameters, and estimates of expected additional recruits that would result from hypothetical repeated experiments summed over the entire 5 years of Chilko Lake fertilization using baseline and narrow (+/- 1 SE) prior probability distributions for model parameters. Models were DI (Density-Independent); DIFI (Density-Independent + Fraser Index); DD (Density-Dependent); DDFI (Density-Dependent + Fraser Index).

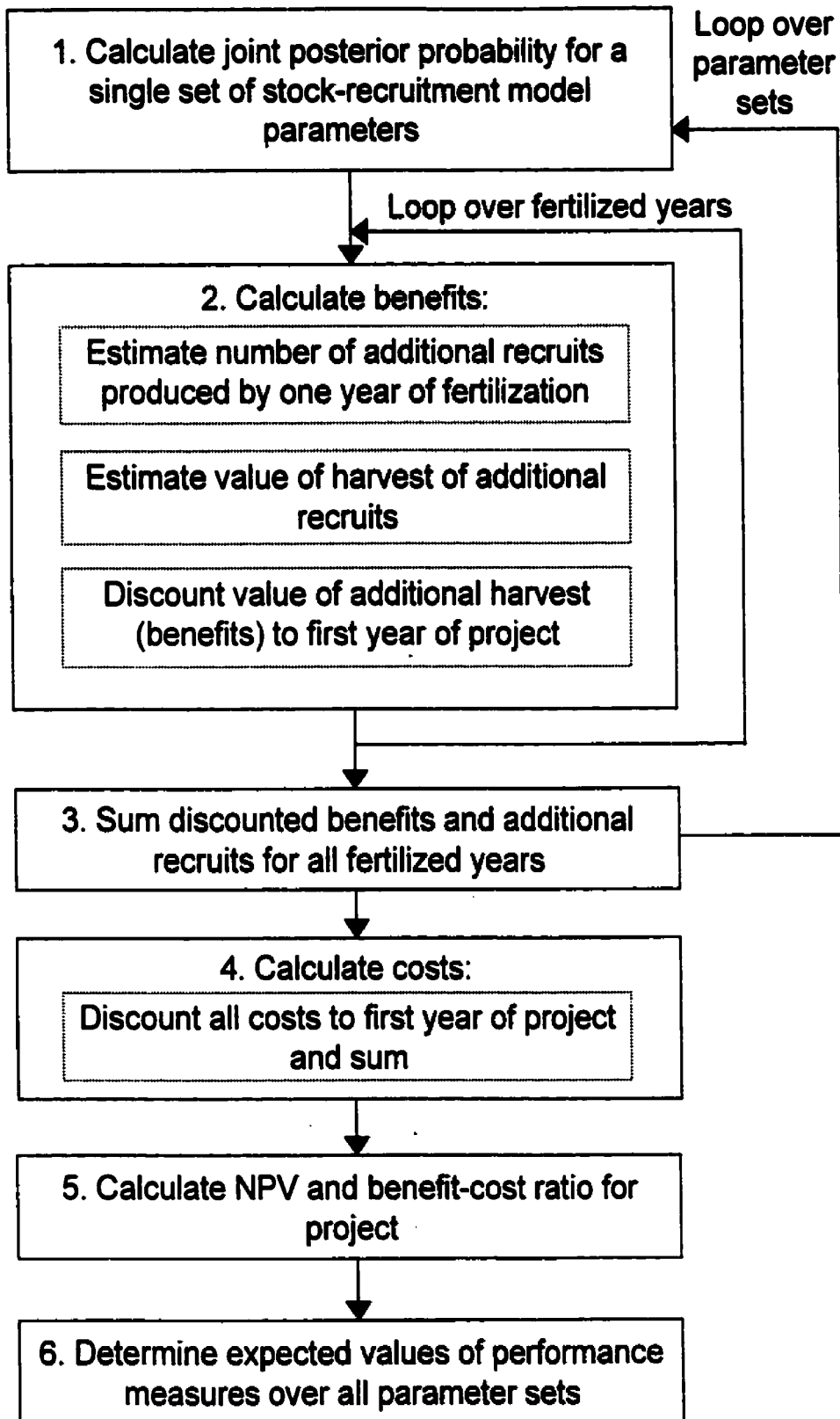
(Expected) Additional Recruits (millions)		Model			
		DI	DIFI	DD	DDFI
Best-fit	1987 fertilized	5.8	5.4	3.3	4.4
	1987 unfertilized	3.2	3.2	0.4	2.1
Baseline priors	1987 fertilized	6.1	5.9	3.9	4.9
	1987 unfertilized	3.5	3.6	1.1	2.6
Narrow priors	1987 fertilized	6.1	5.4	3.4	4.8
	1987 unfertilized	3.3	3.4	0.7	2.5

**Figure 1. Stock-recruitment data for Chilko Lake sockeye (1949 through 1992 brood years). Pre-fertilization brood years are indicated by black circles, fertilized brood years are indicated by open circles. The 1987 brood year is identified by an asterisk because it reared in only a partially fertilized lake. Numbers beside data points identify brood years, and numbers in parentheses indicate the value of that brood year's Fraser Index (that index was from Bradford et al., in press, see text).**



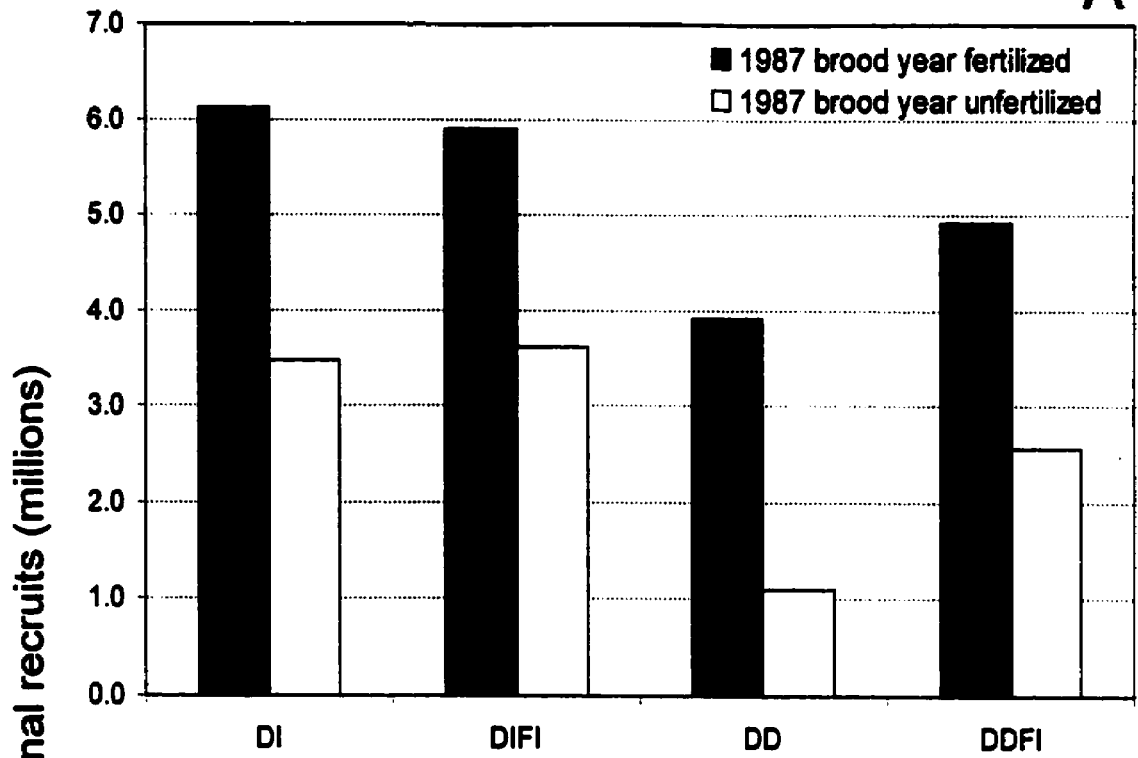
**Figure 2.** Generalized flow chart of the procedure used to estimate the economic value of the Chilko Lake fertilization project.



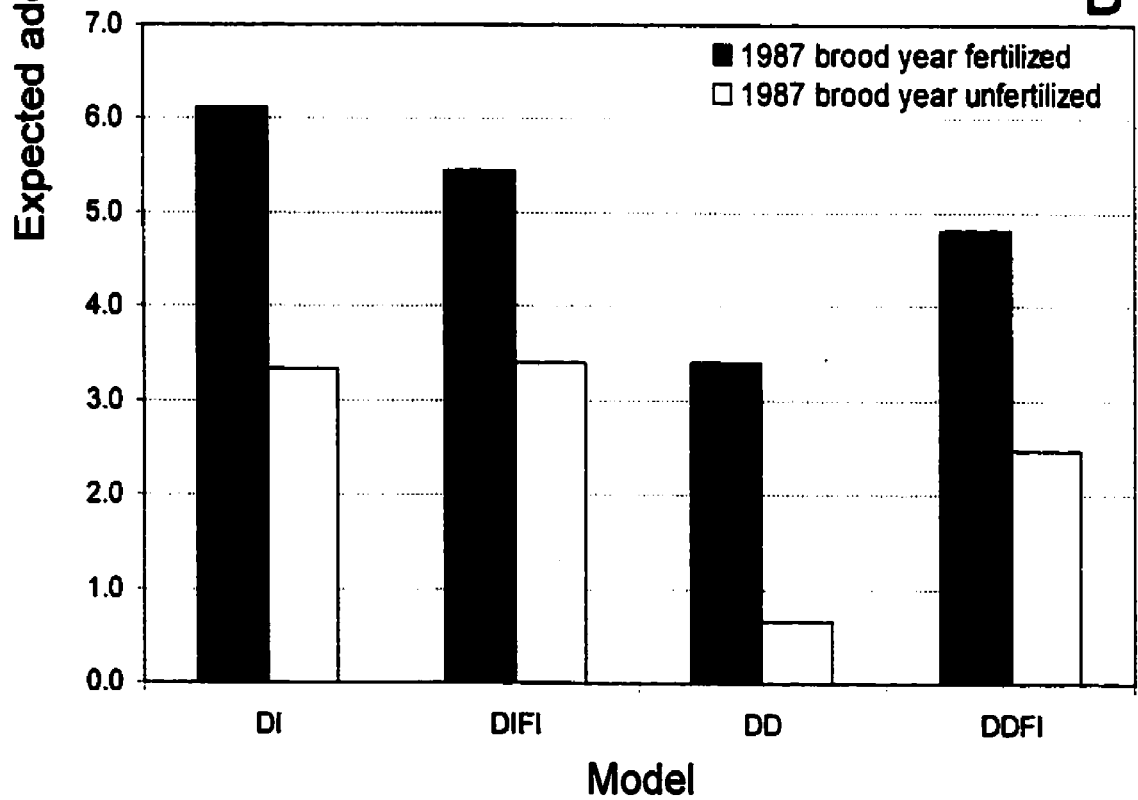


**Figure 3.** Estimates of estimates of expected additional recruits that would result from hypothetical repeated experiments summed over the entire 5 years of the Chilko Lake fertilization project. Models were DI (Density-Independent); DIFI (Density-Independent + Fraser Index); DD (Density-Dependent); DDFI (Density-Dependent + Fraser Index) (see text and Equations 3-6 for further description). Due to the limited fertilization in 1988, solid bars indicate calculations where the 1987 brood year was considered fertilized, open bars indicate calculations where the 1987 brood year was considered unfertilized. Part A is from calculations using baseline parameters; Part B is from calculations using narrower ( $\pm 1$  SE) prior probabilities on parameters.

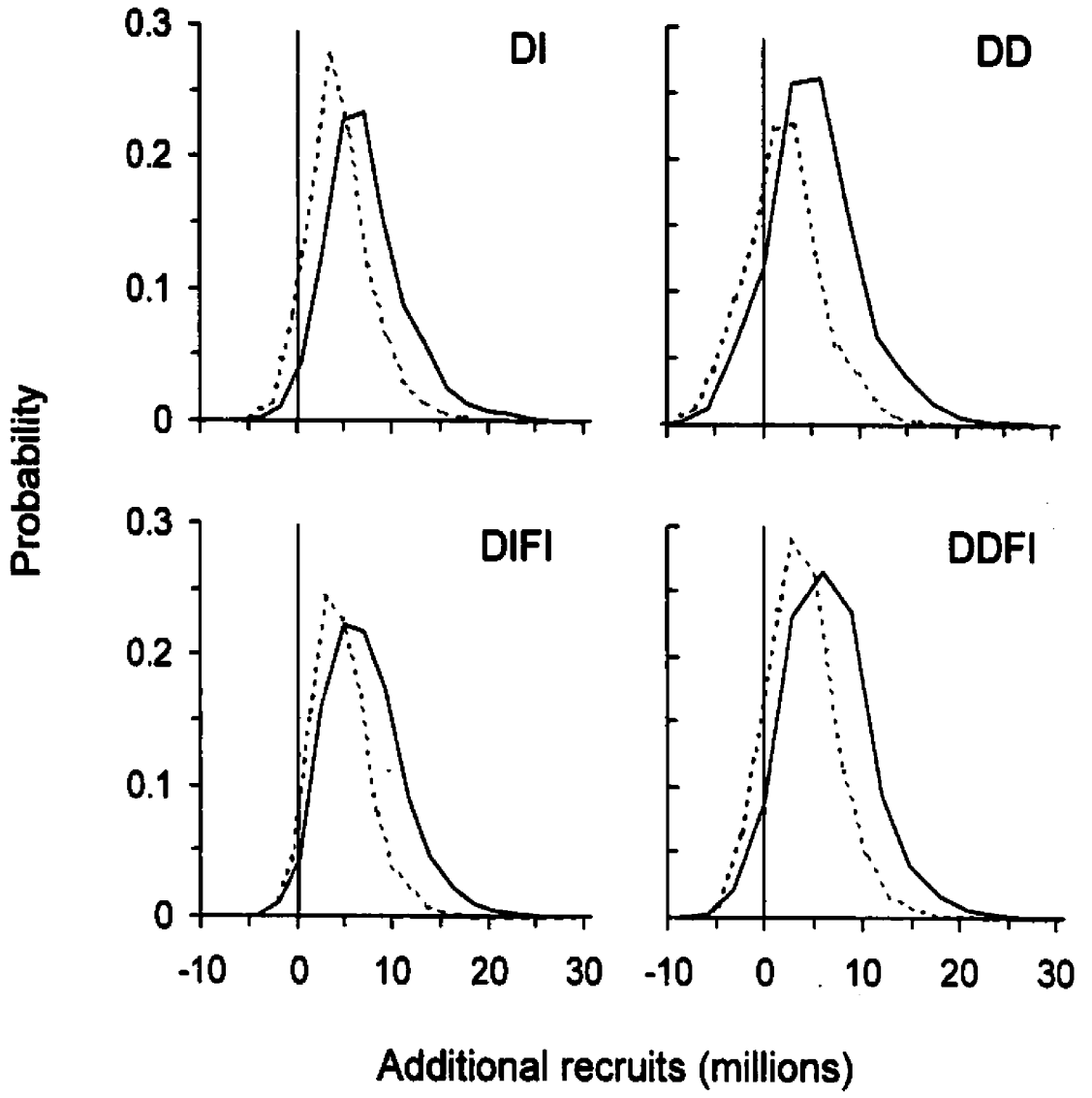
A



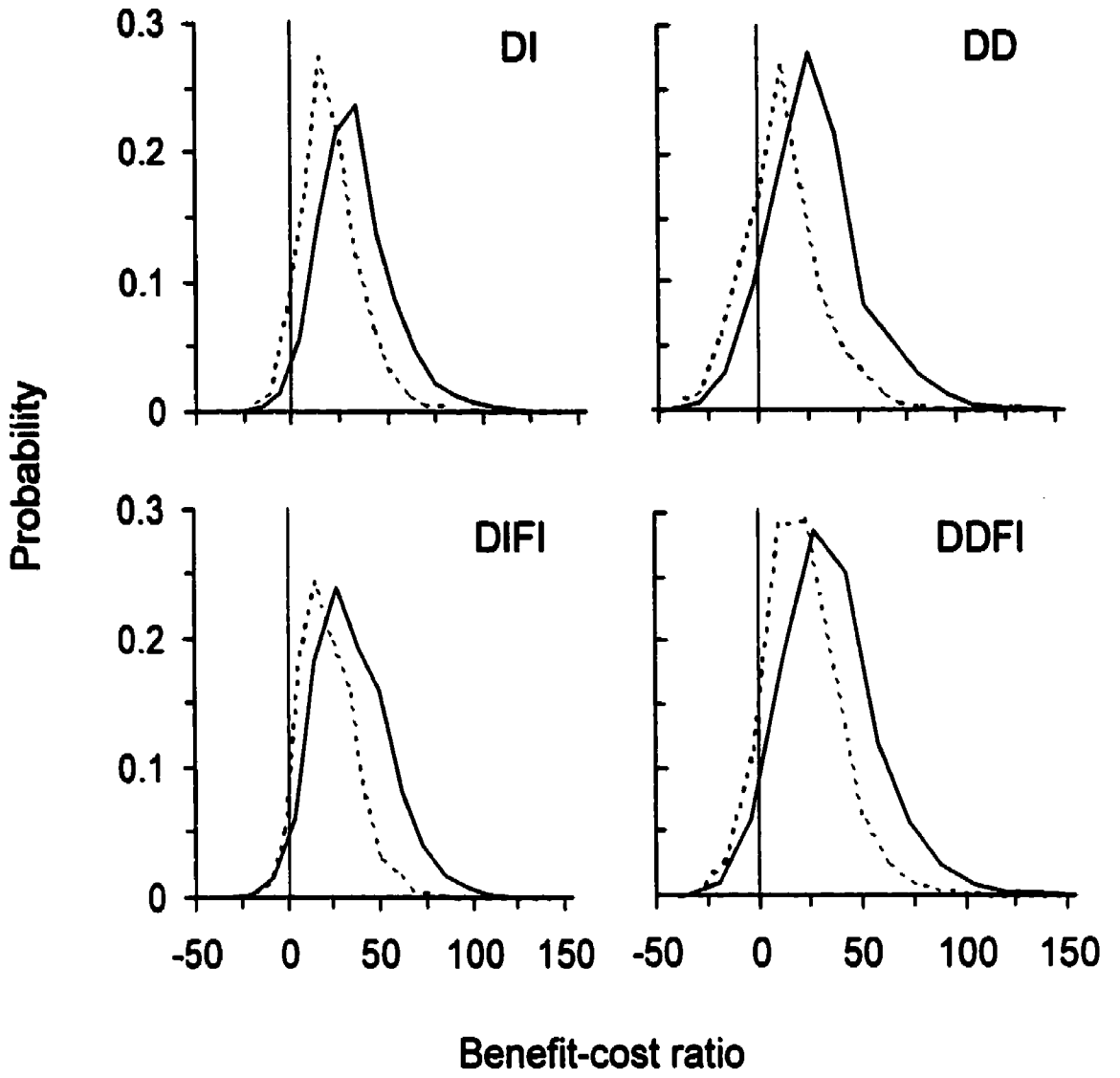
B



**Figure 4.** Probability distributions of additional recruits that would result from hypothetical repeated experiments summed over the entire 5 years of the Chilko Lake fertilization project. Models were DI (Density-Independent); DIFI (Density-Independent + Fraser Index); DD (Density-Dependent); DDFI (Density-Dependent + Fraser Index). Solid lines indicate calculations where the 1987 brood year was considered fertilized, dotted lines indicate calculations where the 1987 brood year was considered unfertilized.

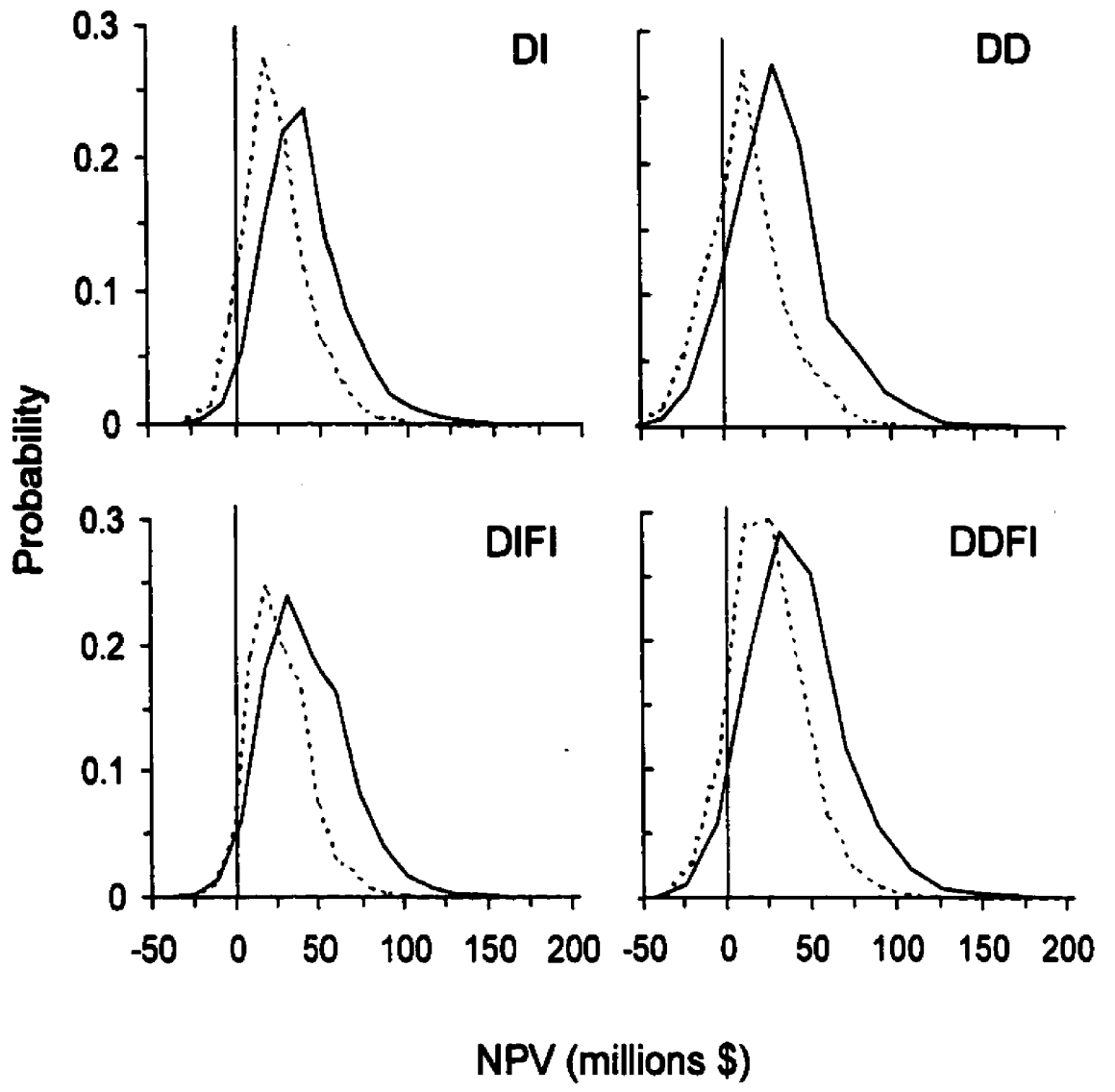


**Figure 5.** Probability distributions of benefit-cost ratio that would result from hypothetical repeated experiments summed over the entire 5 years of the Chilko Lake fertilization project. Models were DI (Density-Independent); DIFI (Density-Independent + Fraser Index); DD (Density-Dependent); DDFI (Density-Dependent + Fraser Index). Solid lines indicate calculations where the 1987 brood year was considered fertilized, dotted lines indicate calculations where the 1987 brood year was considered unfertilized.



**Figure 6.** Probability distributions of net present value (NPV) that would result from hypothetical repeated experiments summed over the entire 5 years of the Chilko Lake fertilization project. Models were DI (Density-Independent); DIFI (Density-Independent + Fraser Index); DD (Density-Dependent); DDFI (Density-Dependent + Fraser Index). Solid lines indicate calculations where the 1987 brood year was considered fertilized, dotted lines indicate calculations where the 1987 brood year was considered unfertilized.





## Appendix A

### SIR Algorithm

The following sequence of steps (from Rubin 1988) was used in the SIR algorithm. (1) I selected an “importance function” to approximate the posterior. For simplicity, I used the joint prior probability distribution of the input parameters to represent this function. Prior probabilities have been used as importance functions in previous analyses (McAllister et al. 1994), and are a reasonable and efficient choice if the likelihood calculation provides reasonable weighting on a large portion of the joint prior distribution (Punt and Hilborn 1997). (2) A parameter set  $\theta_i$  was randomly selected from the joint prior. (3) The model calculated the predicted  $\log_e(R/S)$  using  $\theta_i$  and also  $d_k$ , the difference between the predicted and observed  $\log_e(R/S)$  for data point  $k$ . (4)  $d_k$  was then used to calculate the log-likelihood ( $\log_e L_k$ ) of that data point,  $k$ , given that parameter set,  $\theta_i$ , according to Equation 9. (5) Steps 3 and 4 were repeated for all data points  $k$  in the stock-recruitment data,  $D$ . (6) The joint likelihood of the entire data set ( $L(D|\theta_i)$ ) was calculated according to Equation 10. (7) Steps 2 through 6 were repeated many times (between 60,000 and 400,000 times, depending on the model used). (8) The model calculated the importance ratio (or weight) of each  $\theta_i$  by dividing the likelihood of the stock-recruitment data given that parameter set ( $L(D|\theta_i)$ ) by the sum of all likelihoods across all parameter sets ( $\Sigma L(D|\theta_i)$ ). (9) The parameter set with the greatest weight was then identified. If its weight was greater than 1%, I increased the number of samples in step 7 (Punt and Hilborn 1997) to ensure that the parameter space was sampled sufficiently to yield a reasonably smooth approximation of the posterior. (10) Then, using a binomial sampling algorithm, the model resampled randomly (with replacement) one  $\theta_i$  from the set of previously sampled parameter sets ( $\theta_1, \theta_2, \dots, \theta_m$ ). The probability of

resampling a particular  $\theta_i$  was proportional to its weight, calculated in step 8, and the total number of resamples taken in this step was approximately  $\frac{1}{4}$  of the samples taken in step 7. (11) The posterior probability for this parameter set given the data,  $P(\theta_i|D)$ , was then estimated by taking the ratio of the number of resamples drawn for that parameter set to the total number of resamples taken. (12) After calculating the posterior probability, the model calculated all performance measures (number of additional recruits, net present value, benefit-cost ratio) for  $\theta_i$ . (13) Steps 10 to 12 were repeated until all resamples were taken.

## Appendix B

### Costs and benefits

Table 7. Direct costs of the Chilko Lake fertilization project (thousands of 1997 \$).

	Fertilizer costs	Base costs	Flying costs	Supply and services Canada
1988	45.59	109.14	31.14	0
1989	0	0	0	0
1990	138.16	76.12	168.38	15.11
1991	122.24	72.10	184.76	12.67
1992	112.59	92.98	152.76	0
1993	98.68	69.76	149.02	0

Table 8. Assumed net commercial benefits from the Chilko Lake fertilization project (1997 \$).

	Price per kg for sockeye
Net fishery	5.66
Troll fishery	5.13
First Nations fishery	4.54

Table 9. Components of net commercial benefits for net and troll fisheries (DFO 1996).

Harvesting net benefits	Processing net benefits
= <i>Vessel benefits</i>	= Wholesale value
= Vessel income	- Processing costs
= Landed value	- Processing wages
- Harvesting costs	- Landed value
- Crew share	
- Vessel capitalization	
+ <i>Crew benefits</i>	
= Crew share	
- Crew wages	

## Appendix C

### Canadian Consumer Price Index

Table 10. Canadian Consumer Price Index (CPI) for all economic sectors.

	CPI
1988	84.8
1989	89
1990	93.3
1991	98.5
1992	100
1993	101.8
1994	102
1995	104.2
1996	105.9
1997	107.6