Habitat Manipulations Confound the Interpretation of Sockeye Salmon Recruitment Patterns at Chilko Lake, British Columbia

Scott A. Akenhead[1], James R. Irvine[2], Kim D. Hyatt[2], Stewart C. Johnson[2],
Catherine G.J. Michielsens[3], and Sue C.H. Grant[4]

[1]The Ladysmith Institute, 11810 Fairtide Road, Ladysmith, BC V9G 1K9, Canada
[2]Fisheries and Oceans Canada, Pacific Biological Station,
3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada
[3]Pacific Salmon Commission, 600-1155 Robson Street, Vancouver, BC V6E 1B5, Canada
[4]Fisheries and Oceans Canada, 3-100 Annacis Parkway, Delta, BC V3M 6A2, Canada

Abstract: An examination of metadata associated with a population of sockeye salmon (*Oncorhynchus nerka*) changed our interpretation of the purported benefits of salmon enhancement projects and improved our understanding of the stock-recruitment relationship. Efforts to increase the production of sockeye salmon from Chilko Lake (Fraser River watershed in British Columbia, Canada) included simultaneously fertilizing the lake and operating a spawning channel. To investigate the effects of these manipulations, we analyzed data for spawners, smolts, and returns including metadata associated with these fish and their watershed. Incorporating factors derived from metadata in stock-recruit analyses reduced the total variance to be explained before considering stock density effects, and allowed us to explore the effect of imprecise data. When Beverton and Holt models were applied to data for smolts from spawners and returns from spawners, estimates of productivity and capacity for broods affected by the spawning channel (1988–2003) were lower than for broods before and after its operation. Observations during this period suggested that many salmon fry, emerging from natural spawning areas downstream of the channel and destined for Chilko Lake, entered the channel or could not pass it, and perished. Applying metadata related to the precision of annual return estimates reduced our confidence in published conclusions about a positive effect on egg-to-smolt survival from adding fertilizer to Chilko Lake. We further investigated a factor for smolt-to-adult survival based on the survival of other populations of Fraser River sockeye, noting that this factor, and others, affect estimates for both capacity and productivity. Lastly we investigated changes in the fecundity of spawners and in the primary productivity of Chilko Lake, establishing that both have changed on a decadal scale. In summary, adding categorical and ordinal variables (factors) to account for natural and man-made habitat manipulations reduced the variance to be explained by stock-recruit models, thereby enabling more effective analyses of habitat capacity and density-dependent survival, which should lead to improved fisheries management decisions. The importance of analysts becoming familiar with metadata cannot be overstated.

Keywords: Fraser River, sockeye salmon, stock-recruit, variance factor, Chilko Lake, spawning channel

INTRODUCTION

When investigating time series of adult returns per spawner for Pacific salmon, without information on the relative importance of factors at different stages of the life cycle, there is a tendency to attribute changes to events occurring in the ocean (Beamish et al. 1997, 2012; Mantua et al. 1997; Mueter et al. 2005). It is therefore important to closely examine those few time series for which it is possible to partition mortality into freshwater and marine stages, along with associated metadata (historical information relevant to interpreting data, not necessarily quantitative), in order to improve understanding of the relative importance of these life-history stages. For example, egg-to-smolt survival for sockeye salmon (*Oncorhynchus nerka*) from Chilko Lake (Fig. 1) is marked by a large increase starting with brood year 2004 (Irvine and Akenhead 2013) and brood years 2005 and 2006 produced record numbers
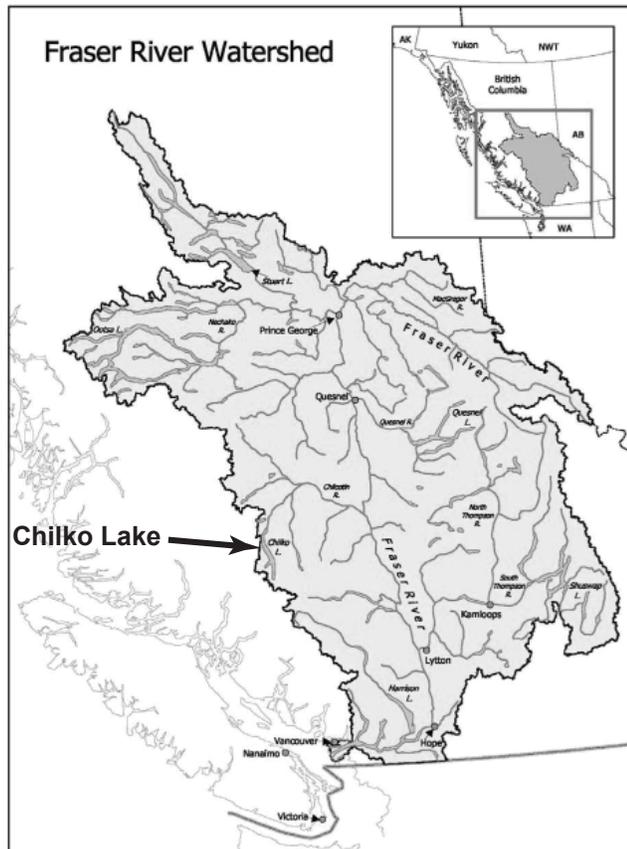
Fig. 1. A map locating Chilko Lake (185 km²; see arrow) in the context of the Fraser River watershed (220,000 km²).

of smolts despite average spawner abundance (Table 1). McKinnell et al. (2012) remarked on "recent, unexplained high freshwater survival of the 2005 and 2006 brood years in Chilko Lake" as did Grant et al. (2011) who noted "freshwater production has been exceptional in recent years; numbers of outmigrating smolts in the 2005 (77 million age-1 smolts) and 2006 (71 million age-1 smolts) brood years were well above average (1954–2009 brood years: 20 million age-1 smolts)." What happened to cause this freshwater-determined increase in smolt numbers, and how important is that to returns of adult salmon? We looked for answers in the associated metadata.

Our metadata for Chilko Lake sockeye salmon ("Chilko sockeye") included information on a spawning channel ~2 km below the outlet of Chilko Lake that operated from 1988 to 2004. The spawning channel was apparently not well used by spawners and, at least in some years, spawning success was also low. Schubert and Fanos (1997) reported that the proportion of total spawners that used the channel for the seven years 1988–1994 was: 1.5%, 2.3%, 1.2%, 1.7%, 1.4%, 1.0%, 0.2%, with a mean of 1.3% (SD = 0.6). They speculated "Because the channel operated from the start of the run and did not provide a means for fish to return to the river, and because actively migrating, shore-oriented lake spawners were more likely to en-

ter the channel, the channel population may have included a substantial number of lake fish which were unsuited to spawning in a riverine environment." The spawning channel was closed in October 2004 after reports that naturally-produced fry migrating upstream in the shallows on the east side of the Chilko River could not navigate past the spawning channel and presumably suffered high mortalities (T. Whitehouse, Timber.Whitehouse@dfo-mpo.gc.ca, pers. comm.) on the way to Chilko Lake. Brood 2004, the first in a series of high egg-to-smolt survivals, did not encounter the spawning channel (in the spring of 2005). To what extent did the spawning channel depress egg-to-smolt survival during the 17 years that it was open?

Following the recommendations of Shortreed and Stockner (1983, also see Shortreed et al. 2001), Chilko Lake was fertilized in 1988, the same year the spawning channel was opened, and again in 1990–1993. About 100 tonnes of inorganic fertilizer (48 mg $P \cdot m^{-2} \cdot year^{-1}$) were applied throughout spring and summer to the central third of Chilko Lake during 1990–1993. The application in 1988 did not extend past spring and only about half the fertilizer of other years was added (Bradford et al. 2000). Primary and secondary production increased greatly each year that fertilizer was applied, but the effect on survival of smolts from eggs was less pronounced and was difficult to determine, in part because smolts were not counted in 1991 when a flood destroyed the smolt counting fence (Bradford et al. 2000). Negative impacts of the spawning channel on smolt production may also have confounded the potential to detect lake fertilization outcomes.

To examine how the analysis of metadata can improve our understanding of time series models of returns per spawner, we examined the influence of freshwater events on recruitment variability for Chilko sockeye. Our primary objective was to evaluate the effects on survival from two factors: fertilizer additions and the operation of a spawning channel. We examined these effects within three life-history intervals: smolts from EFS (pre-smolt survival, entirely in fresh water; EFS is effective female spawners), returns from smolts, (smolt survival, largely marine but includes freshwater periods when smolts are migrating downstream and adults are migrating upstream), and returns from EFS (adult returns per spawner, total survival).

Other factors may contribute to the scatter around stock-recruit curves for these three life-history intervals and potentially confound the interpretation of the fertilizer and spawning channel effects. As examples of those other factors, we investigated:

- natural changes in primary productivity of Chilko Lake,
- the survival of the other conservation units (CU) of Fraser River sockeye salmon, and
- changes in the fecundity of Chilko spawners.

We also evaluated the role of measurement error in the spawner and adult return data by examining a factor related to the relative precision of estimates of adult returns (the proportion of Chilko CU in co-migrating CUs).

Table 1. Chilko sockeye data, broods 1948–2012. E is egg abundance estimated as effective female spawners, EFS $\times 10^{-6}$, S is estimated smolt abundance $\times 10^{-6}$, and R is estimated adult returns $\times 10^{-6}$. Preliminary estimates for R have an asterisk and were not used. Smolts were not counted for brood year 1989.

Brood	E	S	R	Brood	E	S	R
1948	0.365		1.95	1980	0.293	35.0	4.44
1949	0.033		0.62	1981	0.020	1.7	0.21
1950	0.007		0.21	1982	0.143	14.0	1.60
1951	0.058		0.75	1983	0.214	19.7	2.12
1952	0.234	23.0	1.86	1984	0.283	9.8	0.68
1953	0.095		0.62	1985	0.035	5.6	0.57
1954	0.021	3.0	0.71	1986	0.166	18.9	4.80
1955	0.076		1.51	1987	0.268	21.7	4.42
1956	0.369		2.44	1988	0.206	20.9	3.30
1957	0.083		0.14	1989	0.043		3.12
1958	0.070	6.9	0.43	1990	0.498	34.2	2.63
1959	0.273	32.6	2.21	1991	0.598	39.7	1.38
1960	0.245	33.8	1.05	1992	0.320	12.9	1.87
1961	0.015	1.6	0.07	1993	0.322	27.3	3.96
1962	0.042	8.8	0.99	1994	0.254	17.0	1.42
1963	0.057	9.3	1.21	1995	0.298	39.8	1.27
1964	0.132	23.6	2.04	1996	0.505	18.7	1.36
1965	0.021	2.3	0.16	1997	0.509	21.8	0.89
1966	0.108	16.8	0.80	1998	0.468	11.1	0.54
1967	0.090	8.8	2.00	1999	0.433	20.0	1.57
1968	0.182	31.8	2.48	2000	0.396	19.5	0.50
1969	0.026	3.6	0.40	2001	0.331	35.7	1.16
1970	0.051	3.8	0.70	2002	0.215	19.6	1.24
1971	0.091	7.6	0.85	2003	0.335	23.3	0.38
1972	0.332	20.3	2.11	2004	0.049	10.8	0.42
1973	0.030	4.3	0.25	2005	0.285	77.1	0.35
1974	0.071	7.2	0.71	2006	0.262	71.9	4.80
1975	0.134	14.2	1.51	2007	0.157	25.2	0.96
1976	0.228	26.0	1.70	2008	0.069	11.8	1.16
1977	0.020	2.3	0.20	2009	0.127	34.4	1.80
1978	0.086	16.5	1.27	2010	1.181	55.3	2.70
1979	0.148	21.1	1.72	2011	0.458	44.2	0.77*
				2012	0.091	11.4	

MATERIALS AND METHODS

Background

Chilko sockeye eggs are mainly spawned in coarse gravel in the Chilko River in late September, in the outflow of this large lake (185 km², Shortreed et al. 2001). Chilko Lake rarely freezes (Bradford et al. 2000) and its size buffers fluctuations in Chilko River temperature and flow, thereby protecting salmon eggs from freezing and scouring. The eggs hatch during winter and fry emerge in April and May. These fry swim upstream to Chilko Lake where they live and grow for, typically, one year before migrating to the ocean as smolts during a six-week period in the following April and May. About 4% of the fry stay in Chilko Lake for a second year and migrate as age-2 smolts (Irvine and Akenhead 2013). Age-3 smolts are rare; the first recorded at Chilko Lake was in 2010 (brood 2006) despite many thousands of smolts examined annually since 1948. Marine juveniles (post-smolts) generally migrate north through the Strait of Georgia, Johnstone Strait, and Queen Charlotte Strait to the continental shelf, and have been found from Queen Charlotte Sound to Kodiak Island (central Alaska) by the end of July in their first marine summer (Tucker et al. 2009; Beacham et al.

2014). Their location during their first marine winter is not known. Fraser sockeye typically rear for two winters in the Gulf of Alaska before returning to Chilko Lake four years after their parents did. A small fraction return as *jacks*, precocious males, after one marine winter (Healey et al. 2000). Since 1970, an increasing fraction of adults have returned after three marine winters instead of two (Irvine and Akenhead 2013).

Data Sources

There are 24 sockeye salmon CUs in the Fraser River watershed (and five extirpated) that contribute to mixed-stock fisheries managed by the Pacific Salmon Commission (PSC) and Fisheries and Oceans Canada (DFO). A CU is "a group of wild salmon sufficiently isolated from other groups that, if extirpated, is very unlikely to recolonize naturally within an acceptable timeframe" (DFO 2005). Chilko sockeye comprise two CUs, Chilko-ES and Chilko-S (Holtby and Ciruna 2007), parts of the "early summer-run" and "summer-run" of Fraser River sockeye salmon (Grant et al. 2011) that are assessed as a single unit (DFO 2014). A run is a group of co-migrating CUs. Sampling the abundance of spawners and smolts occurred primarily at or below the outlet of Chilko Lake, with the timing of the two Chilko CUs overlapping. Prior to the introduction of DNA identification, it was necessary to aggregate data for the two CUs. Our primary data (Table 1) were the most recent estimates of EFS by brood year, the smolts surviving from those eggs after typically one winter in fresh water and the adult returns surviving from those smolts after, typically, two winters in the NE Pacific Ocean. These data are maintained by DFO Fraser Stock Assessment (www.pac.dfo-mpo.gc.ca/fm-gp/fraser/docs/Escapement/sockeye-rouge-eng.html). Salmon ages are presented as, for example, 1.2, the dominant age class, where the number preceding the dot is the number of winters spent in a rearing lake and the number after the dot is the number of winters in the ocean. For descriptions of how data quality and consistency have been maintained for over 60 years, see Gable and Cox-Rogers (1993), Schubert and Fanos (1997), Grant et al. (2011), and references therein.

Smolt and spawner sampling methodologies were reviewed by Henderson and Cass (1991), Roos (1991), Grant et al. (2011), and Irvine and Akenhead (2013). A counting fence for enumerating smolts from Chilko Lake has been operated with relatively consistent protocols every spring since 1960 with the exception of 1991. The outflow from Chilko Lake in 1991 was the highest recorded before or since, and included mats of filamentous algae that are uncharacteristic of an oligotrophic lake. High flows, plus clogging due to algae, washed out the smolt counting fence in 1991 (brood 1989). The number of Chilko sockeye escaping fisheries and returning to Chilko Lake to spawn were estimated prior to 2009 by mark recapture (e.g., Schubert and Fanos 1997), except for 1967, when they were estimated by expanding visual counts at Henry's Bridge, 12 km below the lake (Grant

et al. 2011). Since 2006, imaging sonar (DIDSON) has been used to estimate spawner abundance (Cronkite et al. 2006; Holmes et al. 2006). DIDSON and mark recapture estimates have been similar enough to rely on DIDSON estimates alone beginning in 2009 (K. Benner, Keri.Benner@dfo-mpo.gc.ca, and T. Cone, Tracy.Cone@dfo-mpo.gc.ca, pers. comm.). Carcasses were sampled to estimate the proportion of eggs successfully spawned, and female escapement estimates were converted to EFS by multiplying by these proportions (Grant et al. 2011). Mixed-stock fisheries for salmon were sampled for stock composition to estimate the numbers of Chilko sockeye caught on their return migration. Allocation of sockeye salmon to discrete CUs was based on distinctive freshwater growth patterns seen on the scales (Gable and Cox-Rogers 1993), supplemented by DNA markers beginning in 2000 (Grant et al. 2011). Annual run size adjustments have also been added to return abundances, to account for en-route loss of adults during their upstream migration, and for error in escapement or catch estimates (Grant et al. 2011). Annual fecundity estimates (1946–2011) were based on random samples of 50 females obtained near the peak of the run, with the exception of two years: five females in 2004, and four females in 2009.

We wanted to clarify stock and environmental effects by applying ordinal (ordered but not quantified) and categorical (unordered) metadata to stock-recruit models for Chilko sockeye. There are many and diverse forms of metadata for Chilko sockeye, including indicators for habitat quantity (e.g., lake area) and habitat quality (e.g., net primary production), indicators for terrestrial and oceanic climate (which are proxy data for changes in salmon habitat), man-made changes to freshwater habitats (e.g., lake fertilization), and changes in sampling methods (e.g., hydroacoustics replacing mark-recapture to estimate spawner numbers).

Metadata for Chilko Lake (Table 2) continue to be assembled (Grant et al. 2011; Grant and Pestal 2012; DFO 2014) and were used to identify potentially influential biological or methodological factors contributing to observed variations in returns of adult Chilko sockeye. These included lake fertilization, spawning channel operation, and a variance factor related to the precision of estimates of Chilko sockeye returns.

Proportion of Run

The variance factor that we explored was the proportion of Chilko sockeye in the summer run each year. For each year, this proportion was estimated from Chilko sockeye EFS divided by EFS summed over all CUs in the summer run (data from Ogden et al. 2015). Two assumptions were made: (1) the early summer run was a negligible component of the amalgamated estimate of EFS for Chilko sockeye, and (2) the fishing mortality within years was similar among CUs so that EFS is representative of adult returns. Further work to improve this factor (using returns by age, year, brood, CU, and run) is indicated. We assumed that Chilko return estimates would be less precise when Chilko

Table 2. Metadata for Chilko Lake sockeye salmon as examples of ordinal and nominal (unordered) data that can be treated as weights (variance factors) or as covariates (productivity and capacity factors) when fitting a stock-recruit curve.

Event or change	Years	Reference	Type of metadata	Type of factor	Used in paper
Mark-recapture estimates for spawners (versus acoustic)	1948–2008	Grant et al. (2011)	ordinal	variance	no
Univariate scale analysis for catch composition (versus multivariate or DNA)	1948–1986	Gable and Cox-Rogers (1993)	nominal	variance	no
Visual count for spawners	1967	Grant et al. (2011)	ordinal	variance	no
Lake fertilization	1988, 1990–1993	Bradford et al. (2000)	nominal	productivity?	yes
Spawning channel open	1988–2004	Grant et al. (2011)	nominal	capacity?	yes
Disease or parasites	1963 spawners 1971 spawners 1973 fry 2007 smolts 2010 spawners	Gilhousen (1990) Williams (1977) Williams and Amend (1976) Miller et al. (2013) Miller et al. (2014)	nominal	productivity	no
Returns for one CU as proportion of returns for all CUs in a run	all years	Run composition from Grant et al. (2011)	rational	variance	yes
Fecundity samples	1945, 1946, 1948, 1956–1976, 1986–present	DFO, unpublished data.	rational	productivity	yes (not as a factor)

sockeye were a small proportion of the summer run timing group than when they were a large proportion, as documented by Gable and Cox-Rogers (1993), Cass and Wood (1994), and Ricker (1997). We explored the impact of this assumption on model results (below) by fitting a parameter that controlled the effect of this variance factor.

Fecundity Data

Changes in fecundity are a possible confounding factor for stock-recruit analysis. Because the mean length of Fraser River sockeye females varies among years and because fecundity increases with length, the number of effective female spawners may not be an accurate indicator of eggs spawned. Fecundity data for Chilko sockeye have been collected since the 1940s, following methods described by Schubert and Fanos (1997) but there were periods when these data were not collected: 1949–1955 and 1977–1985. We did not have access to a separate dataset of annual length distributions, typically 300 observations from multiple samples per year, that could be used to improve the fecundity estimate for each year from a more accurate description of female lengths.

Shared Survival

An accompanying paper (Akenhead et al. 2016) determined that the first principle component of log (Returns / EFS) by year by CU for 11 Fraser sockeye CUs explained 46% of the variance of that variable. The resulting time series identifies the extent to which fluctuations in total survival fluctuations are parallel among CUs, as opposed to idiosyncratic, and was termed "shared survival." About half of the variance in shared survival is due to a trend toward de-

creasing total survival that started about 1990. As a habitat indicator, shared survival has the advantage of being measured by salmon (via their survival), as opposed to human measurements of the environment, but has the disadvantage of not being useful to predict the survival of smolts before they return as adults. We used shared survival after it was scaled to range between 0 and 1, such that "poor" years (as experienced by broods 2003 and 2005) were zero or near-zero, and "good" years (as experienced by many broods prior to 1990) were close to 1; median shared survival = 0.74.

Analysis

Stock-recruit Model

We chose the Beverton and Holt (B&H) stock-recruit model (Beverton and Holt 1957; Walters and Korman 1999) because we wanted to include habitat quality factors to modify productivity (P, the slope at the origin) and capacity (C, the asymptote) following Moussalli and Hilborn (1986), Scheuerell et al. (2006), and Mantua et al. (2009). The B&H model differs from the similar Ricker (1954) model mainly in the response of R (adult returns of all ages, pre-fishery) at levels of E (EFS) above E_{MSY} (EFS required for a theoretical maximum sustainable yield). However, because variance in R is proportional to E, i.e., scatter is homogenous on $\log(R)$ versus $\log(E)$ plots (McKinnell 2008; Akenhead et al. 2016), neither model fits well at high E. Proportional variance was documented for returns from smolts of Fraser sockeye salmon and explained theoretically by Peterman (1981). Furthermore, because salmon fisheries management is designed to prevent an overabundance of E in comparison to E_{MSY}, cases with high E are rare. With few and variable cases to discern

the effects of density-dependent survival, estimates of C will be imprecise.

Capacity was viewed as a measure of the area of limiting habitat, ideally modified by measures of the quality of that habitat. Examples are the area of useful spawning gravel and the area of a rearing lake, the latter potentially improved by considering primary and secondary productivity (e.g., Hume et al. 1996; Hyatt et al. 2004). Spawning channels are an attempt to increase capacity by increasing spawning habitat, with the explicit assumption that spawning habitat limits overall capacity. We expected capacity to be related to area of freshwater habitats for spawning and rearing (i.e., competition for area) and for the area and quality of these habitats to differ among CUs of Fraser River sockeye salmon, but to be constant over time unless there were alterations to the area of habitat such as opening a spawning channel. Productivity was viewed as the quality of habitat, independent of competition effects, and changing from year to year due to weather, predators, or, in this case, lake fertilization. For instance, Peterman et al. (2003) used a Kalman filter to track decadal changes in salmon productivity based on the determination by Adkison et al. (1996) that density effects (i.e., capacity) were small and inconsistent across multiple sockeye stocks.

Parameter Estimation

We took a Bayes/Laplace approach for fitting models to data (Gelman et al. 2013) and used a specialized computer language Stan (Stan Development Team 2014) to generate samples from the joint distribution of parameter estimates for the B&H models we explored. Features of Stan included ease of use, automatic differentiation (similar to ADMB, Fournier et al. 2011), and algorithms that efficiently sample highly dimensional models. For all models, four sets of Monte Carlo sampling chains were run ("MC samples"). Each sampling chain ran for 2,000 samples, the first 1,000 samples were discarded, and the chains were compared to determine convergence to a stationary distribution for the joint posterior distribution of parameter estimates. Convergence was determined with the potential scale reduction statistic of Gelman and Rubin (1992) and all of these relatively simple models converged.

We provided positive non-zero prior distributions for C, P, and σ as gamma $(2, 1/\mu)$ with values for the mode, μ, that were based on fits from trial runs. These are mildly informative priors as recommended by McElreath (2016). The main effect from these priors was avoidance of extremely high estimates of C, precluding a straight line as a stock-recruit curve (infinite capacity). Factors for which near-zero estimates of effect were a possibility had priors that were a normal distribution with mean zero but with negative values rejected for MC samples (i.e., half-normal) and with standard deviations large enough to encompass but not constrain the estimates observed in trial runs.

For all models, the probability distribution of residuals was assumed to be log-normal,

$$\Pr\left(R - \hat{R}\right) = e^{N\left(log\left(\hat{R}\right), \sigma\right)}, \qquad (1)$$

where N refers to the normal distribution, σ is the estimated standard deviation, and $\hat{R}$ is the predicted value for returns:

$$\hat{R}_t = \frac{E_t}{\frac{1}{P} + \frac{E_t}{C}}. \qquad (2)$$

Habitat factors modified values for P and C each year. Our models assumed linear effects proportional to the levels of factors affecting P and C. For a habitat factor G_t that affects capacity C,

$$C_t = C_0 + \gamma_c G_t, \qquad (3)$$

where C_0 is the capacity without G, and γ_C is the estimated effect of G. Similarly, a factor F will have a linear additive effect on base productivity P_0,

$$P_t = P_0 + \gamma_P F_t. \qquad (4)$$

Scheuerell et al. (2006) applied factors as linear and non-linear modifiers to the capacity and productivity terms of the B&H model on the basis of experts' judgment. We estimated γ_P and γ_C as additional parameters for B&H curves in order to calibrate categorical and ordinal factors.

Maximum Sustained Yield

Changes to the uncertainty in a benchmark for fisheries management will demonstrate how additional factors can improve fisheries management decisions by increasing the precision of predictions, or, from adding noisy data and/or imprecise estimates of additional parameters, decrease the precision of predictions. We chose maximum sustainable yield (MSY) as a simplistic but widely recognized benchmark: the number of spawners that maximizes returns after subtracting the number of spawners required to replace themselves. This was calculated as

$$E_{MSY} = \frac{C}{P}\left(\sqrt{rP} - 1\right), \qquad (5)$$

(adapted from Johnston et al. 2002) where C/P is the half-saturation value for the B&H model, and r is the ratio of EFS to returns (the gender ratio of spawners). We assumed 0.5 for r but recognize that a better estimate can be determined by considering (a) annual observations of the gender ratio of returns, (b) fecundity, and (c) pre-spawning mortality of female spawners. R_{MSY} was calculated from E_{MSY} using Equation 2 and both were calculated for 4,000 Monte Carlo (MC) samples of the joint distribution of P and C.

Application of Metadata: Enhancement of Smolt Production at Chilko Lake

Fertilization of Chilko Lake had the potential to affect broods 1987–1992 as parr growing in the lake during the summers of 1988–1993. This period overlapped the period of operation of the spawning channel, which had the potential to affect broods 1988–2003 as fry migrating upstream to Chilko Lake. We examined the effects of lake fertilization and spawning channel operation (as productivity and capacity factors, respectively) for egg-to-smolt survival for Chilko sockeye.

Fertilization was represented as a factor with levels 1 for 1987 and 1989–1992 and 0 for other years. Although the fertilizer added in 1988 was one half that of 1990–1993, the effect on egg-to-smolt survival was not expected to be one half that of years 1990–1993. Despite quantitative information on fertilizer added, this was an ordinal factor: the expected effect from fertilizer in 1988 was merely less than the effect from 1990–1993. There were insufficient data to fit multiple levels for this factor, given that (a) smolts were not counted in spring 1991 after experiencing fertilizer in summer 1990 (leaving four cases), and (b) a modification in only one year of those four. The effect of this factor was quantified by fitting a single additive parameter, γ_{fert}.

The spawning channel was represented as a nominal factor with three levels: before operations (1948–1987), during (1988–2003), and after (2004–present). The possibility of undocumented changes to channel operations during 1988–2003 is recognized (e.g., Shubert 1998). Two estimated parameters quantified the effect of the channel on capacity: γ_{open} for broods affected by the spawning channel, and γ_{shut} for those subsequent to channel effects. Those parameters described a change in B&H capacity relative to the broods before 1988 (before the channel effect). One of the questions examined was whether these channel factors should be used to modify productivity or capacity or both.

Twelve separate B&H models (Equation 2 with residuals as in Equation 1) examined (a) how a change in freshwater habitat (opening spawning channel) would be interpreted when changes in marine habitats were included, and (b) the independence of capacity and productivity parameters. Three life-history intervals were assessed: smolts from EFS, returns from smolts, and returns from EFS. Data from each life-history interval were examined in four periods: before, during, and after the spawning channel, and all years. The same Bayesian priors were used for all four periods.

Effect on Productivity and Capacity of a Marine Habitat Indicator, "Shared Survival"

A factor representing marine habitat quality was available as a time series derived as the first principle component of log(R/E) for 11 CUs of Fraser sockeye salmon (Akenhead et al. 2016). This "shared survival" is an indicator of changes to marine habitats for Fraser sockeye measured as total survival across multiple CUs of sockeye salmon, thus avoiding events and patterns unique to individual CUs. We treated shared survival as a factor H_t, scaled to range from 0 to 1, that affected estimates for both capacity and productivity (having concluded that these are not independent) for returns from EFS for Chilko sockeye. This model also included factors to represent the spawning channel, G_0 before it opened, G_1 during operations, and G_2 after it closed. Because G_0 and G_2 were expected to have a positive effect, and G_1 a negative effect, we fit the capacity (and productivity) with reference to the period when the spawning channel was operating, and then estimated just the effect of G_0 and G_2. Two factors were necessary because egg-to-smolt survival was noticeably higher after the spawning channel was closed compared to before it opened (Fig. 2). These three factors, G_0, G_2, and H, were estimated as additive effects through six linear parameters:

$$P_t = P_0 + \gamma_{PG0}G_{0,t} + \gamma_{PG2}G_{2,t} + \gamma_{PH}H_t$$

$$C_t = C_0 + \gamma_{CG0}G_{0,t} + \gamma_{CG2}G_{2,t} + \gamma_{CH}H_t \qquad (6)$$
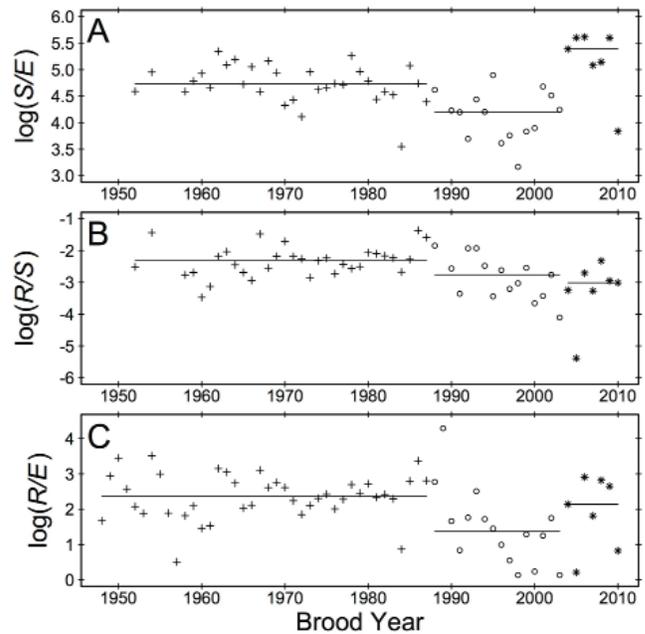
Fig. 2. Temporal patterns of survival for Chilko Lake sockeye salmon. A spawning channel affected survival of fry from brood years 1988 to 2003. Data before, during, and after the spawning channel have different symbols. Horizontal lines indicate the median log survival for each interval. A. Pre-smolt "survival," smolts/EFS, on a log scale. Smolts from brood 1989 were not counted. B. Smolt survival, returns/smolt, on a log scale. Survival of smolts after brood year 1989 has typically been far below the previous mean, with dramatic failures for broods 2003 and 2005. C. Total survival, returns/EFS, on a log scale. Brood 1989 is an outlier.

and the resulting time series, P_t and C_t, were used in Equation 2. Thus, productivity after the channel closed ($G_{0,t} = 0$, $G_{2,t} = 1$) and for the highest shared survival ($H_t = 1$) would be $P_0 + \gamma_{PG2} + \gamma_{PH}$ and similarly for capacity. The distributions of E_{MSY} and R_{MSY} were calculated from MC samples from the joint distribution of P_0, γ_{PG2}, γ_{PH}, C_0, γ_{CG2}, and γ_{CH}.

Variance Factor

The variance factor described how the residuals in a returns-from-EFS regression will be more scattered in those years when observations of returns are relatively imprecise. Variance factors are uncalibrated regression weights, but can be calibrated as part of fitting a regression. Gelman et al. (2013) suggest

$$R_t - \hat{R}_t = N\left(0, \sigma W_t^{-\gamma_W}\right), \qquad (7)$$

where R_t-$\hat{R}_t$ is a residual with a normal distribution about $\hat{R}$, the predicted value for that return (note that we used log-normal residuals), and W_t is a variance factor that expands σ, the standard deviation. The estimated parameter γ_W controls the effect of W. When $\gamma_W = 0$, the variance factor has no effect. When $\gamma_W = 1$, σ is proportional to W (conventional weighted regression). The parameter γ_W acts exponentially on the standard deviation that in turn acts exponentially when applied as a log-normal distribution.

Fecundity

We examined Chilko sockeye salmon fecundity data in relation to the spawning channel via analyses of variance (ANOVA), and as a function of length, year, and age using ordinary linear regression. We calculated the mean of annual mean lengths as a reference length for the predominant age-1.2 females. Because fecundity-at-length can change with time, we calculated the annual fecundity for age-1.2 and -1.3 females at that reference length using regressions of fecundity on length

by year. Only seven years in the time series had more than three fecundity observations for age-1.3 females. We did not use fecundity as a covariate in stock-recruit models.

RESULTS

Stock-recruit Curves for Three Life-history Intervals

To characterize the uncertainty in stock-recruit models for Chilko sockeye salmon, before considering metadata from the salmon escapement and habitat manipulations, three stock-recruit curves were fitted: smolts from EFS (pre-smolt survival), returns from smolts (smolt survival), and returns from EFS (total survival) (Table 3, Fig. 3). Capacity estimates from the three models had CVs (coefficient of variation, standard deviation of samples / mean of samples) that ranged from 22% to 37%, but the distributions for capacity estimates were skewed toward high values, with values for skew measured as (97.5 percentile–50 percentile) / (50 percentile–2.5 percentile) that ranged from 2.1 to 3.1. In contrast, productivity estimates were more constrained, with CVs of 13 to 24% (Table 3). Like capacity estimates, the distribution of productivity estimates also had asymmetrically high values for the 97.5 percentile.

Factors for EFS-to-Smolts Productivity and Capacity

To observe the effects of freshwater factors on the productivity and capacity parameters of a B&H model, we created a baseline model (Table 4A) that was similar to the preceding model for smolts from EFS (Table 3A) with no factors related to lake fertilization or the spawning channel. Small differences between this baseline model and its equivalent in Table 3 are due to the stochastic process of MC sampling.

Table 3. Results from applying the B&H model for three life stages of Chilko Lake sockeye, without factors. The fitted standard deviation of log-normal residuals is σ. Columns marked 2.5%, 25%, etc. are percentiles from 4,000 Monte Carlo samples (after convergence) of the joint posterior distribution of parameter estimates; a subset of those samples was used for the curves in Fig. 3. N means the number of cases (years) used in the regression. SD means "standard deviation" and CV means "coefficient of variation" estimated as SD/mean. NLL means "negative log likelihood" and is a measure of fit expressed as the probability of the data given the model (including priors and constraints). See Appendix 1 for computer code.

Parameter	Mean	SD	CV (%)	2.5%	25%	50%	75%	97.5%
(A) Smolts from EFS N = 54, σ = 0.46, NLL = 30.6								
Productivity	159	20	13	125	145	158	171	205
Capacity	61	19	31	39	49	57	67	99
(B) Returns from Smolts N = 54, σ = 0.64, NLL = 7.2								
Productivity	0.13	0.03	23	0.09	0.11	0.13	0.14	0.19
Capacity	3.8	1.4	37	2.1	2.8	3.4	4.3	7.4
(C) Returns from EFS N = 63, σ = 0.72, NLL = 5.7								
Productivity	21.0	5.0	24	13.0	17.0	20.0	23.0	33.0
Capacity	2.3	0.5	22	1.6	2.0	2.2	2.6	3.6

Models B through E show the results of fitting factors for the state of the spawning channel (via fitted parameters γ_{open} and γ_{shut}) on the capacity and productivity estimates, as indicated in Table 4. Adding a factor for lake fertilization that affected productivity (model B, Table 4) had little effect. The productivity estimate increased from 165 *S/E* (SD = 17) for the unfertilized years to 165 + 9 = 174 *S/E* (SD = 16) during the fertilized years, roughly a 5% increase. That increase was an imprecise estimate with a 17% chance of being zero or less. This weak response might reflect a confounding effect from the spawning channel. In contrast, the effect of the spawning channel on B&H capacity was larger, a decrease from 62 *S/E* (SD =12) before the channel (broods 1950–1987) to 62 – 23 = 39 *S/E* (SD =15) when the channel was open (model B, Table 4), with a 0.5% chance of that effect being zero or greater. Compared to broods before the channel, capacity was lower by 37% during the channel and higher by 42% after the channel. Capacity increased (62 + 26) / (62 - 23) = 225% after the channel compared to during the channel. The unfertilized productivity estimate and the pre-channel capacity estimate for model B were similar to model A, but more precisely estimated. This finding was re-examined in model C (Table 4), a simpler model in which fertilization was ignored and capacity

was modified with one factor: channel open or not. The effect of the channel in this model, compared to model A, was to halve the capacity (44%).

Model D was like model C, but distinguished three states for the channel: before, during, after. In model D, closing the channel increased capacity by (63 + 25) / (63 - 23) = 220%. Model D differed from model B only by dropping the fertilizer effect, and the estimates are nearly identical. This was further evidence that the effect of fertilization on smolts from EFS was small.

To summarize these four models (Table 4, A–D): (a) the spawning channel halved the asymptotic capacity for smolt production compared to previous years, (b) when the spawning channel was subsequently closed, capacity immediately doubled, and (c) lake fertilization had little effect on productivity. From these results, we hypothesized that the greater effect on capacity of closing the spawning channel, compared to opening it, might be due to a coincidental increase in the net primary productivity of Chilko Lake. We therefore redirected the factor γ_{shut} to affect the productivity parameter (Table 4E). The result indicated that smolt-from-EFS productivity had increased by 53% from 1950–2003 (144 *S/E*, SD = 14) to 2004–2008 (221, 19). That new description
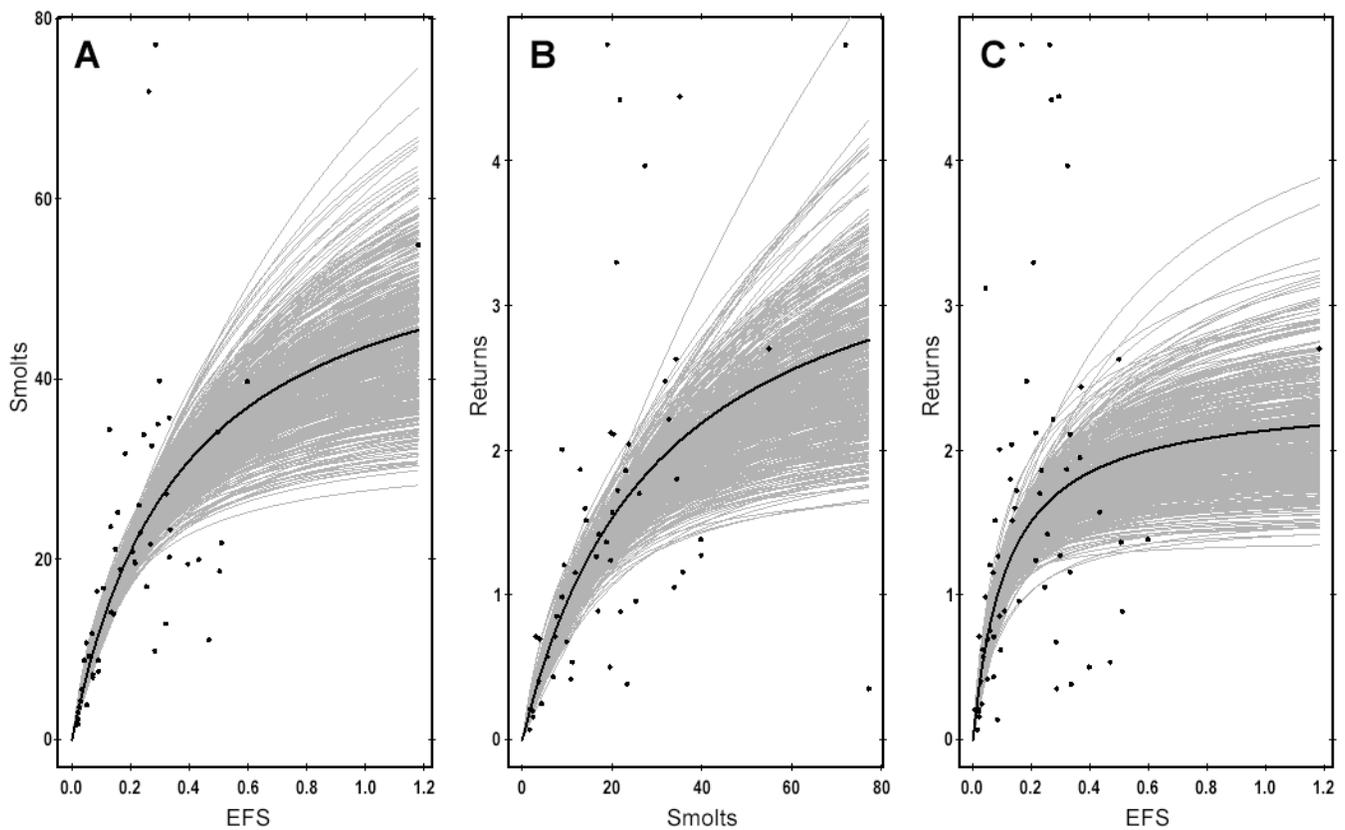
Fig. 3. Bayesian fits for B&H curves that predict Chilko Lake sockeye smolts and adult returns. Points are the observations (in millions) from each brood year, 1948–2010 (Table 1). Statistics for the fitted parameters are in Table 3. The uncertainty of those parameters is demonstrated by 1,000 curves (grey lines) sampled from the joint posterior distribution of estimates for productivity and capacity. The black curve is from the marginal means for productivity and capacity. A. Smolts (S) from EFS (E). B. Returns (R) from smolts. C. Returns from EFS. There are nine more cases for returns from EFS because smolt abundance data were not collected for every brood.

Table 4. Productivity and capacity estimates for B&H curves fitted to Chilko Lake sockeye smolts from EFS. Five models (A to E) with factors affecting productivity and capacity are compared. The factors γ_{open} and γ_{shut} represent a spawning channel which was open to affect fry from broods 1988–2003, and shut for broods 1949–1987 and 2004–2010. The factor γ_{fert} represents lake fertilization that affected parr from broods 1988 and 1990–1993. The factors are linear additive effects. All models had the same mildly informative prior distributions: Productivity was gamma(2,1/150) with mode at 150; Capacity was gamma(2,1/50); and σ was gamma(2,1/2). The prior distribution for γ_{open} was N(10,10), γ_{shut} was N(-20,10), and γ_{fert} was N(20,10). For example, in model E, the fitted mean productivity for broods 2004–2009 is approximately 144 (SD = 14) + 77 (18) = 221 smolts/EFS with SD ≈ $(14^2+18^2)^{1/2}$ = 23, calculated from the marginal distributions. Columns are the same as in Table 3. See Appendix 1 for computer code.

Parameter	Mean	SD	CV (%)	2.5%	25%	50%	75%	97.5%
(A) No factors. σ = 0.45 (SD = 0.05)								
Productivity	160	20	13	125	146	159	174	204
Capacity	60	17	28	39	49	57	68	102
(B) Fertilizer (as productivity), channel (as capacity). σ = 0.41 (0.04)								
Productivity	165	17	10	135	153	164	176	203
γ_{fert}	9.3	10	109	-11	3	9	16	29
Capacity	62	12	19	42	54	62	70	88
γ_{open}	-23	9	39	-41	-28	-22	-17	-6
γ_{shut}	26	9	36	8	19	26	32	44
(C) Channel open (as capacity). σ = 0.43 (0.04)								
Productivity	161	16	10	131	149	160	171	194
Capacity	70	12	17	50	62	69	78	98
γ_{open}	-26	9	33	-43	-31	-26	-20	-9
(D) Channel open and closed (as capacity). σ = 0.42 (0.04)								
Prod	165	17	10	134	153	163	174	202
Cap	63	12	19	42	55	62	70	89
γ_{open}	-23	9	39	-40	-28	-23	-17	-5
γ_{shut}	25	10	38	7	19	25	32	44
(E) Channel open (as capacity) and closed (as productivity). σ = 0.39 (0.04)								
Productivity	144	14	10	118	134	143	153	174
γ_{shut}	77	18	23	42	65	77	89	114
Capacity	77	13	17	55	68	75	84	105
γ_{open}	-27	9	32	-44	-33	-27	-22	-10

of the post-channel years had a similar effect on capacity as opening the channel, (similar γ_{open} among models B–E) but a higher and less precise estimate of capacity from pooling the before-channel and after-channel periods. Whether expressed as productivity or capacity (models D and E), or simply as *S/E* (Fig. 3A), pre-smolt survival improved after the channel was closed (broods 2004–2010) compared to before it was opened (broods 1949–1987).

Three Life-history Intervals and Spawning Channel Operation

The preceding results (Table 4) suggested that a single habitat change (in this case, one that resulted in a brief interval of high mortality events) could affect estimates for both productivity and capacity in the B&H model. We investigated further, considering how productivity and capacity in three life-history intervals (smolts from EFS, returns from smolts, returns from EFS) were affected by the spawning channel (before, during, after, and all years), a total of 12 regressions (Table 5, Fig. 4). For smolts from EFS (Fig. 4A), capacity was halved (-56%) when the channel opened compared to the years before the channel, as per results above, and after the channel was closed, capacity increased by 300% and was 1/3 higher than before the channel. Productivity increased across all three periods, with productivity after the channel twice as high as before the channel.

For adult returns from smolts (Fig. 4B), it is evident that the effect of the spawning channel on smolt survival was small compared to the residual variability, presumably due to freshwater migration mortality and/or marine rearing effects. Productivity estimates were similar for the three periods, whereas capacity estimates were lower by 2/3 for the period during and after the spawning channel, i.e., poor smolt survival 1988–2010. Estimates for both productivity and capacity were imprecise during and after the channel, reflecting highly variable smolt survival.

Table 5. A summary of parameters of B&H models fitted to (A) sockeye smolts from EFS, (B) returns from smolts, and (C) returns from EFS (see Fig. 4). Depending on the life-history interval (A, B, or C) used in the B&H models, parameter values affected by spawning channel operation ("all year" and "during" categories) exhibit variable levels of contrast (A > B > C) relative to "before" and "after" years of no channel effect. Values in brackets are the CV (SD/mean) where SD was estimated from the curvature at the best fit. See Appendix 1 for computer code.

Spawning Channel	Productivity	Capacity	σ
(A) Smolts from EFS			
All Years	161 (12%)	54 (20%)	0.44 (9%)
Before	139 (9%)	76 (37%)	0.33 (12%)
During	207 (61%)	33 (30%)	0.38 (18%)
After	290 (23%)	99 (33%)	0.37 (27%)
(B) Returns from Smolts			
All Years	0.13 (15%)	3.3 (27%)	0.60 (10%)
Before	0.12 (17%)	7.9 (48%)	0.47 (13%)
During	0.13 (85%)	2.5 (72%)	0.61 (18%)
After	0.11 (91%)	2.3 (70%)	0.77 (25%)
(C) Returns from EFS			
All Years	19 (21%)	2.3 (17%)	0.69 (9%)
Before	15 (13%)	4.7 (43%)	0.59 (12%)
During	43 (58%)	1.5 (20%)	0.70 (17%)
After	16 (62%)	2.9 (66%)	0.75 (25%)

For returns from EFS (total survival, Fig. 4C and Table 5C), when the spawning channel was opened the capacity estimate dropped by 2/3 compared to the preceding years (68%), a combination of reduced survival in both freshwater and marine habitats. Reflecting the pattern of smolts from EFS, capacity doubled after closing the spawning channel, but the trend of decreasing returns from smolts resulted in capacity for returns from EFS after the channel being 1/3 less than before the channel (38%). It is evident from Fig. 4C that the capacity estimate for the period after the channel is strongly influenced by the data for brood 2010 ($E = 1.2$, Table 1). Productivity estimates (for returns from EFS) before and after the spawning channel operation were similar, but much higher during channel operation largely due to the influence of the extreme value for R/E for brood 1989.

Factors for Spawning Channel and Shared Survival Affect Productivity and Capacity for Returns from EFS

The effect of three factors (spawning channel, shared survival, precision of returns), individually and in combinations, required 23 regressions (Table 6). Model 6A (Table 6) is the base case for assessing the effect of adding habitat factors and a variance factor and is the same as model 5C "Returns from EFS, All Years" (Table 5) and the results are similar. The datum for brood 1989 was deleted as an outlier for the models in Table 6 (see Discussion: Lake Fertilization). Deleting that point resulted in the high estimate for productivity in our earlier model (i.e., 5C "Returns from EFS" in the period during the spawning channel) declining from 43 R/E
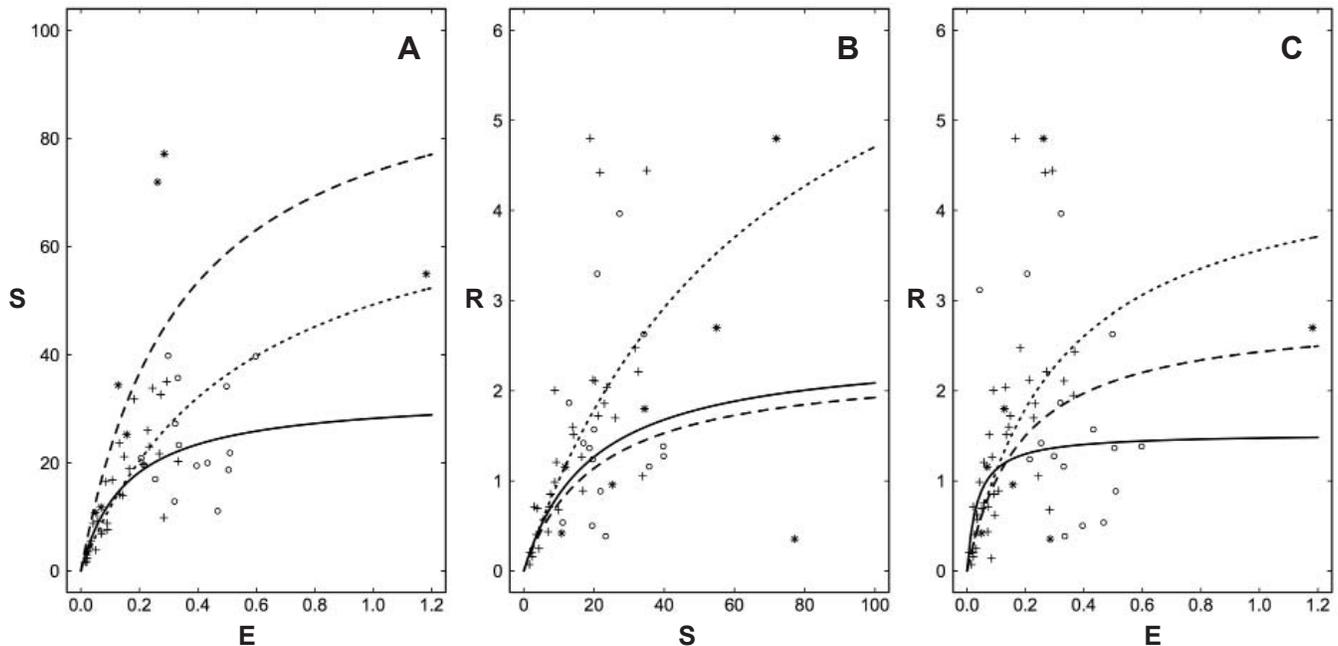
Fig. 4. The spawning channel affected estimates of both productivity and capacity for three intervals of survival for Chilko sockeye. For broods before the channel had an effect, points are marked "+" and the fitted B&H curve is a dotted line; during the channel: "o" and solid line; after the channel: "*" and dashed line. A. Smolts from EFS. B. Returns from smolts. C. Returns from EFS.

Table 6. Eight B&H models for Chilko sockeye returns from EFS, exploring the effects of factors for the spawning channel (before, during, and after) that affected broods 1988–2003, for annual shared survival (ranging from poor to good), and for a variance factor related to the precision of estimates of returns. Data for brood 1989 were not included. The fitted estimates for the effect of these factors (i.e., γ_{PG0} in Equation 6) have been applied (via 4,000 Monte Carlo samples of parameters) to produce estimates for productivity and capacity for the corresponding situations. See text for equations for these models. NLL is the mean of negative log likelihood, an indicator of fit. The abundance of EFS (E, in millions) at maximum sustainable yield is E_{MSY} (again the joint distribution of productivity and capacity) and the corresponding adult returns (in millions) is R_{MSY}. In models B and D, E_{MSY} is for the period after the spawning channel was closed (broods 2004–2010), and for models C and D, E_{MSY} is for the highest shared survival (good). The variance factor was fitted to model D, the most saturated model, yielding median $\gamma_W = 0.20$ (50% range = 0.13–0.27, 95% range = 0.027–0.41). That variance factor was applied without fitting to models A–C to generate the right-hand side of this table. See Appendix 1 for computer code.

| Parameter	No variance factor			With variance factor		
	Median	**50% range**	**95% range**	**Median**	**50% range**	**95% range**
6A. No Factors						
	NLL = 5.3 σ = 0.70			NLL = 3.7 σ = 0.56		
Productivity	17.0	15–20	12–27	20.0	17–24	13–35
Capacity	2.4	2.1–2.8	1.6–4.0	2.3	2.1–2.7	1.7–3.7
E_{MSY}	0.27	0.23–0.32	0.17–0.48	0.25	0.21–0.3	0.16–0.43
R_{MSY}	1.6	1.4–1.8	1.2–2.5	1.6	1.4–1.8	1.2–2.4
6B. Spawning Channel						
	NLL = 5.3 σ = 0.70			NLL = 3.7 σ = 0.56		
Prod. Before	15.0	14–17	11–22	17.0	15–19	12–26
Prod. During	11.0	8.2–13	4.8–18	12.0	9.1–15	5.2–21
Prod. After	15.0	12–18	8.1–27	17.0	13–20	9–29
Cap. Before	4.3	3.5–5.4	2.5–8.8	3.9	3.3–4.9	2.4–7.7
Cap. During	2.2	1.8–2.8	1.3–5.8	2.0	1.7–2.4	1.3–4.6
Cap. After	3.6	2.9–4.7	2.0–8.1	3.4	2.8–4.4	2.0–7.5
E_{MSY}	0.42	0.33–0.55	0.21–1.0	0.39	0.31–0.5	0.21–0.91
R_{MSY}	2.3	1.9–2.9	1.3–4.7	2.2	1.8–2.8	1.3–4.4
6C. Shared Survival						
	NLL = -1.1 σ = 0.60			NLL = -3.1 σ = 0.48		
Prod. Poor	15.0	12–17	7.6–22	17.0	15–20	9.9–28
Prod. Good	18.0	16–20	13–25	20.0	18–23	15–30
Cap. Poor	0.57	0.41–0.82	0.21–1.7	0.54	0.40–0.76	0.21–1.6
Cap. Good	3.7	3.3–4.2	2.6–5.5	3.5	3.2–4.0	2.5–5.1
E_{MSY}	0.41	0.36–0.48	0.27–0.63	0.38	0.33–0.44	0.25–0.58
R_{MSY}	2.5	2.2–2.8	1.8–3.5	2.4	2.2–2.7	1.8–3.3
6D. Spawning Channel and Shared Survival						
	NLL = 1.0 σ = 0.62			NLL = 1.2 σ = 0.49		
Prod. Before+Poor	12.0	9.9–15	6.0–19	14.0	12–17	7.0–23
Prod. During+Poor	8.2	5.5–11	1.7–16	9.9	7.0–13	2.1–19
Prod. After+Poor	13.0	9.5–16	4.0–24	15.0	11–18	5.2–26
Prod. After+Good	16.0	14–19	10–27	18.0	15–21	11–29
Cap. Before+Poor	2.7	1.8–4	0.84–7.5	2.3	1.6–3.3	0.78–6.4
Cap. During+Poor	0.9	0.57–1.6	0.25–4.7	0.8	0.51–1.2	0.25–3.7
Cap. After+Poor	2.1	1.4–3.2	0.62–7.1	1.9	1.3–2.8	0.65–6.0
Cap. After+Good	4.7	3.9–5.6	2.7–9.2	4.4	3.7–5.3	2.8–8.1
E_{MSY}	0.53	0.43–0.65	0.29–1.1	0.49	0.40–0.60	0.29–0.97
R_{MSY}	3.0	2.6–3.6	1.8–5.6	2.9	2.5–3.4	1.9–5

to 11 (model 6B, "Prod. During"). The latter value is more in accordance with the corresponding productivity estimates for smolts from EFS and returns from smolts. We were interested primarily in the magnitude and precision of estimates for

capacity because certainty about density-dependent mortality is important and difficult to ascertain. We were also interested in the precision of E_{MSY} because that integrates most of the uncertainties in the model and is directly related to fisheries

management (e.g., optimal escapement goals). The values for σ and NLL (negative log likelihood) are also important because these describe how well each model predicted the observed returns. The base case values, as medians and 50% ranges, were capacity = 2.4 returns (2.1–2.8) and E_{MSY} = 0.27 EFS (0.23–0.32). We reported medians and MC sample percentiles in Table 6, instead of means and SDs, because some parameter estimates had skewed distributions (Fig. 5) that resulted in MC samples with rare but extremely large estimates that had a misleading effect on the mean and SD.

The spawning channel effect was large (model 6B), indicating that median capacity was twice as high before the spawning channel was opened, and 2/3 higher after it closed. As noted above for freshwater survival, median productivity was higher by 1/3 before and after the channel. The estimate for E_{MSY} for the period after the channel, compared to not including the channel in calculations (models 6B and 6A), increased by 1/2 to 0.42 E (50% range = 0.33–0.55) from 0.27 (0.23–0.32). There were only seven cases for the post-channel estimate of E_{MSY} during a period of highly variable smolt survival (Fig. 2: broods 2004–2010) so it was less precise (MAD/median increased from 24% to 36%, where MAD is the median absolute difference from the median).

The shared survival factor (which ranges from 0 to 1) predicted the observed returns (R) from EFS (E) data better than the spawning channel, as measured by decreased σ and NLL (model 6C). Results marked "Prod. Good", "Prod. Poor", "Cap. Good", and "Cap. Poor" in Table 6C represent the range of effects for this factor when applied as an additive covariate. Shared survival accounts for less than half of Chilko sockeye total survival (r^2 = 39% without brood 1989). The effect of good versus poor shared survival differed greatly between capacity and productivity: capacity changed by a factor of six, but productivity changed by only 1/5. This reflects the strong effect of variability in smolt survival on variability of returns, but also suggests that tracking variability in log(R/E) (Peterman et al. 2003) might be improved by splitting that into Beverton-Holt productivity and capacity and tracking variability in both. The change in median E_{MSY} between years with good shared survival (E_{MSY} = 0.42) and poor shared survival (E_{MSY} = 0.07) reflected that change in capacity. E_{MSY} for years with good shared survival was similar to E_{MSY} for the period after the spawning channel, but was more precisely estimated (E_{MSY} MAD/median = 21% *versus* 37% for model 6B). Despite the fact that the shared survival factor injects
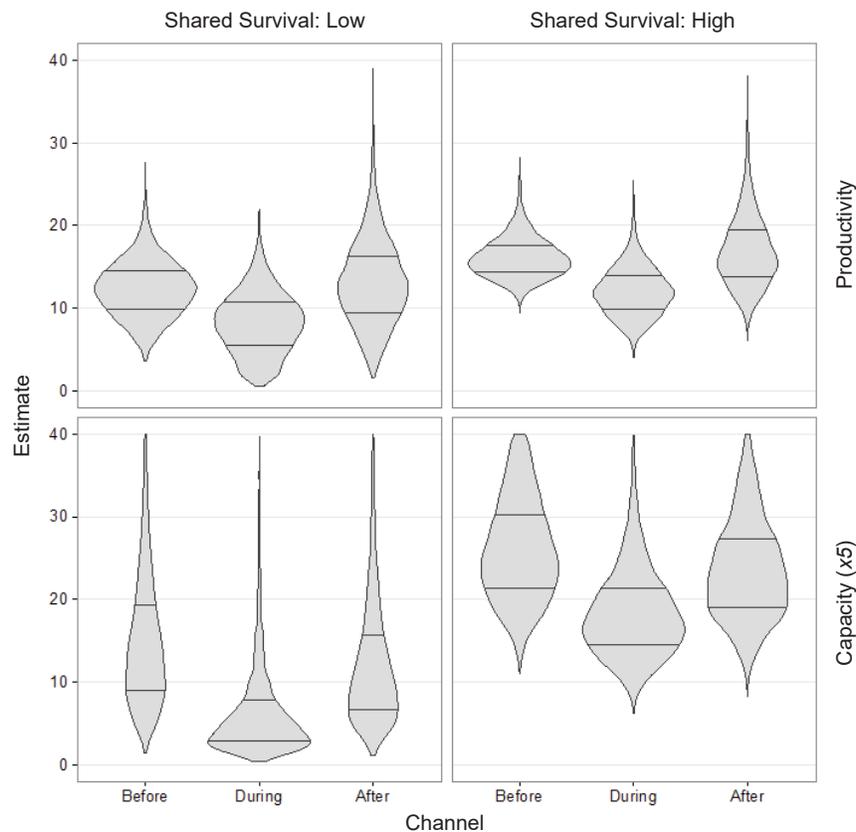
Fig. 5. Distributions for B&H estimates for productivity and capacity corresponding to the spawning channel ("during" refers to broods 1988-2003) and to good and poor years for the shared survival factor. The polygons ("violins") represent the distribution of estimates derived from 4,000 samples of the joint distribution of parameter estimates from the model in Table 6D. Areas of polygons are comparable within panels, but are scaled differently between panels.
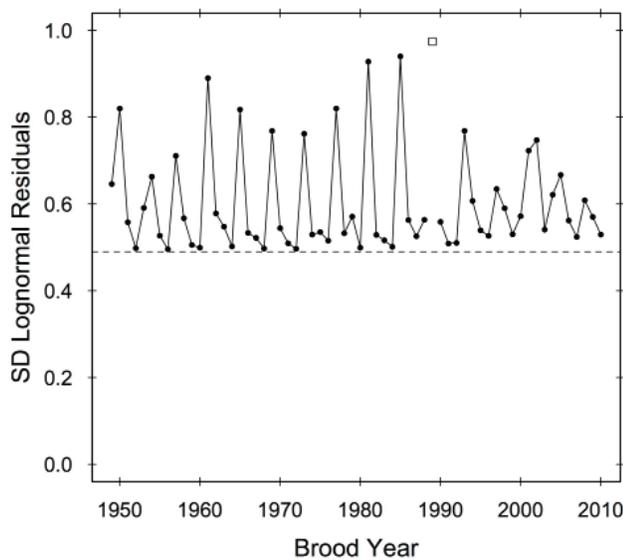
Fig. 6. The proportion of Chilko Lake returns in the summer run of Fraser River sockeye (broods 1949–2010) was used to describe the relative precision of return estimates for Chilko sockeye (a variance factor). The dashed line at $\sigma = 0.49$ (Table 6D) represents the most precise estimates corresponding to a large proportion of the summer run. The dots are fitted values for the lognormal standard deviation (SD) of expected residuals. High values mean less weight for a case. This result highlights a four-year cycle of low abundance (1961, 1965, … 1993) where the SD is 60% to 90% larger. Brood 1989, deleted for the models in Table 6, is marked by a square.

noise into the model, the estimate of capacity in a good year is slightly more precise than when it was estimated without the shared survival factor (E_{MSY} MAD/median = 24% for model 6A).

Separately, both habitat factors appear useful; now we consider them together (model 6D). The two factors are not independent, shared survival was lower after the spawning channel was opened than before (39% of the variance in shared survival is accounted for by that shift). No causation is implied, it is a coincidence that a spawning channel for the Chilko sockeye CU was open during a period when marine survival of many Fraser River sockeye salmon declined in the 1990s. The value for σ (model 6D) was similar to considering just shared survival (6C), and about 12% better than fitting just the spawning channel (model 6B). This model reflects six situations: before, during, and after the spawning channel, and for each of these, good and poor values for shared survival. These two habitat factors operate independently (additive but correlated, no interaction terms) in their effect on productivity. Comparing the best situation (After + Good) to the worst (During + Poor), productivity differed by a factor of two, changing from 8.2 *R/E* (50% range = 5.5–11) to 16 (14–19), while capacity differed by a factor of five, changing from 0.9 *R* (0.57–1.6) to 4.7 (3.9–5.6). The lowest productivity value is ¼ lower than with the spawning channel alone, but the upper level is similar to preceding models. Notably,

the best-case capacity is 30% higher than with the spawning channel alone (6B) or shared survival alone (6C). At present, with the spawning channel closed, this model with these data suggest productivity of 13 to 16 and capacity of 2.1 to 4.7. A reasonable approximation, based on the median shared survival (0.74) is productivity = 15 (MAD = 4.1) and capacity = 4 (MAD = 1.3), leading to $E_{MSY} = 0.46$ and $R_{MSY} = 2.6$ (but note the 95th percentile for E_{MSY} in Table 6D is 1.1 and these estimates involve Bayesian priors that constrain high estimates for capacity). All of the parameter estimates in model 6D involve substantial uncertainty, with MAD/median (this is the CV for normally distributed data) about 25% for productivity and capacity when shared survival is good, and about 38% for productivity and about 58% for capacity when shared survival is poor.

Effect of a Variance Factor

Including "proportion of run" as a variance factor (Equation 7, see the right-hand side of Table 6) suggested a four-year cycle of low returns (including 1989) with increased standard deviations for the distribution of expected residuals for those years (Fig. 6). The estimated regression weights reduced the effect of those cases (down-weighted them). The estimate for the effect of the variance factor was median $\gamma_W = 0.20$ (50% range = 0.13–0.27), based on the
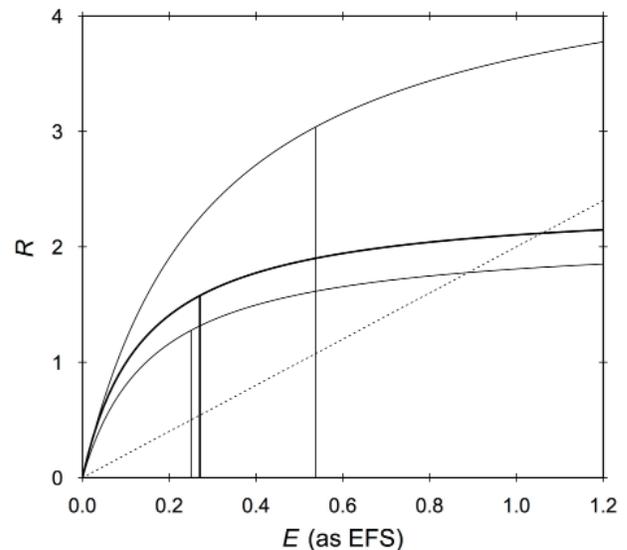
Fig. 7. Beverton-Holt curves for Chilko sockeye with and without factors from metadata for the spawning channel and shared survival. For each curve, E_{MSY} is indicated by a vertical line and the corresponding R_{MSY} is the point where that line intersects the curve. The dotted line has slope = 2 and shows the adult returns (*R*) required to replace the female spawners (*E*). The upper thin curve represents good years for the shared survival factor during the period after the spawning channel closed (broods 2004–2010, Table 6D): Productivity = 16, Capacity = 4.7, $E_{MSY} = 0.53$, $R_{MSY} = 3.0$. The lower thin curve is poor shared survival in the same period: 13, 2.1, 0.25, 1.3. The thick line is for all years (1949–2010, Table 6A) without considering factors from metadata: 17, 2.4, 0.27, 1.6.
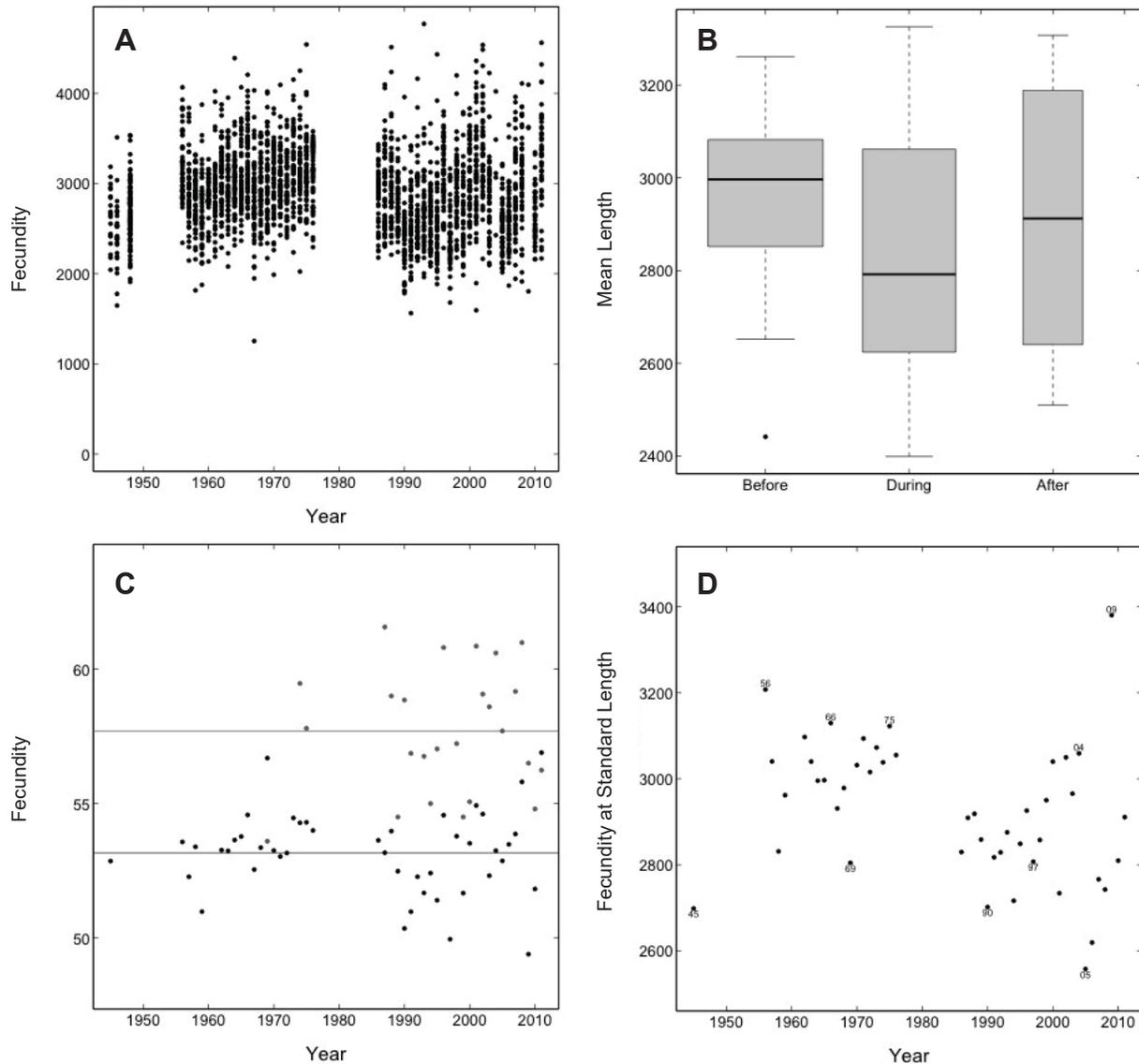
Fig. 8. Fecundity by length for Chilko sockeye. A. Individual fecundity observations by year. Sample size is typically 50 but sample sizes were small in 2004 ($n = 5$) and 2009 ($n = 4$). B. Fecundity in relation to the spawning channel (see Table 7). Median fecundities before, during and after the channel are 2997 (MAD = 159), 2791 (300), and 2912 (433). C. Mean length (cm) by age, from fecundity samples, did not have a temporal trend. Age 1.3 females (grey dots) have increased to about 12% of spawners from near-zero in 1970. D. Fecundity by age at a standard reference length (53.45 cm, the mean) has declined by about 15% between 1950 and 2010. Females of age 1.2 and age 1.3 were pooled for this plot and the high values for 2004 and 2009 are poorly determined.

most complicated model (6D) where an effect of precision would be strongest, essentially as outliers became more distinct. With brood 1989 included, the effect of the precision factor was stronger ($\gamma_W = 0.26$, 0.20–0.32). Brood 1989 had the lowest proportion of run in this 62-year series (0.032) and the SD for log-normal residuals for the 1989 case would have been $0.032^{-0.26} = 2.5$ times larger than the SD for the most precise observations (median $\sigma = 0.49$ (50% range = 0.40–0.60), Table 6D).

In models where this variance factor was included (the right-hand side of Table 6), the residual log-normal variance,

σ, is consistently 20% lower that without the variance factor. It is tempting to see that as evidence that the models fit better, but this inference is unwarranted because the datasets are now different (consider that a case can be essentially deleted with regression weights). A revealing calculation is $n_{eff} = \sum W^\gamma$ to estimate the number of effective observations given that some are downweighted (note change of sign). In this case, $n_{eff} = 51.4$ instead of $n = 61$. It is reasonable to ask how results from the same models with the new dataset differed from results with the previous dataset. Cases with small estimates for R were downweighted, and mainly

Table 7. Analysis of variance showed that annual values of fecundity varied for different states of the spawning channel (before, during, after) in a way that explained only 5% of the variance. There is a 32% chance that the three periods had the same mean fecundity.

Parameter	Estimate	SE	Pr(>|t|)
Before	2956	47.8	<0.001
During	2838	76.1	0.13
After	2913	103.8	0.68
Residuals	SD = 244		
Fit	r^2 = 5%		Pr($F_{2,47}$ > 1.16) = 0.32

before the spawning channel was opened. These are associated with small E (but not always, e.g., broods 1993, 2001, and 2002). Removing cases with small values of R at low values of E should lead to higher estimates for productivity, and, comparing the left and right sides of Table 6, this was always the case. Similar logic applies to capacity, where points above the median for E have the greatest effect, and if the cases that are downweighted are overestimates of R, then capacity should be lower. This was also the case, but the effect is not as pronounced. Taken together, higher productivity and lower capacity means lower E_{MSY} and R_{MSY} and in fact adding this variance factor reduced the estimates for E_{MSY}, however the effect was slight (< 8%).

After addressing one part of precision for one part of the data, are the stock-recruit parameters more precise? We compared the 50% and 95% ranges of MC samples, divided by the median, before and after considering precision of estimates of returns, for all of the parameters determined in the four models in Table 6. The only useful difference was that the capacity estimates had 95% ranges that were smaller by 38% (MAD/median = 95%), apart from those affected by the shared survival factor where the 95% ranges increased by 220% (28%) after considering precision. The overall result, expressed as E_{MSY}, was a decrease of 8.5% (52%) in the 95% range, a small change. The 50% ranges for capacity estimates were all smaller by 6.5% (23%) but there was no improvement in precision for E_{MSY} (smaller by 1.5% for which MAD/median = 99%). In summary, although we have a method for considering the precision of data in stock recruit analyses, the categorical variance factor we used did not usefully improve the precision of parameter estimates.

Our objective, improved understanding of Chilko returns from EFS via factors derived from metadata, can be measured as improved fits between the simplest model (Table 3C) and the most complicated (Table 6D with variance factor). The standard deviation of log-normal residuals, σ, decreased from 0.72 (Table 3C) to 0.70 by eliminating brood 1989 (Table 6A), then to 0.62 by considering the spawning channel and shared survival (Table 6D), and then to 0.49 by considering precision of returns (Table 6D, right-hand side). Similarly, the negative log likelihood (NLL) decreased greatly: from 5.7 (Table 3C) to 1.0 or 1.2 (Table 6D). From a practical perspective, understanding that recent capacity is

somewhere between 2.1 and 4.7 (despite wide 95% confidence limits) depending on marine conditions, instead of 2.3 based on the long-term mean (Tables 6A and 3C) makes a large difference in escapement targets (Fig. 7).

Fecundity as a Potential Confounding Factor

The mean fecundity for 2,420 observations (Fig. 8A) was 2,900 (SD = 455; range = 1,254–4,770) and the mean annual fecundity for 50 years (1945–2011) was also 2,900 (245; 2,399–3,326). The SD among individuals is 1.86 times the SD among years, indicating about half of the variation in fecundity is due to the differences among years. After partitioning the years into before, during, and after the spawning channel was open, the statistics for annual fecundity were compared with ANOVA (Table 7), which indicated that annual mean fecundity did not differ before, during, and after the spawning channel: only 5% of the variance among years was related to the three periods (a value this large or larger has a 32% chance of appearing when the periods actually have the same mean). Increasing variability in fecundity with time was indicated by increasing interquartiles (Fig. 8B) and by the MAD for annual fecundity: before, 159 eggs per female; during, 300; after, 433.

Fecundity at Length

A regression for fecundity against length for all years combined was compared to a similar regression with separate lines before, during, and after the spawning channel. The value for r^2 increased from 25% to 48% (ANCOVAR, Pr($F_{4,42}$ > 4.64) < 0.004). To examine this, we broke fecundity into two constituent parts: length at age and fecundity at length by age. There was no trend in length at age for age 1.2 or age 1.3 females (Fig. 8C), although the variability in length at age for age 1.2 females was greater in recent years. There was, however, a trend of decreasing fecundity corrected to a standard length (Fig. 8D). The loss from 1950 to 2010 has been about 550 eggs per reference-length female. In the fecundity samples there was a strong tendency to an increased proportion of age 1.3 females that were 9% longer (57.9 cm, n = 128, SD = 2.77) than age 1.2 females (53.2 cm, n = 1,968, SD = 2.42) and 20% more fecund (3,459 eggs, n = 129, SD = 499) than age 1.2 females (2,873 eggs, n = 2,201, SD = 434). This corresponds to the observation that age-1.3 returns in Chilko sockeye have increased linearly to 20% of total returns in 2010 from near-zero before 1970 (Irvine and Akenhead 2013).

DISCUSSION

The time series for Chilko sockeye is the longest and most consistently measured survival record for Pacific salmon in Canada. It is valuable for understanding sockeye salmon ecology because survival can be partitioned into presmolt survival (freshwater) and smolt survival (largely ma-

rine). The time series is sometimes used as an index of smolt survival for other populations of Fraser sockeye. A previous study (Irvine and Akenhead 2013) focused on smolt survival in Chilko sockeye. This study focused on pre-smolt survival, particularly the effects of adding and then removing a spawning channel. Even without a reference (control) system in the Fraser River watershed to compare Chilko survival with, detailed examination of metadata, including those pertaining to the habitat manipulations considered here, improved our understanding of factors responsible for recruitment variability.

Lake Fertilization

Our analysis of Chilko Lake fertilization in 1988 and 1990–1993 was limited to survival estimates. We did not examine the length-frequency data for smolts or the survival of the comparatively rare age-2 smolts. Analysis was difficult because the fertilizer effect was confounded by: (1) simultaneously opening a spawning channel in 1988 that reduced the egg-to-smolt survival of broods 1988–2003; (2) an increase in escapement: mean EFS for the five broods exposed to fertilization as parr (1987, 1989–1992) was 2.9 times the mean of the preceding 38 years (0.35 million (SD = 0.22) compared to 1.2 (0.10)); and similarly (3) variable smolt survivals, specifically the low survival rate for smolts from broods 1990 and 1991 (Fig. 3B) compared to broods 1992 and 1993. We note that lower fishing mortality was required for this increase in escapement for broods affected by the fertilizer, particularly when smolt survival was low.

The value for returns from EFS for Chilko sockeye from brood year 1989 was a remarkable outlier (Figs. 3C and 5B), with R/E = 73, which is more than 9 SD from the mean excluding 1989 (mean R/E = 10.6 (SD = 7.6)). In 1989 the proportion of Chilko spawners in the summer run of Fraser sockeye was 0.032, the lowest value in the series. This suggested an overestimate of returns, given that brood 1989 is part of a weak cycle, similar to 1977, 1981, and 1985 (the mean R/E for those three years was 12 (SD = 2.3)). Brood 1989 was one of five that used the lake when it was fertilized but this case is problematic because (a) smolt abundance was not estimated, (b) the returns estimate was an extreme outlier, and (c) the returns estimate had the smallest value for the precision of returns factor (Fig. 5). We did not use brood 1989 when fitting the models in Table 6.

Including fertilizer as a productivity effect in the freshwater survival models (Table 4B) produced an estimate for the fertilizer effect that was small (9.3 R/E higher in fertilized years is an increase of 5.6% over the baseline of 165 S/E) and imprecise (CV= 107%, 95% range = -11–29). In addition, the estimates for productivity and capacity did not change when the factor for fertilizer was excluded (Table 4D).

Smolt production (S/E) from Chilko Lake was higher for broods without fertilizer or a spawning channel (broods 2004 and subsequent) than for broods before those projects were undertaken (broods before 1987). This indicated the possibility of a change within Chilko Lake, as opposed to a change within the salmon population. The mean daily primary production during the May to October growing season in Chilko Lake in 2009–2014 was 126.6 mg C•m⁻²•day⁻¹ (n = 5, SD = 10.6) compared to 73.1 (n = 4, SD = 113.9) in 1985–1995, a 73% increase in about 20 years (Pr($t_{5.5}$ > 6.3) = 0.001) (Dan Selbie, DFO, unpublished data). Recent levels of primary production now exceed those from years when the lake was fertilized (range 65–125, mean 93.1, n = 5, SD = 26.8). At present there is no published explanation for this increase. A time-varying nutrient budget for Chilko Lake may be needed to assess possible effects of naturally varying nutrient loading from retreating glaciers, water replacement time (stream flow), and carcass accumulation from increases in sockeye spawning in streams that enter Chilko Lake and along the shores of Chilko Lake.

It appears that a naturally induced change in the net primary productivity of Chilko Lake increased smolt production more than the intentional lake fertilization. The reasons for this are not clear although McQueen et al. (2007) have previously noted the potential for variable smolt production outcomes given differential responses of algal taxa to consecutive years of similar inorganic fertilizer additions at Woss Lake, BC.

Long-term changes in lake habitat quality further confound analyses of the salmon enhancement projects. This large and recent change in primary production in isolated and pristine Chilko Lake suggests that habitat quality in other sockeye nursery lakes in the Fraser River watershed is not stationary. This suggestion is supported by evidence from Quesnel Lake, where net primary productivity in 2003–2007 (n = 5) was 50% higher than in 1984–1994 (n = 5) (Selbie et al. 2010).

Our conclusion is that a useful increase in the survival rate of Chilko sockeye from lake fertilization could not be demonstrated, especially after excluding the extreme value of R/E for brood 1989. On the other hand, we were able to associate the high values of S/E after 2003, compared to before 1987, with a large but natural increase in primary production. Bradford et al. (2000) concluded that an increase in the length of Chilko Lake smolts was a fertilizer effect, but we note that the effect of smolt abundance on the size of smolts (density-dependent growth) was not considered. Despite the small sample size, we are hopeful that some future close examination of size, condition, and density for parr and smolt —as well as the size and abundance of smolts and returns at various ages—may clarify the effects of Chilko Lake fertilization within the context of similar projects reviewed by Hyatt et al. (2004).

Spawning Channel

The channel at Chilko Lake operated for 16 years despite at least one report (Schubert and Fanos 1997) that indicated little additional spawning. As mentioned for the fertilizer experiment, the effect of the spawning channel was possi-

bly confounded by increased escapement. Escapement was 280% higher when the spawning channel was open compared to previously (mean EFS 1988–2003 = 0.36 (SD = 0.14), mean EFS 1949–1987 = 0.13 (0.11)). This increase in escapement occurred during a period of low smolt survival (Fig. 3) and required a lower fishing mortality. Low fishing mortality and increased competition between spawners in the Chilko River spawning ground could conceivably shift the ratio of lake-spawning sockeye to river-spawning sockeye.

Based on the time series for smolts from EFS (Fig. 3A), pre-smolt survival was lower for broods during spawning channel operation (1988–2003) than either before or after. In conjunction with decreased smolt survival (Fig. 3B), total survival was also lower during spawning channel operation compared to either before or after. Modeled as B&H curves for smolts from EFS, opening the spawning channel in 1988 reduced the capacity for smolts by 57% (from 76 to 33 million, Table 5A) or 37% (from 63 to 40 million, Table 4D). Modeled as B&H curves for returns from EFS (total survival), the channel decreased capacity for returns by 49% (from 4.3 to 2.2 million, Table 6B) or, after removing some of the marine survival effect, by 67% (from 2.7 to 0.9 million, Table 6D). Although it is possible that the decrease in salmon production observed at Chilko Lake during the period of channel operation was due to an unknown factor that coincided with channel operation, we consider this unlikely because after the channel was closed in 2004, the capacity for smolts doubled (Table 4D: (63 + 25) / (63 - 23) = 2.1) or tripled (Table 5A: 99 / 33) compared to when the channel was open. The initial benefits of closing the spawning channel in 2004 were hidden by unusually low spawner abundance for brood 2004 and by low marine survival events in 2005 and 2007 that affected broods 2003 and 2005. Similarly, the drop in capacity for smolts after the spawning channel opened in 1988 was masked by the outlier for estimated returns from EFS for brood 1989 (age-1 smolts were not counted for that brood) and by declining post-smolt survival in the 1990s. This example demonstrates that identification of associated and confounding effects on salmon survival from freshwater and marine events is warranted.

Fecundity

Female length distributions for sockeye salmon have changed substantially over time (Peterman 1984; McKinnell 1995, 2008; Bigler et al. 1996; Pyper and Peterman 1999; Welch et al. 2000). With the exception of 2010, when small females were associated with an unusually large abundance of returns, the female salmon returning to Chilko Lake, after the spawning channel was closed, were usually larger than average, so an increase in fecundity due to an increase in size was a potential explanation for higher pre-smolt survival after the channel was closed. When we examined fecundity before, during, and after the channel, changes in annual mean fecundity appeared to have relatively little effect. Comparing these three periods accounted for only 5%

of the variation in fecundity (small compared to the changes in smolts per EFS, S/E) and in particular did not account for the enormous increase in S/E 2004–2010 compared to 1987–2003. The increasing proportion of age 1.3 females—larger, more fecund, and possibly with better egg survival—may play a role in explaining why S/E 2004–2010 was double that of 1960–1987, but a better explanation seems to be the 73% increase in primary productivity in Chilko Lake.

Density-dependent growth has been documented for sockeye salmon (Peterman 1984; Pyper and Peterman 1999), but our observation of a linear decline in fecundity-at-length from the 1950s to the 2010s is a different phenomenon. Because the skeletal length-at-age of Chilko sockeye salmon females has not changed, but their fecundity has declined, this appears to represent a factor such as less food, increased temperature, or longer migration (or combinations thereof) that affects fecundity after spawners have reached maximum length, perhaps shortly before they reach Chilko Lake. We do not know how the decline in fecundity-at-length might be related to the increasing proportion of age-1.3 females starting in 1970 (Irvine and Akenhead 2013), but shared causation behind these two indicators of adult female energetics is an intriguing possibility. Additional work should examine potential interactions between Fraser River sockeye salmon with pink salmon (*O. gorbuscha*), for instance to detect differences in length and/or fecundity between even and odd numbered years (Ruggerone and Connors 2015).

In most of the earliest years (before 1964, M. Forrest, reichardt@psc.org, pers. comm.), spawning ground age was estimated with scales rather than otoliths. Resorption of portions of scales is typical in sockeye salmon, and leads to the possibility that marine annuli could be lost and age underestimated (S. Latham, latham@psc.org, pers. comm.). Although some age-1.2 females in the early years may have actually been age-1.3 females, the ratio of age-1.3 to age-1.2 females was consistently low before 1970 (Irvine and Akenhead 2013).

The usual protocol at Chilko Lake was to take fecundity samples ($n = 50$) near the day of peak abundance (Schubert and Fanos 1997). Because size, age, and fecundity can vary through the spawning period, those samples may not be representative of the entire population of female spawners, resulting in biased fecundity estimates. The Chilko sockeye CU ("Chilko-ES") that spawns on submerged beaches within Chilko Lake (a) returns before the CU that spawns downstream of the lake in Chilko River (Schubert and Fanos 1997; Grant et al. 2011), (b) is shorter by age, and (c) has a different age structure (Schubert and Fanos 1997; Healey et al. 2000; Grant et al. 2011). If this earlier population was over-represented in fecundity samples, this is another possible source of bias in fecundity estimates (S. Latham, latham@psc.org, pers. comm.). On the other hand, if similar sampling protocols were followed in all years, even if fecundity estimates are biased they may still be relatively precise, reducing concerns regarding these data.

Capacity and Productivity are not Independent

For a Chilko sockeye salmon fry, the process of migrating upstream past the spawning channel outlet, or failing to do so, probably applies to less than one day in its life. Should that effect from the spawning channel be ascribed to productivity or to capacity? We found that this factor (the spawning channel) required fitting two effects instead of one: the capacity and the productivity estimates both changed (Tables 5 and 6). Nevertheless, there really was one event. This suggests there should be a better approach to parameterize the inclusion of habitat factors in stock-recruit models, such that one parameter, not two, describes the effect of a specific change to a specific habitat. In general, the B&H and Ricker models were designed to average across year-to-year variability in the habitats that fishes migrate through. When habitat variables are incorporated into these models, as we are proposing, the result is a different stock-recruit curve for different states of habitat (e.g., spawning channel open or closed) and different ocean climate regimes (i.e., marine survival indicators: Beamish et al. 1997; Chen and Irvine 2001).

Imprecise Estimates (Variance Factor)

Adult returns of Chilko sockeye may be a small fraction of the co-migrating CUs within an abundant summer run of Fraser River sockeye and consequently poorly sampled and imprecisely determined (Millar 1987; Wood et al. 1987; Cass and Wood 1994; Ricker 1997). As mentioned, the smallest proportion of Chilko sockeye in the summer run corresponds to brood 1989, and that brood was exposed to fertilizer effects during their lake year, in 1990. Discounting returns from brood 1989 as imprecise will affect the interpretation of Chilko Lake fertilization. For instance, the conclusion of Bradford et al. (2000) that adding fertilizer in 1990 had a beneficial effect on the survival of this brood (in the absence of a smolt abundance estimate) might need to be re-examined.

We expected that uncertainty about the effect of shared survival (a noisy predictor of R/E for Chilko sockeye) would lead to lower precision in E_{MSY} when shared survival was part of the MSY calculation, i.e., that including this factor would lower the signal to noise ratio in a model. Inspection of Table 6 confirmed that expectation, but the effect was small: the 50% range of MC samples for E_{MSY} is larger with shared survival (0.48 - 0.36 = 0.12, Table 6C) than without (0.32 - 0.23 = 0.09, model 6A), despite the reduction in σ between these models. The largest effect on precision of individual parameters (P, C, γ_{G0}, γ_{G2}, γ_H) and values derived from those parameters (E_{MSY}, R_{MSY}, "Prod. After + Good", etc.) was simply the number of parameters to be estimated. Across the sequence of models in Table 6, the log-likelihood surface became less curved, indicating overall less precision: MAD/median for NLL was 0.22, 0.57, 1.1, 3.3 for models 6A–D, and the number of parameters being estimated (including

σ) was 3, 7, 5, and 9. When we included a variance factor for precision of returns, the models responded (right-hand side of Table 6 compared to left-hand side) in a way that was predictable just from considering the smaller returns to be downweighted. The improvement in precision of E_{MSY} from this particular variance factor was, as stated previously, small and not useful.

We look forward to better factors being extracted from the metadata for Chilko sockeye in order to provide better explanations for historical returns and to improve the precision of reference points for fisheries management such as E_{MSY}. In particular, better indicators of the relative precision of returns appear warranted, perhaps leading to stronger downweighting of cases such as adult returns from brood 1989. In contrast, factors for the relative precision of estimates of spawner abundance will be difficult to compile because of (a) the large number of spawning sites for Fraser River sockeye CUs (Grant et al. 2011), (b) the variety of field approaches that have been used from 1949–present (e.g., Table 2), and (c) different methods by spawning sites and by years were used to estimate the spawners for each CU, and different methods within sites by years (Schubert 1998). The methods explored in this paper can be used to apply improved variance factors that describe the year-to-year changes in the relative precision of spawners, smolts, and adult returns. Estimates of the effect of these variance factors might be improved by analyzing multiple CUs simultaneously (Akenhead et al. 2016). The utility of such variance factors is likely to improve as better habitat factors are applied because that will reveal outliers that can independently be identified as imprecise.

Marine versus Freshwater Effects

McKinnell et al. (2012) noted the CV for total survival for Chilko sockeye was approximately double the CV for pre-smolt survival because the former includes variation in post-smolt survival (from Table 1, CV = 94.5% for returns from EFS and CV = 51.1% for returns from smolts). Consequently, "returns per spawner, the normal measure of Fraser River sockeye salmon productivity, includes significant year-to-year variability from both freshwater and ocean sources. Because it has not been measured routinely at other lakes, the relative influence of each habitat on total survival cannot be determined" (McKinnell et al. 2012, p. 89). We concur and emphasize that the effects of freshwater factors on pre-smolt survival can be confounded by variability in smolt survival. For example, the deleterious effect of the spawning channel on pre-smolt survival was apparently overlooked because of a concurrent decline in smolt survival. An important advance to address this issue is the quantitative sampling, with DNA-based identification to CU, of all sockeye salmon smolts leaving the Fraser River, started in 2010 by DFO (T. Whitehouse, Timber.Whitehouse@dfo-mpo.gc.ca, pers. comm.).

In general, this analysis provides an example of how changes in habitat quality at various life stages can confound

the interpretation of retrospective analyses of returns per spawner. We have not addressed many other factors related to the natural variability in freshwater habitats for Chilko sockeye (Table 2) but we recognize both the complexity and importance of these factors. Applying factors from historical metadata to reduce the scatter in stock-recruit curves for all of the CUs of Fraser sockeye, and for salmon management in general, will require a significant effort, but has the promise of not only increasing our understanding of the sources of variation in returns, but also increasing the precision of estimates of stock-recruit parameters, with attendant improvement in salmon fisheries management.

CONCLUSIONS

This paper demonstrates that it is important to be aware of the metadata for any stock being studied as this can help to explain some of the variance in stock-recruit data.

- This study of Chilko Lake sockeye salmon provided an example of how factors derived from metadata can be usefully incorporated within stock-recruit analyses in order to address natural and man-made habitat manipulations and to determine regression weights from metadata related to the relative precision of observations.
- Adding these factors reduced (a) the total variance to be explained before considering stock-density effects, as demonstrated by adding the spawning channel as a factor that affected productivity and capacity parameters, and (b) uncertainty by removing the effect of large outliers that can be recognized as imprecise estimates, as demonstrated by including proportion of run as a factor that affected the variance of individual residuals.
- Fertilization of Chilko Lake (1988, 1990–1993) had a negligible effect on productivity in B&H models, however the analysis was complicated by overlapping changes in the spawning channel, smolt survival, and spawner abundance (a confounded experimental design) and by missing and rejected values for one of the five cases (brood 1989).
- After the spawning channel was closed, more smolts per EFS were produced than before it opened, an effect we traced to a 73% increase in the net primary production of Chilko Lake in the last 20 years.
- The spawning channel at Chilko Lake (1988–2003) was detrimental to pre-smolt survival for 16 years and lowered the B&H capacity for smolts by about a half, with attendant reductions in adult returns.
- Understanding that important events in pre-smolt life can be hidden by events in post-smolt life highlights the value of monitoring smolts.
- More attention to the assembly and analysis of metadata, including freshwater habitat quality indicators, is warranted for this and other salmon populations, and should lead to better informed, hence improved, fisheries management decisions.

REFERENCES

Adkison, M.D., R.M. Peterman, M.F. Lapointe, D.M. Gillis, and J. Korman. 1996. Alternative models of climatic effects on sockeye salmon, *Oncorhynchus nerka*, productivity in Bristol Bay, Alaska, and the Fraser River, British Columbia. Prog. Oceanogr. 5(3–4): 137–152. doi:10.1111/j.1365-2419.tb00113.x.

Akenhead, S.A., J.R. Irvine, K.D. Hyatt, S.C. Johnson, and S.C.H. Grant. 2016. Stock-recruit analyses of Fraser River sockeye salmon. N. Pac. Anadr. Fish Comm. Bull. 6: 363–390. doi:10.23849/npafcb6/363.390.

Beacham, T.D., R.J. Beamish, J.R. Candy, C. Wallace, S. Tucker, J.H. Moss, and M. Trudel. 2014. Stock-specific size of juvenile sockeye salmon in British Columbia waters and the Gulf of Alaska. Trans. Am. Fish. Soc. 143: 37–41. doi:10.1080/00028487.2014.889751.

Beamish, R.J., C.M. Neville, and A.J. Cass. 1997. Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. Can. J. Fish. Aquat. Sci. 54: 543–554.

Beamish, R.J., C.M. Neville, R.M. Sweeting, and K.L. Lange. 2012. The synchronous failure of juvenile Pacific salmon and herring production in the Strait of Georgia in 2007 and the poor return of sockeye salmon to the Fraser River in 2009. Mar. Coast. Fish. 4: 403–414. doi:10.1080/19425120.2012.676607.

Beverton, R.H., and S.J. Holt. 1957. On the dynamics of exploited fish populations. Chapman and Hall, New York. 533 pp.

Bigler, B.S., D.W. Welch, and J.H. Helle. 1996. A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). Can. J. Fish. Aquat. Sci. 53: 455–465. doi:10.1139/cjfas-53-2-455.

Bradford, M.J., B.J. Pyper, and K.S. Shortreed. 2000. Biological responses of sockeye salmon to the fertilization of Chilko Lake, a large lake in the interior of British Columbia. N. Am. J. Fish. Manage. 20: 661–671. doi:10.1577/1548-8675(2000)020<0661:BROSST>2.3.CO;2.

Cass, A.J., and Wood, C.C. 1994. Evaluation of the depensatory fishing hypothesis as an explanation for population cycles in Fraser River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 51: 1839–1854.

Chen, D.G., and J.R. Irvine. 2001. A semiparametric model to examine stock-recruitment relationships incorporating environmental data. Can. J. Fish. Aquat. Sci. 58:1178–1186. doi:10.1139/f01-037.

Cronkite, G.M.W., H.J. Enzenhofer, T. Ridley, J. Holmes, J. Lilja, and K. Benner. 2006. Use of high-frequency imaging sonar to estimate adult sockeye salmon escapement in the Horsefly River, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. No. 2647. 46 pp.

DFO (Fisheries and Oceans Canada). 2005. Canada's policy for conservation of wild Pacific salmon. (Available at.pac.dfo-mpo.gc.ca/publications/pdfs/wsp-eng.pdf).

DFO (Fisheries and Oceans Canada). 2014. Supplement to the pre-season return forecasts for Fraser River sockeye salmon in 2014. DFO Can. Sci. Advis. Sec. Sci. Rep. 2014/041. (Available at www.dfo-mpo.gc.ca/csas-sccs/Publications/ScR-RS/2014/2014_041-eng.pdf).

Fournier, D.A., H.J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M.N. Maunder, A. Nielsen, and J. Sibert. 2011. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optim. Methods Softw. 27: 233–249. doi:10.1080/10556788.2011.597854.

Gable, J., and S. Cox-Rogers. 1993. Stock identification of Fraser River sockeye salmon: methodology and management application. Pac. Salmon Comm. Tech. Rep. 5. 36 pp.

Gelman, A., and D.B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statist. Sci. 7: 457–472.

Gelman, A., J.B. Carlin, H.S. Stern, D.B. Dunson, A. Vehtari, and D.B. Rubin. 2013. Bayesian data analysis, Third Edition. Chapman and Hall, New York. 661 pp.

Gilhousen, P. 1990. Prespawning mortalities of sockeye salmon in the Fraser River system and possible causal factors. Int. Pac. Salmon Fish. Comm. Bulletin XXVI. 58 pp. (Available at www.psc.org/pubs/IPSFCbulletinXXVI.pdf).

Grant, S.C.H., and G. Pestal. 2012. Integrated biological status assessments under the Wild Salmon Policy using standardized metrics and expert judgement: Fraser River sockeye salmon (*Oncorhynchus nerka*) case studies. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/206. 132 pp.

Grant, S.C.H., B.L. MacDonald, T.E. Cone, C.A. Holt, A. Cass, E.J. Porszt, J.M.B. Hume, and L.B. Pon. 2011. Evaluation of uncertainty in Fraser sockeye (*Oncorhynchus nerka*) wild salmon policy status using abundance and trends in abundance metrics. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/087. 183 pp.

Healey, M.C., M.A. Henderson, and I. Burgetz. 2000. Precocial maturation of male sockeye salmon in the Fraser River, British Columbia, and its relationship to growth and year-class strength. Can. J. Fish. Aquat. Sci. 57: 2248–2257. doi:10.1139/cjfas-57-11-2248.

Henderson, M.A., and A.J. Cass. 1991. Effect of smolt size on smolt-to-adult survival for Chilko Lake sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 48: 988–994.

Holmes J., G. Cronkite, H. Enzenhofer, and T. Mulligan. 2006. Accuracy and precision of fish-count data from a "dual-frequency identification sonar" (DIDSON) imaging system. ICES J. Mar. Sci. 63: 543–555. doi:10.1016/j.icesjms.2005.08.015.

Holtby, L.B., and K.A. Ciruna. 2007. Conservation units for Pacific salmon under the wild salmon policy. DFO Can. Sci. Advis. Sec. Res. Doc. 2007/070. 350 pp. (Available at www.dfo-mpo.gc.ca/CSAS/Csas/DocREC/2007/RES2007_070_e.pdf).

Hume, J.M.B., K.S. Shortreed, and K.F. Morton. 1996. Juvenile sockeye rearing capacity of three lakes in the Fraser River system. Can. J. Fish. Aquat. Sci. 53: 719–733.

Hyatt, K.D, D.J. McQueen, K.S. Shortreed, and D.P. Rankin. 2004. Sockeye salmon (*Oncorhynchus nerka*) nursery lake fertilization: review and summary of results. Environ. Rev. 12: 133–162. doi:10.1139/a04-008.

Irvine, J.R., and S.A. Akenhead. 2013. Understanding smolt survival trends in sockeye salmon. Mar. Coast. Fish. 5: 303–328. doi:10.1080/19425120.2013.831002.

Johnston, N.T., E.A. Parkinson, A.F. Tautz, and B.R. Ward. 2002. Biological reference points from deterministic stock-recruit relations. Province of British Columbia Fish. Proj. Rep. No. RD100 (manuscript). 43 pp. (Available at www.env.gov.bc.ca/wld/documents/fisheriesrpts/FPR100.pdf).

Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace, and R.C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bull. Am. Meteorol. Soc. 78: 1969–1080.

Mantua, N.J., N.G. Taylor, G.T. Ruggerone, K.W. Myers, D.B. Preikshot, X. Augerot, N.D. Davis, B. Dorner, R. Hilborn, R.M. Peterman, P. Rand, D. Schindler, J. Stanford, R.V. Walker, and C.J. Walters. 2009. The salmon MALBEC project: A North Pacific-scale study to support salmon conservation planning. N. Pac. Anadr. Fish Comm. Bull. 5: 333–354. (Available at www.npafc.org).

McElreath, R. 2016. Statistical rethinking: A Bayesian course with examples in R and Stan. CRC Press. Taylor & Francis, Boca Raton. 469 pp.

McKinnell, S.M. 1995. Age-specific effects of sockeye abundance on adult body size of selected British Columbia sockeye stocks. Can. J. Fish. Aquat. Sci. 52: 1050–1063.

McKinnell, S.M. 2008. Fraser River sockeye salmon productivity and climate: A re-analysis that avoids an undesirable property of Ricker's curve. Prog. Oceanogr. 77: 146–154. doi:10.1016/j.pocean.2008.03.014.

McKinnell, S.M., E. Curchitser, K. Groot, M. Kaeriyama, and K.W. Myers. 2012. PICES advisory report on the de-

cline of Fraser River sockeye salmon *Oncorhynchus nerka* (Steller, 1743) in relation to marine ecology. PICES Sci. Rep. No. 41. 149 pp. (Available at www.pices.int).

McQueen, D.J., K.D. Hyatt, D.P. Rankin, and C. Ramcharan. 2007. Changes in algal species composition affected juvenile sockeye salmon production at Woss Lake, British Columbia: a lake fertilization and food web analysis. N. Am. J. Fish. Manage. 27: 369–386.

Millar, R.B. 1987. Maximum likelihood estimation of mixed stock fishery composition. Can. J. Fish. Aquat. Sci. 44: 583–590.

Miller, K.M, M. Trudel, D.A. Patterson, A. Schulze, K. Kaukinen, S. Li, N. Ginther, T. Ming, and A. Tabata. 2013. Are smolts healthier in years of good ocean productivity? N. Pac. Anadr. Fish Comm. Tech. Rep. 9: 165–168. (Available at www.npafc.org).

Miller, K.M, A. Teffer, S. Tucker, S. Li, A.D. Schulze, M. Trudel, F. Juanes, A.Tabata, K.H. Kaukinen, N.G. Ginther, T.J. Ming, S.J. Cooke, J.M. Hipfner, D.A. Patterson, and S.G. Hinch. 2014. Infectious disease, shifting climates, and opportunistic predators: cumulative factors potentially impacting wild salmon declines. Evol. Appl. 7: 812–855. doi:10.1111/eva.12164.

Moussalli, E., and R. Hilborn. 1986. Optimal stock size and harvest rate in multistage life history models. Can. J. Fish. Aquat. Sci. 43: 135–141.

Mueter, F.J., B.J. Pyper, and R.M. Peterman. 2005. Relationships between coastal ocean conditions and survival rates of Northeast Pacific salmon at multiple lags. Trans. Am. Fish. Soc. 134: 105–119.

Ogden, A.D., J.R. Irvine, K.K. English, S. Grant, K.D. Hyatt, L. Godbout, and C.A. Holt. 2015. Productivity (recruits-per-spawner) data for sockeye, pink, and chum salmon from British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 3130. 57 pp.

Peterman, R.M. 1981. Form of random variation in salmon smolt-to-adult relations and its influence on production estimates. Can. J. Fish. Aquat. Sci. 38: 1113–1119. doi:10.1139/f81-151.

Peterman, R.M. 1984. Density-dependent growth in early ocean life of sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 41: 1825–1829.

Peterman, R.M., B.J. Pyper, and B.W. MacGregor. 2003. Use of the Kalman Filter to reconstruct historical trends in productivity of Bristol Bay sockeye salmon (*Oncorhynchus nerka*). Fisheries 824: 809–824. doi:10.1139/F03-069.

Pyper, B.J., and R.M. Peterman. 1999. Relationship among adult body length, abundance, and ocean temperature for British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*), 1967–1997. Can. J. Fish. Aquat. Sci. 56: 1716–1720. doi:10.1139/cjfas-56-10-1716.

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Bd. Canada. 11: 559–623.

Ricker, W.E. 1997. Cycles of abundance among Fraser River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 54: 950–968. doi:10.1139/cjfas-54-4-950.

Roos, J.E. 1991. Restoring Fraser River salmon: a history of the International Pacific Salmon Fisheries Commission 1937–1985. The Pacific Salmon Commission. Vancouver, Canada. 438 pp.

Ruggerone, G.T., and B.M. Connors. 2015. Productivity and life history of sockeye salmon in relation to competition with pink and sockeye salmon in the North Pacific Ocean. Can. J. Fish. Aquat. Sci. 72: 818–833. doi:10.1139/cjfas-2014-0134.

Scheuerell, M.D., R. Hilborn, M.H. Ruckelshaus, K.K. Bartz, K.M. Lagueux, A.D. Haas, and K. Rawson. 2006. The Shiraz model: a tool for incorporating anthropogenic effects and fish-habitat relationships in conservation planning. Can. J. Fish. Aquat. Sci. 63: 1596–1607.

Schubert, N.D. 1998. The 1994 Fraser River sockeye salmon (*Oncorhynchus nerka*) escapement. Can. Tech. Rep. Fish. Aquat. Sci. 2201. 62 pp.

Schubert, N.D., and B.P. Fanos. 1997. Estimation of the 1994 Chilko River and Chilko Lake sockeye salmon (*Oncorhynchus nerka*) escapement. Can. Man. Rep. Fish. Aquat. Sci. 2428. 54 pp.

Selbie, D.T., M.J. Bradford, M.J. Hague, J.M.B. Hume, E.A. MacIsaac, and D.A. Patterson. 2010. Are freshwater habitat conditions in the Fraser River watershed an important contributor to the Fraser sockeye situation? *In* Synthesis of evidence from a workshop on the decline of Fraser River sockeye: June 15-17 2010. *Edited by* R.M. Peterman and D. Marmorek. Pacific Salmon Commission, Vancouver. pp. 79–82.

Shortreed, K.S., and J.G. Stockner. 1983. A comparative limnological survey of 19 sockeye salmon (*Oncorhynchus nerka*) nursery lakes in the Fraser River system, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1190. 62 pp.

Shortreed, K.S., K.F. Morton, K. Malange, and J.M.B. Hume. 2001. Factors limiting juvenile sockeye production and enhancement potential for selected BC nursery lakes. DFO Can. Sci. Advis. Sec. Res. Doc. 2001/098. 69 pp.

Stan Development Team. 2014. Stan modeling language user's guide and reference manual. (Available at www.github.com/stan-dev/stan/releases/download/v2.6.0/stan-reference-2.6.0.pdf).

Tucker, S., M. Trudel, D.W. Welch, J.R. Candy, J.F.T. Morrison, M.E. Thiess, C. Wallace, D.J. Teel, W. Crawford, E.V. Farley, Jr., and T.D. Beacham. 2009. Stock-specific migrations of juvenile sockeye salmon along the west coast of North America: Implications for growth. Trans. Am. Fish. Soc. 138: 1458–1480. doi:10.1577/T08-211.1.

Walters, C.J., and J. Korman. 1999. Revisiting the Beverton-Holt recruitment model from a life history and multispecies perspective. Rev. Fish Biol. Fish. 9: 187–202.

Welch, D.W., B.R. Ward, B.D. Smith, and J.P. Eveson. 2000. Temporal and spatial responses of British Columbia steelhead (*Oncorhynchus mykiss*) populations to ocean climate shifts. Fish. Oceanogr. 9: 17–23.

Williams, I.V. 1977. Investigation of the pre-spawning mortality of sockeye in Chilko River in 1971. Int. Pac. Salmon Fish. Comm. Prog. Rep. 35. New Westminster, BC. 22 pp.

Williams, I.V., and D.F. Amend. 1976. A natural epizootic of infectious hematopoietic necrosis in fry of sockeye salmon (*Oncorhynchus nerka*) at Chilko Lake, British Columbia. J. Fish. Res. Board Canada 33: 1564-1567.

Wood, C.C., S. McKinnell, T.J. Mulligan, and D.A. Fournier. 1987. Stock identification with the maximum-likelihood mixture model: sensitivity analysis and application to complex problems. Can. J. Fish. Aquat. Sci. 44: 866–884.

Appendix 1. Computer code for Stan models in Tables 3–6.

```
data {
    int      N;                              # number of years
    vector[N]  X;                            # parents
    vector[N]  Y;                            # survivors
    vector[N]  H;                            # habitat factor, shared survival, 0 to 1
    vector[N]  G0;                           # habitat factor, before channel,  0 or 1
    vector[N]  G2;                           # habitat factor, after channel,  0 or 1
    vector[N]  W;                            # variance factor, 0 to 1
    vector[10] P;                            # priors
}


parameters {
    real<lower=0> Prod;                      # inital productivity
    real<lower=0> g_PG0;                     # effect on Prod of G0
    real<lower=0> g_PG2;                     # effect on Prod of G2
    real<lower=0> g_PH;                      # effect on Prod of H
    real<lower=0> Cap;                       # asymptotic capacity
    real<lower=0> g_CG0;                     # effect on Cap of G0
    real<lower=0> g_CG2;                     # effect on Cap of G2
    real<lower=0> g_CH;                      # effect on Cap of H
    real<lower=0> sigma;                     # SD of lognormal residuals
    real<lower=0> g_W;                       # effect on sigma of W
}


model {
# internal variables
    vector[N] p;                            # Prod by year
    vector[N] c;                            # Cap by year
vector[N] s;                                # sigma by year
    vector[N] Yfit;                         # predicted, compare to data
# prior distributions.
Prod    ~ gamma(2,1/P[1]);
    g_PG0       ~ gamma(2,1/P[2]);
    g_PG2       ~ gamma(2,1/P[3]);
g_PH    ~ normal(0, P[4]);
Cap ~ gamma(2,1/P[5]);
    g_CG0       ~ gamma(2,1/P[6]);
    g_CG2       ~ gamma(2,1/P[7]);
    g_CH        ~ normal(0, P[8]);
    sigma       ~ gamma(2,1/P[9]);
    g_W ~ normal(0, P[10]);
```

```
# factor effects
    c <- Cap  + g_CG0*G0 + g_CG2*G2 + g_CH*H;
    p <- Prod + g_PG0*G0 + g_PG2*G2 + g_PH*H;
    for(n in 1:N){s[n] <- sigma*pow(W[n],-g_W);} # weighted SD
# prediction and likelihood
    Yfit <- X ./ ( 1 ./ p  + X ./ c);
    Y ~ lognormal(log(Yfit), s); # add to log likelihood
}


generated quantities {
    real Prod0; real Prod2; real Prod3;
    real  Cap0; real  Cap2; real  Cap3;
real Emsy;      real Rmsy;
    Prod0 <- Prod+g_PG0; Prod2 <- Prod+g_PG2; Prod3 <- Prod+g_PG2+g_PH;
Cap0  <-  Cap+g_CG0;  Cap2 <-  Cap+g_CG2;  Cap3 <-  Cap+g_CG2+g_CH;
    Emsy <- (Cap3/Prod3) * (sqrt(0.5*Prod3) -1.0);
    Rmsy <- Emsy / (1.0 / Prod3 + Emsy / Cap3);
}
```