A life history model for assessing alternative management policies for depressed chinook salmon

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Population and fishery dynamics are modelled to assess performance of alternative harvest policies for chinook that spawn in western North America. The sensitivity of model performance to variations in stock productivity and patterns of environment variation are explored to evaluate the trade-off between risk of extinction and benefits from harvest. Results indicate maximum economic benefit and low risk of extinction is not likely under the present harvest policy. Even with a conservative harvest-threshold policy, wherein harvest rates are reduced at low stock size and are zero if the stock size declines below an abundance threshold, the risk of extinction is significantly reduced compared to fixed harvest rate policies. Simulated abundance forecast errors within the historical range degraded model performance only slightly. With the constraint that risk of extinction be held below an acceptable level, socio-economic indicators reveal an optimal harvest-threshold policy at a fractional harvest of surplus abundance of about 0.45 and a threshold near 100 female spawners per stock. Based on coded-wire tag results for a major hatchery population, the mean historical harvest rate (1983–1991) was 0.6.

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Introduction

The stock assessment of most Pacific salmon populations suffers from weak information or short time periods of more quantitative information. The results are uncertainty in parameter estimates, disagreement about management goals, and frequently, a lack of management action. The latter results from denial of causes by users or governments leading to delay of appropriate responses. The consequences of these problems have become increasingly apparent as the status of many Pacific salmonid populations deteriorates (Nehlsen et al., 1991; Slaney et al., 1996), and, recently, as a decline in marine production in these populations (see Hare et al., 1999).

These issues apply particularly to the management and conservation of chinook and coho salmon in British Columbia, which consist of hundreds of small to medium-sized populations with very little information for assessment and management available for each. Stock-recruitment data are lacking and the results can be misleading (Hilborn and Walters, 1992). These species have been heavily exploited in large mixed-stock ocean fisheries that may not respond to changes in production from natural populations, due to the enormous numbers of chinook and coho salmon released from hatcheries (NPAFC, 1998) and mixed with the natural production.

Given this situation and the need to conserve natural populations, we have examined an alternative assessment process that synthesizes information from multiple sources and examines the effect of uncertainty on harvest policies. In general, the model integrates biological processes (implemented as sequential life stages) with fishery exploitation patterns and rates, and information on environmental variation. These models can be easily generalized but to be informative require data representative of specific stocks and areas. To demonstrate the procedure, we present the model to assess the consequences of alternative harvesting policies for chinook salmon along the west coast of Vancouver Island (WCVI), British Columbia, Canada. This example was

developed following the sudden decline in ocean production of these populations associated with the extended El Niño conditions during the early 1990s (Trenberth and Hoar, 1996). Poor marine survival of chinook entering the ocean in these years was predicted to result in only tens of females spawning in many of the natural populations.

Harvest of WCVI chinook has recently been managed under fixed-catch limits (ceilings) in most ocean fisheries (Pacific Salmon Treaty, 1985). Fixed-catch ceilings can not effectively limit harvest impacts, however, if abundance declines and ceilings are not reduced proportionately. Given the sudden reductions in production, there was a critical need to develop a harvest policy that would maintain spawning populations above a level that minimizes risk of extinction, and within that constraint, allows for economic benefits from the resource. The sensitivity of model performance to variations in stock productivity and patterns of environmental variation is explored to evaluate the trade-off between risk of extinction and benefits from harvest.

WCVI Chinook salmon

Chinook salmon have been recorded to reproduce in over 100 rivers along the west coast of Vancouver Island. Spawner abundance is highly variable with numbers exceeding 100 000 in the largest enhanced system (Robertson Creek Hatchery in the Somass/Stamp River) and down to hundreds in the natural populations (approximately 40 streams are believed to still support natural populations). Spawning occurs in mid to late autumn and juveniles migrate to sea in the following spring. Smolts remain in nearshore waters for a few months but then migrate northward into central British Columbia and through Alaskan coastal waters. Chinook are partially recruited to fisheries at age 3 (catch year minus brood year) due to size limits in many ocean fisheries and become fully recruited by age 4. Fishing mortality is caused principally by the southeast Alaskan and northern B.C. fisheries, and subsequently in terminal fisheries (i.e. near the natal streams). Mature adults principally return to natal streams during August and September. Age-at-maturity varies between sexes with males maturing, on average, 1 year earlier than females. These fall migrant (reference to adult migration), ocean-type (less than 1 year freshwater) chinook constitute the vast majority of production harvested in ocean fisheries from Washington State through SE Alaska.

Much of the information used to represent this stock has been collected through coded-wire tagging of chinook reared in hatcheries. In particular, the Robertson Creek Hatchery fish, which have been consistently tagged since 1971, has been used as the "indicator" stock for WCVI chinook. Indicator stocks have been widely utilized in chinook and coho assessments to
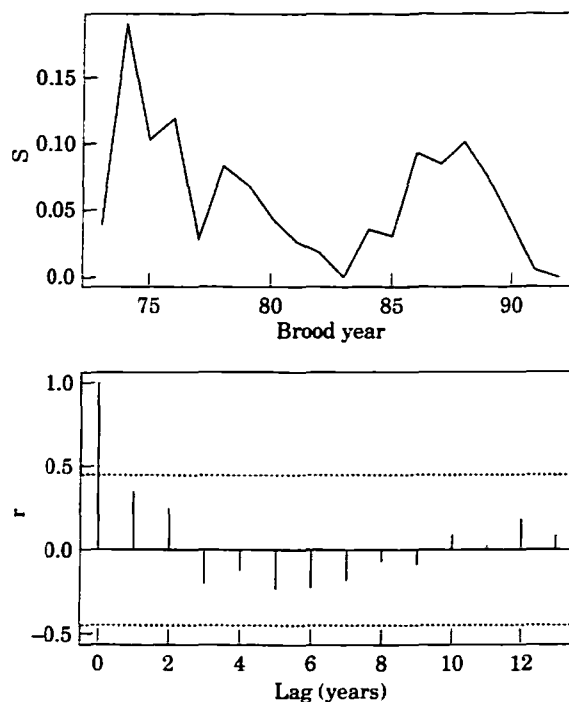

Figure 1. Time series of smolt-to-age-2 survival rates (S) and autocorrelation (r) of survival rates.

compensate for the limited information on natural populations (Chinook Technical Committee, 1996). These assessments assume that the ocean distributions, fishery exploitation patterns and rates, maturity rates, and survival variation measured in the hatchery-reared groups are indicative of the associated natural populations. This assumption is difficult to test since tagging of wild chinook smolts reduces survival. However, the similarity of variations in age structure between years and populations, the repeatability of distributions between multiple tagged populations, and the timing of terminal runs each support the assumption that this indicator is representative of variation in the natural populations.

Production of chinook has been highly variable depending on marine survival conditions. Estimates of smolt-to-age-2 survival, for the Robertson Creek indicator stock, vary over two orders of magnitude and are moderately autocorrelated ($r=0.4$ at lag 1), with extremely poor survival from the 1983 and 1992 cohorts (Figure 1).

Methods

We generated 1000 trial runs of 50 years each with starting population sizes fixed in the first 5 years to fill

the abundance-at-age matrix (maximum age of 5). The smolt-to-age-2 mortality rates estimated for 1989–1993 were used to fix the population age structure in year 6 at levels comparable to 1995. The abundance of later generations was controlled in an annual time step by the effects of natural and fishing mortality, maturity, and fecundity at age. Ocean survival (smolt-to-age-2) and exploitation rates used rely on information from coded-wire tagged (CWT) chinook from Robertson Creek Hatchery (production data available since 1971). Unbiased estimates of exploitation are available by fishery since 1983. The initial spawning population was set at 400 females, which is considered the typical size of the natural populations before the recent stock collapse.

The abundance of smolts $N_{0,t}$ in a particular year t is a function of egg abundance in year $t-1$ and egg-to-smolt survival S_0:

$$N_{0,t} = eggs_{t-1} * S_0 \exp(\sigma_0 \varepsilon_{t-1}) \tag{1}$$

where σ_0 is the standard deviation of the residuals and ε_{t-1} is a standard normal deviate. Unfortunately, estimates of ocean-type chinook egg-to-smolt survival rates are few and we used mean values ($S_0 = 0.087$) and standard deviations ($\sigma_0 = 0.689$) reported for chinook from Big Qualicum River (pre-hatchery) on the east coast of Vancouver Island (Fraser *et al.*, 1983; Bradford, 1995). These parameter values are within the range estimated for a variety of populations of ocean- and stream-type life histories sampled from British Columbia, Washington, and Oregon (Bradford, 1995).

The form of density dependency for wild stocks is not known. We used a simple rectilinear stock–recruit function that has a linear ascending left limb described by the above equation and a flat right limb (slope=0) to simulate the effect of freshwater carrying capacity. Other stock–recruitment functions are plausible, for example, that result in diminished smolt abundance at high stock size, i.e. a Ricker (1954) function. For purposes of evaluating dynamics at low stock sizes, a rectilinear relationship is considered the most parsimonious. Density-dependent factors are not particularly relevant since we are more concerned about factors affecting productivity at the lower end of the stock–recruitment relationship. The freshwater carrying capacity was set at 2000 female spawners or five times the initial spawning population. This number was sufficiently large to result in a negligible effect on extinction rates.

The abundance of age-2 chinook $N_{2,t}$, the first vulnerable age to fishing, is computed as the product of smolt abundance $N_{0,t}$ and smolt-to-age-2 survival (Figure 1):

$$N_{2,t} = N_{0,t} * \exp(-M_t) \tag{2}$$

where M represents natural mortality. To simulate long-term environmental effects on survival, we used an autoregressive random process $M_t = M_t + d_t$, where $d_t = rd_{t-1} + \omega_t$ has lag-1 and autocorrelation $0 \le r \le 1$, normally distributed changes ω_t with mean zero and standard deviation $\sigma = 1.37$. Given the short time series of smolt-to-age-2 survival rates the appropriate value of r is not clear. We tested the sensitivity of model performance at increments of $r = (0.3, 0.5, 0.8)$. We also tested the effect of simulating recruitment correlation by repeating the observed time series of smolt-to-age-2 survival throughout the 50-year run.

Age 2–5 chinook are vulnerable to fisheries. Pre-fishery survival was computed in annual time steps first by applying fixed age-specific natural survival rates S (age 2–5 = 0.6, 0.7, 0.8, 0.9) and second by applying age and ocean fishery-specific exploitation rates μ. The estimates of S applied here were derived from Ricker (1976) in Healey (1991). Exploitation rates were applied stochastically by randomly sampling the empirical year and fishery-specific exploitation rates based on CWT chinook (1983–1991 brood years). Catch at age i was computed as the abundance times the exploitation rates μ_{ij} for ocean fishery j summed over n fisheries:

$$C_{i,t} = N_{i,t} \sum_{j=1}^{n} \mu_{ij} \tag{3}$$

Escapement E from ocean fisheries was computed by applying fixed age-specific maturity rates MR:

$$E_{i,t} = MR_i(N_{i,t}S_i - C_{i,t}) \tag{4}$$

Maturity rates were also estimated from CWT data and for ages (2, 3, 4) = (0.037, 0.152, 0.586). All fish surviving to age-5 are assumed to reach maturity (MR = 1).

The annual time step to obtain the abundance of a particular age group in a particular year as a function of survival less catch and escapement in the previous year is summarized as follows:

$$N_{i+1,t+1} = N_{i,t}S_i - (C_{i,t} + E_{i,t}) \tag{5}$$

Terminal fisheries were simulated by applying a fixed terminal exploitation rate of 20% to mature components of age 2–5 chinook. Female escapement was computed using estimates of female proportions (FP) at age (2, 3, 4, 5) = (0.0, 0.07, 0.5, 0.75) based on average annual values for Robertson Creek. Note that almost all of the age-2 and age-3 returns are males. The number of eggs contributing to future smolt production was computed as the fecundity-at-age for ages 3–5 times the female abundance-at-age:

$$eggs_t = \sum_{i=3}^{5} (FP_i * E_{i,t} * fecundity_i) \tag{6}$$

Mean number of eggs per female (fecundity) was fixed at mean values for ages (3, 4, 5)=(4000, 4400, 4800) computed from relationships in Healey and Heard (1984).

Annual pre-season forecasts of abundance are used to develop management plans in order to achieve escapement targets. Forecasts are based on sibling regression models that predict older aged cohorts from maturing younger aged chinook from the same cohort. Mean forecast error (10%) has been remarkably low. However, the time series is short and the long-term prediction error may be underestimated. Forecasts were incorporated to assess effects of forecast error whereby $N_t'=N_t \exp(v_t)$. Here, v_t represent independent annual forecast errors in population abundance. Fishery performance indicators are expected to degrade in proportion to the amount of forecasting error and the effect was evaluated at increments of mean error equal to ± 0, 10, and 100%.

Alternative harvest policies consisted of fixed fractional removals f of surplus abundance ranging from f=(0.2–0.7). Surplus abundance is the population abundance minus the threshold. We used thresholds expressed as females ranging from 0 to 300 chinook. If the forecast of female abundance was above the specified threshold, a fixed harvest on surplus abundance was applied. If the harvest was sufficient to result in forecasts below the threshold, the fishery was closed once the threshold was reached.

The performance indicators used to evaluate alternative fishery policies are: (1) probability of extinction; (2) long-term catch; (3) catch variance; and (4) the frequency of fishing closures. The stock was considered "extinct" if the 3-year running sum of female escapement declined to 10% of the initial population. Risk of extinction was quantified as the mean probability of the stock becoming extinct within 20 years following implementation of a particular harvest policy. As reproductive output is derived from three overlapping age classes (age-3 to age-5), unacceptably low escapements in three consecutive years were considered sufficient to eliminate the mitigating effect of a potential recruitment buffer that might still exist after 3 years. The choice of an initial 400 female spawning population infers a 3-year running sum of 40 females at extinction.

Maximizing the long-term catch is obviously desirable and is akin to the traditional biological objective of maximum sustainable yield. The long-term catch was computed as the median cumulative catch derived from 1000 simulations. The coefficient of variation (CV) of the long-term catch was computed within each trial and then averaged over 1000 simulations. The probability of a fishery closure was computed as the mean frequency of closures within a 20 year period after implementation of a specific harvest policy.
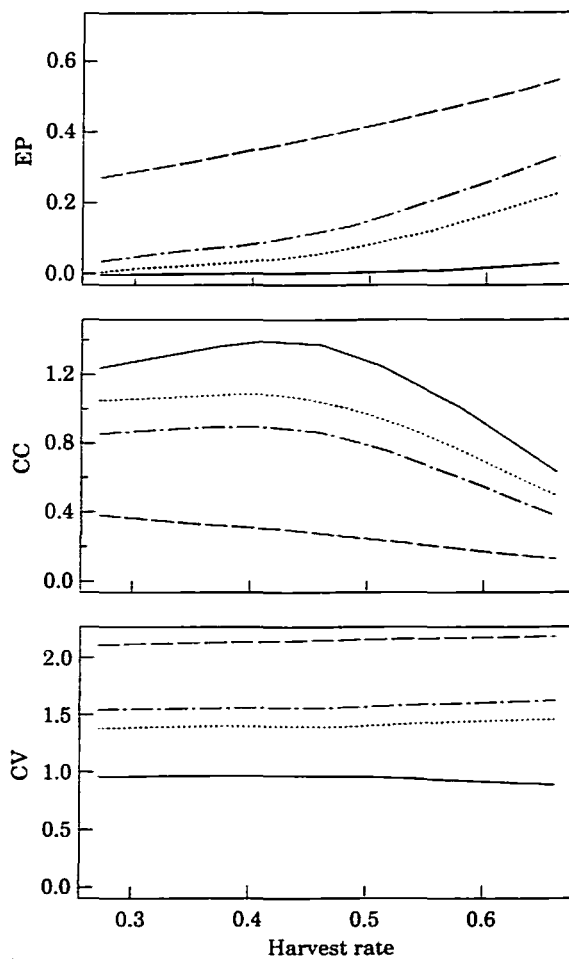

Figure 2. Effect of recruitment autocorrelation (r) on extinction probability in 20 years (EP), cumulative 50-year catch × 100 000 (CC), and catch coefficient of variation (CV): "empirical" (——) refers to simulations where the observed trend in survival was repeated throughout the 50-year time series (· · ·, r=0.3; – · – ·, r=0.5; – – –, r=0.8).

Results

Simulation results under a fixed harvest rate policy (zero threshold) result in the largest long-term catches at exploitation rates of 0.4–0.5 (Figure 2). The risk of extinction increases rapidly at exploitation rates >0.5. The catch CV is independent of exploitation rate. All performance indicators are sensitive to the degree of autocorrelation in ocean survival (Figure 2). Performance indicators under assumptions of high correlated survival (r=0.8) are seriously degraded to the point where stock collapse would likely have already occurred under the present harvest policy. Even under low harvest regimes ($\mu=0.3$), highly correlated survival rates result in an extinction probability of nearly 0.3 in 20 years. At moderate correlations in survival (r=0.5), the risk of
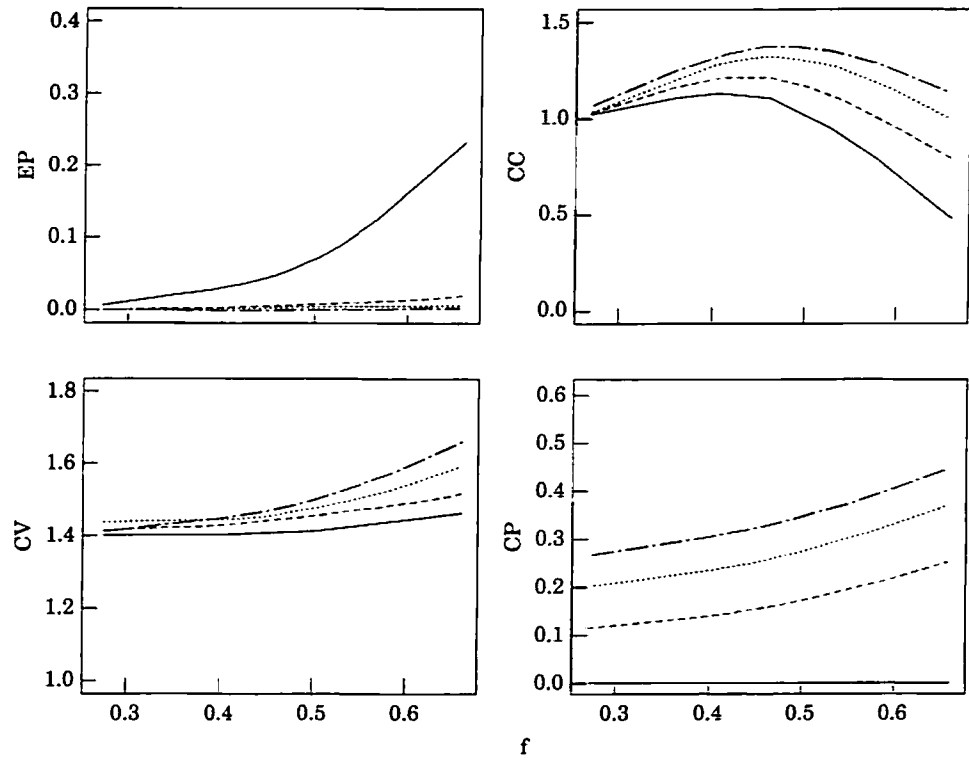
Figure 3. Effect of different harvest-threshold policies on extinction probability (EP), cumulative catch (CC), catch coefficient of variation (CV), and fishing closure probability (CP): thresholds in numbers of females (——, 0; – – –, 100; · · ·, 200; – · – ·, 300); harvest rate (f) is the fractional removal of surplus abundance; autocorrelation r=0.36; zero forecast error.

extinction is still high (0.2) at harvest rates near the historical mean (0.6 for WCVI stocks).

Threshold harvest policies reduce the risk of extinction compared to policies without a threshold (Figure 3), even when a conservative threshold of 100 female spawners is applied. Also the long-term catch is increased as the immediate effect of maintaining spawning escapements during low survival periods. The downside of threshold harvesting is inter-annual instability in catch.

Threshold harvesting requires abundance forecasts. Forecast error reduces long-term catch, increases catch CV and increases the risk of extinction (Figure 4). As we chose to model forecast error with lognormal error, closure probability is lower because fisheries more often remain open as a result of incorrectly forecasting escapements above the threshold. Forecast errors within the range of 0 to 100% result in relatively low performance degradation.

Clearly, reducing harvest rates from 0.6 (historical mean) to 0.45 increases long-term yield. Such a reduction coupled with thresholds may dramatically reduce risk of extinction. Gradients of extinction in response to harvest-threshold combinations increases disproportionately as fractional removals of surplus abundance increase beyond 0.5 and at thresholds <50 females

(Figure 5). The ultimate choice of an appropriate harvest-threshold policy is obviously constrained by the level of extinction risk deemed to be acceptable. Gradients of model performance resulting from various combinations may be used for measuring the socio-economic trade-off at various levels of extinction risk. At recruitment correlations near the value computed from the available data (r=0.36) and mean forecast errors of 10%, extinction probabilities hardly change in response to harvest rates <0.45 and at thresholds >100 females (Figure 5). The simulations predict that further reductions in probabilities of extinction to less than 0.6% in 20 years are difficult to achieve without severe constraints on fishing. Conversely, small increases in fractional surplus removals above 0.5 and/or reductions in the threshold below 100 females result in disproportionately larger risks of extinction. Extinction gradients occur in broad regions of threshold-harvest rate space. Once an acceptable level of risk is agreed upon, the threshold-harvest rate combination that maximizes yield and minimizes catch variance or frequency of fishery closures may be chosen (Figure 5). For instance, at an extinction probability of 0.6% in 20 years, the optimal harvest policy that combines a near maximum long-term catch and a minimal catch variance would be to set a threshold near 100 females and to implement a harvest f of 0.45.
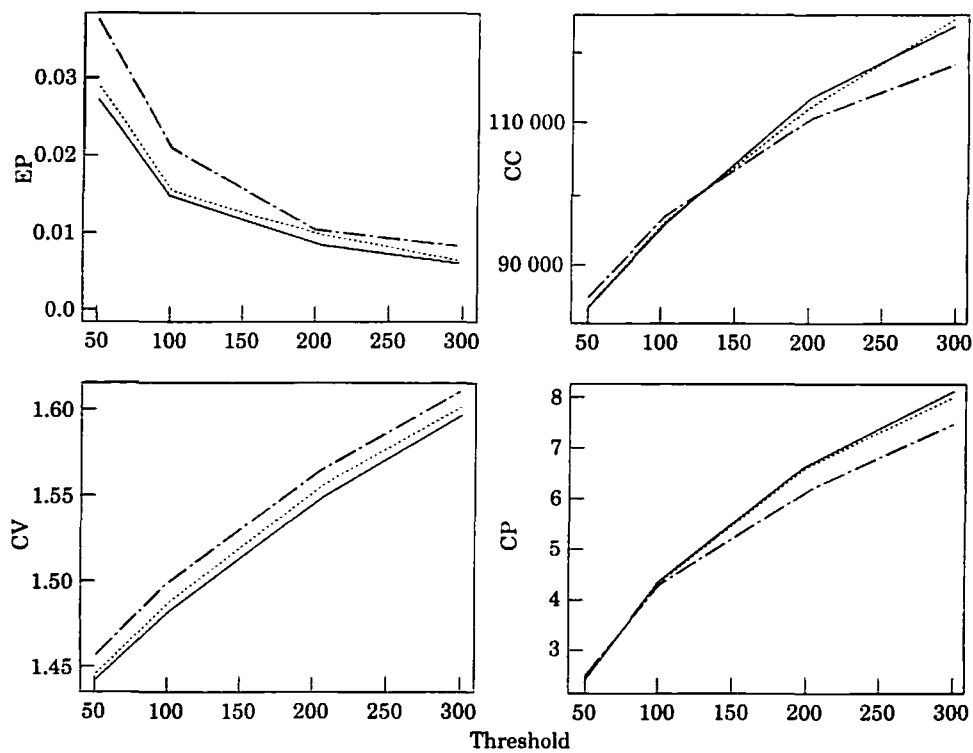
Figure 4. Effect of forecast error (——, 0%; ⋯, 10%; · – · –, 100%) on model performance indicators (see Figure 3): autocorrelation r=0.36; fixed harvest rate of 60%, zero threshold.

The corresponding probability of a closure would be about once every 10 years.

Discussion

Previous methods for the development of chinook management plans within the Pacific Salmon Commission have relied upon a deterministic but comprehensive model of coast-wide stocks and fisheries extending from Alaska to Oregon. The utility of this deterministic model in forecasting production trends has recently been compromised by the extreme variability observed in marine survival. Stochastic life history models, such as described here, allow incorporation of parameter variability when evaluating exploitation policies for sustaining future production.

The large variability in observed ocean survival rates and the sensitivity of model performance to assumptions about the pattern of recruitment variation imply that chinook in the north Pacific are at risk under the present harvest policy. Indeed, forecasts of abundance in 1996 indicated that conservation goals were not attainable under the present harvest regime as a result of prevailing poor ocean survival rates. This prompted conservation measures by restricting Canadian fisheries in order to increase the chance of meeting conservation goals. In addition, terminal Indian fisheries were likely

to be compromised by excessive harvests in ocean fisheries.

Neglecting the possibility of extinction from stochastic processes, Parma (1990) and Walters and Parma (1996) concluded that fixed harvest rate strategies (catch is proportional to abundance) are optimal for stocks with cyclic or autocorrelated survival patterns and should result in long-term performance that is within 15% of the theoretical optimum for a wide variety of populations. Also, their study shows that fixed escapement policies are only optimal when environmental effects are stationary and uncorrelated. Lande *et al.* (1995, 1997) showed that a constant harvest rate policy results in a greater risk of extinction than when a population threshold is specified below which harvest rate is set to zero.

Our simulation results indicate that even conservative thresholds are effective in reducing the risk of stock collapse. Depending on the degree of autocorrelation in recruitment, thresholds are also likely to increase long-term yield through immediate effects of sustained escapement during periods of low survival. Fisheries managers need to consider the trade-off between risk, yield, and catch instability in response to particular management strategies. Long-term yield increases over a broad range of thresholds. Higher thresholds result in larger variations in annual catches and more frequent
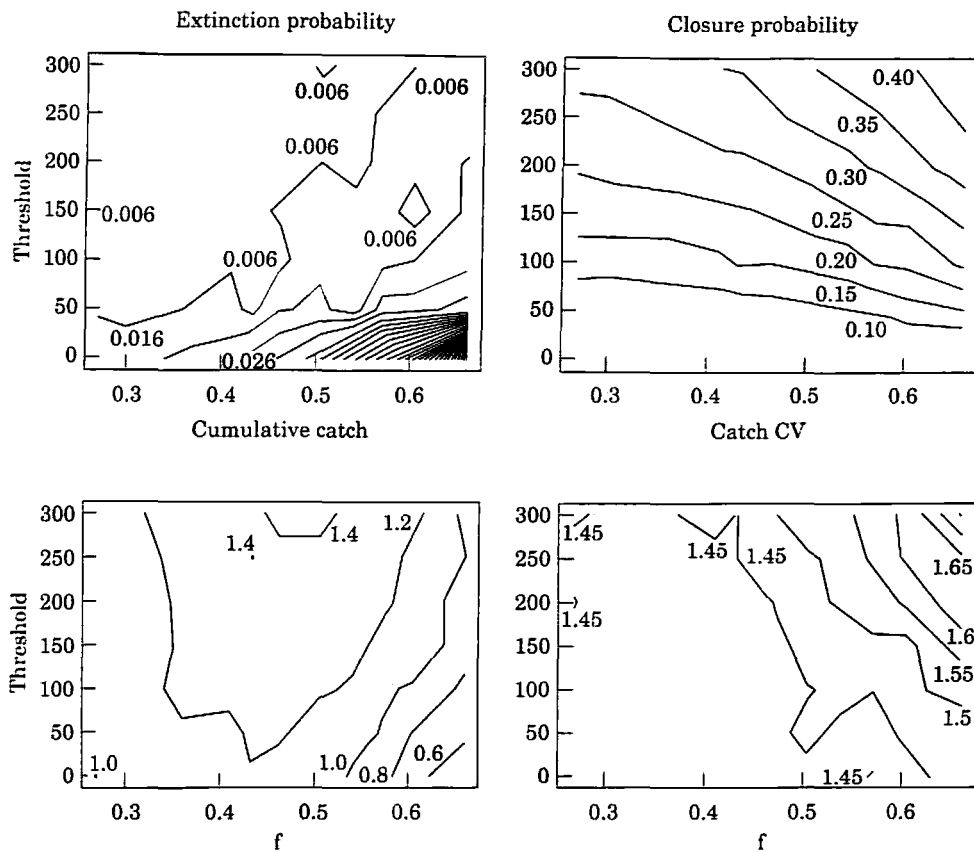
Figure 5. Gradients of model performance indicators (see Figure 3) measured as response to fractional harvest rate of surplus abundance and threshold: autocorrelation r=0.36; forecast error=10%.

fishing closures. Recognizing that equal gradients of risk, long-term catch, and catch variance occur along broad regions of threshold-harvest rate space, optimal threshold-harvest combinations can be identified that maximize economic benefit (high yield and low fishery disruption) conditional on an acceptable level of risk.

Fisheries in other management regions ultimately affect the effectiveness of management policies imposed upon particular fisheries aimed at reducing risk during periods of low survival. Because chinook that spawn in Canada are fished outside Canada's management zone, those fisheries, in the absence of a fishing agreement, simply act as a source of uncontrolled mortality. To achieve a specified level of risk, more restrictive harvesting regimes may therefore be required locally (i.e. more frequent closures/higher thresholds) than suggested here if the burden of the restrictions is not shared equally among all fisheries.

The simulation model presented does not include all facets of the life history and fishery dynamics of WCVI chinook. In particular, effects of interactions among individual populations and metapopulation dynamics

are not considered. Also, the model does not fully explore the range of plausible harvest policies and performance indicators. Thus, the simulations rather represent a first step in utilizing the available life history and fishery data. Future development logically extends to the multi-stock and fishery situations that exist in all ocean fisheries for chinook salmon along the Pacific coast of North America.

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