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In-Season Forecasting of Coho Salmon Marine Survival via Coded Wire Tag Recoveries

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Abstract.—Calculation of in-season marine survival rate forecasts for coho salmon *Oncorhynchus kisutch* can provide valuable support for in-season harvest management decisions because annual variability in marine survival accounts for a large proportion of total recruitment variability. We present a new forecasting model that utilizes coded wire tag (CWT) recovery information from early occurring fisheries to provide in-season marine survival forecasts that are timely enough to inform harvest management decisions for subsequent fisheries. We evaluate performance of the CWT model by using retrospective analyses on four coho salmon indicator stocks from northern British Columbia, Canada. For each stock, model selection analysis was used to identify which of three time-varying fishery catchability models used within the CWT model maximized forecasting performance. A Bayesian approach to parameter estimation was then applied to the best CWT model to generate probabilistic forecasts of marine survival rate for six consecutive weeks of in-season forecasting in each year. Although forecasted posterior distributions were wide in some cases, the posterior mode tracked marine survival relatively well in comparison with postseason marine survival estimates based on recoveries from all fisheries and the spawning grounds. Average percent forecast biases based on posterior modes were −1, −4, 19, and 57% for the four indicator stocks in the final week of forecasting. The lower tails of the posterior distributions were well defined, which is most relevant to identifying years of conservation concern due to extremely low marine survival. We conclude that timely in-season recovery and analysis of CWT information could improve the level of information available to inform in-season harvest management decisions.

Annual forecasts of smolt-to-adult survival in the marine environment can provide valuable support for Pacific salmon harvest management decisions because high interannual variations in marine survival cause large fluctuations in recruitment. For North Pacific populations of coho salmon *Oncorhynchus kisutch*, variability in marine survival accounts for 48–68% of the total variability in recruitment, the remainder being attributed to smolt production (Shaul et al. 2007). For this reason, marine survival estimates, along with estimates of freshwater productivity, are critical for determining sustainable exploitation rates for coho salmon (Bradford et al. 2000). A large amount of effort has been invested in studying environmental variables affecting coho salmon marine survival over the past two decades (e.g., Nickelson 1986; Coronado and Hilborn 1998; Hobday and Boehlert 2001). However, retrospective analyses show that predictive abilities of these relationships inevitably fail in some years because of unexplained biological and physical factors (Cole et al. 2001; Logerwell et al. 2003). Furthermore, high local and regional variability in the response of Pacific salmon marine survival to environmental variables (Coronado and Hilborn 1998; Peterman et al. 1998; Quinn et al. 2005) will require these types of predictive relationships to be continually redefined for different management areas, as well as through time.

We present a new forecasting model that utilizes coded wire tag (CWT) recovery information from early occurring fisheries to provide in-season forecasts of marine survival that are timely enough to inform harvest decisions about subsequent fisheries. In-season management regimes attempt to achieve conservation and harvest objectives by revising harvesting decisions throughout the fishing season as new and presumably more informative data become available. Preseason recruitment forecasts based on factors such as spawning stock abundance, previous years' recruitment levels, environmental variables, and recruitment of sibling age-classes (i.e., jacks that return to spawn after only one summer at sea as opposed to two summers for the normal adults) remain an important part of most

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salmon management procedures because they allow harvesters and managers to plan for upcoming fisheries. However, the generally poor performance of preseason forecasting models in retrospective analyses (Haeseker et al. 2008) has led to an increased reliance on in-season forecasts to make decisions about when and where to open fisheries (Claytor 1996; Su and Adkison 2002; Hyun et al. 2005). Typically, in-season forecasting methods have focused on estimating total return abundance; however, in mixed-stock fisheries where total abundance is difficult to define, estimates of marine survival can play an important role in in-season forecasting. For example, marine survival rates can be combined with estimates of total smolt production to predict the total abundance of fish from a given stock recruiting to fisheries and spawning grounds. Where estimates of smolt production are not available, marine survival rate estimates will still provide valuable insight into the potential for low adult returns.

We evaluate performance of the CWT return forecasting model using retrospective analyses on four coho salmon indicator stocks from northern British Columbia, Canada. These stocks are a good example of the above challenges to preseason and in-season forecasting for several reasons. First, preseason forecasts of return abundance for northern British Columbia coho salmon have historically been generated using time-series and sibling analyses; however, these forecasting methods have performed poorly due to high interannual variation in marine survival and low proportions of fish returning to inland rivers as jacks (Sawada et al. 2003). As a consequence, unreliable forecasts for the 1997 return year led to an approximately 55% exploitation rate being applied to one of the lowest recruitments on record. Second, coho salmon are encountered as directed and incidental catch in six mixed-stock fisheries in both Alaska and northern British Columbia, which makes it difficult to obtain reliable stock-specific recruitment information. Although catch levels for southeast Alaska and northern British Columbia stocks have been correlated during the past few decades, they have also shown periods of strong divergence (PSC 2002). The feasibility of using catch indices from Alaskan and Canadian mixed-stock fisheries to forecast total return abundance has been examined; however, predictive abilities are generally poor (Holtby 2000). Finally, extremely low marine survival rates and escapement levels throughout the 1990s have led to conservation concerns for several northern British Columbia coho salmon stocks (PSC 2002). In light of these challenges, early identification of years in which stocks will experience undesirably low marine survival rates before the opening of Canadian commercial fisheries has been identified as a key management requirement (Holtby 2000). Because Canadian commercial fisheries are managed using effort control, triggering of the early warning signal for any one indicator stock would result in Canadian commercial fisheries remaining closed for the year.

The coordinated, coastwide CWT program has been maintained between Canadian and U. S. fisheries management agencies since the late 1970s (Johnson 2004). This program allows the fate of specific groups of Pacific salmon to be tracked from the time of tagging as juveniles to tag recovery in fisheries or terminal spawning areas. A standardized sampling and reporting protocol has been established, and information is shared among agencies in both countries via an online database. The primary purpose of the CWT program is to monitor stock composition of catch and to estimate stock-specific exploitation and marine survival rates in the postseason. The CWT information is not commonly used for forecasting purposes; however, the interception of British Columbia-bound fish by Alaska fisheries several weeks before the opening of the Canadian fishery, as well as the relatively quick turnaround time for tag processing and data entry (approximately 2 weeks), provides an ideal opportunity to apply this information to in-season harvest decisions.

Methods

We used a Bayesian approach to parameter estimation to generate posterior probability distributions that describe uncertainty in forecasts of marine survival rates. The calculation of a probabilistic forecast is beneficial because it provides decision makers with a simple, visual representation of uncertainty in estimated rates. In the case of northern British Columbia coho salmon, we are interested in providing in-season management support in the form of a statement about the probability that marine survival is below a threshold level that has historically been associated with poor return abundance. This type of information will help Canadian fishery managers make informed decisions about whether or not to open Canadian commercial fisheries.

We present our methods in three sections: (1) the context for our application of the CWT model to northern British Columbia coho salmon; (2) descriptions of the CWT model, a model selection analysis conducted on time-varying fishery catchability models used within the CWT forecasting procedure, and the Markov Chain Monte Carlo (MCMC) method used to generate probabilistic forecasts of marine survival rate;

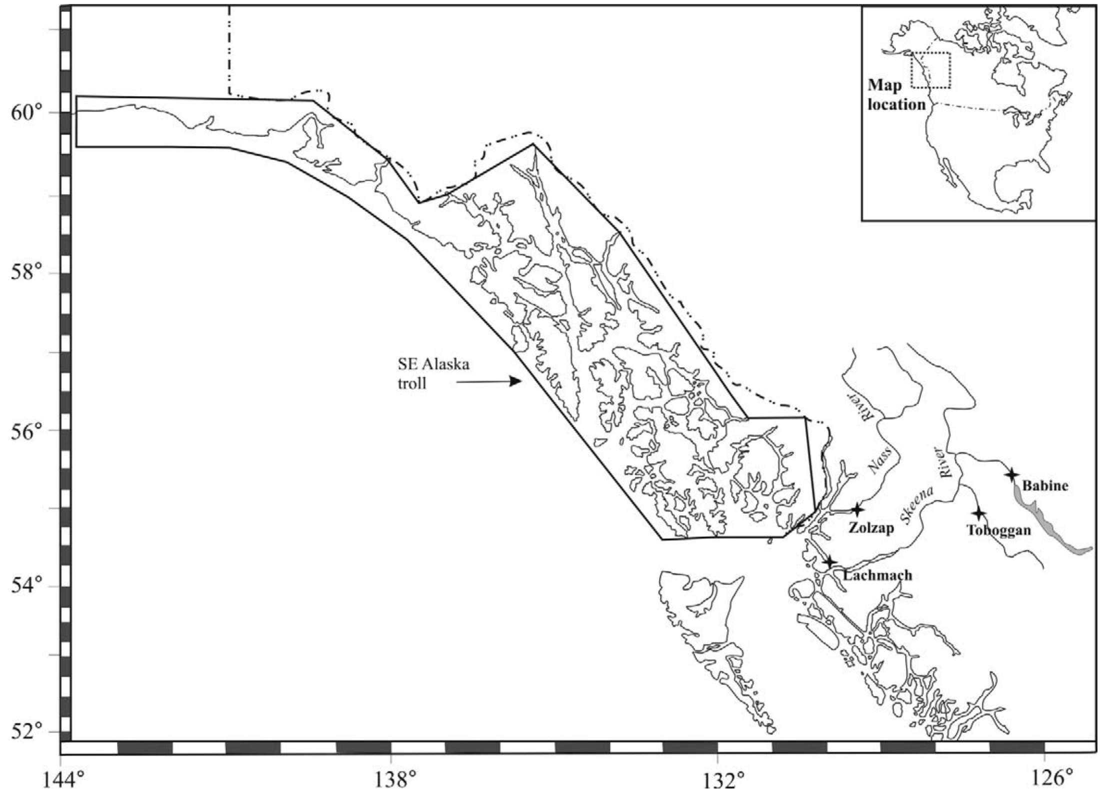

FIGURE 1.—Locations of four northern British Columbia streams (indicated with stars) containing coho salmon indicator stocks, and the area fished by the southeast Alaska troll fishery, from which coded-wire-tagged fish were recovered.

and (3) details of the retrospective analysis used to evaluate forecasting performance.

Application to Northern British Columbia Coho Salmon

Biological and fishery considerations.—Two of the four northern British Columbia coho salmon indicator stocks, the Babine River and Toboggan Creek stocks, are located in the Skeena River watershed (Figure 1). The third stock is located in Zolzap Creek within the Nass River watershed, and the fourth stock is found in the Lachmach River, a coastal system located between the Skeena and Nass rivers. These four systems differ from each other in several respects, including location (coastal versus interior), average recruitment level, and average marine survival rate (Table 1). The predominant life cycle for northern British Columbia coho salmon extends 3 years. Spawning occurs in October and November, and fry emerge from the gravel the following spring. Juveniles spend 1–3 years in freshwater before migrating to sea as smolts between April and June. Marine CWT recoveries of northern British Columbia coho salmon are mostly from fisheries in southeast Alaska and northern British Columbia (including the Queen Charlotte Islands), which suggests a northerly ocean distribution pattern along the British Columbia coast and the Alaskan panhandle (Weitkamp and Neely 2002). All females and most males spend about 16 months at sea before returning to their natal streams to spawn. A small proportion of males from coastal streams, including the Lachmach River indicator stock, return to spawn as jacks after spending only 4 or 5 months in the ocean. The Toboggan Creek, Zolzap Creek, and Babine River indicator stocks have no jacks. Migrating adults pass through Alaskan and northern British Columbia fisheries en-route to their natal streams between late June and September, and those heading to interior streams migrate earlier than those destined for coastal streams (PSC 2002).

During their migration back to spawning streams, northern British Columbia coho salmon are encountered in up to six mixed-stock ocean fisheries and two freshwater fisheries. Ocean fisheries include the southeast Alaskan troll fishery that intercepts the fish as they migrate from Alaska back to northern British

TABLE 1.—Comparison of coded wire tag (CWT) data and stock characteristics for northern British Columbia coho salmon indicator stocks of Toboggan Creek, Lachmach River, Babine River, and Zolzap Creek. Single numerical values are averages, and ranges are given in parentheses.

	Indicator stock			
Variable	Toboggan	Lachmach	Babine	Zolzap
CWT time series	1988–2005	1988–2003	1994–2001 2003–2004	1993–2004
Stock type	Hatchery	Wild	Hatchery	Wild
Recruitment	6,167 (848–11,853)	2,823 (1,173–5,973)	15,849 (1,002–33,050)	3,453 (1,025–9,552)
Marine survival	0.040 (0.005–0.104)	0.106 (0.030–0.188)	0.025 (0.006–0.051)	0.063 (0.020–0.115)
Exploitation rate (%)	47 (15–74)	56 (22–76)	56 (33–87)	53 (24–75)
Number tagged	33,219 (30,354–40,351)	10,255 (1,169–24,408)	36,930 (26,014–59,965)	19,721 (10,166–33,923)
Number recovered	67 (6–160)	66 (1–206)	79 (8–244)	67 (36–164)
Proportion sampled[a]	0.40 (0.28–0.57)	0.38 (0.28–0.54)	0.37 (0.26–0.45)	0.38 (0.30–0.47)

[a] Both observed and expanded estimates of tag returns were extracted from the Regional Salmon Mark Recovery database maintained by the Pacific States Marine Fisheries Commission, Portland, Oregon (http://www.rmpc.org/contacts.html). The proportion of catch sampled was calculated based on extractions from the database by dividing the number of tags observed from the fishery by the expanded estimate of total tags caught in the fishery.

Columbia, three Canadian commercial fisheries (troll, gill-net, and seine), a Canadian First Nations fishery, and a Canadian sport fishery. Freshwater fisheries include First Nations harvest and an in-river sport fishery. Exploitation rates (Table 1) were generally higher in the late 1980s and early to mid-1990s, reaching as high as 74–87% of total recruitment. Poor returns in the late 1990s, including one of the lowest escapements on record (1997), caused management actions in Canada that resulted in sharp reductions in exploitation rates. Fishing opportunities and effort levels in southeast Alaska have remained relatively constant through time; however, there was a slight decline in effort between 2001 and 2003 in response to low fish prices (Shaul et al. 2007). For the Toboggan Creek indicator stock, which has the most complete time series, Alaskan troll fishery catches take, on average, 25% of the total return run before the fish enter Canadian waters. The Alaskan troll fishery operates from mid-July (week 27) to September (week 39); northern British Columbia coho salmon account for the largest portion of this Alaskan mixed-stock catch in late July and early August. The remaining catch is divided up among the seven Canadian fisheries. Between 1988 and 1997, average Canadian exploitation rates of Toboggan Creek coho salmon were 13% in the troll fishery, 6% in the gill-net fishery, and 6% in the seine fishery. Between 1997 and 2005, exploitation rate averages for these gear types were 6, 0, and 1%, respectively, with Canadian fisheries remaining closed in several years (J.S., unpublished data). Openings for Canadian commercial fisheries currently occur from July to September.

The CWT model described below makes three key assumptions. First, we assumed that juveniles with CWTs migrate to the ocean as smolts in the year of tagging. In the two indicator streams with wild stocks, Lachmach River and Zolzap Creek, this assumption is valid because fish were captured and tagged using methods that specifically target smolts during their downstream migration. Hatchery-reared coho salmon from Toboggan Creek and Babine River are tagged at age 1 and released into freshwater. Although these tagged juveniles may remain in freshwater habitats for an additional 1 or 2 years after release, analysis of CWT recovery information shows that this behavior is rare. Approximately 99% of Toboggan Creek and 100% of Babine River CWT recoveries are from fish that spent only 1 year in freshwater. Second, we assumed that the proportion of jacks returning to Lachmach River is constant among years, despite observed among-year variability of 3–15% from 1988 to 2003. This assumption was necessary, however, given a lack of preseason or in-season information on jack return rates. The third and final assumption made in the CWT model is that fish are not subject to natural mortality during the fishery. This assumption is common to most methods for in-season forecasting of run strength because natural mortality information in ocean environments is very rarely available on a weekly basis.

Data.—The CWT model requires three types of input data for each indicator stock: (1) the annual number of coded-wire-tagged fish released, (2) estimates of the number of tagged fish recaptured in fisheries during each week before the timing of in-season management decisions, and (3) weekly in-season estimates of fishing effort for recapture fisheries. We used data from the southeast Alaskan commercial troll fishery between 1988 and 2005 as input to the CWT model for our retrospective analysis of northern British Columbia coho salmon. Numbers of tagged coho salmon released from each indicator stock and estimates of the corresponding numbers of tagged fish recovered weekly in Alaskan troll fisheries were obtained from the Regional Salmon Mark Recovery Program (MRP) database (Table 1). The number of CWTs recovered from Alaskan fisheries is estimated based on the proportion of the total catch that is inspected for tags each week and the number of tags observed in the inspected samples (see Johnson 2004 for details on sampling and estimation methods). The number of years for which CWT data are available differs among stocks and ranges from 10 to 18 years; only the Toboggan Creek indicator has operated consistently over the study period (1988–2005). In-season decisions about whether to open Canadian fisheries are made within 6 weeks after opening of the Alaskan troll fishery, so we only used the first 6 weeks of in-season catch data each year in the retrospective analysis. Data on troll fishing effort (boat-days) for these 6 weeks were obtained from the Alaska Department of Fish and Game (ADFG; L. Shaul, Commercial Fisheries Division, Douglas, personal communication). Troll fishery effort was collected in-season using aerial overflights.

Annual postseason estimates of marine survival, which we used in the retrospective analysis, are calculated for northern British Columbia coho salmon at the end of the spawning season using tag recovery information from the spawning grounds as well as from all Canadian and U.S. commercial, sport, and First Nations fisheries. These estimates were derived from the MRP database.

Coded Wire Tag Catch Model

Likelihood.—A sampling distribution for CWT recoveries was constructed by assuming that the probability of observing a CWT catch of $C_{t,w}$ in week w of year t follows a Poisson distribution of the form

$$C_{t,w} \sim \text{Poisson}\left[\hat{N}_{t,w}(1 - e^{-q_{t,w}\hat{E}_{t,w}})\right], \qquad (1)$$

where $q_{t,w}$ is week-specific troll fishery catchability, $\hat{E}_{t,w}$ is an in-season estimate of fishing effort for week w of year t, and $\hat{N}_{t,w}$ is the expected number of tagged coho salmon available to the fishery at the start of week w of year t. The state variable $\hat{N}_{t,w}$ is calculated using the marine survival-depletion model:

$$\hat{N}_{t,w} = \begin{cases} s_t R_{t-1}(1-r) & w = 1 \\ s_t R_{t-1}(1-r) - \sum_{j=1}^{j=(w-1)} C_{t,j} & 2 \le w \le 6, \end{cases} \qquad (2)$$

where s_t is the marine survival rate for fish returning in year t, R_{t-1} is the number of coded-wire-tagged smolts released in year $t-1$, r is the stock-specific average jack rate that applies only to the Lachmach River stock, and j is an index used to denote all weeks before the current week w. We define jack rate as the proportion of fish from a release cohort in year t that return to spawn in that same year after only 4–5 months at sea. The jack rate is applied to R_{t-1} to account for the proportion of fish from release abundance R_{t-1} that are not available to the fishery in year t because they have already spawned as jacks. Coho salmon jacks are not taken in troll fisheries; thus, the presence of jacks that entered the ocean in year t does not affect fishery catch rates. The value of r for the Lachmach River stock was set to the average jack rate observed between 1989 and 2002, which was 0.08 (SD = 0.036; J.S., unpublished data). The value of r was set to zero for the other three indicator stocks.

In each year of forecasting, the CWT model is fit to catch data from the current year as well as all previous years, which means that a time series of annual marine survival rates is estimated for each year and for six weekly catchability coefficients. Specifically, marine survival rate forecasts are based on a weighted combination of CWT catch and fishing effort information for (1) all years and weeks up to $T-1$ and (2) week 1 to the forecasting week W in year T. Therefore, the Poisson distribution for the complete CWT data set is of the form (note that we suppress notation for dependence on fishing effort, CWT releases, and the assumed jack rate):

$$p(\mathbf{C} \mid \mathbf{s}, \mathbf{q}) = \prod_{t=4}^{T-1} \prod_{w=1}^{w=6} \frac{1}{C_{t,w}!} \hat{C}_{t,w}{}^{C_{t,w}} e^{-\hat{C}_{t,w}} \times \prod_{w=1}^{W} \frac{1}{C_{T,w}!} \hat{C}_{T,w}{}^{C_{T,w}} e^{-\hat{C}_{T,w}}, \qquad (3)$$

where the matrix $\mathbf{C}$ of observed CWT catches has T rows and six columns. Note that in the forecasting year, row T represents the in-season CWT catch component, and thus it only contains observations for week 1 to week W. Parameter $\mathbf{s} = (s_4, s_5, \ldots s_T)$ is a vector of estimated marine survival rates for year 4 to year T; $\mathbf{q} = (q_1, q_2, \ldots q_6)$ is a vector of estimated weekly catchability coefficients (or matrix, depending on the catchability model used); and $\hat{C}_{t,w}$ is the expected catch in each week w of year t, which is the Poisson expectation in square brackets in equation (1). Although the two components of the likelihood equation can be combined, we chose to partition equation (3) into prior years (first term) and the forecasting year (second term) to highlight the in-season component. As each in-season CWT catch observation is added to the final row of **C**, all model parameters, including those in prior years, are updated. As is evident from equation (3), however, most of the weight in this refitting will be given to the prior years of data.

Prior distributions.—Generating an in-season marine survival forecast for any year T and week W requires estimating year-specific marine survival rates (s_t) and potentially time-varying weekly catchability coefficients ($q_{t,w}$). These parameters will be partially confounded because changes in the mean catchability cannot be distinguished from changes in marine survival rates, especially during the first few years of the time series when there is little contrast in fishing effort. Specifying an informative prior distribution for marine survival rates allows joint estimation of all model parameters. We assumed that annual changes in marine survival followed a random-walk process:

$$p(s'_t \mid s'_{t-1}, \sigma_s^2) = \frac{1}{\sqrt{2\pi\sigma_s^2}} \exp\left[-\frac{(s'_t - s'_{t-1})^2}{2\sigma_s^2}\right], \quad (4)$$

where s'_t is the logit transformation of the marine survival rate: $\text{logit}(s_t) = \log[s_t/(1 - s_t)]$. Marine survival rate parameters were estimated on the logit scale to constrain values between 0 and 1. We used a random-walk model because this form of variation has been shown to perform well for tracking temporal trends in salmon life history variables that covary with changes in ocean conditions (Peterman et al. 2000) and several previous studies have shown relationships between coho salmon marine survival and ocean conditions (e.g., Nickelson 1986; Hobday and Boehlert 2001; Logerwell et al. 2003). The prior variance σ_s^2 is not estimable from the CWT data alone (without an informative prior); therefore, we fixed σ_s^2 to the mean of among-year variances in logit marine survival rates from southeast Alaska indicator coho salmon stocks. We calculated $\sigma_s^2 = 0.26$ on the logit scale using published estimates from Shaul et al. (2004). The first prior value (s'_t) was parameterized using the stock-specific postseason marine survival rate estimates from year $t = 1$. We examined the effects of σ_s^2 on retrospective forecasting performance by setting σ_s^2 equal to 0.13 and 0.39, representing a 50% increase and decrease, respectively, in σ_s^2. We assumed uniform prior distributions for all catchability parameters.

Selection of CWT catchability model.—There is a wide range of potential mechanisms that could lead to changes in fishery catchability over time. For example, changes in fishing gear efficiency, altered behavior and migration patterns of fish through space and time, and the search and capture behavior of harvesters can potentially give rise to temporal trends in catchability (e.g., Peterman and Steer 1981; Winters and Wheeler 1985; Robins et al. 1998). We therefore used a model selection analysis of three different time-varying catchability models proposed by Wilberg and Bence (2006) to describe how catchability might change through time. Relative performance of the alternative catchability models was measured based on retrospective analyses of the precision and bias of in-season marine survival forecasts (see next section).

In the first model (constant catchability), weekly catchability coefficients were assumed constant across all years for each week up to and including the current forecast year T. Six catchability coefficients were estimated for each stock ($q_{\bullet,w=1}, q_{\bullet,w=2}, \ldots q_{\bullet,w=6}$, where the bullet symbol indicates that the parameter applies to all years t). In the second model (abrupt shift), catchability was allowed to shift from one long-term average to another at a single point in time. Alaskan troll fishery catchability is believed to have increased sharply between 1995 and 1996 when economic pressures raised the minimum catch per unit effort (CPUE) that fishers were willing to tolerate to continue fishing a given location (L. Shaul, personal communication). Total fishing effort decreased during this period; however, catchability is believed to have increased because the remaining effort was concentrated on high CPUE fishing times and areas. To mimic this behavior, we allowed catchability to shift as follows,

$$q_{t,w} = \begin{cases} q_w^1 & \text{if } t < 1996 \\ q_w^2 & \text{if } t \geq 1996. \end{cases} \quad (5)$$

There is reason to suspect that a subsequent downward shift in coho salmon catchability for the Alaskan troll fishery may have occurred in 2002 and 2003 because fishers targeted highly abundant Chinook salmon *O. tshawytscha* instead of coho salmon during these years. In an initial examination, abrupt shift models for these years performed poorly and were not considered further. In the third model (density-dependent), the following power function was used to describe catchability as a function of coho salmon abundance:

$$q_{t,w} = \alpha_w \hat{N}_{t,w}^{\beta_w}, \quad \beta_w < 0, \quad \alpha_w > 0, \quad (6)$$

where $\hat{N}_{t,w}$ is the abundance of tagged coho salmon available to the fishery in week w of year t, as predicted by equation (2). Note that the negative constraint on β means that we only allow for an inverse relationship between catchability and coho salmon abundance.

Bayesian posterior simulation.—Combining the likelihood and prior gives the posterior distribution for marine survival rates using only data up to and including year T and week W, where T and W represent the year and week in which forecasts are being made (note that lowercase t and w index all years and weeks prior to T and W). For each year t, we computed the joint posterior distribution for all marine survival rates, including the forecast, and all catchability coefficients. The posterior distribution can be written as follows:

$$p(\mathbf{s}, \mathbf{q} \mid \mathbf{C}, \sigma_s^2) \propto p(\mathbf{C} \mid \mathbf{s}, \mathbf{q}) \times \prod_{t=4}^{t=T} p(s'_t \mid s'_{t-1}, \sigma_s^2). \quad (7)$$

An approximation to the joint posterior distribution of all model parameters was generated using a Metropolis-Hastings algorithm (see Appendix).

Retrospective Evaluation of Forecasting Performance

Year $t = 4$ was the first year evaluated in the retrospective analysis. The first 3 years of CWT data were used to define the prior distribution for year 4. For each forecasting week W and year T, we generated model parameter estimates by using only data that would have been available to managers at that time. Such retrospective information consists of complete catch and effort data for weeks 1–6 in all years up to and including $T - 1$ and catch and effort data for week 1 to week W in the forecasting year T. Forecasting performance was quantified based on how close the in-season CWT model forecasts were to postseason estimates, which we assume are more accurate than in-season forecasts because they incorporate tag recovery information from multiple fisheries and the spawning grounds.

Retrospective performance for catchability model selection was based on maximum posterior density estimates of marine survival s_t produced by the CWT model. The Bayesian estimation procedure was not used for this analysis because we were only interested in using a single point estimate (i.e., the most likely value) to evaluate forecasting performance under alternative assumptions about catchability and σ_s^2. We used mean percent error (MPE) and root mean square error (RMSE) to quantify forecasting performance in each week over $T - 3$ years. The MPE and RMSE values were calculated individually for each indicator stock in each of the six forecasting weeks. The MPE characterizes the average marine survival forecast bias in each week W over $T - 3$ years as a percentage of the observed postseason estimate:

$$\mathrm{MPE}_W = \frac{1}{T-3} \sum_{t=4}^{t=T} \left(\frac{\tilde{s}_{t,W} - \hat{s}_{\mathrm{Post},t}}{\hat{s}_{\mathrm{Post},t}} \right) \times 100, \quad (8)$$

where $\hat{s}_{\mathrm{Post},t}$ is the postseason estimate and $\tilde{s}_{t,W}$ is the posterior mode of the marine survival rate in week W of year t. The RMSE characterizes the accuracy and precision of annual forecasts in week W over $T - 3$ years,

$$\mathrm{RMSE}_W = \sqrt{\frac{1}{T-3} \sum_{t=4}^{t=T} (\tilde{s}_{t,W} - \hat{s}_{\mathrm{Post},t})^2}. \quad (9)$$

We selected the best catchability model for each stock as the one that provided the lowest RMSE and lowest absolute MPE values for the greatest number of weeks.

We used the stock-specific best catchability model within the fully Bayesian CWT model to generate probabilistic forecasts of s_t in each week W. Forecasted posterior distributions were used to evaluate retrospective performance in two ways. First, for each week of in-season forecasting, we examined the number of years in which the 95% highest posterior density (HPD) region of the posterior distribution included the postseason estimate of marine survival and how well the posterior mode tracked postseason estimates. This included an examination of how the bias and precision of forecasted posterior distributions changed over weeks as more information became available. Second, we calculated the forecasted probability that marine survival in a given year t would be lower than a critical value, s_{crit}, and compared the probability statement with the observed postseason value. Values of s_{crit} were set equal to 50% of average postseason marine survival rate estimates ($s_{\mathrm{crit}} = 0.02$ for Toboggan Creek, $s_{\mathrm{crit}} = 0.05$ for Lachmach River, $s_{\mathrm{crit}} = 0.03$ for Zolzap Creek, and $s_{\mathrm{crit}} = 0.01$ for Babine River). This level was selected because it results in s_{crit} values that are slightly greater than those experienced in the 1992, 1995, 1997, and 1998 return years for most stocks (i.e., the 4 years that Holtby 2000 identified as having undesirably low marine survival rates) and smaller than the rates experienced in all other years. In general, our evaluation of retrospective performance of the Bayesian procedure has the benefit of hindsight because we selected the best catchability model based on the full data sets.

Overall model fit, in terms of how well predicted CWT catches from the Bayesian estimation procedure replicated observed catches, was assessed by comparing the modes of posterior predictive distributions for CWT catch with observed catch levels. The posterior predictive distribution is defined as the distribution of model-simulated data that could have been observed conditional on the observed data (Gelman et al. 2004). In other words, it is the distribution of CWT catches obtained when we use the posterior samples of s_t and $q_{t,w}$ to calculate expected values for $C_{t,w}$.

TABLE 2.—Mean percent error (MPE) of maximum likelihood estimates of coho salmon marine survival from the coded wire tag model under alternative assumptions about time-varying catchability. Results for each of the six in-season forecasting weeks are averaged over all years for each of the four northern British Columbia indicator stocks. The lowest absolute error values for each stock are indicated in bold font.

	MPE for week:					
Stock and model type	1	2	3	4	5	6
Toboggan Creek stock						
Constant	−24.5	**−2.6**	**12.5**	**18.3**	14.9	28.8
Abrupt shift	−35.2	−31.9	91.6	−22.8	**−9.3**	**−7.5**
Density dependent	**4.2**	59.7	110.5	156.4	167.9	181.2
Lachmach River stock						
Constant	40.7	50. 9	47.0	43.3	28.7	40.1
Abrupt shift	**7.1**	**8.1**	**15.1**	**11.7**	**6.9**	**10.4**
Density dependent	74.2	124.5	243.1	313.1	326.7	370.3
Zolzap Creek stock						
Constant	34.2	29.3	**7.9**	11.5	17.2	13
Abrupt shift	**-8.2**	**0.8**	−8.1	**−3.1**	**−2.6**	**−2.6**
Density dependent	123.4	209.0	304.0	404.0	480.5	539.7
Babine River stock						
Constant	130.0	84.3	**69.4**	**54.4**	**33.9**	80.2
Abrupt shift	**106.4**	**76.9**	74.9	74.7	48.8	**45.3**
Density dependent	183.5	297.3	369.3	459.1	452.1	511.3

Results

Catchability Models

Measures of MPE and RMSE varied with catchability model and among weeks for all indicator stocks (Tables 2, 3). For Lachmach and Babine River stocks, weekly estimates of marine survival rate tended to be positively biased for all catchability models, whereas for Zolzap and Toboggan Creek stocks the direction of bias was dependent on the catchability model and forecast week. The catchability model that produced the least biased estimates (closest to zero) did not necessarily produce estimates with the lowest variance (Tables 2, 3). To simplify in-season application of the CWT model, we selected a single model for each stock to be used in our retrospective Bayesian forecasting procedure. This choice required us to make tradeoffs among the amount of bias, the direction of bias (positive, negative), and the amount of variance in our forecast error that we were willing to accept in each week. We chose to weight all weeks equally in our selection because in-season decisions about when to open the fishery were made in each week. The best catchability model for each stock was selected as the one that provided the lowest MPE and RMSE values for the greatest number of combined weeks. As an example, the constant catchability model was selected over the abrupt shift model for the Babine River stock because it ranked first for 3 weeks using MPE and for 4 weeks using RMSE. In this case, the constant model was ranked first for a combined 7 weeks, whereas the abrupt shift model was only first for a combined 5 weeks. The selection of a catchability model was more straightforward for the Toboggan Creek, Lachmach River, and Zolzap Creek stocks than for Babine River fish. For Toboggan Creek and Babine River stocks, the constant catchability model was the best of the three models considered, whereas for Lachmach River and Zolzap Creek stocks the abrupt shift model was best (Tables 2, 3) .

With the exception of the Toboggan Creek stock, the density-dependent catchability model performed considerably worse than the other two models, with MPE and RMSE values being 10–40 times those of the density-independent models. Compared with the constant catchability model, which would most likely be used in initial years when data are sparse, the percent reduction in MPE and RMSE achieved by using the abrupt shift model for Lachmach River and Zolzap Creek stocks shows that forecasting performance averaged over all weeks was improved by 1–22% for RMSE and by 76–78% for MPE through our use of hindsight in model selection.

Estimates of weekly catchability coefficients produced in each year of the retrospective analysis show a general trend of low catchability during early weeks and higher catchability for later weeks (Figure 2). The two stocks for which the abrupt shift catchability model was best (Lachmach River and Zolzap Creek) showed high variability arising from occasional sharp spikes in estimated coefficients, especially in weeks 5 and 6. The effect of the abrupt shift model on annual trends in estimated catchability coefficients was apparent for the

TABLE 3.—Root mean square error (RMSE) of maximum likelihood estimates of coho salmon marine survival from the coded wire tag model under alternative assumptions about time-varying catchability. Results for each of the six in-season forecasting weeks are averaged over all years for each of the four northern British Columbia indicator stocks. The lowest error values for each stock (bold font) indicate the best model for each week.

	RMSE for week:					
Stock and model type	1	2	3	4	5	6
Toboggan Creek stock						
Constant	**0.048**	**0.021**	**0.023**	0.032	**0.017**	0.025
Abrupt shift	0.053	0.021	0.243	**0.019**	0.022	**0.018**
Density dependent	0.060	0.062	0.082	0.089	0.097	0.103
Lachmach River stock						
Constant	0.094	0.088	0.077	0.069	0.052	0.059
Abrupt shift	**0.087**	**0.062**	**0.059**	**0.048**	**0.043**	**0.042**
Density dependent	0.169	0.178	0.314	0.359	0.385	0.419
Zolzap Creek stock						
Constant	0.081	0.044	**0.026**	**0.021**	**0.026**	0.041
Abrupt shift	**0.069**	**0.041**	0.030	0.029	0.031	**0.038**
Density dependent	0.137	0.171	0.241	0.305	0.347	0.389
Babine River stock						
Constant	0.092	**0.041**	**0.030**	**0.016**	**0.011**	0.026
Abrupt shift	**0.067**	0.048	0.034	0.027	0.021	**0.021**
Density dependent	0.115	0.101	0.122	0.127	0.135	0.151

Lachmach River stock, which showed an abrupt increase in catchability during 1996 for weeks 2, 4, and 5. The effect of the abrupt shift model on estimated catchability coefficients for the Zolzap Creek stock could not be examined retrospectively because the year of the hypothesized shift (1996) was also the first forecasting year for this stock. Estimated coefficients for Toboggan Creek and Babine River stocks (for which the constant catchability model was used) fluctuated less than those for the other two stocks, with a gradual increase in catchability occurring in later years.

Bayesian Forecasts

Posterior distributions for marine survival rate forecasts were positively skewed, and the mass of the probability distribution was concentrated on smaller values (Figure 3). In most years, postseason estimates occurred within the 95% HPD region of the forecasted posterior distribution for several if not all of the 6 weeks of in-season forecasting. The long tails of posterior forecasts often resulted in large 95% HPD regions; however, the mode of the posterior distribution for week 6 tracked postseason estimates reasonably well (Figure 3). Average percent bias in posterior modes for week 6 (average over all years calculated using MPE, equation 8) was −1% for the Toboggan Creek stock, −4% for the Lachmach River stock, 19% for the Zolzap Creek stock, and 57% for the Babine River stock. There was a subset of years for each stock, however, in which posterior distributions did not cover postseason estimates. For example, at the end of week 6, the 95% HPD region for the Babine River stock overlapped the postseason estimate in only 5 out of 7 years (71% of years; Figure 3D). Forecasting performance in week 6 was improved for Toboggan Creek and Zolzap Creek stocks; postseason estimates occurred within the 95% HPD region for 12 out of 15 years for the Toboggan Creek stock (80%; Figure 3A) and 8 out of 9 years for the Zolzap Creek stock (89%; Figure 3C). Forecasting performance was poorest for the Lachmach River stock, with forecasted posterior modes diverging substantially from postseason estimates in later years (Figure 3B). Although the 95% HPD region overlapped postseason estimates in all 13 years, this overlap was due to low precision in forecasted posterior distributions rather than accurate forecasts.

Precision of marine survival rate forecasts for a given year generally increased with each additional week of in-season CWT information. In years when the CWT model performed well, bias in forecasted posterior modes remained low throughout the season and precision either improved with each additional week of in-season information or remained constant (Figure 4C, D). In years when the model performed poorly, posterior distributions showed high bias but were generally precise throughout the season, sometimes even showing increases in precision, leading to a false confidence in apparently biased estimates (Figure 4A).

Despite wide 95% HPD regions in some cases, the

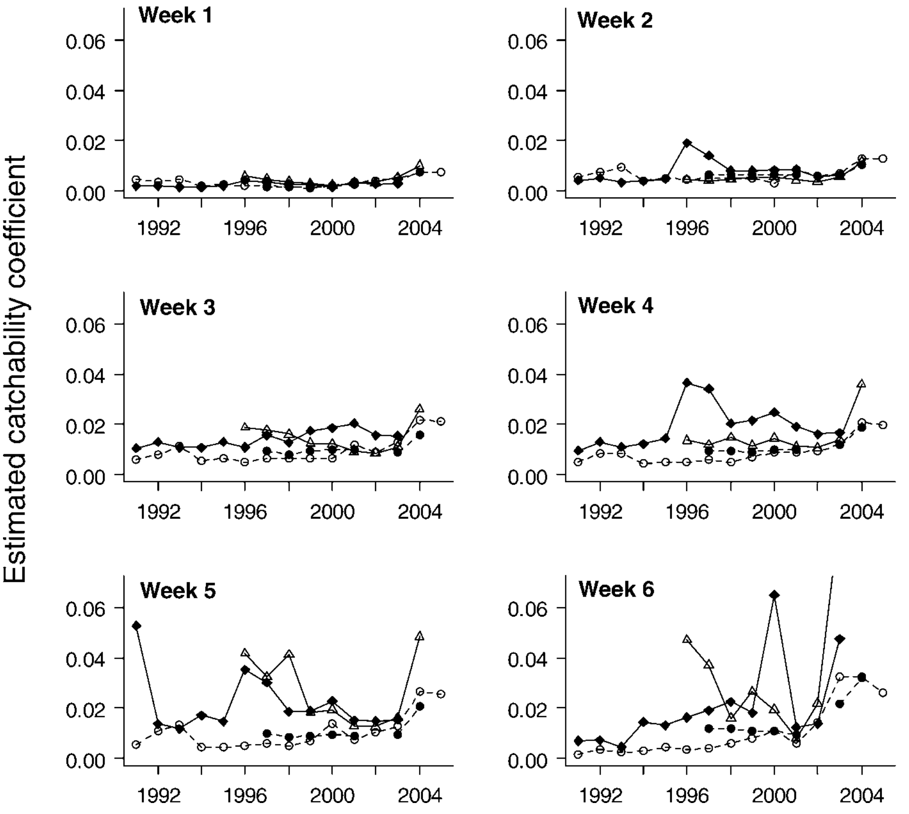

FIGURE 2.—Annual trends (1991–2005) in estimated coho salmon catchability coefficients for weeks 1–6 for four northern British Columbia indicator stocks: Toboggan Creek (open circles), Lachmach River (black diamonds), Zolzap Creek (open triangles), and Babine River (black circles). Estimates represent the median of posterior distributions obtained for each year of retrospective forecasting. Note that two estimates for Zolzap Creek in week 6 (0.097 in 2003 and 0.115 in 2004) are not shown so that the scale can remain consistent among panels.

lower ends of the regions were reasonably well defined for most stocks, which is the area of the HPD region most relevant to identifying conservation concerns. For example, the Zolzap Creek stock forecasts for all weeks in 1997, which was a critical marine survival year ($\hat{s}_{\text{Post},1997} = 0.023$, $s_{\text{crit}} = 0.03$), had relatively wide 95% HPD regions extending from 0.01 to 0.10 but were able to predict a minimum 0.52 probability that s would be less than s_{crit} in all weeks (Figure 4C). In general, the CWT model was successful at providing at least some indication of critically low marine survival for all years that had postseason estimates below the threshold. False-safe signals did occur in which postseason estimates were near or below the critical threshold, but the majority of forecasted posterior distributions, including the modes, fell above the threshold (e.g., Toboggan Creek in 1996; Lachmach River in 1997; Zolzap Creek in week 6 of 2000; Figure 3); the CWT model predicted a greater than 0.50 probability that s would be less than s_{crit} in at least 1 of the 6 weeks for all years with critically low postseason estimates. Furthermore, during these years, there was never a week in which the forecasted probability of s being lower than s_{crit} was zero. In each case, weekly forecasted probabilities that s would be lower than s_{crit} did not drop below 0.06 and more often ranged from 0.4 to 0.9. If CWT forecasts had been available during these years, fisheries managers would have been given at least some indication that marine survival could be critically low.

False-alarm signals in the final forecasting week, in which the majority of forecast posterior distributions fell below the threshold but postseason estimates were above the critical threshold, only occurred for the Toboggan Creek stock. All three of these signals occurred in the last 4 years. Despite triggering a false alarm, the CWT model actually performed well at forecasting Toboggan Creek marine survival rates in these years (Figure 3A). Forecasted survival rates based on posterior modes were within 1–2% of the

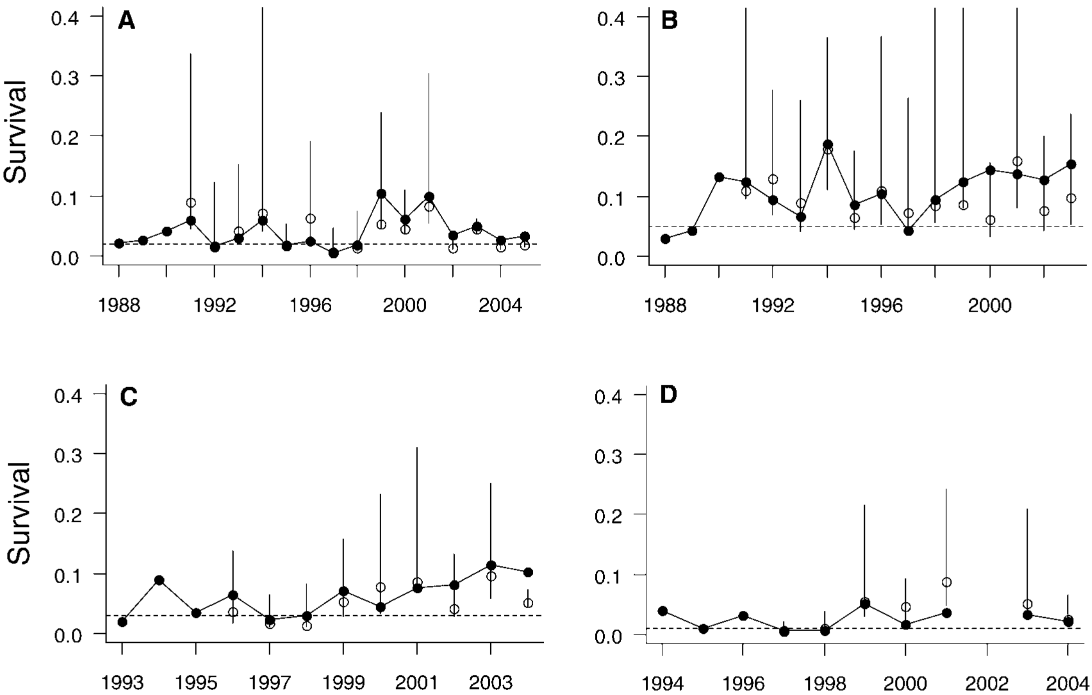

FIGURE 3.—Posterior modes (open circles) and 95% highest posterior density regions (vertical lines) of posterior predictive distributions for marine survival rate in week 6 for four northern British Columbia coho salmon indicator stocks: **(A)** Toboggan Creek, **(B)** Lachmach River, **(C)** Zolzap Creek, and **(D)** Babine River. Annual postseason estimates are shown with black circles, and the critical marine survival rate threshold is represented by the dashed line.

postseason estimates, which were also only slightly above the threshold (i.e., forecasted and observed survival rates differed by 0.01–0.02). Furthermore, forecasts correctly indicated high confidence that marine survival rates were near the critical threshold. The ranges of forecasted posteriors for other stocks occasionally overlapped the critical level in years with above-critical postseason estimates; however, posterior modes remained above the critical threshold in these cases.

Comparison of the posterior predictive distribution for CWT catch with observed catch values based on the complete data set (all years and weeks) did not indicate a consistent lack of fit for any stocks or weeks, although there were some potential outliers (Figure 5).

Sensitivity to Prior Variance

The sensitivity of marine survival rate forecasts to the assumed prior variance, σ_s^2, of the random-walk distribution was considerable in some cases. For example, a 50% increase in σ_s^2 (high σ_s^2) caused posterior modes of marine survival rate forecasts to shift by an average of 19% for the Toboggan Creek stock (relative to mode for baseline σ_s^2), 40% for the Lachmach River stock, 16% for the Zolzap Creek stock, and 48% for the Babine River stock. The effect of a 50% decrease in σ_s^2 (low σ_s^2) had a lesser influence on posterior modes for most stocks; average deviations were 5% for the Toboggan Creek stock, 18% for the Lachmach River stock, 65% for the Zolzap Creek stock, and 8% for the Babine River stock. Such deviations in posterior modes for marine survival rate forecasts lead to changes in forecasting bias. Forecasting bias for all stocks, measured in terms of MPE, was highest in the high σ_s^2 case. The average change in MPE of marine survival rate forecasts over 6 weeks was positive for all stocks: 4% for the Toboggan Creek stock, 19% for the Lachmach River stock, 24% for the Zolzap Creek stock, and 25% for the Babine River stock. Forecasting bias for three of the stocks (Toboggan Creek, Lachmach River, and Babine River) decreased in the low σ_s^2 case but increased for the Zolzap Creek stock. Average changes in MPE were −5, −8, and −22% for the Toboggan Creek, Lachmach River, and Babine River stocks, respectively, whereas the average change was 8% for the Zolzap Creek stock.

Discussion

Forecasts of coho salmon marine survival rates can be used to improve in-season abundance estimates and

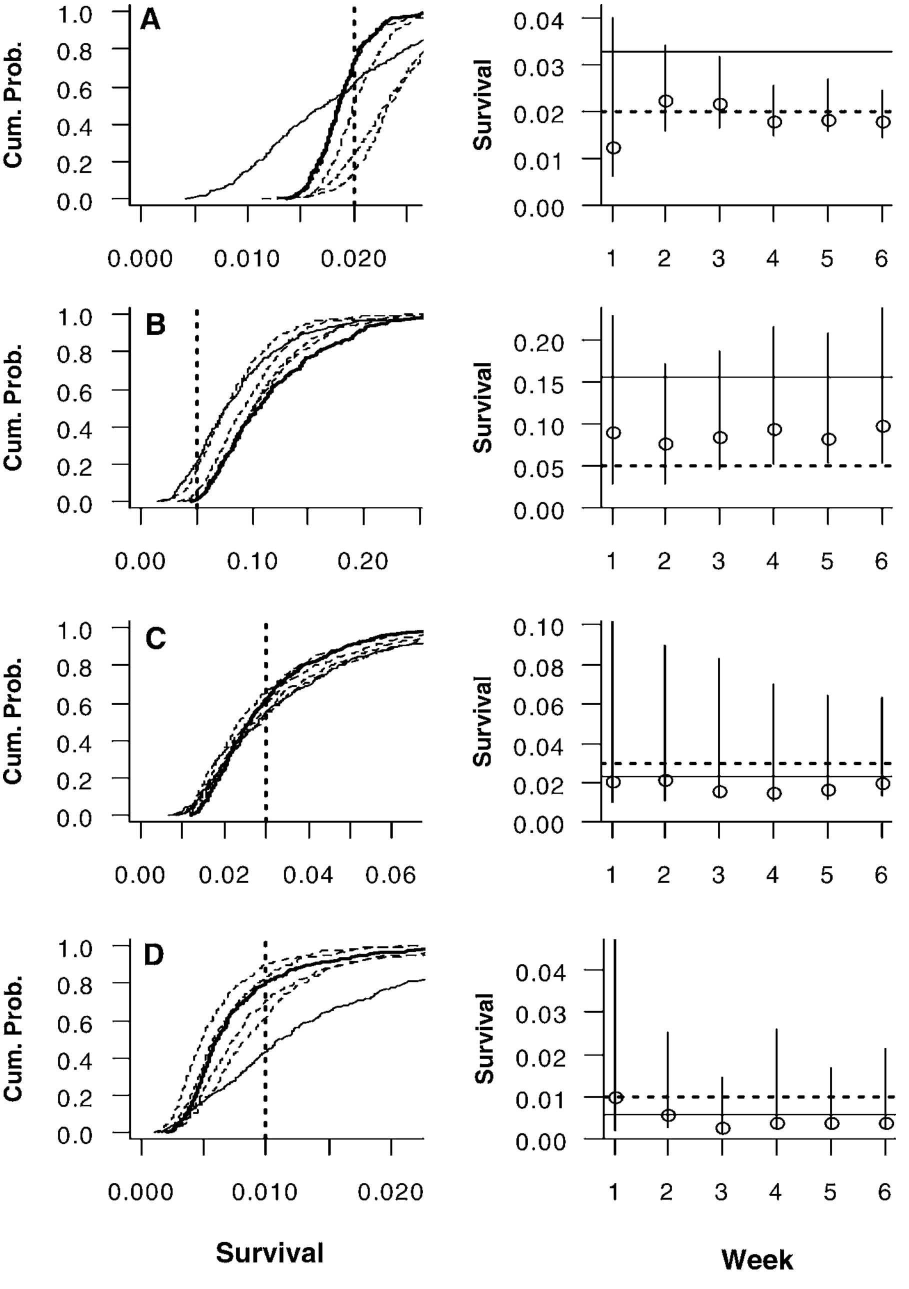

FIGURE 4.—Survival data examples for four northern British Columbia coho salmon indicator stocks: **(A)** Toboggan Creek in 2005, **(B)** Lachmach River in 2003, **(C)** Zolzap Creek in 1997, and **(D)** Babine River in 1997. Panels at left show weekly cumulative probability (cum. prob.) profiles for a subset of marine survival rate forecasts for the first week (thin solid lines), intermediate weeks (dashed lines), and the last week (thick solid lines); the critical survival rate level (s_{crit}) is also indicated (dashed vertical lines). Panels at right show weekly highest probability forecasts (posterior modes) of annual marine survival (open circles), postseason estimates of marine survival (solid lines), s_{crit} (dashed line); the 95% highest posterior density regions of forecasted posterior distributions are indicated by the solid vertical lines.

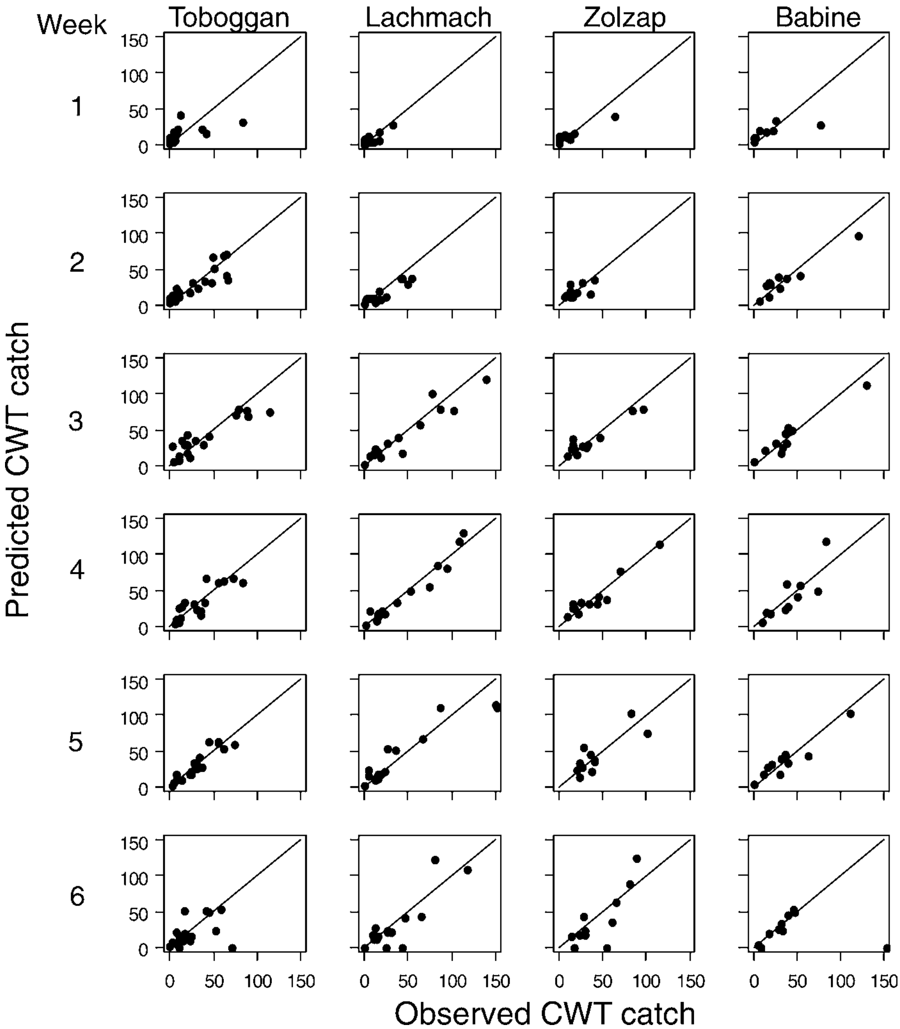

FIGURE 5.—Comparison of the modes of posterior predictive distributions for coded-wire-tag (CWT) catch (predicted CWT catch) in weeks 1–6 with observed CWT catch in week 6 of the final year of retrospective analysis for each of four northern British Columbia coho salmon indicator stocks: Toboggan Creek in 2005, Lachmach River in 2003, Zolzap Creek in 2004, and Babine River in 2004. The solid line is the 1:1 line.

subsequent harvest decisions. Our results indicate that in-season returns of coded-wire-tagged coho salmon from commercial troll fisheries in southeast Alaska can provide reasonably reliable and timely forecasts of marine survival rates for some northern British Columbia indicator stocks. Although coho salmon CWT recoveries have been used in the past as an index of marine survival (PSC 2002), our approach to modeling in-season tag recoveries provides absolute marine survival rate estimates that account for changes in fishing effort, number of tags released, and potential changes in fishery catchability. We developed a simple application of the CWT model to assist harvest management decisions regarding northern British Columbia coho salmon. This forecasting procedure is used as an early warning signal of years in which marine survival is below a critical threshold level. We defined this threshold as the level of marine survival for each stock that has historically been associated with abundances low enough to warrant closing the Canadian commercial fishery. There were a few instances in our retrospective evaluation in which the CWT model provided false-safe results (forecast indicates $s \geq s_{\text{crit}}$, but postseason estimate $\hat{s}_{\text{Post}} < s_{\text{crit}}$), which is undesirable from a conservation standpoint because resulting fisheries are likely to cause overexploitation. Fortunately, however, all years in which false-safe signals occurred had conflicting signals throughout the season, which would have provided at least some indication that marine survival could be poor. Furthermore, forecasted posterior distributions of marine survival were often well defined at the lower limits, which is most relevant to conservation concerns. On the other hand, strong false-alarm signals were never observed in the final week of forecasting. The potential for overexploitation or, conversely, lost fishing opportunities will be dependent on the quantile(s) of the marine survival forecast posterior distribution used in decision making. For example, managers weighing conservation more heavily than lost fishing opportunities may choose a lower quantile, whereas those who place equal weight on catch and conservation outcomes may choose a more central quantile.

Fishery catchability is often assumed constant in stock assessments. Our retrospective performance results based on fitting three types of catchability models suggest that such an assumption is not unreasonable for modeling CWT catches in coho salmon troll fisheries in Alaska provided that catchability assessments are updated annually. For example, despite their name, constant catchability model parameters changed from year to year depending upon information contained in the CWT catch and in-season effort data. We initially expected that catchability estimates would be less likely to make large jumps later in the time series as estimates became increasingly dependent on the data before year *T*. However, this constraint did not appear to be a problem over the timelines we examined. The constant catchability models do a reasonably good job of predicting marine survival rates and catches in later years, and catchability was estimated to increase gradually over a 10-year period, followed by a more rapid change over the most recent years.

For the other two stocks, Lachmach River and Zolzap Creek, an abrupt shift catchability model provided slightly better retrospective performance than the constant catchability model. The high among-year variation in estimated catchability coefficients for these two stocks in week 6, especially in later years, suggests that the success of the abrupt shift model is at least partially due to weaker constraints on catchability estimates caused by lower numbers of tag releases. The Lachmach River and Zolzap Creek stocks are both wild stocks and have lower levels of recruitment and CWT releases than the other two (hatchery) stocks. Alternatively, large changes in catchability estimates may be explained by unusually late run timing through the fishery. The CPUE of fish with CWTs ($CPUE_{CWT}$) for the Lachmach River stock in both 2000 and 2003 was highest in week 6, but in most other years it peaked in weeks 3 or 4. The CWT model would be expected to adjust to these high catch rates by either increasing annual marine survival rates or increasing catchability. Presumably, the random-walk model that we used to constrain estimates of marine survival rates forced the latter. Although the CWT model still did a good job of predicting CWT catches in the final year of the retrospective analysis, the high catchability estimate caused the marine survival rate forecast to be negatively biased. A shift to later run timing also appears to have occurred for the Zolzap Creek stock between 2002 and 2004. For instance, before 2002, the $CPUE_{CWT}$ in week 6 accounted for an average of 20% (range = 18–33%) of the total weekly $CPUE_{CWT}$ over all 6 weeks. For 2002, 2003, and 2004, $CPUE_{CWT}$ in week 6 accounted for 48, 56, and 66%, respectively. Similar to the Lachmach River stock, CWT model forecasts of marine survival for the Zolzap Creek stock were negatively biased in all of these years. Regardless of the cause of changes in catchability, we suggest that similar model selection analyses be used in applications of the CWT model to new stocks and that the analysis be repeated on a regular basis to ensure detection of changes in the best catchability model.

The observed sensitivity of marine survival rate forecasts to σ_s^2 demonstrates the importance of carefully selecting an informative prior distribution. We selected a random-walk model and parameterized σ_s^2 based on neighboring coho salmon stocks in southeast Alaska. In hindsight, it appears that a smaller σ_s^2 value could have improved forecasting performance for three of the northern British Columbia stocks. However, we selected our prior distribution based on a source for prior information that was, to our knowledge, the best available for northern British Columbia stocks. It is possible that our simple averaging of marine survival rate variances did not remove unrelated sources of variation, such as that arising from observation errors or among-stock variation. A hierarchical Bayesian approach would potentially allow for estimation of a pure process error variance σ_s^2 for each stock by borrowing information from other stocks; however, the hierarchical approach would not be particularly effective if based on only four stocks. Future applications of the CWT model could also incorporate environmental variables that are known to influence local marine survival rates into the estimation procedure to supplement prior information. In addition, prior information on run timing may improve estimation of catchability coefficients.

Our in-season estimates of marine survival rates were similar to postseason estimates derived from both

Alaskan and Canadian fishery recoveries and returns from spawning grounds. In only a few cases did the in-season estimates differ substantially from the postseason estimates. In particular, differences were greatest for the Lachmach River wild stock, for which forecasts showed some large errors after 1996. Such differences could arise for a number of reasons for this stock. First, the number of fish tagged and released was lower for the Lachmach River stock than for the other three stocks. Bias and imprecision in in-season estimates could therefore be due to the effects of small sample size. Second, poor performance may be due to biases in postseason estimates and from in-season estimation errors. Smolt trapping and enumeration methods have changed over time for the Lachmach River stock, and such changes could potentially cause biases in postseason marine survival rate estimates. Thus, we do not necessarily place more weight on the postseason estimates for the wild stocks. In-season estimates agreed closely with postseason estimates for the interior hatchery stocks, for which smolt counts are known with much greater precision and in which jack life history types are rare. Future attempts to apply the CWT model to coastal coho salmon stocks with high jack returns would benefit from investigating ways to forecast jack rates. Several biological and physical factors, including sea entry timing, smolt body size, sea surface temperatures, and conditions during freshwater rearing, have been linked to coho salmon jack rates and may provide a basis for these types of forecasts (Bilton et al. 1982; Briscoe et al. 2005; Koseki and Fleming 2007).

A key limitation with this study, as with all retrospective analyses, is that the performance of the CWT forecasting model can only be evaluated based on conditions that occurred during the retrospective time series. In our case, inferences about forecasting performance are limited to the observed range of variation in marine survival, return abundances, CWT catches, catchability, and life history strategies. A model that has performed well in the past may not perform well in the future under different conditions, such as higher levels of interannual variability in marine survival or lower tagging rates. We attempted to address this limitation by evaluating model performance for four different indicator stocks over 10–18 years; however, an informative extension would be to test the forecasting procedure under a wider range of scenarios for population and fishery dynamics (e.g., Peterman et al. 2000; Wilberg and Bence 2006). Previous evaluations of in-season assessment and management models have shown simulation modeling to be a useful tool for assessing the value of in-season estimates of abundance (Link and Peterman 1998) and for determining optimal harvest strategies using in-season abundance data (Su and Adkison 2002).

Mass marking of hatchery-reared coho salmon is not currently done in northern British Columbia or southeast Alaska; however, the trend towards mass marking of hatchery salmon and mark-selective fisheries in some areas could affect future applications of the CWT forecasting model. Historically, only coded-wire-tagged fish had their adipose fins clipped as an external mark, regardless of whether they were of hatchery or wild origin (Johnson 2004). The heads of all fish with adipose fin clips were retained during catch inspections and sent to laboratories for tag processing. Under mass-marking programs, all hatchery-reared fish (with or without CWTs) receive adipose fins clips, and mark-selective fisheries only retain marked hatchery fish (Expert Panel on the Future of the Coded Wire Tag Program 2005). Unmarked wild fish are released as bycatch for conservation reasons. Mass marking could affect the CWT forecasting model because coded-wire-tagged fish no longer possess a distinctive external marking. As a result, the entire catch would need to be electronically scanned for CWTs. This change in sampling methods could lead to a change in the probability of tag detection. If the magnitude of change is known, it could be incorporated into the CWT model, but if it is unknown then the performance of the CWT model could be compromised. In addition, the CWT forecasting model cannot be used for wild stocks in mark-selective fisheries because wild fish do not receive adipose clips and are therefore not retained as catch. However, unmarked wild fish are expected to experience some catch-and-release mortality from mark-selective fisheries, so marine survival rates of wild stocks may still be of interest when deciding whether or not to open fisheries. In this case, information about marine survival rates for wild stocks would have to be inferred from neighboring hatchery stocks.

Calculation of the Bayes posterior probability distribution summarizes uncertainty about estimated marine survival rates in a simple, visual way that is also of practical use for precautionary fishery management (Walters and Punt 1994; Wade 2000). For example, the posterior distribution for marine survival could be used in harvest decision rules that are compliant with Canada's commitment to the precautionary approach to fishery management (Fisheries and Oceans Canada 2006). Such decision rules would take either output control (e.g., harvest quotas) or input control (e.g., effort limitation) forms. Forecasts of total return abundance that are required for output control rules depend upon estimates of total smolt production and marine survival rates. Unfortunately, reliable estimates of total smolt production are not currently available for northern British Columbia coho salmon, which essentially precludes the use of harvest quotas for fishery management. Setting quotas without reliable forecasts of total return abundance would not be precautionary unless such quotas were set at extremely low levels. Thus, fishery decisions for northern British Columbia coho salmon will probably continue to be based on input control measures that limit exploitation rates by limiting the times and areas of fishery openings. Sustainable exploitation rates for coho salmon depend strongly on marine survival (Bradford et al. 2000), so accounting for natural variation in marine survival rates and uncertainty in forecasts is consistent with the precautionary approach. Precautionary harvest rules for mixed-stock salmon fisheries should also account for among-stock variability in sustainable exploitation rates because some stocks are at a higher risk of overfishing than others. An investigation of the performance of different weighting schemes for combining run strength forecasts from multiple indicator stocks into a single harvest rule would be a useful extension of CWT forecasting methods.

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References

Bilton, H. T., D. F. Alderdice, and J. T. Schnute. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. Canadian Journal of Fisheries and Aquatic Sciences 39:426–447.

Bradford, M. J., R. A. Myers, and J. R. Irvine. 2000. Reference points for coho salmon (*Oncorhynchus kisutch*) harvest rates and escapement goals based on freshwater production. Canadian Journal of Fisheries and Aquatic Sciences 57:677–686.

Briscoe, R. J., M. D. Adkison, A. Wertheimer, and G. S. Taylor. 2005. Biophysical factors associated with the marine survival of Auke Creek, Alaska, coho salmon. Transactions of the American Fisheries Society 134:817–828.

Claytor, R. R. 1996. In-season management of Atlantic salmon (*Salmo salar*): an example using southern Gulf of St. Lawrence rivers. Canadian Journal of Fisheries and Aquatic Sciences 53:1345–1359.

Cole, J., G. Boehlert, and L. de Witt. 2001. Forecasting coho salmon survival in the Oregon Production Index region. Pages 22–24 *in* R. Beamish, Y. Ishida, V. Karpenko, P. Livingston, and K. Myers, editors. Workshop on factors affecting production of juvenile salmon. North Pacific Anadromous Fish Commission, Vancouver.

Coronado, C., and R. Hilborn. 1998. Spatial and temporal factors affecting survival in coho salmon (*Oncorhynchus kisutch*) in the Pacific Northwest. Canadian Journal of Fisheries and Aquatic Sciences 55:2067–2077.

Expert Panel on the Future of the Coded Wire Tag Program for Pacific Salmon. 2005. Pacific Salmon Commission, Technical Report 18, Vancouver. Available: www.psc.org/pubs/psctr18.pdf. (June 2009).

Fisheries and Oceans Canada. 2006. A harvest strategy compliant with the precautionary approach. Fisheries and Oceans Canada, Canadian Science Advisory Secretariat, Science Advisory Report 2006/023.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian Data Analysis, second edition. Chapman and Hall, New York.

Haeseker, S. L., R. M. Peterman, Z. Su, and C. C. Wood. 2008. Retrospective evaluation of preseason forecasting models for sockeye and chum salmon. North American Journal of Fisheries Management 28:12–29.

Hobday, A. J., and G. W. Boehlert. 2001. The role of coastal ocean variation in spatial and temporal patterns in survival and size of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 58:2021–2036.

Holtby, L. 2000. In-season indicators of run-strength and survival for northern British Columbia coho. Canadian Stock Assessment Secretariat, Research Document 2000/153.

Hyun, S., R. Hilborn, J. J. Anderson, and B. Ernst. 2005. A statistical model for in-season forecasts of sockeye salmon (*Oncorhynchus nerka*) returns to the Bristol Bay districts of Alaska. Canadian Journal of Fisheries and Aquatic Sciences 62:1665–1680.

Johnson, J. K. 2004. Regional review of coded-wire tagging of anadromous salmon and steelhead in northwest America. Paper updated from 1989 to current year 2004. Available: www.psc.org. (August 2007).

Koseki, Y., and I. A. Fleming. 2007. Large-scale frequency dynamics of alternative male phenotypes in natural populations of coho salmon (*Oncorhynchus kisutch*): patterns, processes, and implications. Canadian Journal of Fisheries and Aquatic Sciences 64:743–753.

Link, M. R., and R. M. Peterman. 1998. Estimating the value of in-season estimates of abundance of sockeye salmon

(*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 55:1408–1418.

Logerwell, E. A., N. Mantua, P. W. Lawson, R. C. Francis, and V. N. Agostini. 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fisheries Oceanography 12:554–568.

Martin, A. D., and K. M. Quinn. 2006. The Markov chain Monte Carlo (MCMC) Package. Available: www.cran.r-project.org. (July 2008).

Nickelson, T. E. 1986. Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho (*Oncorhynchus kisutch*) salmon in the Oregon production area. Canadian Journal of Fisheries and Aquatic Sciences 43:527–535.

Peterman, R. M., B. J. Pyper, and J. A. Grout. 2000. Comparison of parameter estimation methods for detecting climate-induced changes in productivity of Pacific salmon (*Oncorhynchus* spp.). Canadian Journal of Fisheries and Aquatic Sciences 57:181–191.

Peterman, R. M., B. J. Pyper, M. F. Lapointe, M. D. Adkison, and C. J. Walters. 1998. Patterns in covariation in survival rates of British Columbian and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. Canadian Journal of Fisheries and Aquatic Sciences 55:2503–2517.

Peterman, R. M., and G. J. Steer. 1981. Relation between sport-fishing catchability coefficients and salmon abundance. Transactions of the American Fisheries Society 110:585–593.

PSC (Pacific Salmon Commission). 2002. Status of coho salmon stocks and fisheries in the Northern Boundary Area. PSC Northern Boundary Technical Committee, Report TCNB(02)-3.

Quinn, T. P., B. R. Dickerson, and L. A. Vollestad. 2005. Marine survival and distribution patterns of two Puget Sound hatchery populations of coho (*Oncorhynchus kisutch*) and chinook (*Oncorhynchus tshawytscha*) salmon. Fisheries Research 26:209–220.

R Development Core Team. 2007. R: a language and environment for statistical computing. R Development Core Team, Vienna. Available: www.R-project.org.

Robins, C. M., Y. G. Yang, and D. Die. 1998. The impact of global positioning systems and plotters on fishing power in the northern prawn fishery, Australia. Canadian Journal of Fisheries and Aquatic Sciences 55:1645–1651.

Sawada, J., L. B. Holtby, and B. Finnegan. 2003. Forecast for northern British Columbia coho salmon in 2003. Canadian Science Advisory Board Secretariat, Research Document 2003/084.

Shaul, L., S. McPhearson, E. Jones, and K. Crabtree. 2004. Stock status and escapement goals for coho salmon in Southeast Alaska. *In* H. J. Geiger and S. McPherson, editors. Stock status and escapement goals for salmon stocks in Southeast Alaska. Alaska Department of Fish and Game, Division of Sport Fish and Commercial Fisheries, Special Publication 04-02, Juneau.

Shaul, L., L. Weitkamp, K. Simpson, and J. Sawada. 2007. Trends in abundance and size of coho salmon in the Pacific Rim. North Pacific Anadromous Fish Commission Bulletin 4:93–104.

Su, Z., and M. D. Adkison. 2002. Optimal in-season management of pink salmon (*Oncorhynchus gorbuscha*) given uncertain run sizes and seasonal changes in economic value. Canadian Journal of Fisheries and Aquatic Sciences 59:1648–1659.

Wade, P. R. 2000. Bayesian methods in conservation biology. Conservation Biology 14:1308–1316.

Walters, C., and A. Punt. 1994. Placing odds on sustainable catch using virtual population analysis and survey data. Canadian Journal of Fisheries and Aquatic Sciences 51:946–958.

Weitkamp, L., and K. Neely. 2002. Coho salmon (*Oncorhynchus kisutch*) ocean migration patterns: insight from marine coded-wire tag recoveries. Canadian Journal of Fisheries and Aquatic Sciences 59:1100–1115.

Wilberg, M. J., and J. R. Bence. 2006. Performance of time-varying catchability estimators in statistical catch-at-age analysis. Canadian Journal of Fisheries and Aquatic Sciences 63:2275–2285.

Winters, G. H., and J. R. Wheeler. 1985. Interactions between stock area, stock abundance, and catchability coefficient. Canadian Journal of Fisheries and Aquatic Sciences 42:989–998.

Appendix: Metropolis-Hastings Procedure

We used a Markov Chain Monte Carlo (MCMC) procedure with a Metropolis-Hastings algorithm from the MCMC package for R software (MCMC pack) to construct the joint posterior distribution and the marginal posterior distributions for marine survival and catchability coefficients (Martin and Quinn 2006; R Development Core Team 2007). Initial iterations of the MCMC procedure showed that the acceptance rate of simulations was low compared with the optimal acceptance rate of 0.44 (Gelman et al. 2004). Reducing the scale of the jumping distribution to 0.40 achieved acceptance rates ranging from 0.38 to 0.55. Initial runs produced high autocorrelations for all estimated parameters; lag 1 autocorrelation coefficients ranged from 0.80 to 0.95, where lag values are expressed relative to thinning intervals. Evaluation of the autocorrelation function at increasing levels of lag showed that autocorrelation decreased slowly with increasing lag values for all parameters and that a lag value of 125 was generally necessary to achieve autocorrelation near zero. Based on initial examinations of the Markov chains and posterior distributions, we ran 100,000 MCMC iterations and sampled every 125th value to avoid autocorrelation. The first 50,000 samples were discarded for burn-in, resulting in a total of 400 posterior sample points that were used to make inferences about parameter values.

We assessed convergence for each estimated parameter by visual inspection of three independent MCMC chains and by computing a potential scale reduction factor, $\Re$ (Gelman et al. 2004). An $\Re$ statistic of 1.0 is the target value used to indicate posterior convergence; however, $\Re$ values less than or equal to 1.1 are generally considered acceptable (Gelman et al. 2004). Chains were made independent by initiating each at a different (overdispersed) starting point.

Visual inspections of simulated posterior distributions for marine survival rate and catchability parameters did not indicate a lack of convergence of MCMC chains on the target distribution. All posterior distributions were unimodal, and the average parameter values within chains remained stable after the burn-in period was removed. The $\Re$ value for each parameter also indicated approximate convergence had been achieved for all posterior distributions ($\Re < 1.1$).