Incorporating the Effects of Migratory Behaviour and River Conditions into Estimates of Steelhead Escapement

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Abstract

Estimating escapement from repeated counts will be uncertain when catchability is low during periods of peak abundance or late in the run. We analyzed four years of radio telemetry and snorkel count data to examine the effects of physical and biological factors on the catchability, survey life, and departure timing of a winter-run steelhead population, and integrated these relationships and data into a maximum likelihood procedure to estimate escapement and run timing. Date of entry and gender explained 65% of the variability in survey life and relationship did not vary significantly among years. The timing of immigration into the survey area was similar across genders, but the departure schedule of male spawners was significantly later than for females and there were significant differences in departure timing across years. The ratio of horizontal visibility to discharge explained about 50% of the variation in catchability in a subset of the data, and there was weak evidence that catchability increased later in the run due to behavioural changes associated with spawning. Use of the model predicting catchability based on river conditions improved the precision of escapement estimates in years when survey-specific estimates of catchability were available. Use of both departure timing and survey life data greatly reduced the uncertainty in escapement estimates by providing better definition of run timing.

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1.0 Introduction

Population size of returning adult salmon and steelhead is often estimated by obtaining repeated counts of the number of fish present in a survey area over the course of the run. Catchability, the proportion of fish present on each survey that are enumerated, and the proportion of the total run that is present on the surveys, must be determined to calculate the total escapement. Catchability can be estimated using standard mark-recapture techniques, but determination of the proportion present is more difficult as it depends on the difference between the cumulative proportions that have arrived and departed by each survey date. The most common approach to determine the proportions present is to estimate parameters that define an arrival timing function, and in conjunction with data or assumptions about the time a fish resides in the survey area (survey life), calculate the departure schedule. The likelihood of the arrival timing parameters can then be determined based on how well the proportion of fish present on each survey predicted by the model fit the temporal pattern in the repeated count data. Hilborn et al. (1999) used a maximum likelihood approach to estimate escapement and arrival timing parameters based on the assumptions that survey life was constant and that counts were measured with error but that, on average, all fish present in the survey area were counted. Su et al. (2001) assumed there was a relationship between survey life and date of entry to account for decreasing survey life over the duration of the run. Korman et al. (2002) used a similar survey life model and developed a likelihood structure for using mark-recapture information to estimate survey-specific catchabilities.

In may rivers, catchability of visual-based surveys will be temporally heterogeneous, especially for winter-run steelhead where migration timing occurs over a period of months when there are very large differences in flow and water clarity. Catchability estimates can be very imprecise at the peak or late in the run when discharge is high and clarity is low. Catchability may be spatially heterogeneous within the survey area due to differences in river morphology and tributary inputs of fine sediment, and if within-river migratory patterns change the proportion of fish in these different environments over time, the overall extent of temporal variation in catchability may increase.

Escapement estimates will be uncertain if there are no postpeak counts (Hilborn et al. 1999, Adkison and Su 2001) or if peak and postpeak surveys occur during periods of low catchability (Korman et al. 2002). In these situations, the possibility of a large number of fish entering at the peak or late in the run cannot be discounted in the estimation process because there is little information about arrival timing in the repeated count data. Su et al. (2001) used a hierarchical Bayesian model to 'borrow' information on arrival timing from years when it was better defined to improve estimates of escapement and timing in years when few or no counts are made after the peak of escapement. The approach has utility for escapement programs with many years of data and where timing is well defined in at least some years, but is not very useful in programs with less data and/or where escapement timing is never well defined due to deterioration in catchability at the peak or end of the run.

Improving our understanding of the components that effect catchability and migratory timing, and incorporating this information into an escapement estimation scheme, is necessary to obtain more reliable escapement estimates when arrival timing is poorly defined and catchability is temporally heterogeneous. The combination of snorkel surveys and radio tagging can provide much useful information in this regard. Direct observations of fish and the physical environment are useful in the formulation of hypotheses about factors potentially effecting catchability. Radio tracking can be used to describe the spatial distribution of fish in the survey area and in conjunction with counts of tagged fish, can be used to quantitatively evaluate the influence of biological and physical factors on catchability. Radio telemetry data can also be used to directly measure survey life and departure timing that can in turn be related to biological factors and physical conditions.

In this paper we analyze four years of radio telemetry and snorkel count data for a steelhead population that spawns in the Cheakamus River, BC. We examine the effects of physical and biological factors on catchability, survey life, and departure timing. We modify the escapement estimation approach of Korman et al. (2002) to make better use of this information and account for uncertainty in all component relationships. The new estimation procedure predicts catchability based on river conditions, and combined with tag-derived estimates of catchability, predicts the number of fish present on each survey. Using data on survey life and departure timing, posterior distributions of escapement and run timing are derived using Markov Chain Monte Carlo (MCMC) simulation.

On August 5th 2005, a CN train derailment in the Cheakamus Canyon resulted in a spill of 41,000 litres of caustic soda into the Cheakamus River. The most severely affected were rearing juvenile steelhead/rainbow trout, with approximately 90% mortality in four age classes (McCubbing et al. 2005). We developed a simple spreadsheet model using steelhead escapement and age data from the Cheakamus River and information on stock productivity and marine survival from the Keogh River, to estimate how long it will take the Cheakamus steelhead population to recover to pre-spill abundance levels. This projection is presented in Appendix A.

2.0 Methods

Information from radio telemetry surveys of steelhead conducted in 2001, and 2003-2005 was used in conjunction with snorkel counts for individual years from 1996-2005 to develop annual escapement estimates. Details of the snorkel surveys and radio telemetry programs, model structure and parameter estimation, and analytical methods are provided in Sections 2.1-2.4.

2.1 Snorkel Surveys

The Cheakamus River is a 5^{th} order glacially-fed river with an unregulated mean annual discharge of 65 $m^3 \cdot sec^{-1}$ that drains an area of 1032 km^2 of the Coastal Mountain range in southwestern B.C. (Fig. 1). River flow, is in part, regulated by the BC Hydro and Power Authority through Daisy Lake Reservoir and the Cheakamus generating plant, a 155 MW storage and diversion project. The Cheakamus River, downstream of the reservoir, extends 26 km to its confluence with the Squamish River. Only the lower 17.5 kilometers of this river are accessible to anadromous salmon and steelhead. The survey area was limited to the upper 14.5 km of the anadromous portion of the river that extends from ca. 500 m below the natural barrier to the confluence with the Cheekeye River.

On average between 1996 and 2004, 9 surveys have been conducted annually, typically between early March and mid- to-late May (Table 1). On each survey, a team of three divers floats the entire study area (14.5 km of river) in about six hours. Divers float side-by-side in lanes spaced equidistant along the channel cross-section. The number of tagged and untagged steelhead, char (bull trout or Dolly Varden), and resident rainbow trout greater then 20 cm in fork length are recorded by river section (Table 2) on each survey. Diver horizontal visibility (HV) was estimated by measuring the maximum distance from which a diver could detect a dark object held underwater at 1 m depth. Horizontal visibility was measured in sections 4 and 21 to index conditions in the upper and lower survey areas, respectively (Table 2, Fig. 1).

Hourly water temperatures were recorded with an Onset Tidbit temperature logger placed in section 13. Mean daily discharge (Q) over the survey period was computed from the Water Survey of Canada (WSC) hourly discharge record for the Cheakamus River at Brackendale (WSC 08GA043, Section 27, Fig. 1).

2.2 Radio Telemetry

Steelhead were captured by volunteer anglers fishing both within and downstream of the survey area (Fig. 1). Upon capture, a MCFT-3A radio tag (Lotek Engineering Inc.) was placed in the stomach of each fish and a 6-inch fluorescent pink spaghetti tag was attached through the dorsal muscle mass, so that divers could visually identify that the fish was radio tagged. Fork length and gender were recorded during tagging. Fish were held in a submersible holding tube for a minimum of one-half hour prior to release to ensure that the radio tag was properly placed, and that tag regurgitation had not occurred. In addition, the movement of tagged fish was monitored closely for the first 48 hrs to ensure that migration behavior was not adversely affected by handling.

The movements of radio-tagged steelhead were determined using data from two fixed telemetry stations and mobile tracking conducted during the snorkel surveys. Fixed stations were located at the downstream ends of the upper and lower survey areas (Fig. 1). Lotek SRX_400 receivers with CODE LOG W17 and W20 firmware were used at fixed telemetry stations to record upstream and downstream movements. The fixed station at the downstream end of the lower survey area was configured so it could also record movement of fish up and down the Cheekeye River. Telemetry stations consisted of a 12-volt deep cycle battery, a watertight enclosure, three 4-element Yagi antennas, double insulated coaxial cable fitted with BNC connectors and an ASP-8 antenna-switching unit. The antennas were pointed in the upstream and downstream directions of the Cheakamus River. A third and fourth antenna were added to the lower station and orientated in the upstream and downstream directions of the Cheekeye River. The direction of travel was determined based on the relative signal strength detected by each antenna (Koski et al. 1993). Receivers at fixed telemetry stations were set up to continuously scan all frequencies in use. When a steelhead outfitted with a digitally encoded tag moved into detection range, the date, time, channel, code, signal strength and the antenna number were recorded within the receiver's memory. Receiver data were downloaded when the fixed stations were retrieved at the end of spawning and kelting period (late June).

During snorkel surveys, a raft with one technician piloted by a river guide followed 50-100 meters behind the divers. The technician determined the presence of tagged steelhead in each river section using a Lotek SRX 400 version 4.01/W5 mobile receiver outfitted with a 3-element Yagi antenna (model F-3FB). The upstream boundary of the snorkel survey was ca. 1.5 km upstream from the raft put-in. Prior to commencing the raft survey, a technician hiked behind the divers to the upstream end of the survey area to check for the presence of tags in this section (section 0) and upstream of the upper survey area (section –1).

Five years of radio telemetry were conducted between 2000 and 2005 (Table 1). The telemetry program in 2000 was a pilot study used principally to determine spawning distribution. Survey life, date of departure, and on the temporal distribution of tags in the survey area was not measured. Although the total number of tags deployed was low, fish with radio tags received an external mark, so it was possible to estimate catchability on some surveys. In this analysis, the tagging information from 2000 is used to estimate escapement in that year, but the data was not used in the multi-year analyses of catchability, survey life, and departure timing.

2.3 Model Structure and Parameter Estimation

The proportion of the total escapement entering the survey area on each day (PA_i) of the simulated run is predicted by a beta distribution,

(1) $$PA_i = \Theta_i^{\alpha-1}(1-\Theta_i)^{\beta-1}$$

where, α and β are parameters of the beta distribution and Θ_i represents the proportional day of the run for day *i*, ranging from 0 to 1 on the assumed first (January 1) and last (June 30) day, respectively. The number of days a fish spends in the survey area is predicted using a negative logistic relationship,

(2) $$SL_i = SL_{\max}(1 - \frac{i^{SL_{sl}}}{SL_{half}^{\ \ SL_{sl}} + i^{SL_{sl}}})$$

where SL_i is the mean survey life in days for fish entering on day *i*, SL_{max} is the maximum survey life possible, SL_{half} is the day at which survey life is half the maximum, and SL_{sl} is the slope of the relationship. The mean departure day, *d*, for any fish arriving on day *i* is simply $d = i + SL_i$. The proportion of fish that arrive on day *i* and depart on day *j* is predicted from a normal distribution with mean *d* and standard deviation σ_{sl},

(3) $$PAD_{i,j} \sim Normal(j,\ d,\ \sigma_{sl})$$

PAD values are standardized so that proportions across all departure days for each arrival day sum to 1, that is, all fish must have left the survey area by the assumed last day of the run. The proportion of fish departing on each day is computed from,

(4) $$PD_j = \sum_i PA_i * PAD_{i,j}$$

Note that departure timing depends on both arrival timing and the survey life relationship that defines PAD. Finally, the number of fish present in the survey area on each day (U_i) is the product of the total escapement (*E*) and the difference between the cumulative arrivals and departures on that day,

(5) $$U_i = E * (\int_1^i PA - \int_1^i PD)$$

Note that *E* represents the escapement of unmarked fish so the total escapement is simply the sum of this value and the total number of fish that are tagged. The difference between the cumulative values of *PA* and *PD* on any date represents the proportion of the total run that is present.

Escapement, arrival timing, and survey life parameters are jointly estimated in a maximum likelihood framework that integrates mark-recapture data collected in a single year with the telemetry data collected from 2001-2005. The likelihoods of observing unmarked (L_u) and marked (L_m) fish on any survey day are assumed to follow a Poisson distribution,

(6) $$r_i \sim Poisson(q_i R_i)$$

(7) $$u_i \sim Poisson(q_i U_i)$$

where, R_i is the total number of marked fish present on a survey (determined from telemetry data), r_i is the number of marked fish that are observed, U_i is the predicted number of unmarked fish that are present (predicted from eqn. 5), u_i is the number of unmarked fish observed, and q_i is the catchability or observer efficiency. L_u and L_m were computed by summing the log-transformed probabilities returned from the Poisson model across all surveys conducted over the run. Catchability is a nuisance parameter that can be omitted from the fitting procedure by evaluating it at its conditional maximum likelihood estimate (Korman et al. 2002) and is calculated from,

(8) $$q_i = \frac{r_i + u_i}{R_i + U_i}$$

That is, catchability is simply the ratio of the total number of fish seen to the total number present. Values of U_i are not independent across surveys because they are linked through the model structure and parameters, thus the number of unmarked fish observed can contribute to the estimate of catchability.

The likelihood of survey life parameters (L_{sl}) was computed assuming normally distributed error,

$$(9) \qquad slobs_i \sim Normal(SL_i, \sigma_{sl})$$

where, $slobs_i$ is the observed survey life for the i^{th} tagged fish for which survey life and date of entry could be determined, and SL_i is the predicted survey life for the same fish based on its date of entry (eqn. 2). Note that σ_{sl} is a nuisance parameter that is calculated at its conditional maximum likelihood value of $\sqrt{\frac{\sum(slobs_i - slpred_i)^2}{nsl}}$, where nsl is the number of survey life observations (Walters and Ludwig 1996). Probabilities returned from the normal distribution were log-transformed and summed across all survey life observations ($nsl = 33$) obtained between 2001 and 2005.

The likelihood of the predicted departure schedule (L_{pd}) was computed assuming multinomial error,

$$(10) \qquad nexit_i \sim Multinom(Texit, PD_i))$$

where, *Texit* is the total number of radio tagged fish for which an exit date could be determined (n = 104) between 2001 and 2005, $nexit_i$ is the number of radio tagged fish that departed on the i^{th} day, and PD_i is the predicted departure proportions for these days (from eqn. 4).

Korman et al. (2002) found that the ratio of horizontal visibility to discharge was reasonably reliable predictor of catchability computed from the ratio of tags observed to tags present on each survey. Such predictions are required to estimate the number of fish present on individual surveys in years when there is no tagging. In this analysis, we recognize that physically based predictions of catchability can also be used in years with tagging information to increase the precision of estimates of the numbers present. The precision of the tag-based estimate of catchability will be very poor when the total number of tags present or the true catchability is very low. In this situation, the contribution to the estimate of catchability from the physically based model could be important. The model used to predict catchability in the escapement estimation procedure was,

$$(11) \qquad qp_i = LOGIT^{-1}\left[(B_0 + B_1 \log\left(\frac{HV}{Q}\right)\right]$$

where qp_i is the physically-based prediction of observer efficiency, B_o and B_1 are the intercept and slope of the model, HV is the horizontal visibility (in meters), Q is discharge (in $m^3 \cdot sec^{-1}$), and $LOGIT^{-1}$ is the inverse logit transformation used to constrain predicted catchabilities between 0 and 1. Two additional likelihoods for the number of marked (L_{pm}) and unmarked (L_{pu}) fish observed were computed by replacing the conditional catchabilities in eqn.'s 6 and 7 (q_i) with catchability values predicted by the physical model (eqn. 11).

The likelihood for any set of model parameters ($\theta = E, \alpha, \beta, SL_{max}, SL_{half}, SL_{sl}, B_0, B_1$) was determined by summing all component log-likelihoods (L_{total}),

$$(12) \qquad L(data \mid \theta) = \frac{L_m + L_{pm}}{2} + \frac{L_u + L_{pu}}{2} + L_{sl} + L_{pd}$$

The denominator of 2 in eqn. 12 accounts for the fact that observations of marked and unmarked fish are essentially double-counted in the overall likelihood because they are evaluated using both conditional MLE values (eqn. 8) and physically-based predictions of catchability (eqn. 11). The first term of eqn. 12 does not contribute to the total likelihood in years with no tagging or for surveys where no tags are present in years when tagging is conducted. Posterior distributions of model parameters were estimated using a Markov Chain Monte Carlo analysis (MCMC). $E, \alpha, \beta,$ and S_{sl} were estimated in log-space as their values cannot be less than zero. SL_{max} and SL_{half} were constrained between the first (day=1) and last (day=181) day of the simulated run, using an arc tangent transformation (Hilborn and Mangel 1997). B_0 and B_1 were not constrained in the estimation but predictions were transformed by the inverse logit function to constrain values between 0 and 1. Parameters were estimated using the MCMCMetrop1R MCMC algorithm available in the MCMCPack package called from 'R'. The standard deviations of the proposal distributions were tuned to obtain an acceptance rate of 30%. Posterior distributions were then created from a systematic subsample of 7500 points drawn from an MCMC sample of 75,000. Prior to sampling, 10,000 burn-in simulations were conducted. Diagnostic procedures available in the CODA package were used to determine convergence of posterior distributions for all model parameters (see Appendix B of Su et al. 2001).

Highest likelihoods of the objective function will occur when escapement, arrival, and survey life parameters maximize the survey-specific likelihoods L_u and L_m, but model parameters also need to predict a departure schedule that is consistent with observations, and a set of catchabilities consistent with what would be predicted from the physically-based model. Unlike most mark-recapture models, by using continuous functions to estimate U_i, we are assuming that these values are not independent over time. The overall likelihood function assumes that the relationship between river conditions and catchability, survey life and date of entry, and departure timing, are exchangeable among years. A variety of alternate structures for the objective function are possible by removing various terms from eqn. 12 to account for differences in data availability or assumptions about exchangeability (Table 3). Likelihoods associated with the physical model predicting catchability can be removed (L_{pu} and L_{pm}) in years when fish are tagged if there is concern about the exchangeability of catchabilities among years, perhaps due to changes in river morphology or observers. The exchangeability of departure timing among years could be a concern if the survey life relationship is exchangeable, but arrival timing is not. It may be difficult to measure survey life in some cases, if, for example, one cannot catch fish downstream of the survey area. In this case parameters of the survey life model will move towards values that explain as much of the variability in count and departure timing data as possible. In the case of the Cheakamus and likely for other similar programs, tagging and telemetry may only be possible in a limited number of years to establish catchability and survey life relationships and departure schedules. In latter years when fish are no longer tagged, only likelihoods for unmarked components can be included in the objective function. Korman et al. 2002 only evaluated the uncertainty in escapement estimates by likelihood profiling and therefore did not integrate over the uncertainty in survey life as is done here. They did not use departure schedule data or combine information from the physical model predicting catchability in years when tagging information was available. In this analysis, we apply many of these alternate likelihood formulations to the same datasets to examine how they affect the extent of uncertainty in escapement estimates.

2.4 Data Analysis

We explored a range of model structures for important functional relationships or data used in the escapement estimation procedure. Combining relevant telemetry data from 2001 –2005, we used a maximum likelihood approach (Hilborn and Mangel 1997) to examine: 1) alternate structural forms of the survey life – date of entry relationship and the effects of the covariates gender and year; 2) alternate structural forms for predicting catchability based on horizontal visibility, discharge, date, water temperature, and the spatial distribution of tagged fish; and 3) the effects of year and gender on departure timing. The analysis of departure timing consists of a set of nested models, thus a likelihood ratio test was used to determine if the additional variance explained by more complex models outweighed the predictive cost associated with the additional parameters. Twice the difference between the negative log-likelihoods (-2L) of two models is χ^2 distributed, with degrees of freedom equal to the difference in the number of parameters between models. We used the Akaike Information Criterion (AIC) to evaluate alternate catchability and survey life models, which in many cases were not nested. For each model, the AIC is computed as the sum of the log-likelihood and 2 times the number of parameters; the model with the lowest AIC value is considered best. We followed the stepwise-AIC model selection approach of Maunder (2001). Each explanatory variable was evaluated in a separate model and ranked according to its AIC value. To determine the best combination of variables to use in a multivariate additive linear model, the one with the lowest AIC value was added first. Other variables were then added one at a time based on their individual AIC scores, and the process was repeated until the AIC for the multivariate model no longer declined.

We examined linear and logistic forms of the survey life model and assumed a normal error structure. We examined additive linear models with and without interaction terms for predicting catchability. A Poisson error structure was used to account for differences in the amount of information in each catchability estimate. Estimates determined when few tags were present or when the probability of seeing a tag was very low are more uncertain than estimates obtained under the opposite conditions, and the Poisson model correctly weights each value in the estimation. We repeated the analysis assuming a normal error structure to examine the sensitivity of the assumed error structure on model ranking. An inverse logit transformation of predicted catchability was used to constrain values between 0 and 1. To examine variation in departure timing by gender and year, we fitted beta-distributions to the data assuming multinomial error. Most likely parameter estimates were computed for all models using a nonlinear iterative search procedure that maximized the sum of log-transformed normal, poisson, or multinomial probabilities across all observations.

3.0 Results

A total of 137 steelhead were tagged between 2001 and 2005 (Table 1). Fish predominantly resided in either the upper or lower survey areas with few fish spending significant amounts of time in both (Table 4). Typically, about 10% of fish that had entered the lower survey area made downstream movements and entered or attempted to enter Brohm River (Table 5). Variability in this percentage could reflect natural variation driven by river conditions or natal homing, but could also be driven by annual differences in the spatial distribution of tagging effort. In March, when discharge is typically low and water temperatures are cool (Fig. 2), tagged fish predominantly concentrated in a limited number of holding areas that were mostly in the in the lower survey area (Fig. 3). As the season progressed, fish distribution became less concentrated and there was increased use of the upper survey area (Fig. 4). Spawning, as evidenced by the presence of redds and examination of radio tracking records, was confirmed in both upper and lower survey areas and began by mid-April when water temperatures exceeded 6.5-7.0 ^{0}C.

The relationship between survey life and date of entry could only be evaluated using data from 33 of the 137-tagged fish. Date of entry in to the survey area was unknown for the many fish caught in the survey area, and date of departure could not be established for fish that died, regurgitated their tags, or were not recorded leaving the survey area (Table 4). Average survey life was 45 days with a standard deviation of 21 days (model 1, Table 6). Survey life for females and males was 39 and 51 days with standard deviations of 20 and 23 days, respectively (model 2). Date of entry explained 50% of the variation in survey life (Fig. 5) based on logistic (model 4, eqn. 2) or linear models (model 3). Most likely parameter estimates for the logistic survey life model were SL_{max} = 78, SL_{half} = 97, SL_{sl} = 4.2, and σ_{sl} = 15 days. A linear fit to the survey life data was more parsimonious than the logistic model as evidenced by its lower AIC score (Table 6). Estimating different slopes and intercepts for the linear models for each gender (model 6) resulted in a further reduction in the AIC, but the most parsimonious gender-based model had a common intercept and different slopes and explained 65% of the variation in survey life (model 5). Without accounting for gender there was little evidence of the effect of year on survey life (models 7 and 8). A model which accounted for both gender and year (model 9) had the second lowest AIC of all models that were evaluated.

Steelhead began exiting the survey area no sooner than mid-April (Fig. 6a) with the exception of two males in 2003 that subsequently migrated into the Brohm River. Females begin to emigrate from the Cheakamus River by mid- to late-April. This timing is coincident with a period when water temperature increased from 6 to 8 ^{0}C (Fig. 2) and our first observations of steelhead redds. Males and females had a similar entry schedule (Fig. 5a), but males had a much later departure schedule (Fig. 6a) because of their longer residence time (Fig. 5b). Individual beta distributions fit to the sex-specific departure schedules provided a significant improvement in fit ($p<0.001$) relative to a single relationship fit to all the data based on a likelihood ratio test. There were year-to-year differences in departure schedules when averaged across sexes (Fig. 6b) and year-specific beta distributions provided a significantly better fit to the data relative to the average relationship ($.01<p<0.05$) even when gender-specific differences were not accounted for.

We evaluated the utility of a suite of independent variables to predict catchability, computed as the ratio of tags observed to tags present. Catchability averaged 0.22, 0.27, and 0.13 over the entire, lower, and upper survey areas, respectively (Table 7). The lower survey area has a narrower wetted width due to extensive dyking which creates pools where steelhead are relatively easy to observe when horizontal visibility exceeds 4.5-5.0 m. The lower survey area also has a lower gradient that limits the spatial extent of high velocity and turbulent water where steelhead can hold, but are unlikely to be seen. The analysis was not stratified by survey area because of the limited number of tags.

Catchability estimates from 45 surveys between 2001 and 2005, could be explained both by physical conditions in the river as well as other variables related to fish behaviour and spatial distribution (Table 8). Discharge was a better predictor of catchability (model 10) than horizontal visibility (model 12). Models that used both variables independently, with and without an intercept (models 9 and 8, respectively) had lower AIC scores than the univariate models. Discharge and horizontal visibility were weakly correlated, so the model using the ratio of horizontal visibility to discharge (model 3) had only a slightly lower log likelihood than the multivariate models (models 8 and 9). However, with one less parameter, the HV/Q model (model 3) had a lower AIC than the model where HV and Q had independent slopes (model 9). There was a slight non-linear pattern in the catchability-HV/Q relationship and a log transformation (model 1) increased the log-likelihood and therefore decreased AIC relative to the untransformed relationship (model 3). Accounting for the year of the survey (model 11) in the log(HV/Q) model resulted in a slight reduction in the log-likelihood, but the additional 3 parameters resulted in a much larger AIC score.

When river conditions were accounted for through the log(HV/Q) model, catchability increased as the season progressed as indexed by the day of the run (model 2). This model had the lowest log likelihood and explained more variance than any of the other models, but the reduction in the log-likelihood was not sufficient to offset the effect of the additional parameter in the AIC calculation. Catchability increased with water temperature (model 4), after the onset of spawning (model 6), or with an increase in the proportion of tags in the lower survey area (model 7). The reduction in the log-likelihoods in all these cases was not sufficient to decrease the overall AIC scores. The percentage of tags in the lower survey area decreased over the duration of the run (Fig. 4) and its effect was therefore potentially confounded with increasing catchability as the run progressed (model 2, 4, or 6). The addition of the interaction term Ptags*Day, which limits the extent of confounding, was positively related to catchability but did not significantly reduce the log-likelihood. The log(HV/Q) model had the lowest AIC score (Table 7) as was therefore used in the escapement estimation procedure. This model only explained 25% of the variance in 45 catchability estimates between 2001 and 2005. However, much of the variance in predictions was associated with surveys with few tags present when there is very large uncertainty in catchability (Fig. 7). The HV/Q model explained over 50% of the variation in catchability when it was evaluated using only data from surveys with 10 or more tags present (n=33).

The joint estimation of escapement, arrival timing, survey life, and parameters predicting catchability as a function of river conditions provided good fits to all data components. Taking most likely parameter estimates for 2005 as an example (Fig. 8), the model predicted that the peak number of fish present in the survey area occurred in late-April. The numbers present curve provides good fits to the number of fish present on individual surveys as determined from the number of untagged fish observed expanded by either the ratio of tags observed to total tags present (Fig. 8a), or expanded based on the HV/Q catchability model (Fig. 8b). Survey life and arrival timing parameters that provided good fits to the count data were consistent with the 2001-2005 departure schedule (Fig. 8c) and survey life – date of entry data (Fig. 8d) data. The arrival timing parameters required to do this were low, implying a relatively consistent and low immigration rate over most of the run. The HV/Q model did a good job of predicting the seasonal trend in catchability as indexed by the ratio of tags observed to tags present in 2005 (Fig. 8e) while also explaining catchability estimates over the entire 2001-2005 period (Fig. 8f). This was expected as there was no significant year effect in the physical model predicting catchability (Table 8).

The estimation procedure provided plausible estimates of run timing in all survey years (Fig. 9) although this inference is quite limited in early years when few surveys were conducted. Escapement estimates were more uncertain in 1996 and 1997 (CV = 0.25) compared to later years when the number of surveys was at least doubled (2003-2005 CV = 0.17-0.19, Fig. 9). With the exception of 2004, we were unable to obtain postpeak estimates of the numbers present. In all years, uncertainty in the numbers present was higher during the peak or late in the run as catchability declined due to higher discharge and decreased water clarity. The inter-annual trend in median escapement estimates shows relatively low but variable escapement between 1996 and 2000 (avg. = 180 with CV = 0.47), followed by generally higher and more stable escapements (average = 390, CV = 0.16, Fig.'s 10 and 11). The average of the median values of escapement between 1997 and 2005 was 290 spawners.

There was considerable correlation among estimated parameters (Fig.12). Arrival timing parameters were strongly correlated. Low and moderate escapements could occur under a range of arrival timing values, however higher escapements were more likely when arrival timing values were low, implying consistent immigration rates over the run. Survey life parameters were strongly correlated with each other. This not surprising as a 3 parameter logistic model, while provides a plausible structure when the duration of the entire run is considered, was not the most parsimonious model over the range of survey life data that was available (Table 6, Fig. 5a). High escapements were more likely when SL_{max} was low or when SL_{half} or SL_{sl} were high which resulted in low values of survey life. Parameters of the HV/Q model predicting catchability were strongly correlated with each other which is not surprising considering the relatively weak relationship and uncertainty in low catchability estimates (Figure 7, Table 8). Variation in HV/Q model parameters had little effect on escapement or survey life parameters. To index the next effect of arrival timing and survey life parameters, we predicted the proportion of the run present on May 1st. Higher escapements were most likely when this proportion was low, which occurred when arrival timing was very consistent but low (low α and β) and to a lesser extent when survey life was low.

We evaluated the effect of including different types of information in the assessment on escapement estimates by sequentially removing each term from the overall likelihood (Table 3, Fig. 13). It was not possible to get posterior distributions to converge when some likelihood components were removed. We therefore added a weak prior on escapement assuming a normal distribution with a mean equal to the most likely escapement estimate and a CV of 1. As the prior was very uninformative, it had very little to no effect on the escapement distribution but was useful in stabilizing the model in most cases. Escapement estimates were only slightly more uncertain when tagging data from the year of the survey was not included in the assessment. This is not surprising as there is considerable variability in survey-specific estimates of catchability due to low tag numbers and generally low efficiency, and the prediction of catchability from the physical model is generally consistent with the tag-based estimates (e.g. Fig. 8e). Escapement estimates were a bit more uncertain if multi-year data defining the physical model predicting catchability was omitted. Tag-based estimates of catchability are highly uncertain for swims late in the run (Fig. 9). The physical model, which averages such estimates over multiple years, provides a more reliable prediction of the numbers present at the end of the run that in turn reduces the likelihood of higher escapements.

Escapement estimates were much more uncertain and tended to increase when departure timing or survey life data were removed from the assessment procedure (Fig. 13). There is little information about run timing in the count data because of the lack of reliable peak or postpeak estimates of the numbers present. Compounding this deficiency, there is little information on survey life late in the run from (Fig. 5a). Thus, without the departure timing data, very late arrival timing patterns are not penalized, allowing many fish to enter late in the run resulting in large escapement estimates. When survey life data were removed from the assessment the posterior distribution of escapements did not converge except in 2005. Without any survey life data, the three parameters of the survey life model are determined solely based on the temporal pattern in the count data and departure timing information. This highly overparameterized situation resulted in a very unstable model that did not converge in 2001, 2003, and 2004, and to very large uncertainty in escapement estimates in 2005.

4.0 Discussion

Repeated counts of steelhead or salmon numbers will likely contain little information about run timing if there is large uncertainty about the numbers present at the peak or late in the run. The use of both survey life and departure timing information in the assessment model was critical in reducing uncertainty in escapement estimates in this situation. Entry into the survey area was similar across genders, but females had shorter survey lives and left the survey area earlier compared to males. Females are probably emigrating shortly after spawning and defense of their redds, while males remain in the system longer, likely to increase the probability of spawning again. Gender-stratified survey life and departure timing relationships were much less variable, and would therefore increase the precision of escapement estimates. However, since we are unable to reliably determine the gender of fish from snorkel surveys, a gender-stratified analysis is not possible.

Discharge and horizontal visibility did explain some of the variation in catchability across surveys, although the relationship was quite variable. Part of this variability was caused by the considerable uncertainty in many of the survey-specific catchabilities estimates, resulting from low numbers of tags coupled with generally low catchability. In the multivariate models where river conditions were controlled through the horizontal visibility to discharge ratio, there was weak evidence that catchability increased later in the run. Warmer temperatures could increase activity levels of fish thereby increasing their probability of being seen. There appeared to be a temperature trigger of 6.5-7 ^{0}C above which spawning began. It is also possible that other factors, such as discharge, day length, or turbidity, stimulated the onset of spawning. Regardless of the mechanism, once spawning had begun, fish exhibited a much reduced flight response, were seen in pairs or larger groups, and were observed in habitats such as pool tail-outs where they were more likely to be seen. This behavioral effect, though present, was not significant in multivariate models because of the temporal covariation among measurements. Most observations occurred either during periods of good river conditions early in the run before spawning when most fish were in the lower survey area where catchability was higher, or later in the run after spawning had begun, when river conditions were poorer and a higher proportion of fish were in the upper survey area. To tease-out the effects, sufficient replication across the full range of conditions for all predictor variables is required, but this is difficult to achieve given normal patterns in spawn timing and hydrology.

Use of the HV/Q model predicting catchability improved the precision of escapement estimates in some years even though the relationship was relatively uncertain. Mark-recapture based estimates of the numbers present can be imprecise in many cases, or can be very biased if the catchability of the tagged fish is not representative of untagged ones. For example, the total number of fish present on a survey can be grossly overestimated if the majority of tagged fish are in the upper survey area where catchability is lower, and a large group of fresh unmarked fish enters the river and moves into the lower survey area. If this occurs on a survey late in the run after which there are few if any reliable estimates of the numbers present to correct the run timing curve, the estimation model can substantially overestimate the escapement and/or the upper confidence bound. Using the HV/Q relationship, which is based on multiple-years of data, produces a more robust estimate of catchability because it averages over multiple surveys with similar river conditions. Furthermore, the HV/Q model allows the use of count data early and late in the run where there are no or very few marked fish present in the survey area, and is essential in years when tagging is not conducted.

The two-parameter linear survey life – date of entry model was more parsimonious than the three-parameter logistic model based on the AIC criterion. Why then, did we use the latter when estimating escapement? Although not shown here, an arc-tangent transformed linear model provided more precise estimates of escapement while still meeting the model assumption that all fish exit the survey area by the last day of the run. We were wary of using the linear model because it likely masks the true uncertainty in survey life during the early and late part of the run when there is little data. With its extra parameter, the logistic model allows for a wider range of survey lives during these periods, and therefore admits more uncertainty in run timing. As there is little information on the relative abundance of fish late in the run from the count data, the overall effect of the more flexible survey life model is to increase the probability of larger escapement estimates. The departure timing data, which do not show large number of fish exiting late in the run, was very useful in minimizing this potential estimation problem.

The structure of maximum likelihood approaches to estimate escapement from repeat count data is evolving. Hilborn et al. (1999) used the restrictive structural assumptions of normal arrival timing and constant survey life to constrain their estimates. Su et al. (2001) increased flexibility in survey life dynamics, salvaging the estimation in years where run timing was poorly defined in the count data by borrowing information from other years where it was better defined using a hierarchical Bayesian approach. Korman et al. (2002) did not use departure timing information, and in the absence of a historical time series of informative count data, were forced to constrain arrival timing parameters. In this analysis, we have avoided the use of arbitrary constraints or priors by using the additional information in run timing provided by the observed departure schedule.

We have assumed that data defining the relationships between catchability and river conditions, survey life and date of entry, and departure timing are completely exchangeable among years and can therefore be pooled. The effect of year on both catchability and survey life relationships was weak, however departure timing was significantly different among years. Pooling the departure timing data could therefore result in an underestimate of the uncertainty in run timing and escapement estimates. The logical next step in our analysis would be to employ a hierarchical modelling approach where the year-to-year variation in data is considered. Such an analysis is warranted as the program matures, but is premature at this point given the small sample size for some component relationships and the limited number of years of telemetry data.

5.0 References

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Table 1. Number and range of dates for steelhead snorkel surveys conducted on the Cheakamus River and summary of the total number of radio tags applied in each year of study.

Year	Number of Surveys	First Survey Date	Last Survey Date	Total Tags Applied
1996	4	23-Apr	23-May	0
1997	6	10-Mar	26-Apr	0
1999	5	16-Mar	11-May	0
2000	8	2-Feb	15-May	17
2001	9	7-Feb	21-May	31
2002	9	26-Feb	21-May	0
2003	16	3-Mar	20-May	33
2004	9	12-Mar	4-Jun	36
2005	14	3-Mar	12-May	37

Table 2. List of river sections in the Cheakamus River used in the analysis of snorkel count and telemetry data. The table shows the relationship between these sections, the ones used in the 2003 analysis, the original reach break designations used in previous analyses, as well as the relationship to the upper and lower survey areas shown in Figure 1.

2004+ Section	Upstream Boundary Description	Survey Area	1997-2001 Section	2003 Section
-1	Above swimmer put-in			-1
0	Swimmer put-In to raft put-in	Upper	CYER	0
1	Raft put-n	Upper	ERCU	1
2	Large rock/powerlines	Upper	ERCU	2
3	Huge boulder at Start of Pool	Upper	ERCU	3
4	End of pool/rock on RR; Small pool	Upper	ERCU	4
5	Suspension bridge to sweepers on RL at start of riffle	Upper	ERCU	5
6	Sweepers to u/s of Culliton confluence	Upper	ERCU	6
7	Pool starting just u/s of Culliton	Upper	CUCA	7-8
8	Long boulder rapid	Upper	CUCA	9
9	Big rock on RR (orange tape)	Upper	CUCA	10
10	Above upper Campground; Logjam on RR	Upper	CUCA	11
11	Below giant gravel dump on RL	Upper	CAHB	12
12	Below split channels	Upper	CAHB	13
13	Original lunch spot at old cableway	Upper	CAHB	14
14	First pool above tree-fort (new lunch spot)	Upper	CAHB	15
15	First pool below wife wanted (Don's Pool, includes riffle d/s of new wood on RR)	Upper	CAHB	16
16	Right corner (orange tape)	Upper	CAHB	17-18
17	End of pool (orange tape)	Upper	CAHB	19
18	Boil in pool (orange tape)	Upper	CAHB	20
19	Lower Campground (orange tape)	Upper	CAHB	21
20	Orange tape on River Left above Bailey Bridge	Upper	CAHB	22
21	Bailey Bridge	Lower	HBCC	23
22	Riffle above side channel that is now gone	Lower	HBCC	24
23	Tenderfoot Confluence	Lower	HBCC	25
24	Riffle just below Al's Rock	Lower	HBCC	26
25	NVOS pool	Lower	HBCC	27
26	NVOS Tailout	Lower	HBCC	28
27	Gauge pool (warning sign on RR at start of pool)	Lower	HBCC	29
28	RST pool to below longhouse	Lower	HBCC	30
29	Top of riffle; Woody pool below longhouse	Lower	HBCC	31
30	Start of Dry section where most flow goes RR into trees	Lower	HBCC	32
31	Start at confluence with new channel. Log sticking out of water on RR	Lower	HBCC	33-34
32	Tree lying along RL	Lower	HBCC	35
33	Start of gravel bar (RL); Hydro lines above	Lower	HBCC	36
34	Frog pond; Ends at Cheekeye	Lower	HBCC	37
35	Below Cheekeye confluence			38

Table 3. Alternate likelihood formulations based on different structural assumptions and data availability.

Structural Assumptions or Data Limitations	Components of objective function
Full Likelihood (eqn. 12) – No Prior	$L_u + L_m + L_{pu} + L_{pm} + L_{sl} + L_{pd}$
No Tags in Year of Survey	$L_u + L_{pu} + L_{sl} + L_{pd}$
No q-HV/Q Relationship (eqn. 11)	$L_u + L_m + L_{sl} + L_{pd}$
No Departure Timing Data	$L_u + L_m + L_{pu} + L_{pm} + L_{sl}$
No Survey Life Data	$L_u + L_m + L_{pu} + L_{pm} + L_{pd}$
Korman et al. 2002 (tags in year of survey)	$L_u + L_m$ conditional on MLE survey life parameters
Korman et al. 2002 (no tags in year of survey	$L_{pu} + L_{pm}$ conditional on MLE survey life parameters

Table 4. Summary of movement of radio tagged steelhead from 2003-2005 by river section. Yellow and green colors denote whether a fish was in the upper or lower survey areas, respectively. See Table 1 for definition of sections.

2005

						upper	lower												
Chan. Code	Date of Capture	Date of Exit	Loc. Capture	% Time in Lower	2 10-Mar	3 18-Mar	4 23-Mar	5 31-Mar	6 14-Apr	7 15-Apr	8 19-Apr	9 21-Apr	10 3-May	11 4-May	12 5-May	13 10-May	14 12-May	15 26-May	16 11-Jun
Fish using mostly upper survey area																			
1.57	11-Mar	18-Apr	28	0		-1	-1	0	**2**	1									
3.78	11-Mar	22-May	28	0		11	2	2	8	8	8	6	9	9	**10**	8	9		
1.66	24-Mar		27	0				6	**2**	2	0	0	0	0	0	1	0	1	1
3.81	13-Apr	11-May	11	0					14	14	14	15	12	12	11	11			
3.90	13-Apr	28-May	5	0					6	1	1	-1	1	1	3	**1**	0	1	
3.93	13-Apr	2-Jun	11	0					14	14	**14**	14	11	8	8	0	2	1	
3.89	21-Apr	8-May	29	0									11	11	11				
3.84	28-Mar	28-May	27	9				**13**	14	**7**	5	9	1	4	1	**1**	1	27	
1.68	28-Mar		29	20				**27**	**27**	**17**	**17**		20	19	20	19	19	20	
3.86	3-Apr	19-May	35	29							34	**24**	2	4	3	1	1		
3.76	18-Apr	11-May	28	33							25	25	8	14	14	13			
Fish using both upper and lower survey areas																			
3.88	21-Mar	15-May	27	36			**29**	**29**	9	6	**5**	5	9	9	**9**	25	25		
3.66	7-Mar		28	43	18	18	18	15	14	14	21	21	21	21	21	21	10	1	
1.69	14-Apr	16-May	31	60						29	**27**	25	**3**	0					
3.91	14-Apr	11-Jun	29	64					29	**25**	**21**	21	14	7	8	21	35	28	18
Fish using mostly lower survey area																			
3.82	14-Apr	4-May	29	67					29	29	29	25	18	12					
3.92	21-Apr		35	67									28	28	**28**	23	19		16
1.70	22-Apr	31-May	29	67									21	21	20	21	21	6	
1.53	25-Mar	14-May	29	70				25	**25**	**25**	**25**	**20**	18	23	19	33	34		
1.60	3-Mar	7-May	29	73	27	26	27	26	**27**	**26**	**26**	26	18	18	18				
1.67	29-Mar	4-May	28	86				28	**29**	**28**	28	15	28				35		
1.61	21-Apr		27	86								27	21	21	21	21	21	19	
3.83	14-Apr	11-May	29	88					29	28	25	12	21	25	25	27			
3.85	23-Mar	11-May	29	89				27	27	27	27	29	27	27	27	**18**			
1.63	10-Mar	12-May	29	100		29	29	29	29	29	29	29	**24**		29	27	28		
3.67	15-Mar	12-May	35	100						29	**27**		29	29	29	35	35		
3.80	15-Mar	18-May	28	100		25	25	**25**	25	25	25	25	25	25	35	26	25		
3.95	4-Apr	20-May	28	100					35	**35**			31		31		30		
1.65	6-Apr	5-May	31	100					**25**	**25**	**25**	**25**	28	29	29				
1.64	14-Apr		35	100							31			25	25	25	25	28	
3.77	19-Apr		25	100							25								
5.11	29-Apr	19-May	35	100									29		29	21	25		
Spat Tag, Died, or Did Not Enter Survey Area																			
1.58	3-Mar		29		25	**25**	25	25	**25**	**25**	**25**	**25**	25	25	25	25	25	25	25
1.62	10-Mar		35																
3.87	15-Mar		28			27	**27**	**27**	27	**27**	27	26	27	27	27	27	27	27	27
3.94	20-Mar		35																
4.38	23-Apr	24-Apr	29																

Table 4. Con't.

2004

Chan. Code	Date of Capture	Date of Exit	Loc. Capture	% Time in Lower	1 12-Mar	2 23-Mar	3 6-Apr	4 19-Apr	5 22-Apr	6 26-Apr	7 29-Apr	8 14-May	9 28-May	10 3-Jun	11 4-Jun
Fish using mostly upper survey area															
3.62	24-Mar		25	0			10	3	10	9	9	10	10	9	9
1.59	1-May	22-Jun	4	0									4	0	0
1.41	10-Mar	11-May	21	0	17	11	10	14	14	14	14				
3.63	17-Mar	19-May	29	0		14	4	4	2	0	0				
3.70	26-Mar	30-Apr	32	0			-1	19		7					
1.52	1-Apr	5-Jun	25	0			15	14	14	15	12	15	15	14	15
1.47	4-Apr	3-May	29	0				19	0	0	1				
3.68	27-Apr	29-May	29	0									14		
1.42	11-Mar	22-May	35	17	35	9	-1	11	3			0			
3.73	21-Apr	8-Jun	29	17					27	12		0	0	0	0
3.79	28-Apr		35	20							35	5	5	5	5
1.48	8-Apr	15-Jun	29	25								27	8	1	6
3.74	27-Apr	7-Jun	35	25							34	1		8	8
1.33	22-Mar	7-May	29	33		27	15	14	18	20	23				
3.72	14-Apr	2-Jun	29	33				18	20	22					
Fish using both upper and lower survey areas															
1.31	22-Feb	23-Apr	28	40	23	23	20	19	20						
1.35	6-Mar	23-Apr	35	40	28	28	14	14	14						
3.69	24-Mar	20-May	21	40			20	21	21	20	19				
1.45	24-Apr	12-Jun	35	40						35	30	14	14	14	
1.34	6-Mar	15-May	35	50	28	28	28	14	14	14	12	27			
Fish using mostly lower survey area															
1.55	30-Mar	21-May	29	75				25	25	22	8				
3.64	20-Mar	21-May	23	83		14	29	29	29	29	25				
1.43	11-Mar	6-May	35	100		34	34	29	29	28	29				
3.65	13-Mar	21-May	35	100		34	34								
1.46	25-Mar	7-May	29	100			29	32	32	32	32				
3.71	6-Apr	29-May	25	100				27	25	26	26	23	23		
1.54	12-Apr	24-Apr	34	100				32	32	35					
1.51	14-Apr	10-May	29	100				29	32	34	34				
3.75	20-Apr	5-Jun	28	100					29	29	29	29	29	29	29
1.44	27-Apr		29	100							27	21	23	25	25
1.56	7-May	27-May	29	100								29			
Spat Tag, Died, or Did Not Enter Survey Area															
1.32	12-Feb		35												
2.40	19-Mar	21-May	32												
3.61	25-Mar		29				20	14	14	14	14	14	14	14	14
1.49	2-Apr		28				25	25	25	25	25	25	25	25	25
1.50	5-May	10-May	29												

Table 4. Con't.

2003

Chan. Code	Date of Capture	Date of Exit	Loc. Capture	% Time in Lower	1 03-Mar	2 10-Mar	3 26-Mar	4 04-Apr	5 07-Apr	6 14-Apr	7 18-Apr	8 22-Apr	9 23-Apr	10 25-Apr	11 29-Apr	12 01-May	13 05-May	14 08-May	15 12-May	16 20-May
Fish using mostly upper survey area																				
2.13	25-Feb	25-Mar	24	0	9	20														
2.17	20-Mar	1-Jun	30	0			15	0	5	7	9									
3.21	21-Mar		35	10			23	15	5	0		0	0	0	0	0				5
3.22	21-Mar	3-Jun	35	20			26	25	15		13	12	11				12	12	12	12
1.1	20-Mar		35	21			23	9	7	34	34	0	0	0	0	0	0	0	0	0
1.4	5-Mar	1-May	35	30		32	24	18	18	18	18	18	18	18	28					
2.15	23-Mar	18-May	35	31			29	15	15	15	7	0	0	0	0	0	28	28	34	
2.38	25-Apr	5-May	23	33										34	12	11				
Fish using both upper and lower survey areas																				
2.20	24-Mar	26-May	35	36			30	24	24	24	24	14	18	19	15	16	19	14	11	7
2.18	1-Apr	25-Apr	35	50						20	20	21	21							
2.12	11-Apr	13-Jun	35	55						34	34	24	24	18	20	20	20	18	21	21
1.6	18-Feb	16-Apr	25	60	7		0	29	29	29										
1.10	10-Apr		35	63								34	34	34	34	34		0	0	2
Fish using mostly lower survey area																				
3.25	7-Apr	27-May	35	82						29	23	30	29	29	29	29	27	28	2	7
3.26	12-Apr	29-May	35	82						29	29	29	29	29	25	25	25	25	7	0
1.9	18-Feb	23-Apr	28	100	32	32	29				31	31	31							
2.11	25-Feb	23-Mar	24	100	23	23														
3.30	8-Apr	10-May	35	100						32	32	32	34	34						
1.8	8-Apr	6-May	35	100						31	31	31	31	31	31	33	32			
3.28	8-Apr	27-May	28	100						32	32	32	32	31	32					
3.24	9-Apr	13-May	35	100						35	34	34	34	34	25	25	25	25	25	
3.27	12-Apr	1-Jun	35	100						35	34	25	30	29		29	29	30	29	29
2.36	17-Apr	8-May	35	100										29	29	29	29			
2.37	25-Apr		35	100										21	34		34			
Spat Tag, Died, or Did Not Enter Survey Area																				
1.5	16-Feb		35																	
1.2	17-Feb		23																	
2.14	5-Mar		35																	
1.3	5-Mar		35			25	23	23	23	23	23	23	23	23	23	23	23	23	23	23
1.7	19-Mar		35				29	29	29	29	29	29	29	29	29	29	29	29	29	29
2.16	20-Mar		23				29	29	29	29	29	29	29	29	29	29	29	29	29	29
3.23	21-Mar		35																	
2.19	24-Mar		28				29	29	29	27	24	28	29	29	29	29	29	29	29	29
3.29	10-Apr		35																	

Table 5. Number of total tags applied to steelhead in each year of study and the number and % migrating into Brohm or Cheekeye Rivers.

Year	Total Tags	Tags in Brohm or Cheekeye	% Tags in Brohm or Cheekeye
2000	17	7	41
2001	31	3	10
2003	33	7	21
2004	36	4	11
2005	37	4	11

Table 6. Alternate models predicting survey life as a function of date of entry (Day). The number of parameters for each model (# Pars), log likelihood (Log Like), squared Pearson correlation coefficient (r^2), and Akaike information criteria (AIC) are shown. M and F denote Male and Female, respectively. Day is in units of 1 (first day) to 181 (last day). Year (Yr) is in units of 1 (2001) to 5 (2005).

Model #	**Model Name**	**Model Form**	**# Pars**	**Model Parameters** B_0	B_1	B_2	B_4	B_5	**Log Like**	r^2	**AIC**
1	Mean	B_0	1	44.67					-64.32	0.00	130.64
2	Mean - Gender	M:B_0, F:B_1	2	50.63	39.06				-63.78	0.07	131.56
3	Linear	$B_0 + B_1$*Day	2	117.72	-0.80				-59.41	0.50	122.82
4	Logistic	$B_0*(1-Day^{B_2}/(B1^{B_2} + Day^{B_2}))$	3	77.99	96.92	4.20			-59.39	0.50	124.79
5	Linear - Gender/Slope	B_0+ (M:B_1*Day, F:B_2*Day)	3	124.66	-0.79	-0.97			-56.86	0.65	119.73
6	Linear -Gender/Full	(M:$B_0 + B_1$*Day), (F:$B_2 + B_3$*Day)	4	132.50	-0.87	117.57	-0.89		-56.76	0.65	121.53
7	Linear - Year/Intercept	(01:B_0, 03:B_1, 04:B_2, 05:B_3) + B_4*Day	5	107.24	93.47	100.62	89.08	-0.58	-58.65	0.55	127.31
8	Linear - Year/Slope	$B_0 + B_1$*Day + B_2*Yr	3	117.42	-0.73	-2.73			-59.26	0.51	124.51
9	Linear-Gender/Year	B_0 + (M:B_1*Day, F:B_2*Day) + B_3*Yr	4	124.34	-0.73	-0.91	-2.36		-56.70	0.65	121.40

Table 7. Summary of tagging and snorkel count data.

Date	Total Tagged	Entire Survey Area Tags R	Entire Survey Area Tags Observed r	Entire Survey Area Untagged Observed U	Lower Survey Area Tags R	Lower Survey Area Tags Observed r	Lower Survey Area Untagged Observed U	Upper Survey Area Tags R	Upper Survey Area Tags Observed r	Upper Survey Area Untagged Observed U
2005										
3-Mar	0	0	0	40	0	0	21	0	0	19
10-Mar	5	3	0	14	2	0	7	1	0	7
18-Mar	10	7	2	38	5	2	23	2	0	15
23-Mar	13	8	3	30	6	3	13	2	0	17
31-Mar	18	15	6	64	10	5	45	5	1	19
14-Apr	29	22	10	63	13	8	42	9	2	21
15-Apr	29	24	10	57	15	9	36	9	1	21
19-Apr	30	27	9	60	20	7	39	7	2	21
21-Apr	34	26	5	35	17	3	24	9	2	11
3-May	37	31	5	42	14	4	20	17	1	22
4-May	37	29	2	24	15	2	12	14	0	12
5-May	37	27	6	35	13	3	19	14	3	16
10-May	37	24	5	24	12	2	11	12	3	13
12-May	37	18	0	2	8	0		10	0	2
2004										
12-Mar	7	4	0	16	3	0	8	1	0	8
23-Mar	12	10	1	27	6	0	18	4	1	9
6-Apr	22	16	2	26	7	1	14	9	1	12
19-Apr	26	20	4	27	8	2	11	12	2	16
22-Apr	28	22	6	49	10	3	15	12	3	34
26-Apr	29	19	8	57	8	3	23	11	5	34
29-Apr	33	19	2	23	10	1	8	9	1	15
3-Jun	36	9	1	10	2	1	4	7	0	6
4-Jun	36	7	1	9	2	0	2	5	1	7

Table 7. Con't.

Date	Total Tagged	Entire Survey Area			Lower Survey Area			Upper Survey Area		
		Tags	Tags Observed	Untagged Observed	Tags	Tags Observed	Untagged Observed	Tags	Tags Observed	Untagged Observed
		R	**r**	**U**	**R**	**r**	**U**	**R**	**R**	**U**
2003										
3-Mar	6	4	1	35	2	1	12	2	0	36
10-Mar	9	5	0	18	4	0	10	1	0	18
26-Mar	19	13	3	18	10	2	13	3	1	20
4-Apr	20	11	3	26	6	2	17	5	1	28
7-Apr	21	10	2	18	4	2	7	6	0	20
14-Apr	30	15	0	12	11	0	8	4	0	12
18-Apr	31	18	5	27	13	3	16	5	2	30
22-Apr	31	18	6	45	13	6	27	5	0	51
23-Apr	31	16	2	34	12	2	15	4	0	36
25-Apr	33	15	3	38	10	2	22	5	1	40
29-Apr	33	13	2	50	9	1	22	4	1	51
1-May	33	12	5	66	9	5	43	3	0	71
5-May	33	11	5	47	8	4	28	3	1	51
8-May	33	8	1	54	5	0	17	3	1	54
12-May	33	10	1	53	4	1	29	6	0	54
20-May	33	9	4	52	2	0	19	7	4	52
2001										
7-Feb	0	0	0	8	0	0	5	0	0	3
23-Feb	2	0	0	40	0	0	33	0	0	7
8-Mar	6	6	3	17	5	3	12	1	0	5
20-Mar	13	9	0	9	8	0	3	1	0	6
24-Mar	16	13	1	18	8	1	8	5	0	10
4-Apr	27	23	14	27	17	14	19	6	0	8
11-Apr	31	25	14	94	19	13	81	6	1	13
3-May	31	19	1	7	14	1	0	5	0	7
21-May	31	18	1	31	6	0	15	12	1	16

Table 8. Alternate models predicting catchability as a function of horizontal visibility (HV), discharge (Q), the day of the run (Day), a seasonal categorical variable for surveys before and after April 14th (the beginning of spawning), water temperature (H20Temp), and the proportion of tags present in the lower survey area (Ptags). The number of parameters for each model (# Pars), log likelihood (Log Like), squared Pearson correlation coefficient (r^2), and Akaike information criteria are shown (AIC).

Model #	Model	# Pars	B_0	B_1	B_2	Log Like	r^2	AIC
1	$B_0 + B_1$*Log(HV/Q)	2	1.74	3.99		-35.51	0.25	75.02
2	$B_0 + B_1$*Log(HV/Q) +B_2* Day	3	0.64	4.92	0.02	-34.71	0.33	75.41
3	$B_0 + B_1$*(HV/Q)	2	-3.04	9.42		-36.14	0.19	76.27
4	$B_0 + B_1$*Log(HV/Q) + B_2*H2OTemp	3	1.19	4.46	0.12	-35.18	0.30	76.36
5	$B_0 + B_1$*log(HV/Q) + B_2*Ptags*Day	3	1.12	3.95	0.01	-35.20	0.30	76.41
6	(<Apr14:B_0, >=Apr14:B_1) + B_2*Log(HV/Q)	3	2.15	2.51	4.92	-35.39	0.28	76.79
7	$B_0 + B_1$*log(HV/Q) + B_2* Ptags	3	1.69	3.97	0.06	-35.51	0.25	77.02
8	B1*HV + B_2*Q	2		0.21	-0.08	-36.52	0.24	77.03
9	$B_0 + B_1$*HV + B2*Q	3	-1.52	0.41	-0.06	-35.85	0.25	77.69
10	$B_0 + B_1$*Q	2	0.86	-0.08		-37.96	0.19	79.92
11	B_0*(01) + B_1*(03) + B_2*(04) + B_3*(05) + B_4*log(HV/Q)	5	B_0=1.71 B_1=1.27	B_2=1.80 B_3=1.90	B_4=1.77	-35.39	0.26	80.78
12	$B_0 + B_1$*HV	2	-3.85	0.55		-39.23	0.19	82.46
13	B_1*(HV/Q)	1		-3.90		-56.07	0.25	114.13

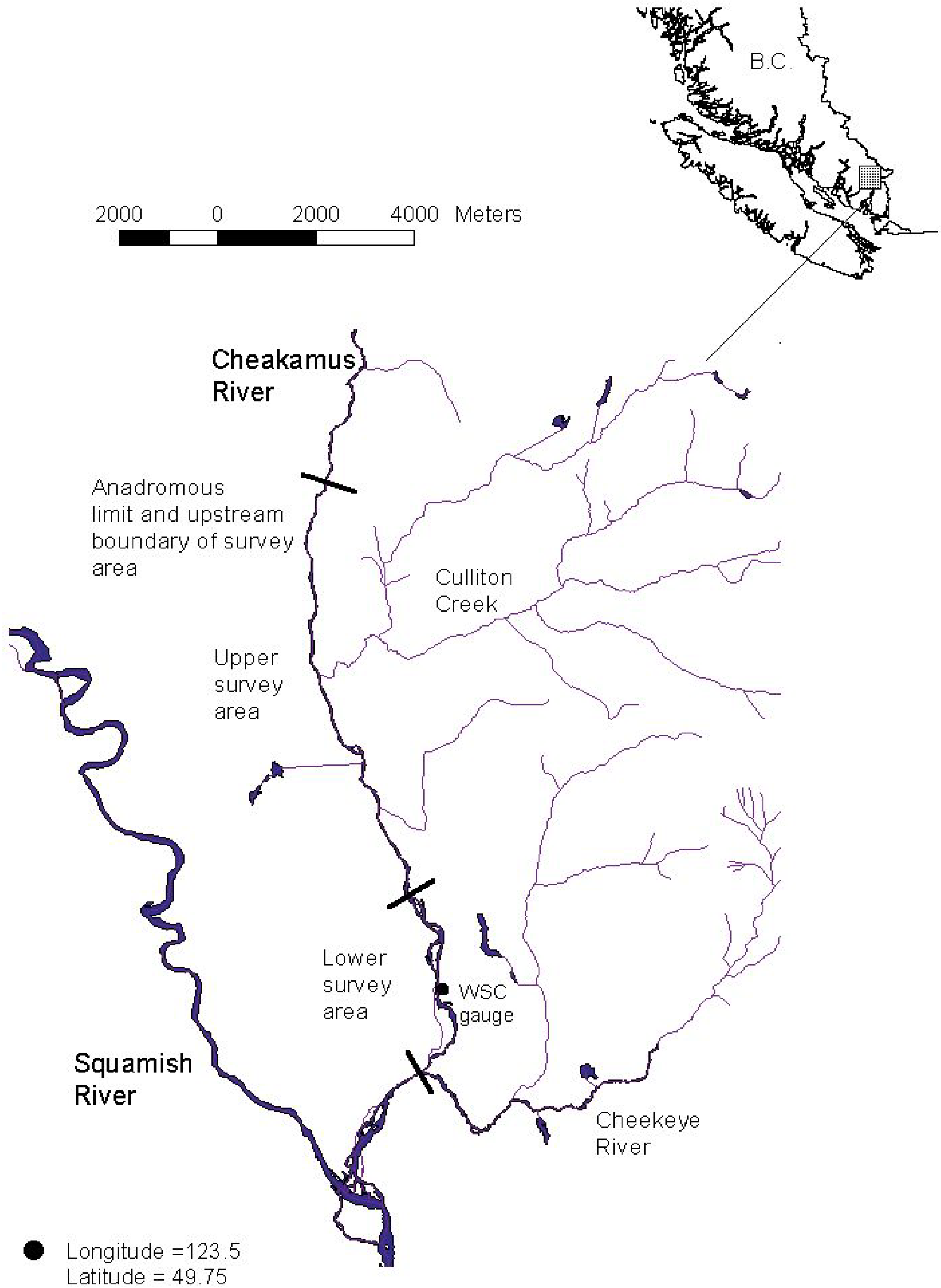


Figure 1. Map of the anadromous portion of the Cheakamus River showing the locations of the upper and lower survey areas. Brohm River is the major tributary of the Cheekeye River that runs parallel to the mainstem Cheakamus.

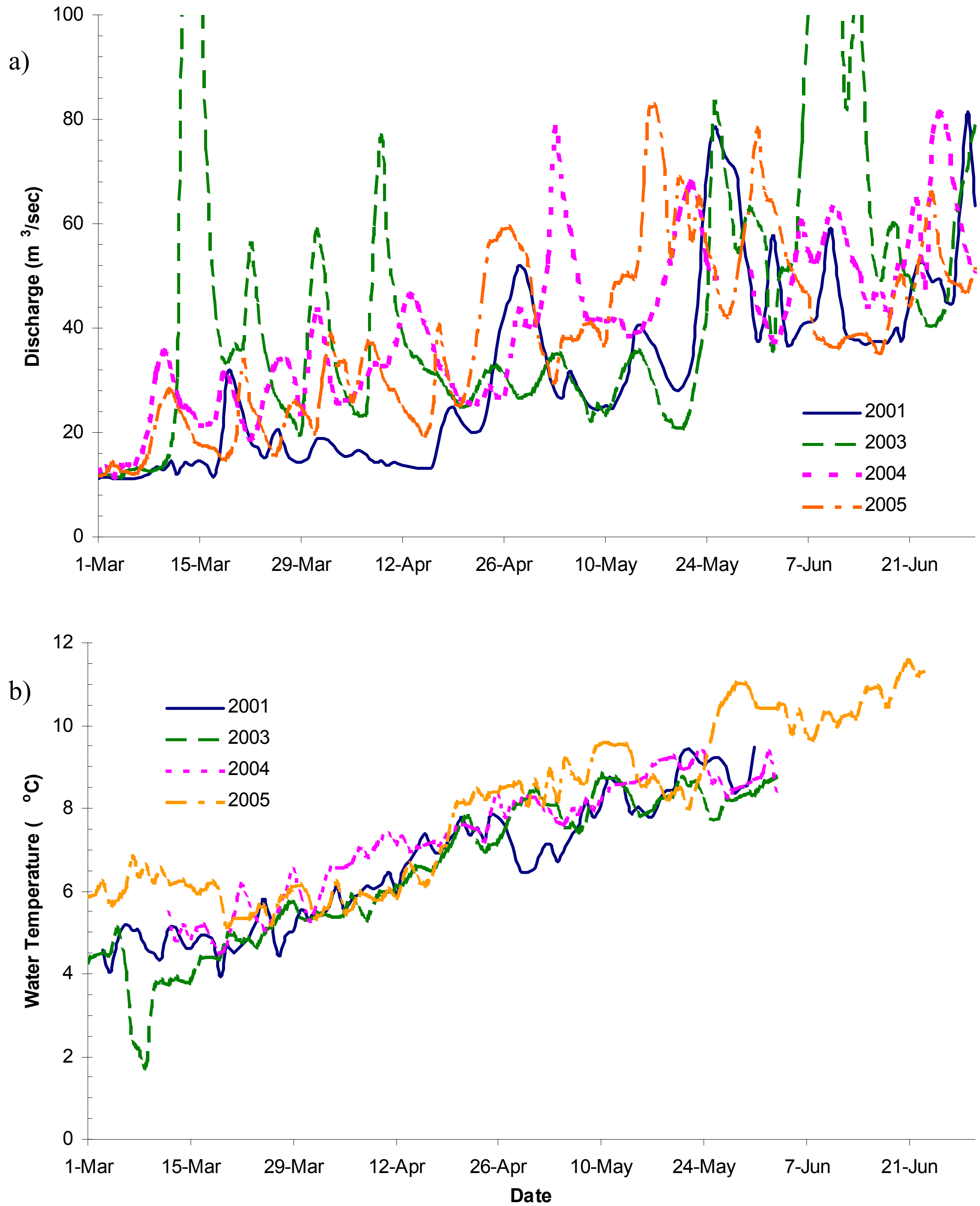


Figure 2. Discharge (a) and water temperature (b) during the majority of the steelhead migration and spawning period in years when tagging was conducted.

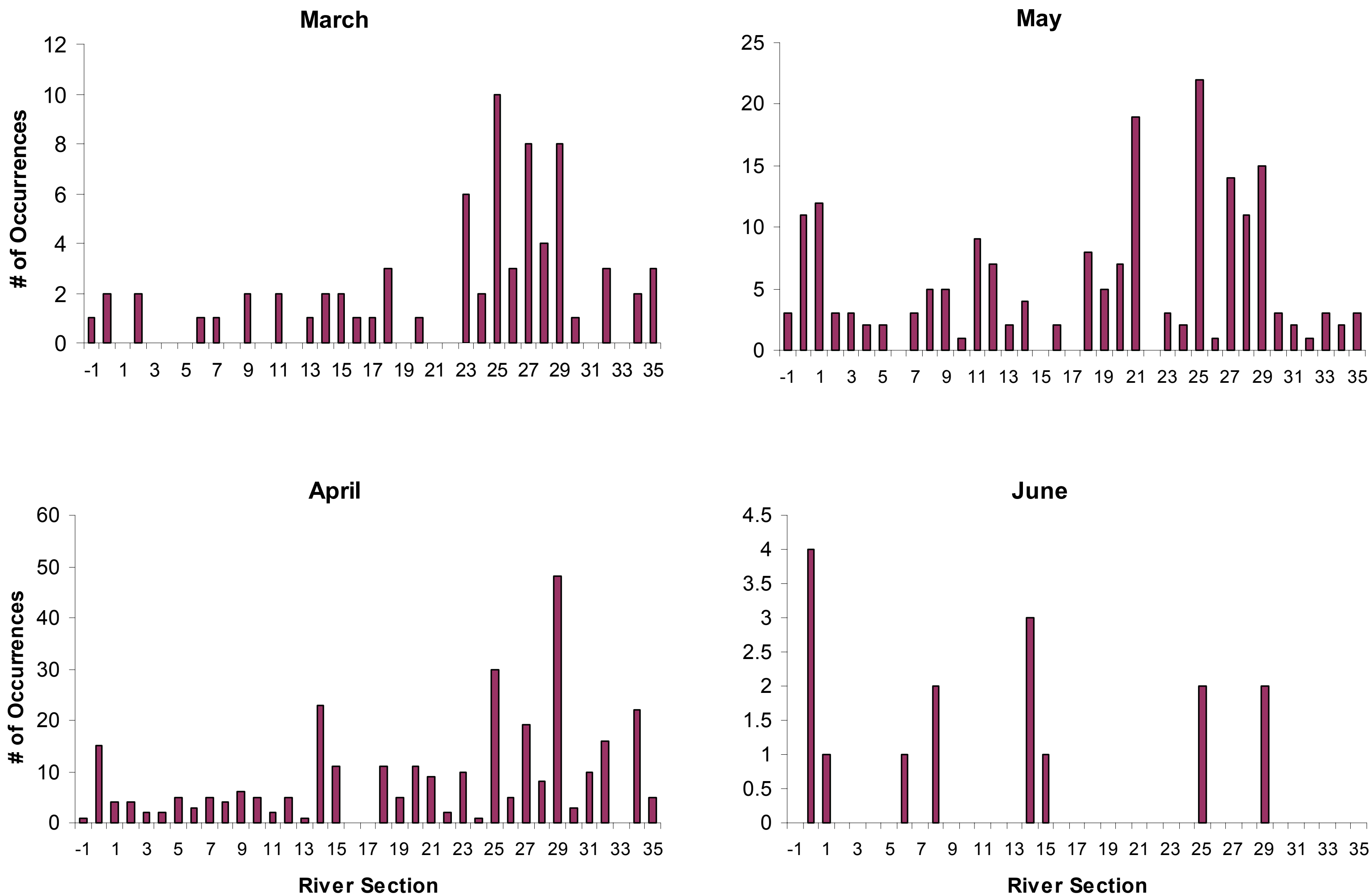


Figure 3. Location of tagged steelhead between 2003 and 2005 based on a total of 596 occurrences. River sections are ordered from upstream (-1) to downstream (35). See Table 1 for a description of river section locations. Data from 2001 was not included because location was recorded using the much longer 1997-2001 river section breaks.

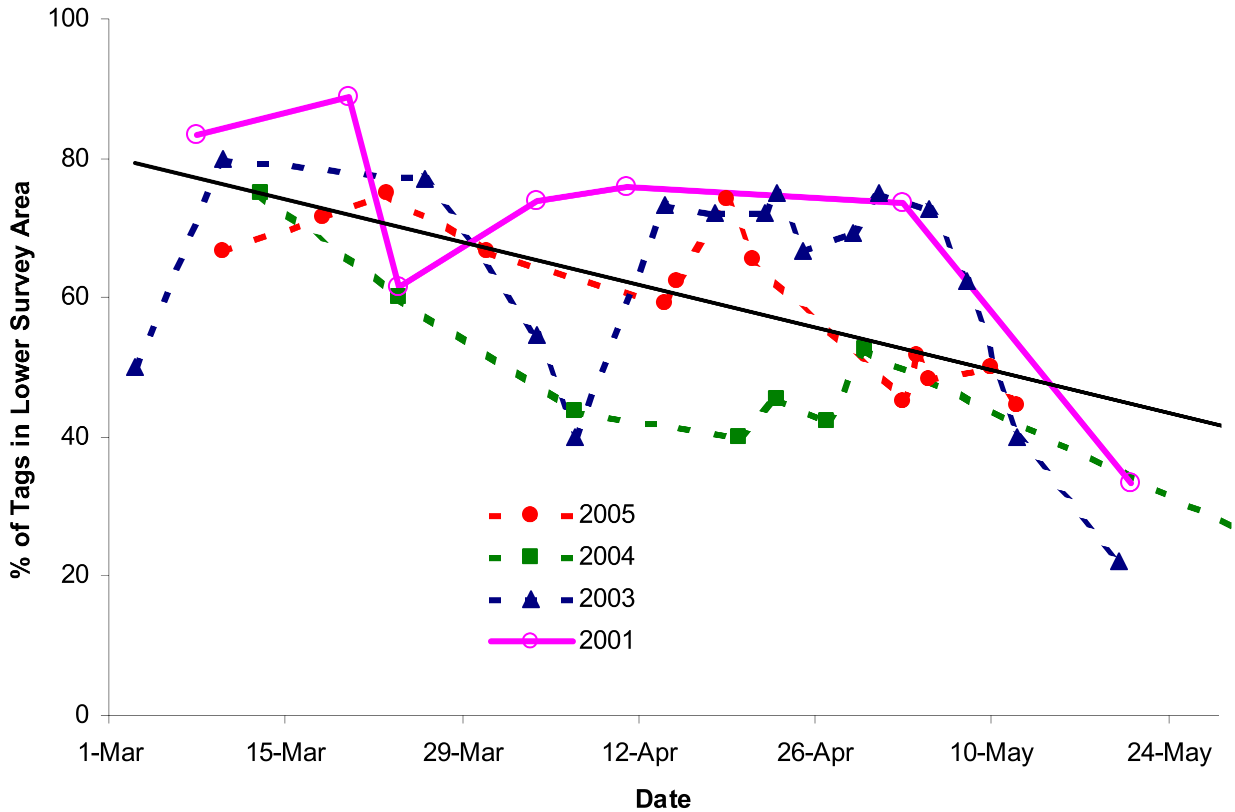


Figure 4. Percentage of tags in the lower survey area as a function of survey date, stratified by year. Black line is a linear regression fit to all years of data.

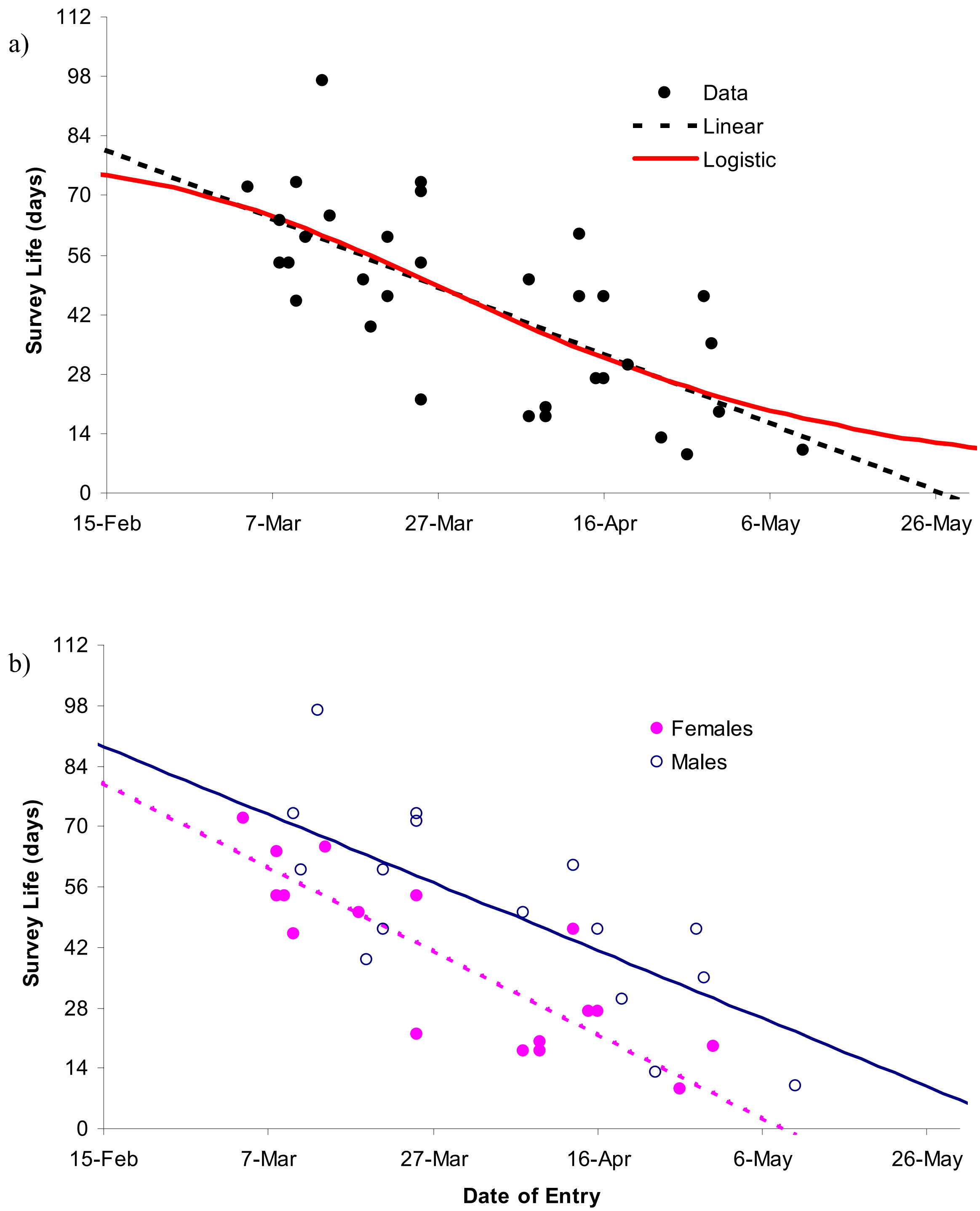


Figure 5. Relationship between survey life and date of entry into the survey area. a) shows best-fit linear and logistic models (Table 6). b) shows data stratified by gender and the most parsimonious model fit assuming a common intercept but different slopes.

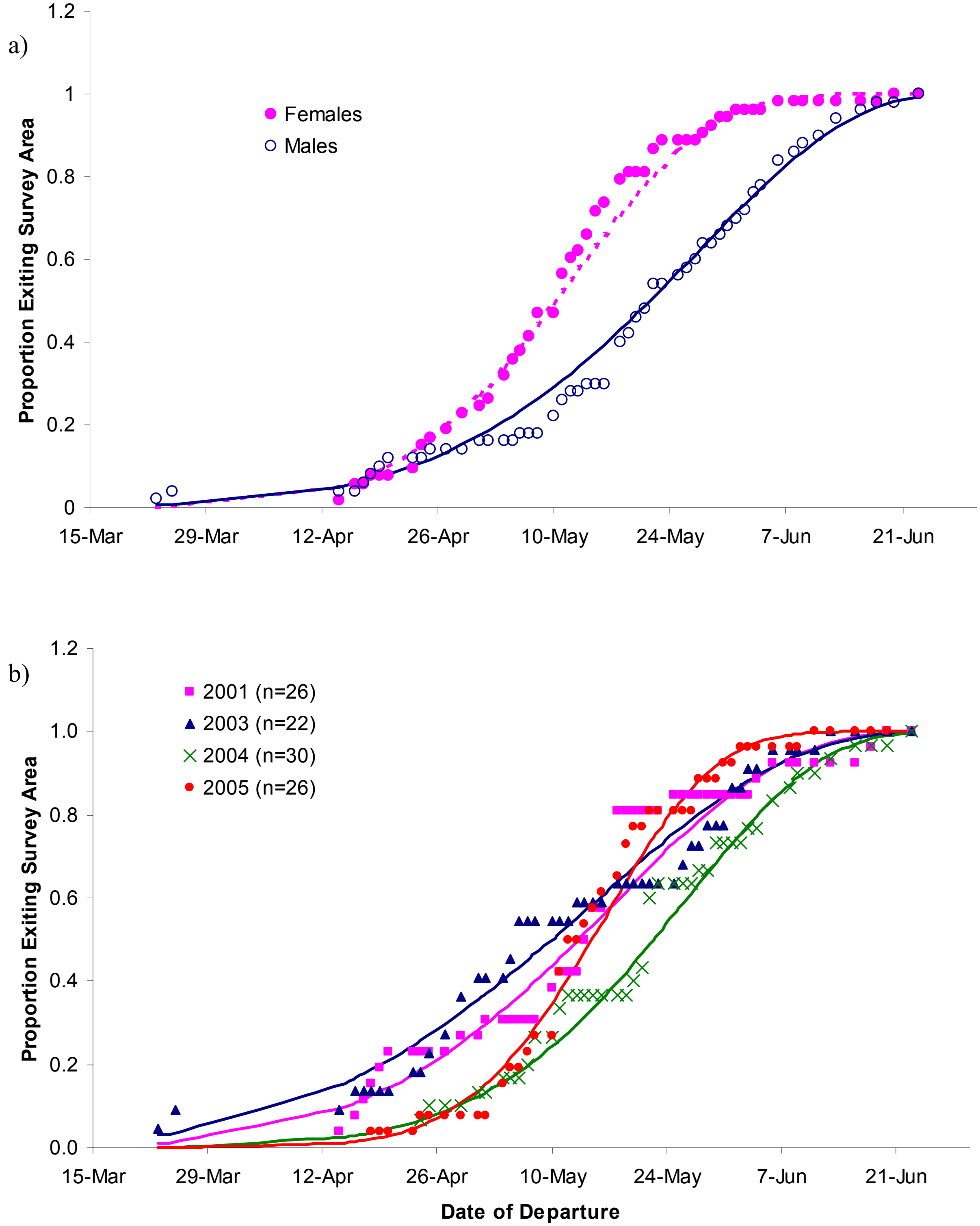
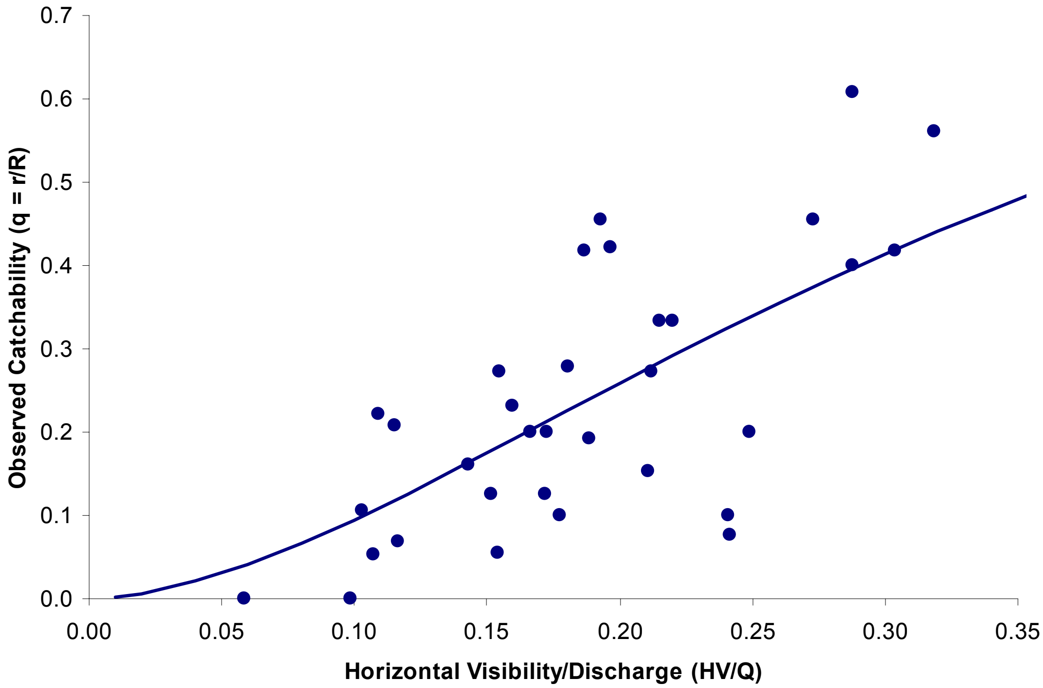


Figure 6. Cumulative proportion of tagged fish exiting the lower survey area in a downstream direction by sex (a) and year (b) with best-fit beta distributions.

a)



b)

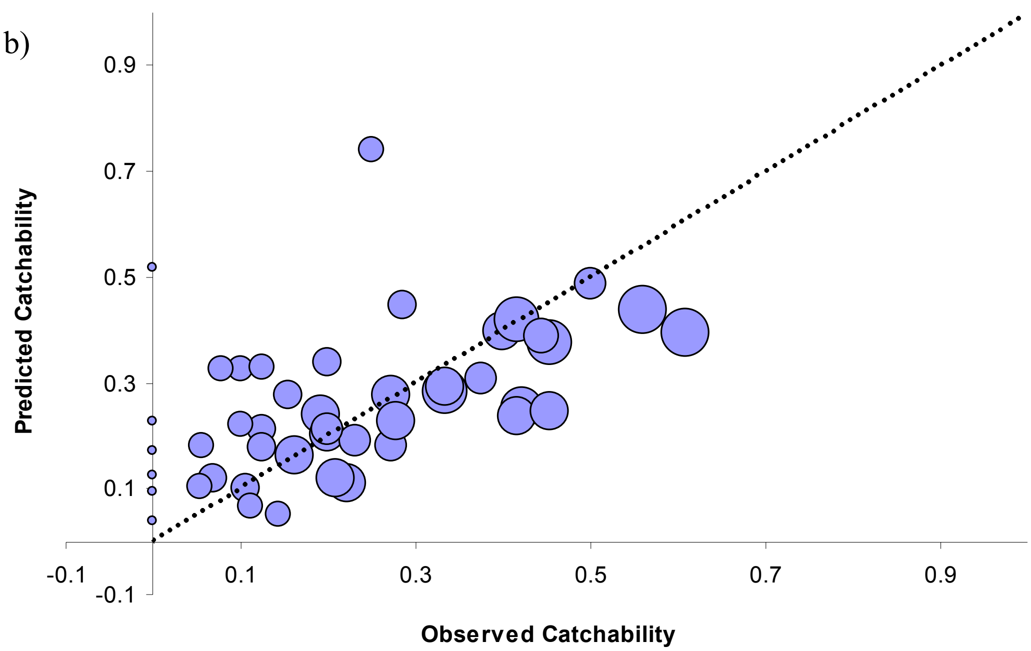


Figure 7. Relationship between most likely estimates of catchability (r/R) and the ratio of horizontal visibility to discharge with best-fit model ($q = B_0 + B_1$*Log(HV/Q)), showing data from 33 of 45 surveys when 10 or more tags present (a), and a comparison of predicted and observed catchabilities showing data from all 45 surveys (b). The size of the data points in b) is proportional to the precision of each estimate, as indexed by the inverse of the coefficient of variation. The largest or most precise observations have a CV of 0.25.

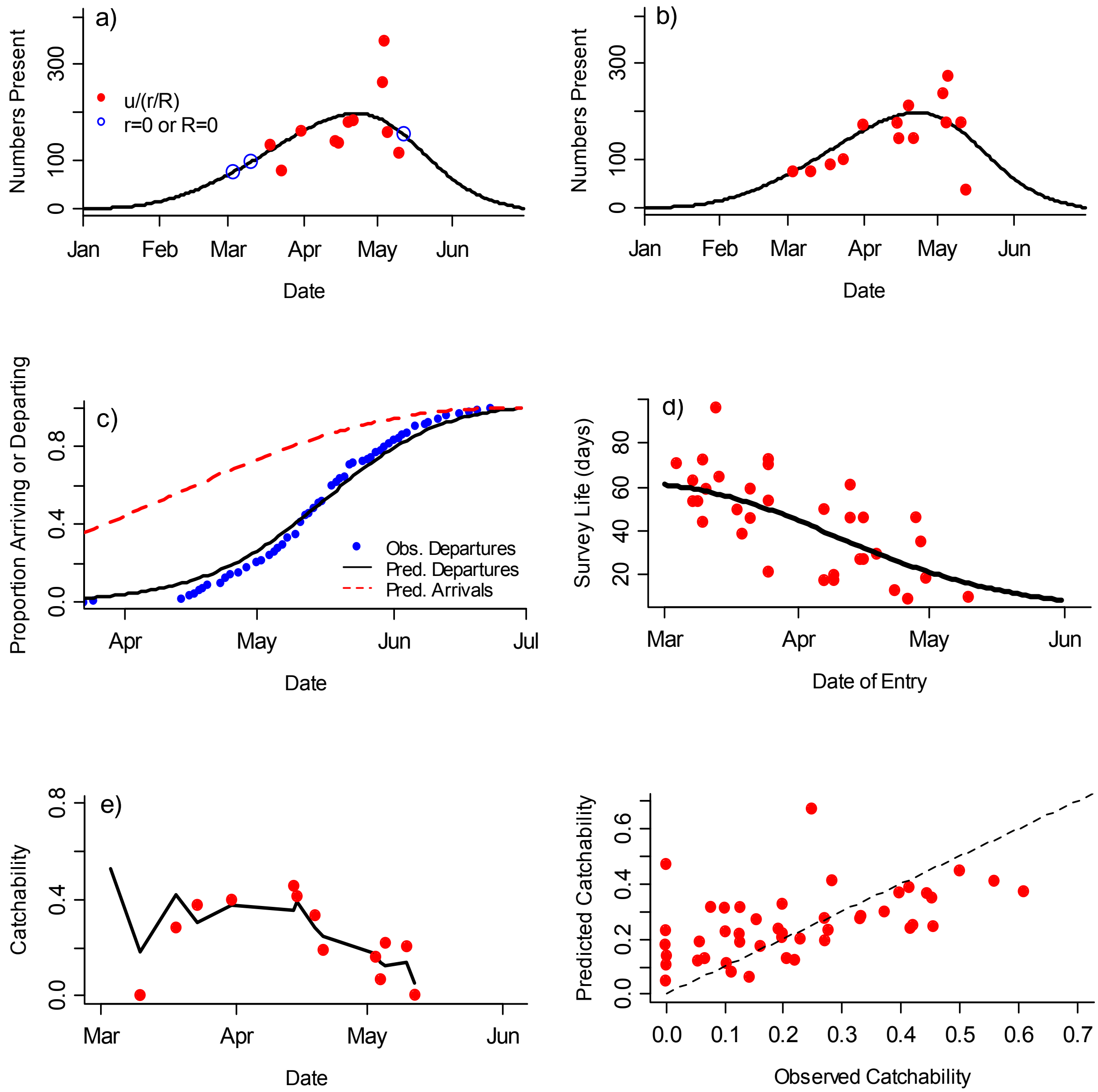


Figure 8. Most likely fit to the tagging data from 2005 and 2001-2005 telemetry data. a) shows the predicted number of fish present (line) and the estimated number of fish present on individual surveys (points) based on the ratio of tags observed to tags present (u/(r/R)). b) shows the same prediction compared to the estimated number present on individual surveys predicted from the best-fit 2005 HV/Q model (eqn. 11). c) shows the predicted cumulative arrival and departure schedules for 2005 and the observed departure schedule from the 2001-2005 telemetry data. d) shows the 2001-2005 survey life data and best-fit survey life model for 2005. e) shows the observer efficiency in 2005 (points) and the predicted values from the 2005 best-fit HV/Q model (line). f) shows how well the best-fit 2005 HV/Q model predicts the catchability from 2001-2005.

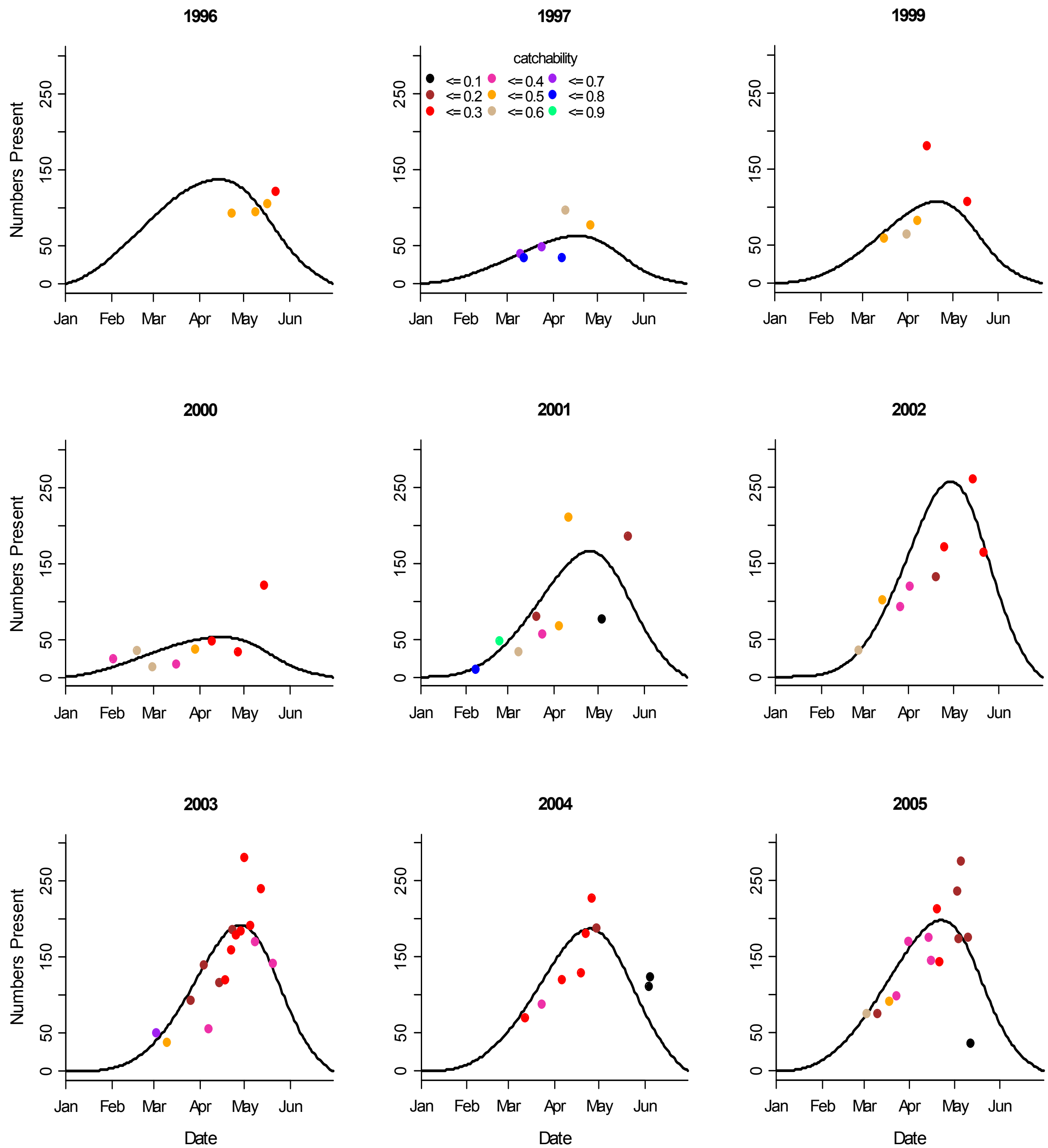


Figure 9. Most-likely estimates of the number of fish present from 1996 through 2005 compared to numbers present on individual surveys computed by expanding the total counted by the catchability predicted by the ratio of horizontal visibility to discharge. Colors of points denote the predicted catchability on each survey.

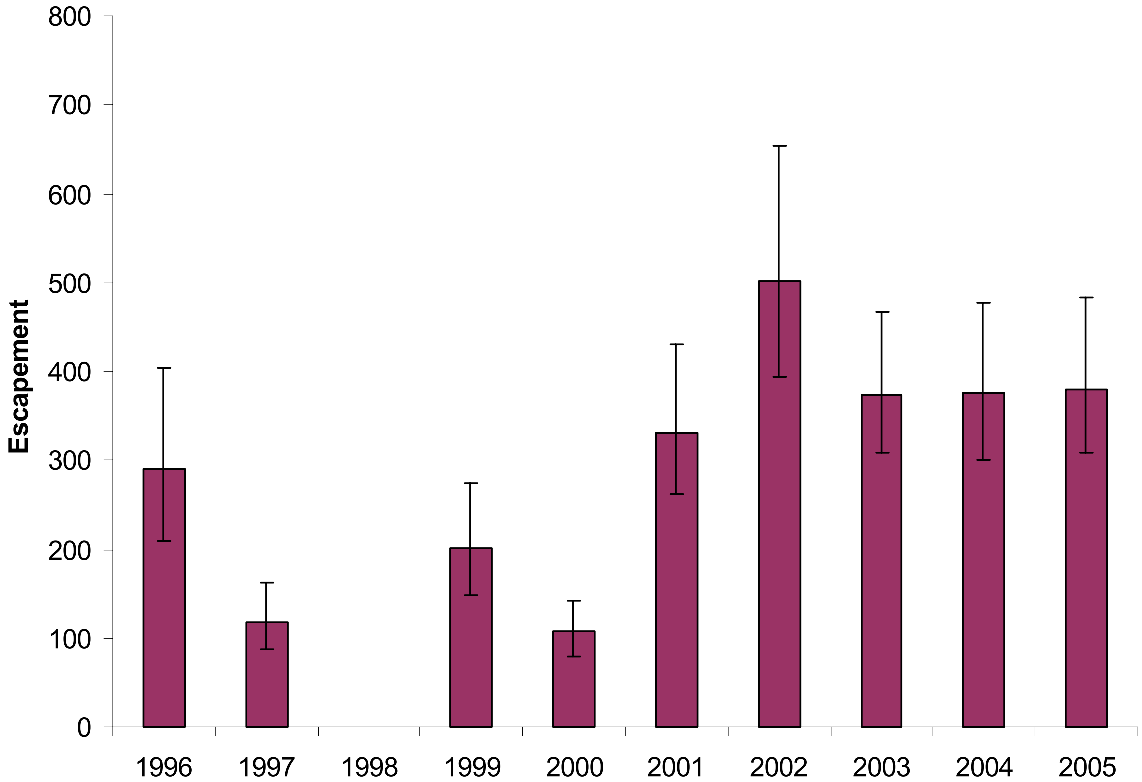


Figure 10. Median steelhead escapement estimates and 80% credible intervals.

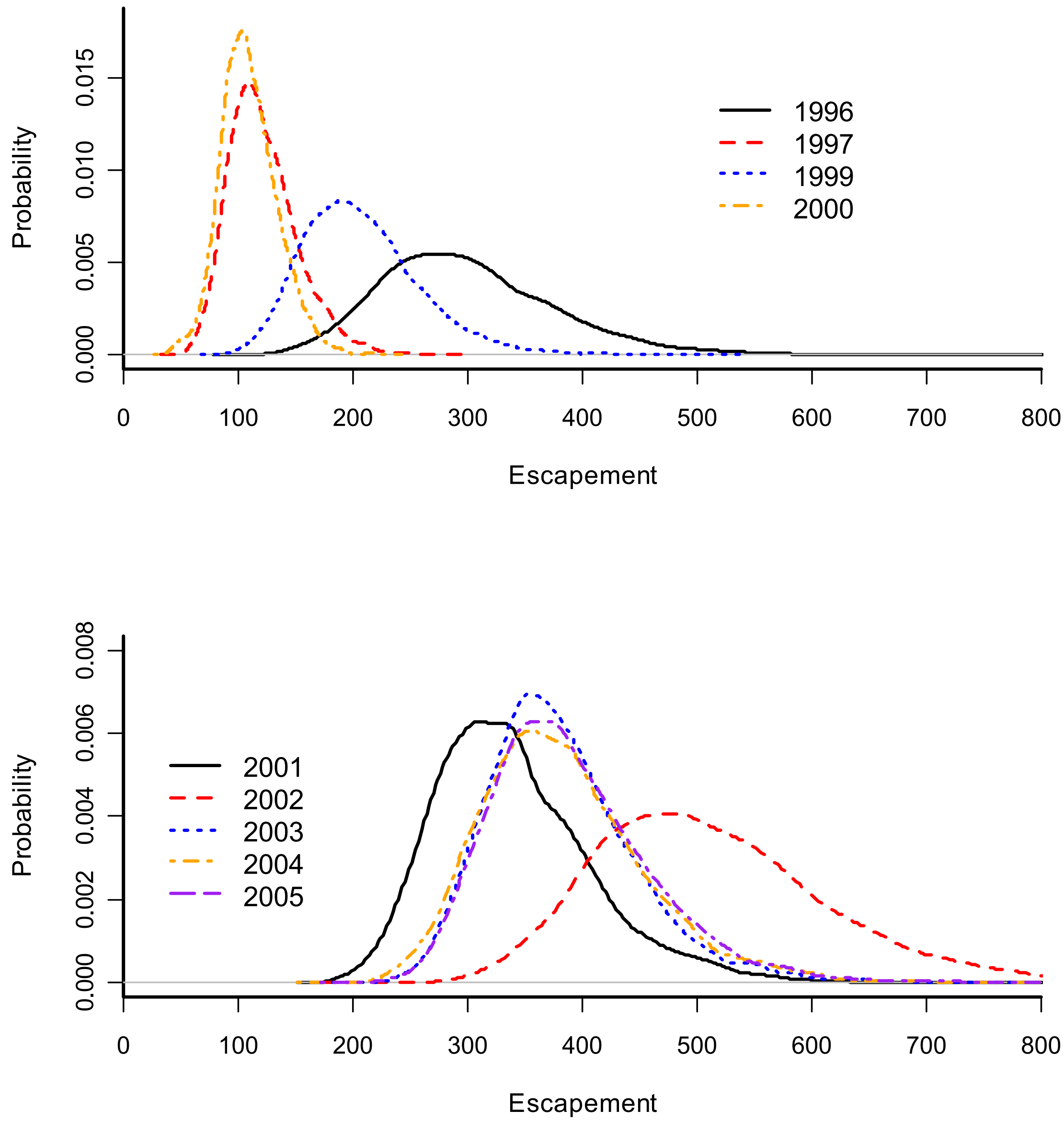


Figure 11. Posterior distributions of escapement by year based on the full likelihood model (eqn 12).

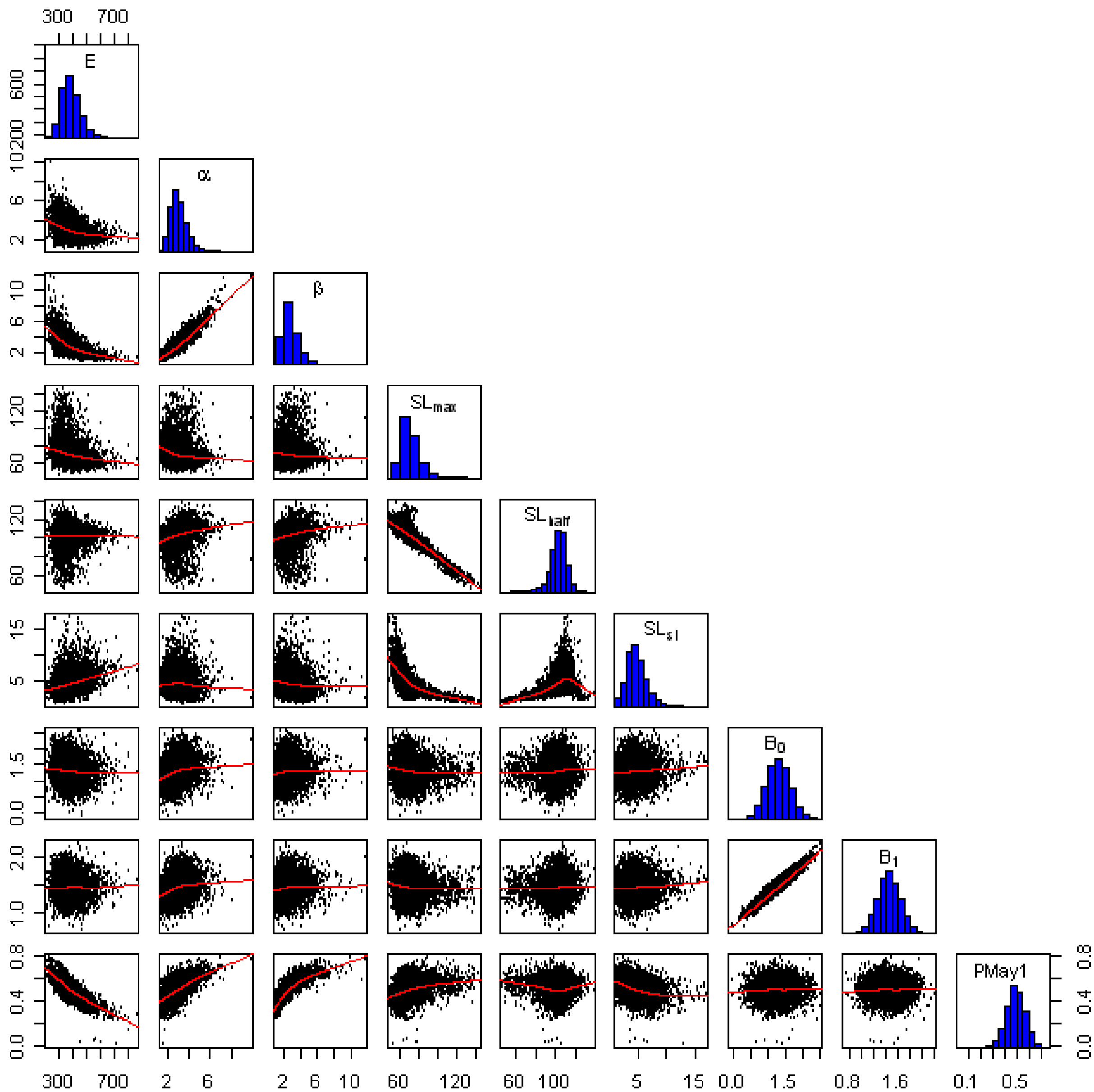


Figure 12. Correlation among 7500 parameter values for 2005 taken systematically from an MCMC total sample length of 75,000. The posterior distribution for each parameter is shown in the top diagonal. Note that the proportion of the run present on May 1 (PMay1) is not an estimated parameter but is predicted from the model based on arrival timing (α, β) and survey life (Sl_{max}, SL_{half}, and SL_{sl}) parameters.

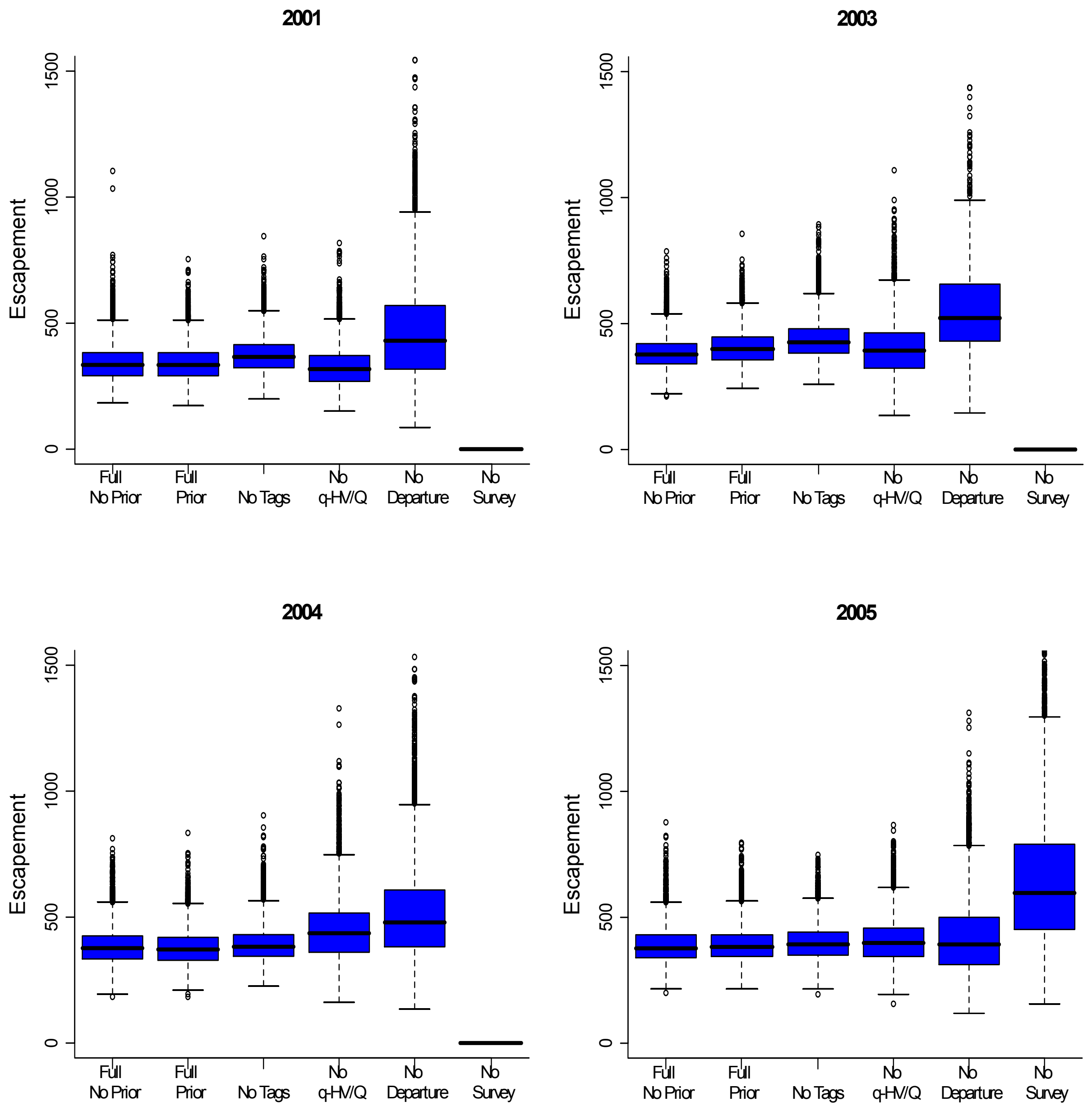


Figure 13. Posterior distributions of escapement under different likelihood structures (see Table 3). The centerline and edges of the box (hinges) represent the median and the first (25%) and third (75%) quartiles, respectively. The box width represents the 50% credible interval. The whiskers show the range of values that fall within the interquartile range (12.5% and 87.5%) equivalent to the 75% credible interval. It was not possible to compute posterior distributions for the likelihood that did not use survey life data for 2001, 2003, and 2004.

Appendix A: Assessment of the Effects of the CN Caustic Soda Spill on Future Steelhead Escapement to the Cheakamus River

On August 5th 2005, a CN train derailment in the Cheakamus Canyon resulted in a spill of 41,000 litres of caustic soda into the Cheakamus River. It is likely that most of the free-swimming fish occupying the mainstem Cheakamus River at the time of the spill were killed. The most severely affected were rearing juvenile steelhead/rainbow trout, with approximately 90% mortality in four age classes (McCubbing et al. 2005). We developed a simple spreadsheet model using steelhead escapement and age data from the Cheakamus River and information on stock productivity and marine survival from the steelhead population of the Keogh River, to estimate how long it will take the Cheakamus population to recover to pre-spill abundance levels.

The model predicts the annual abundance of smolts and adult returns by freshwater and at-sea age from 1997 through 2050. We assume a hockey-stick relationship between spawner and smolt abundance (Bradford 1999) and a constant marine survival rate. The historical time series of escapements to the Cheakamus River was used as input to the spawner-to-smolt relationship to predict the total number of smolts that have been produced from 1997 through 2005. For years after 2005, the predicted adult returns from the model were used as input to the spawner-to-smolt relationship. Smolt production in each year was divided into 3 smolt age groups based on available ageing data. The adult returns of each age class produced from each smolt group was computed as the product of number of smolts in each smolt age class, the marine survival rate, and the proportion of that adult returns in each adult age-smolt age class, again determined from available ageing data. To simulate the effect of the spill, we applied a 90% mortality rate to all smolt age classes in the river at the time of the spill. We compared the population trajectory assuming no mortality, with the trajectory assuming 90% mortality.

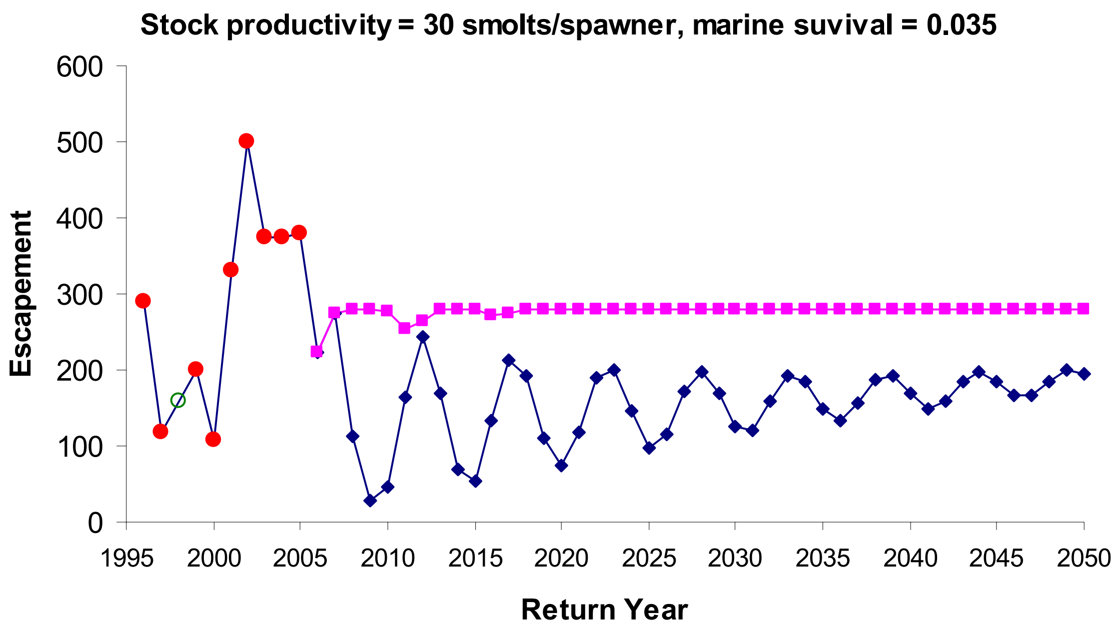
There is no marine survival rate data available for the Cheakamus River, and the time series of steelhead smolt and escapement estimates is to short to develop a spawner-to-smolt relationship. We therefore had to assume that the data for the Keogh River steelhead population is representative of the Cheakamus population. We assumed a marine survival of 0.035, which is the average rate for the Keogh River population using the last 5 yrs of available data (1993-2005, Ward 2000 and Ward et al. 2005). The number of smolts produced per spawner at low stock size was assumed to be 30 (Ward et al. 2005). The estimated carrying capacity for smolts at the Keogh River is 211 smolts/km. The anadromous length of the Cheakamus mainstem covered by our adult surveys is 14 km. This translates to approximately 3,000 total smolts, which produces a return of only 100 fish under a marine survival rate of 0.035. As the actual returns have averaged 3-fold higher since 1997, it is likely that the smolt capacity of the Cheakamus River is much higher, or alternately, that marine survival is higher. We assumed the former, and estimated the carrying capacity for the Cheakamus River by diving the average historical escapement from 1997-2005 for the Cheakamus population (280) by the assumed marine survival rate of 0.035 resulting in a smolt carrying capacity of 8000 fish.

The proportion of freshwater and at-sea ages for the Cheakamus steelhead population have been summarized by Van Dischoeck (2002) and are as follows: 2.2=0.1; 2.3=0.03; 3.2=0.48, 3.3=0.29; 4.2=.08, 4.3=0.02. Thus, over 75% of juvenile steelhead leave as 3 yr smolts and over 65% return after spending 2 winters at sea. Based on the freshwater age structure, the model assumes that the spilled reduced 90% of the production from the following spawning cohorts: 2002: age 4 smolts; 2003: age 3 and 4 smolts; 2004 and 2005: age 2, 3, and 4 smolts. Put in even simpler terms, the spill has an equivalent impact of killing almost all of the steelhead returns from 2003 through 2005.

No surprisingly, the impact of the spill on future returns is severe. Assuming constant marine survival and freshwater production, the model predicts that the return in 2008 will be at least half the current level, with near zero returns in 2009 and 2010 (Figure A1). As the assumed adult recruits per spawner, which is simply the product of freshwater productivity and marine survival, is only 1.05, the population exhibits a very slow recovery under our baseline simulation. Full recovery is not achieved by 2050.The overlap of generations does not mitigate the effects of the spill in any substantive way.

Two and 4-yr. old smolts produced by unaffected cohorts help fill in the hole in population structure created by the spill, but this smearing comes at the cost of reduced productivity of the unaffected cohorts. Smearing of age classes does not change the overall rate of recovery.

The rate of population recovery is completely dependent on the assumed future recruits per spawner. Assuming that marine survival rate remains at 0.035 but that freshwater productivity doubles to 60 smolts/spawner results in full population recovery by 2017. Between 2006 and 2017, about 5 of the 12 years will have escapements well below half of what they would had been in the absence of a spill.



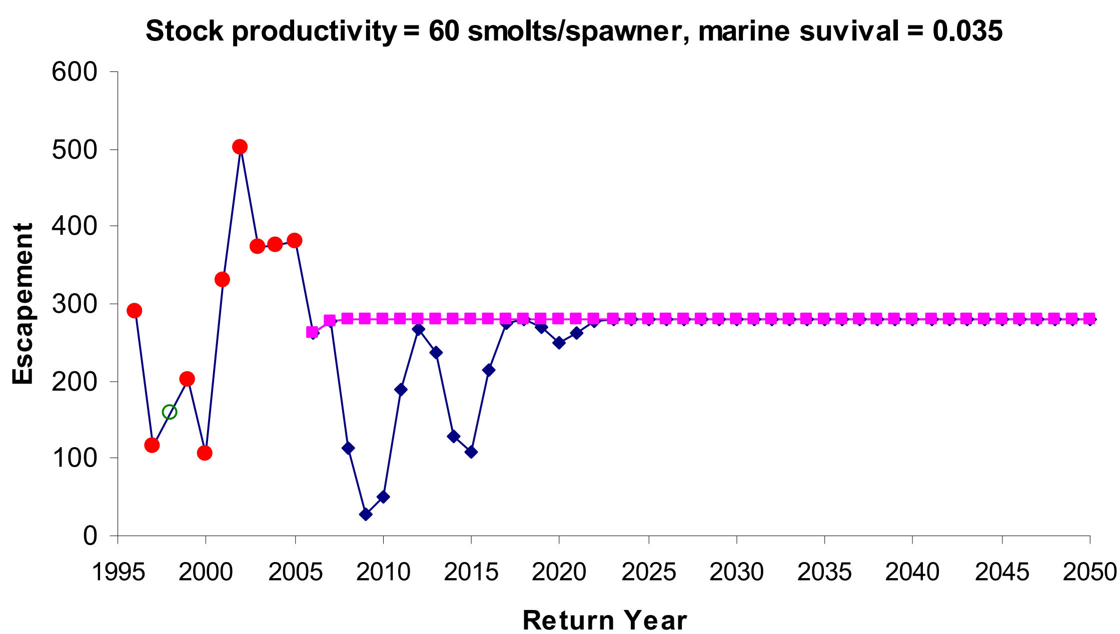


Figure A1. Observed and predicted steelhead escapement to the Cheakamus River. Red circles show estimated escapements from 1997-2005. Escapement was not estimated in 1998 as identified by the open circle, and the average of 1997 and 1999 values were used for this year. Predicted escapements for 2006 and beyond, assuming a 90% loss of freshwater production due to the spill, are shown by the lines with diamond characters. The lines with square characters show the predicted future escapements with no spill impact. The top and bottom projections are based on freshwater productivities of 30 and 60 smolts per spawner.

References for Appendix A

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