# EFFECTS OF CATCHABILITY VARIATION ON PERFORMANCE OF DEPLETION ESTIMATORS: APPLICATION TO AN ADAPTIVE MANAGEMENT EXPERIMENT

by

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# 1 INTRODUCTION

Assessing the abundance of organisms is a basic but crucial task for management biologists. Depletion (or 'removal') sampling is one approach widely used to estimate abundance, and involves the sequential removal of individuals from a defined area (Leslie and Davis 1939; Moran 1951). The pattern of decreasing catches over removal passes is used to infer both the total population size and the catchability (the probability of an individual being captured on a given pass). There is extensive theoretical and practical literature on the merits and limitations of depletion sampling, with on-going development of the statistical models used to estimate abundance and catchability from the catch series. Classic estimators assume equal catchability across sampled individuals and across passes (Zippin 1956, 1958; Carle and Strub 1978), but it is known that this assumption is often violated (Bohlin and Sundström 1977; Riley and Fausch 1992; Peterson et al. 2004). If constant catchability is incorrectly assumed, population estimates are negatively biased, and calculated confidence bounds indicate unwarranted precision. A variety of models have been developed that explicitly consider non-constant catchability (e.g. Schnute 1983, Wang and Loneragan 1996, Mäntyniemi et al. 2005). Although these models may improve performance under certain conditions, there is a lack of rigorous evaluation of performance characteristics.

Depletion sampling is a common assessment technique for freshwater fish populations, particularly stream resident juvenile salmonids (Bohlin et al. 1989; Guy and Brown 2007). Results are often used in an experimental context to measure response to treatment, or in stock assessment programs, to track juvenile abundance over time. In both contexts, it is crucial that estimators avoid bias and avoid overestimating precision, because these errors may lead to incorrect conclusions when comparing results between treatments or over time. If the bias of an estimator is constant across sites, time and treatments, this might not affect attempts to detect differences in abundance. However, differences in estimator behaviour between sites, over time, or between treatments may affect tests for change over time or due to experimental treatment. Similarly, overstated confidence in results may lead to an erroneous conclusion of difference.

Depletion sampling via electrofishing has been used to monitor juvenile salmonid response to flow over two experimental treatments between 1996 and the present. The intent is to infer a relationship between river discharge and juvenile salmonid productivity. The absence of supplementary information means that assessment of the accuracy and precision of abundance estimates must rely on the three and four pass removal series. I examined the extent to which trends in catchability, and therefore in the bias and precision of abundance

# 2 EFFECTS OF CATCHABILITY VARIATION ON PERFORMANCE OF DEPLETION ESTIMATORS

## 2.1 Introduction

Estimating the abundance of organisms within a study area is fundamental to ecology and field biology. In freshwater fisheries assessment, depletion sampling using electrofishing is widely applied to estimate the total population size within a site (Otis et al. 1978; Peterson et al. 2004). Fish captured during consecutive events are removed, and

Depletion models can be applied to both open and closed populations, but are simplest to use where the population is closed to immigration, emigration and recruitment, and when all mortality can be attributed to experimental removals or fishing (Hilborn and Walters 1992). In small streams, it is reasonable to assume that these conditions hold, especially for the net-enclosed sites commonly used to estimate juvenile salmonid abundance. For such sites, depletion estimators depend on distinct, consecutive fishing events (hereafter called "passes"), often using an electrofisher. Although not specifically required (Leslie and Davis 1939; DeLury 1947), depletion estimators often assume equal effort on each pass. The simplest depletion model defines the vector of catches $C_i$ as a function of the initial abundance $N$ and the probability of capture, or "catchability" $q_i$, i.e.,

$$C_i = q_i\left(N - T_{i-1}\right),\ i = 1, \dots, k, \tag{2.1}$$

where $T_i$ is the cumulative catch to pass $i$, and $k$ the total number of depletion passes (Leslie and Davis 1939; Moran 1951). If catchability is assumed constant ($q_i = q$), the catches can be considered as a regression of catch against cumulative catch up to the previous pass (Figure 2.1). The $x$-intercept estimates the initial abundance (the catch if fishing was continued indefinitely), and the slope estimates the catchability coefficient (Hayne 1949; Ricker 1975; Hilborn and Walters 1992). Non-independence in observed catches, and correlation between catch and cumulative catch, are not modelled by linear regression (Hilborn and Walters 1992), but can be addressed with other statistical

(Hilborn and Mangel 1997; McCarthy 2007). Maximum likelihood estimates are those parameter values that make the observed data most likely to have happened (Bolker 2008). The approach provides inference about future data given a hypothesis (a parameter value) and permits statements about the proportion of confidence intervals, constructed on the basis of hypothetical future experiments, which are expected to contain the true parameter value. Bayesian methods provide inference about a hypothesis given observed data, as well as permitting the incorporation of prior beliefs. The Bayesian approach assesses the probability distribution for an unknown parameter, given collected data, and so is logically more consistent with the questions posed in depletion estimators (McCarthy 2007). Bayesian results provide clear probabilistic statements about parameter values, and well characterise uncertainty. Hierarchical Bayesian models (e.g. Wyatt 2002; Dorazio et al. 2005; Rivot et al. 2008) permit information sharing among similar sites, allowing well defined results to contribute to estimation at similar sites with less informative depletion data (Wyatt 2002).

Both maximum likelihood and Bayesian estimation approaches have been used to develop constant catchability depletion models. Moran (1951) and Zippin (1956) develop the likelihood for a binomial model of fish capture, and use iterative or graphical maximum likelihood procedures to estimate abundance for depletion data. Alternative maximum likelihood estimators are available using iterative (Carle and Strub 1978) or numerical optimisation methods (Schnute 1983). Wyatt (2002) provides a Bayesian approach for a constant catchability depletion model.

Constant catchability depletion estimators remain in widespread use, despite evidence that catchability often changes over the course of removal samples (Bohlin and

Sundström 1977; Peterson and Cederholm 1984; Riley and Fausch 1992; Peterson et al. 2004; Rosenberger and Dunham 2005; Dauwalter and Fisher 2007; Korman et al. 2009). Catchability may change over passes due to variation among individuals, with more vulnerable fish captured first. Catchability may also vary as a function of fish size (Anderson 1995; Dolan and Miranda 2003), operator skill, electrofisher settings (Dolan and Miranda 2003), habitat (Peterson et al. 2004; Rosenberger and Dunham 2005), temperature or fish abundance (Bayley and Austen 2002). For juvenile bull trout and cutthroat trout, Peterson et al. (2004) found a reduction in catchability of between 1.15 and 1.96 times by pass (e.g. pass 1/pass 2, etc.).

Biased depletion estimates with inaccurate uncertainty measures, based on an unwarranted assumption of constant catchability, are acknowledged as a common problem in stock assessment (Hilborn and Walters 1992). Models that incorrectly earlier passes. However, some models (e.g. Schnute 1983; Wang and Loneragan 1996) do not assume that sequential catches decline monotonically. Both maximum likelihood (e.g. Otis et al. 1978; Schnute 1983; Wang and Loneragan 1996; Wang 1999; White and Burnham 1999; Dorazio and Royle 2003) and Bayesian (e.g. Warren 1994; Mäntyniemi et al. 2005) approaches to parameter estimation are applied to depletion models. Despite widespread discussion of the risks associated with assuming constant catchability, and great attention to the development of alternative, non-constant catchability depletion models, no definitively preferred model has emerged for the analysis of removal data. The alternative models encompass disparate assumptions about the patterns of change in catchability, and perform differently. Testing of depletion methods is recommended to select an appropriate approach for a given dataset (Hilborn and Walters 1992).

Simulation experiments allow more precise assessment of the statistical behaviour

maximum likelihood estimation procedures for *Models 1*, *2,* and *3*

$$\hat{C}_i = q_1(1-q_1)^{i-1}N\text{, } i = 1, \ldots, k. \tag{2.3}$$

### 2.2.3 ***Model 2*** **(Schnute 1983): stepped catchability**

*Model 2* (Schnute 1983) assumes that catchability on the first pass differs from all subsequent passes, but remains constant thereafter (i.e., $q_1 \neq q_i$ and $q_i = q$, $i = 2, \ldots, k$); catchability may increase or decrease after the first pass. The three parameters, $i$

Mäntyniemi et al. (2005) show (Appendix B) that only the expected value of the distribution of catchabilities on each pass, is required to model the depletion series. Mean catchability declines over passes, and is described by a parametric function analogous to the Schnute (1983) models:

$$\frac{\quad}{\quad + \quad - 1}$$

four MCMC chains initialised at different values in the parameter space. To avoid manual inspection of each simulation for convergence, I used the Gelman-Rubin potential scale reduction statistic ( $\hat{R}$ ; Gelman and Rubin 1992) to assess whether the posterior samples obtained on the posterior distribution for each parameter. This statistic compares the variance within an MCMC chain of length $l$ to the variance between multiple MCMC chains to estimate the factor by which the scale of the posterior distribution for a given parameter might be reduced if simulations were continued in the limit $l \rightarrow \infty$ (Gelman et al. 2004). If the potential scale reduction is high ( $\hat{R} >> 1$ ), additional simulation iterations are expected to improve the MCMC sample of the posterior distribution. Because MCMC chains tend to be autocorrelated, I used the $n_{eff}$ statistic (Gelman et al. 2004) to track the effective number of simulations. I continued simulations until $\hat{R} < 1.1$ and $n_{eff} > 100$ for all estimated parameters (Gelman et al. 2004), up to a maximum of 60 000 simulations. The $n_{eff}$ statistic was not tracked for $\eta$ in *Model 4*, because depletion series rarely contained enough information to provide more than 100 independent samples for this parameter.

One of the strengths of Bayesian analysis is that the resulting posterior distributions represent probabilistic statements about parameter values. However, to compare results in a simulation context, a point estimate is required. I used simulation to compare the performance of the mean and the median of posterior densities as point estimates for parameters $N$ and $q_i$ (Appendix D). The median was a less biased estimator if catchability was constant, and was similar to the estimate obtained from maximum likelihood estimation (the mode of the likelihood; Appendix A). However, the mean is a less biased point estimate if catchability declines (Appendix D). As my focus was to examine the effects of declining catchability, I selected the mean of posterior distributions as the appropriate point measure. To represent uncertainty in estimates, I calculated Bayesian 95% posterior intervals based on the 2.5% and 97.5% quantiles of posterior samples.

### 2.2.7 Prior distributions

Bayesian estimation requires prior distributions, which describe prior beliefs about parameter values before depletion sampling. The Bayesian approach uses collected catch data to update prior beliefs and produce posterior probability distributions for unknown parameters. If there is no information to support prior beliefs, the standard approach is to use non-informative priors. I tested the impact of different prior distributions on results for all four depletion models. I conducted simulations using both informative and non-informative prior distributions.

#### *Non-informative prior distributions*

Non-informative priors are appropriate where no data are available to describe abundance, catchability or variation in catchability before the completion of a depletion experiment. I followed Mäntyniemi et al. (2005) in assigning non-informative priors for *Models 1 – 4*. I assigned uniform priors for $\log(N)$ and $\log(\eta)$, and uninformative Beta priors for $q$

available for a given species and habitat combination within a watershed or region. An upper bound on the site population ($N$) may also be known from previous studies, and (after sampling), a lower bound is defined by the total catch $T_k$. However, when the number of passes is small, there is little information about the variation of catchability in the data, and even a weakly informative prior distribution dominates the posterior (e.g. for $\eta$ in *Model 4*; Mäntyniemi et al. 2005).

I assigned an informative Beta prior (Table 2.1) for the first pass catchability (*Models 1 - 3* = $q_1$, *Model 4* = $\varepsilon$) based on the true simulated initial catchability ($q_0$; see following section). Each $q_0$ scenario therefore had its own prior for first pass catchability (Figure 2.2). I parameterised the prior using the method of moments approximation (Gelman et al. 2004, p. 582) with mean = $q_0$ and standard deviation = 0.1, i.e.,

$$\textit{Models 1 – 3:}\ q_1 \sim \textit{Beta}\,(\alpha, \beta)$$

$$\textit{Model 4:}\ \ \mu \sim \textit{Beta}\,(\alpha, \beta);$$

$$\alpha = q_0 \;\; \frac{q_0(1-q_0)}{\mathrm{var}(q)} - 1 \;\; ; \quad \beta = (1-q_0) \;\; \frac{q_0(1-q_0)}{\mathrm{var}(q)} - 1 \;\; ;$$

$$q_0 = \{0.2, 0.4, \ldots, 0.8\}; \quad \mathrm{var}(q) = (0.1)^2 . \tag{2.8}$$

I defined the lower limit of the prior for $N$ using the total catch, i.e.,

$$\log\,(\;N\;) \sim \textit{Uniform}\,(\;\log(T_k), 10\;). \tag{2.9}$$

As the models are highly sensitive to the prior distributions related to the variation in catchability, I used non-informative priors for $q$, $a$ and $\eta$, as appropriate (Table 2.1).

### 2.2.8 Simulation approach

The three variables of interest for simulation include the true total population $N$, the vector of catchability over passes $q_i$, ($i$ = 1, 2, …, $k$) and the number of passes ($k$; Table 2.2). Catchability is defined by both initial (pass 1) conditions, and by the function defining pattern of change over passes. I simulated three and four pass depletion experiments, with true population $N = \{25, 100\}$. Based on empirical results for juvenile salmonids (Riley and Fausch 1992; Peterson et al. 2004; Rosenberger and Dunham 2005), I simulated true initial catchability over the range $q_0 = \{0.2, 0.4, 0.6, 0.8\}$. To examine whether or not estimates were improved by collecting additional depletion samples, I also simulated eight pass removal experiments for $N$ = 100.

As a simulation model to generate data, I used the Peterson et al. (2004) expression, i.e.,

$$q_i = q_0 \frac{1}{r}^{\,i-1}, \quad i = 1, \ldots, k, \tag{2.10}$$

where $q_0$ is the initial catchability and $r$ defines the rate of decline by pass (i.e. $r = 1$ = constant catchability, $r = 2$ = catchability declines by ½ = 50% each pass. This function can be parameterised such that the form is similar to *Model 3* (Equation 2.5), *Model 4* (Equation 2.6) or to an alternative such as an exponential function, i.e.,

$$q_i = q_0 e^{-\lambda(i-1)}, \quad i = 1, \ldots, k. \tag{2.11}$$

However, because the simulation model (Equation 2.10) is different from the estimation models (*Models 1 – 4*), none of the depletion estimators fit the simulated pattern of declines exactly. Based on empirical evidence for reductions in catchability for juvenile salmonids (mean $r$ = 1.71 for bull trout *Salvelinus confluentus* and westslope cutthroat trout *Oncorhynchus clarki lewisi*; Peterson et al. 2004), I simulated values of $r$ in the range {1.0, 1.2, …, 2.0}.

I simulated catch data series using random draws from the binomial distribution, i.e.,

$$C_i = Binomial \quad N - \sum_{j=0}^{i-1} C_j , q_i \quad , \quad i = 1, \ldots, k. \tag{2.12}$$

Each $N$, $q_0$ and $r$ combination represents a simulation scenario (Table 2.2). For each of the candidate depletion models, and for each scenario, I calculated total population and catchability estimates for $M = 500$ Monte Carlo trials.

### 2.2.9 Performance measures

I defined performance measures for estimates of the total population $N$, the initial catchability $q_0$, and the variation in catchability. The total population estimate is generally of most interest to researchers applying depletion models. However, I found that the bias in estimates of $N$ is largely a function of the magnitude and variation of catchability. It is therefore of interest to examine how well depletion models define these parameters. Accurate measures of the catchability and variation in catchability might be applied to predict the degree of bias in estimates of $N$, and, in particular, to assess changes in expected bias between habitat types, over time, or between experimental treatments. I defined performance measures for $N$ that track the bias, variation, confidence interval coverage and confidence interval width for the eight depletion estimators I examined. I calculated these summary statistics over all simulations for each scenario. I examined the bias and variation of estimates of $q_1$ and $q_4$. I examined only bias in estimates of the change in catchability over depletion passes.

Prior to the calculation of summary statistics, I removed simulations for which: (1) posterior samples failed to converge for any one estimated parameter ($\hat{R} > 1.1$); (2) fewer than 100 effective samples were obtained for an estimated parameter ($n_{eff} < 100$; η in *Model 4* excepted); or, (3) the estimated population $\hat{N}$ was more than twice the true population *N*.

*Performance measures for estimates of abundance*

I calculated mean square error (MSE) for each scenario directly from successful simulations ($M^*$), i.e.,

$$MSE = \frac{\sum_{m=1}^{M^*} \left(\hat{N}_m - N\right)^2}{M^*}, \tag{2.13}$$

where $\hat{N}_m$ is the abundance estimate for each simulation *m*, and *N* is the known true value. Root mean square error (RMSE) is often used as a model performance measure, because it incorporates both accuracy and precision, and is in the same units as the estimate. However, I was interested in both components of mean square error (MSE = *variance* + *bias*$^2$). To facilitate comparisons across scenarios where *N* varies, I calculated the bias component of MSE and standardised by the true value (*N*) to obtain the mean percent error ($\text{MPE}_N$), i.e.,

$$MPE_N = \frac{\sum_{m=1}^{M^*} \frac{\hat{N}_m - N}{N}}{M^*} \bullet 100\,. \tag{2.14}$$

I standardised the variance component of MSE by calculating the simulation based ‘coefficient of variation’ as the ratio of the standard deviation of estimates across all successful simulations ($s_{M*}$) to the true value ($N$):

$$= \frac{}{N} \bullet 100$$

$$\rho_m = \frac{L_{2,m} - L_{1,m}}{N}, \tag{2.16}$$

where $L_{2,m}$ and $L_{1,m}$ are the upper and lower confidence bounds, respectively. Because confidence limits for uninformative depletion series were infinite, reporting the mean confidence interval width was not useful. As a statistic to coBec1d5f12.015 0 7(i)-

*Performance measures for estimates of variation in catchability*

I calculated the estimated change in catchability between pass 1 and pass 4 ($\Delta\hat{q}$), for the base case, $N = 100$, $k = 4$ as the mean, over all successful simulations of the difference between the estimate for $q_4$ and the estimate for $q_1$. I calculated the mean percent error in estimates of $\Delta q$, i.e.,

$$MPE_{\Delta\hat{q}} = \frac{\sum_{m=1}^{M^*} \Delta\hat{q}}{M^*} \bullet \frac{100}{\Delta q}. \tag{2.19}$$

### 2.2.10 Model selection approaches

Model selection approaches, such as the likelihood ratio test (Kendall and Stuart 1979; Hilborn and Mangel 1997), the Akaike information criterion (AIC; Akaike 1974) or the deviance information criterion (DIC; Spiegelhalter et al. 2002) can be used to compare the fits of competing models applied to the same dataset. The likelihood ratio test requires that models are nested (i.e. of a suite of models compared, the more complex models reduce to the simpler models under certain conditions; e.g. *Models 1 – 3*). The DIC and AIC approaches do not require models to be nested, and trade-off model complexity with model fit. AIC and DIC use the penalised deviance to test model fit, where deviance is -2 times the log likelihood (i.e. -2 times the logarithm of the probability of the data, given estimated model parameters; Gelman and Hill 2007). A smaller deviance value thus represents a better fit. Adding a parameter to a model is expected to improve the fit, even if the new parameter provides no additional information. For this reason, model selection approaches evaluate model fit using a penalty function incorporating the number of parameters.

## 2.3 Results

I present results for abundance estimates for $N = 100$, $k = 4$, $q_0 = \{0.2, 0.4, 0.6, 0.8\}$ as a base case. I present sensitivity to changes in abundance and sampling intensity by comparing conclusions from this base case to results for $N = 25$ and $k = \{3, 8\}$. I then present results for estimates of catchability and change in catchability for the base case. Finally, I present results for the relative effects of abundance, initial catchability and the rate of decline in catchability on abundance estimates derived using *Model 3*.

### 2.3.1 Estimation failure

Estimation failures were rare for *Models 2* and *3* (< 1%, aggregated over all simulated catchability scenarios; Table 2.3). For *Model 1* and *Model 4* small, positive, bias in estimates of abundance with low variance (Table 2.4). Because estimates were well defined in the constant catchability case, confidence interval coverage tended to be 100%, with narrow intervals (standardised interval width ρ was uniformly less than *N*).

If catchability was high, and declined over consecutive passes, total catch was, as expected, less than the true abundance. The constant catchability estimator (*Model 1*

substantial negative bias (-57.0% to -19.7%) for declining catchability. *Model 4* also provided confidence interval coverage closer to the target 95% than other estimators. However, at low catchability, with strong declines ($q_0 = 0.2$, $r = 2.0$), few fish were being captured, and there was little information in the depletion series (MPE = -57.0%, CI coverage = 22.2%).

### *Incorporating prior information*

As would be expected, informative prior distributions for catchability and the minimum population, based on true simulation parameters and the total catch (Table 2.1, Figure 2.2), generally improved the performance of estimators (Table 2.5). In general, priors reduced the bias of estimates, reduced the variability of estimates, improved confidence interval coverage and reduced confidence width. However, for declining catchability, estimates remain negatively biased, particularly for low catchability and for severe reductions in catchability (i.e. $r = 2.0$).

### *Incorporating additional depletion passes ($N = 100$, $k = 8$)*

Collecting additional information in the form of additional passes universally decreased the variance of estimates, and generally reduced bias and confidence interval width (Table 2.6). However, if catchability was low, estimates remained substantially biased, particularly if catchability was not constant.

### *Reducing the number of depletion passes ($N = 100$, $k = 3$)*

If the number of passes was reduced, it might be expected that the reduction in observations would negatively impact estimator performance. However, this was not universally the case. For high catchability, and constant catchability conditions, three pass estimates were more biased than the analogous four pass estimates (Table 2.7). However, if catchability was low, and declined by pass, the three pass estimates were generally less biased than the four pass equivalent. Uncertainty in estimates was generally increased, with wider confidence intervals. Because confidence interval coverage for many four pass scenarios was less than the target 95%, wider intervals in three pass scenarios generally improved confidence interval coverage (i.e. closer to 95%).

### *Impact of low true abundance ($N = 25$, $k = 4$)*

If the true total population was low ($N = 25$, $k = 4$), estimates at constant catchability, or near constant catchability ($r = \{ 1.0, 1.2 \}$) were generally more biased than was the case for $N = 100$ (Table 2.8; *cf.* Table 2.4)

However, if catchability declined over passes, performance relative to the $N = 100$ base case depended on initial catchability. At high initial catchability ($q_0 = 0.8$), *Model 1* was less biased for $N = 25$ than for $N = 100$. *Models 2, 3* and *4* were generally more biased at low $N$

biased and more variable for lower true catchability than for higher true catchability, and were more biased if true catchability declined over passes, relative to constant true catchability.

Three and four pass depletion series generally contained too little information to accurately estimate parameters defining the change in catchability over successive depletion passes (for an example, see Appendix D). As a result, estimates of catchability for latter passes were both biased and highly variable (e.g. $q_4$ for $k = 4$; Table 2.10). Severely biased estimates for $q_4$ were not necessarily associated with biased estimates of abundance. For example, for $q_0 = 0.8$ and $r = >1.2$, estimates of $q_4$ were badly biased (MPE = 63.2% to 737.6%), but estimates of abundance were relatively unbiased (MPE = -8.3% to 4.4%).

### 2.3.4 Effects of catchability variation on depletion estimates of change in catchability over depletion passes

Despite bias and high uncertainty in estimates of late pass catchability, if true catchability declined over passes, non-constant catchability models did track this decline. All models substantially underestimated the change. At moderate and high catchability ($q_0 = \{ 0.6, 0.8\}$), *Model 3* estimates of the change in catchability were least biased (e.g. -23.0% - - 45.8% for $q_0$

and *3* erroneously estimated, on average, that catchability increased between pass 1 and pass 4.

### 2.3.5 Model selection approaches

Three and four pass depletion series did not contain sufficient information to reliably estimate all parameters of more complex non-constant catchability models. Although simulation results showed that application of these models was justified under used simulation to rigorously test the performance of these non-constant catchability depletion estimators.

My simulation results showed that, for the three and four pass depletions commonly completed by freshwater fisheries biologists, estimators explicitly designed to address non-constant catchability did not substantially reduce the bias of abundance estimates. Estimator performance was driven by catchability and the change in catchability, rather than by abundance. As might be expected, performance was particularly poor for low catchability, as well as for large declines in catchability by pass. Confidence intervals for non-constant catchability models were more likely to contain the true value than was the case for constant catchability models. These confidence intervals could be very wide, accurately reflecting the high uncertainty in estimates of abundance. Improved estimates (reduced bias, reduced variance and reduced confidence interval width) were obtained if additional information was incorporated in the form of informative prior distributions. The collection of additional depletion passes reduced the variance of estimates, but generally did not substantially reduce bias. Confidence interval coverage was generally reduced (often detrimentally so, with increased certainty indicated for biased results).

### 2.4.1 Bayesian parameter estimation versus maximum likelihood estimation

If catchability declines, Bayesian abundance estimates were less biased than maximum likelihood estimates (Appendix A). In the case where non-informative priors are assumed, this difference reflects the way in which point estimates and confidence intervals are calculated. If little information is supplied by prior distributions, the Bayesian posterior distribution will be similar to the likelihood. I calculated Bayesian point estimates for *N* as the mean of posterior distributions (Appendix D). Maximum likelihood estimates are the mode of the analogous likelihood. For depletion models with declining catchability, posterior distributions and likelihood profiles for *N* tend to be skewed right by the possibility that catchability is very low (Schnute 1983; Appendix D). As a result, the mean of these distributions (i.e. the Bayesian point estimate) will tend to be less biased than the mode (i.e. the maximum likelihood estimate).

Bayesian methods might also be preferred on conceptual grounds, because: (1) posterior distributions represent probabilistic statements about parameter values, so results are easily interpreted; (2) if prior data are available for any parameters of a given model, there is an explicit mechanism to include this information, and (3) Bayesian models are amenable to hierarchical analyses likely to be appropriate for depletion data collected over a network of related sites in a given study (e.g. Wyatt 2002; Rivot et al 2008).

### 2.4.2 Selecting an appropriate depletion model

If data are available to show that catchability is constant, constant catchability depletion models are preferred. If supplementary information is not available to test this assumption, biologists must determine if it is better to erroneously assume constant catchability, or to erroneously assume non-constant catchability. Empirical results suggest that catchability is probably not constant for juvenile salmonids (Bohlin and Sundström 1977; Gatz and Loar 1988; Riley and Fausch 1992; Peterson et al. 2004; Rosenberger and Dunham 2005; Carrier et al. 2009) as well as for other fish (Dauwalter and Fisher 2007).

The cost of assuming constant catchability, and being wrong, can be high, because constant catchability models provide biased estimates with inappropriate confidence limits if capture efficiency is in uses a likelihood ratio test to compare the fits of *Models 1 – 3*; I apply this approach to

For the range of parameters values that I examined, the effects of true abundance on bias were overwhelmed by the effects of initial catchability and the rate of decline in catchability.  This might not be the case

not reflect the sampling conditions experienced in the collection of the field data (Bohlin and Sundström 1977) used by Mäntyniemi et al. (2005).

Informative priors for the change in catchability are also expected to improve estimates from depletion estimators. Substantial literature evidence for non-constant depletion experiments to estimate juvenile abundance in small (Peterson et al. 2004; Rosenburger and Dunham 2005; Sweka et al. 2006; Carrier et al. 2009) and large (Korman et al. 2009) rivers. All recommend the use of mark-recapture experiments to obtain unbiased estimates of abundance and catchability.

Using field experiments and simulation, Korman et al. (2009) show that, for backpack and boat electrofishing on a large river, mark-recapture studies provided less biased estimates of capture probability than did maximum likelihood depletion methods. Mark-recapture methods were able to detect a change in catchability between successive passes, while depletion data did not resolve the difference, based on AIC comparison of fits for both constant and non-constant catchability models.

### *Additional information from related sites*

Perhaps the most promising approach to incorporate additional information is to use data from sites that are likely to have similar catchability conditions (for example, sites that are nearby, or sites with similar habitat). Hierarchical Bayesian models (e.g. Dorazio et al. 2005; Wyatt 2002; Rivot et al. 2008) provide a framework to permit analyses of this kind, facilitating information sharing between appropriately similar sites, allowing well defined results to contribute to estimation at sites with more poorly defined estimates. Hierarchical models represent partial pooling of site data. As a result, site-specific estimates might become biased towards the mean of the sites. However, if the interest in a stock assessment or experimental context is in the aggregate, this partial pooling may improve estimates.

### 2.4.8 Choosing an appropriate sampling method

My results summarise the precision and accuracy expected from depletion sampling across a range of parameters, and can be used to determine whether removal experiments are appropriate. If depletion sampling is selected, my results can be used to select the level of effort (the number of passes) appropriate to research objectives. Simple field rules can be developed to determine when collected data do not provide the required resolution, and additional passes are therefore required (Schnute 1983). Alternatively, depletion models can be run using a laptop computer in the field. Sampling would be continued until pre-determined accuracy and precision targets are met. Alternatively, additional passes at a subset of sites, or concurrent, independent measures of catchability might be used to guide selection of an appropriate estimation model, and to develop the prior distributions that improve Bayesian model results. Poor performance of all depletion models under low catchability conditions suggests that researchers should make all reasonable efforts to ensure moderate or high capture efficiency. This might be accomplished through appropriate sampling efforts, fishing technique, and electroshocker settings.

## 2.5 Recommendations

1. Where practical, independent measures should be obtained to determine whether catchability is constant in surveyed populations. Results will help to inform selection of an appropriate depletion estimator, and to develop priors for Bayesian depletion models.

2. Practical field rules should be developed to determine when a depletion experiment does not meet pre-defined precision requirements, and additional

passes are therefore required. Schnute (1983) suggests using the ratio of successive catches to roughly estimate the escapement fraction ($p_i$ = 1 - $q_i$). Where $p_i > 0.75$ or $p$ increases by a factor of more than 3 after the first fishing, additional passes should be considered.

3. Low catchability results in poor depletion estimates. Reasonable measures to obtain high catchability, such as standardised electrofisher settings, should be undertaken, within the usual constraints of depletion sa

# 3 EXAMINING THE IMPACT OF CATCHABILITY AND ON CONCLUSIONS DRAWN FROM A LARGE SCALE, LONG TERM ADAPTIVE MANAGEMENT STUDY

## 3.1 Introduction

Depletion sampling was selected to test fish population response to increased flow in the context of a long-term, adaptive management experiment on the regulated lower Bridge River, BC. The study examines the effects of experimental discharge manipulation on fish abundance. Two flow treatments have been monitored to date, with surveys between 1996 and 1999 representing historical flow conditions. In 2000, flows were increased, substantially changing both habitat and sampling conditions. Previously dry habitats in the upper river were wetted (and so subsequently sampled), and augmented flows provided different habitat and sampling conditions in some lower river sites. The challenge is to detect a response to treatment, against a background of potential treatment-induced changes in the sampling efficiency, as well as high natural variability. Effective analysis of the available depletion data is imperative if robust conclusions are to be drawn from the adaptive management experiment. If the change in sampling conditions affects the precision or bias of results, this might affect conclusions; if the treatment does affect fish abundance, this might not be detected.

Depletion models use the sequence of captures to infer both the total number of fish present in sampled sites and catchability, the probability of capturing an individual during a given sampling pass. The models are subject to bias and reduced confidence interval coverage if catchability is low or highly variable (Chapter 2). The performance of depletion estimators for the lower Bridge River dataset is therefore affected by prevailing catchability conditions. Furthermore, because the experimental treatment substantially altered habitat and sampling conditions, catchability may have changed. If so, estimator performance may, in part, be a function of treatment. If there is a flow effect on estimator performance, this may affect subsequent tests for a treatment effect on juvenile salmonid abundance. I therefore had two linked objectives for Chapter 3:

1. to assess the performance of depletion estimators for lower Bridge River data, as a function of catchability and variation in catchability; and,
2. to assess how treatment may have altered catchability conditions, and therefore the performance of depletion estimators.

### 3.1.1 Treatment mediated effects on catchability and bias

Electrofishing catchability is affected by factors such as stream size (Peterson et al. 2004; Rosenberger and Dunham 2005), habitat complexity (Peterson et al. 2004), fish size and species (Bagenal 1979; Anderson 1995; Peterson et al. 2004; Korman et al. 2009), fish density (Korman et al. 2009), substrate (Peterson et al. 2004), temperature, turbidity, and methods applied, such as electrofisher settings, and the use of block nets (Dauphin et al. 2009). Factors that influence variation in catchability are less well studied. Because both the magnitude and variance of catchability affect the performance of depletion estimators, changes in sampling conditions with experimental treatment may affect tests designed to detect response to that treatment.

Augmentation of flow in the lower Bridge River is explicitly designed to alter conditions, with the intention of improving salmonid rearing habitats. It is therefore reasonable to expect that the treatment may also affect sampling efficiency. For example, some sites in Reach 3 had been completely isolated during Treatment 1 using two nets across the width of the river. Higher Treatment 2 flows dictate the use of three nets to establish sites along the stream margin. Treatment 2 may have caused a system-wide reduction in sampling efficiency by introducing colder, more turbid water from the reservoir. Changes in fish behaviour may also have affected sampling efficiency. Increased flows permit bull trout, an efficient predator of juvenile salmonids, to move into upper sections of the river from which they were previously absent. It is likely that juvenile fish distribution and behaviour changed with the immigration of this predator. Consequences for sampling efficiency are unclear and untested. In addition, catchability may have changed over the relatively long time-frame of an adaptive management experiment, as a function of researcher behaviour (e.g. learning over repeated sampling, changes in personnel, refinements of methods, etc). There has been remarkable stability in senior field staff over the study period, suggesting continuity of approach; however, subtle changes might be expected as experienced crews sample familiar sites. Although site locations and sampling protocol were standardised, electrofisher settings were initially left to crew discretion. Systematic differences between crews with respect to settings may affect capture efficiency and therefore the performance of calculated estimates.

In this section, my objective was to detect systematic treatment effects on catchability. Because such effects might reduce the power of statistical tests for experimental response, it might be possible to develop corrective models linking catchability conditions with site characteristics (Rosenberger and Dunham 2005). I therefore examined the impact of a wide variety of site characteristics on catchability estimates derived from a depletion model tested in Chapter 2.

Low and heterogeneous catchability both affect the performance of depletion estimators (Chapter 2). There are two approaches to assess the magnitude and variation of catchability, and thus assess estimator performance: (1) independent measures of catchability can be obtained from mark-recapture studies (Riley and Fausch 1992; Peterson et al. 2004; Rosenberger and Dunham 2005; Carrier et al. 2009); or, (2) a depletion estimator that permits heterogeneity in catchability (Chapter 2) can be applied.

I used depletion models with known performance characteristics to estimate population, catchability and variation in catchability for sampled sites in the lower Bridge River. I assessed performance by comparing estimates with my simulation results from Chapter 2. My objective was to determine whether changes in sampling conditions during the lower Bridge River adaptive management experiment may affect tests designed to detect a treatment effect.

## 3.2 Methods

### 3.2.1 Study area

The Bridge River is a sixth order tributary to the Fraser River, near Lillooet, British Columbia. Prior to impoundment the river supported significant populations of resident and anadromous salmonids (*Oncorhynchus* spp.). The lower river (below the dam) likely functioned as a migration corridor to access rearing habitat upstream, as high flows in a confined channel probably precluded more widespread use (mean annual discharge = 100 $m^3 \cdot s^{-1}$, maximum historical flow ~ 950 $m^3 \cdot s^{-1}$; Higgins and Bradford

2001). Completion of the Terzaghi Dam, approximately 40 km upstream of the Fraser River, blocked upstream fish migration and diverted flows from the upper Bridge River into Seton Lake, in an altogether separate watershed. Almost all flows were diverted, with the exception of rare were selected using solicited expert opinion and decision analysis (Failing et al. 2004). Five flow regimes (0, 3, 1, 6 and 9 $m^3 \cdot s^{-1}$) over 4 - 5 year treatment periods were selected to permit response over at least one salmonid generation (~3-5 years) within each treatment. The discharge label for a flow regime (e.g. 0, 3 $m^3 \cdot s^{-1}$) represents the annual average, with seasonal discharge linked to the natural hydrograph of the Yalakom River. Flexibility in treatment order and implementation was anticipated, with the progress of the experiment informed by early results. Only two of the planned flow treatments have been applied to date. No discharge from the dam occurred between dam completion and August 2000, when flows were increased to an annual average of 3 $m^3 \cdot s^{-1}$.

### 3.2.2 Juvenile salmonid stock assessment

Juvenile salmonids were selected as a key response metric because adult abundance is affected by conditions external to the experiment, such as marine survival and fishery interceptions. Given high spatial and temporal variation in juvenile densities (Higgins et al. 2000), monitoring of water quality, primary and benthic productivity, and fish behaviour (Bradford and Higgins 2001), were also undertaken, to provide context and a ‘weight of evidence’ argument if abundance data lacked power to discriminate between treatment effects. Standardised assessments of juvenile salmonid densities have been conducted annually between 1996 and 2008. Sampling between 1996 and 1999 represents baseline ‘Treatment 1’ conditions of zero dam discharge. Flows during the ‘Treatment 2’ period (August 2000 – present) average 3 $m^3 \cdot s^{-1}$ over each year. Due to the flow increase in August 2000, data for this year represent a transition period.

Representative sample sites were estab

reaches 2 and 3. With flow releases beginning in 2000, additional sites were established in Reach 4 (where no wetted habitat had existed previously); between 2001 and 2008, 48 – 50 sites were sampled. Sampling locations were permanently marked and the same locations were generally sampled annually, although not all sites were sampled in all years. A total of 525 sites were sampled between 1996 and 2007. Site conditions may have varied within a treatment due to natural changes in riparian vegetation and substrate composition and configuration. Some interannual variation in flow conditions did occur within a given flow treatment. However, all data were collected during the fall low flow period (September), with flow and water temperature conditions broadly similar across years within treatments (Sneep 2005).

Within each sampling site, an area of approximately 100 $m^2$ (mean = 96, range = 20 – 273 $m^2$) was entirely isolated using block nets anchored with stones. During Treatment 1, some Reach 3 sites used two block nets stretched across the entire width of the channel. The remainder of Reach 3 sites and all Reach 2 sites used three nets to isolate an area along the channel margin. At higher Treatment 2 flows, all sites were three-sided. At each site, a three (n = 277) or four (n = 246) pass depletion was conducted by a three person crew using a Smith-Root backpack electrofishing unit (at two sites, only two passes were completed). Electrofisher settings were initially determined at operator discretion, with some standardization in later years. All sampled fish were identified to species, weighed, measured, and were returned to sites unharmed after sampling was complete. Captured fish were assigned to age classes based on post-capture length frequency analysis. Descriptive information was collected for each site, including habitat type, substrate composition, depth, velocity and area enclosed by block nets. Habitat type was recorded as pool, riffle, run, cascade or sidechannel. Between 1996 and 1999, substrate type was recorded as the mean particle size, both for the exposed streambank and for the wetted site. Beginning in 2000, the substrate composition, as percent fines (< 2mm), gravel (2 – 64mm), cobble (> 64 – 265mm) and bolder (> 256 mm), and $D_{90}$, the intermediate axis dimension of the 90% percentile of substrate particles, were also recorded. Three depth and velocity transects were recorded in each site following removal of block nets.

### 3.2.3 Data analysis

*Performance of lower Bridge*

electroshocker voltage) on estimates of catchability. The Bridge River adaptive management experiment is a repeated measures design, with the same sites sampled both within and across treatments. However, the design is not balanced, as Reach 4 sites were dry during Treatment 1 and so were not sampled. Reach 3 sites are not ‘repeat measures’ between treatments; although site locations were identical during both treatment periods, site character and block net placement changed with the augmented flows.

A hierarchical or non-linear mixed effects model is likely required for the complete analysis of treatment effects on fish abundance and catchability. My intent here was to examine depletion data for flaws that might invalidate such tests. I ignored the complexities of the repeated measures design, and used a non-parametric approach. I used conditioning plots (Cleveland 1993) to examine the influence of a suite of variables on first pass catchability $(\hat{q}_1)$ estimated from the depletion data using *Model 3*. I fitted non-parametric, locally weighted regression (loess) models (Cleveland and Devlin 1988). This approach ignored the non-independence of repeated measures data, but provided for rapid visualisation of relationships that may warrant further testing. This was adequate to identify potential correlations between catchability and variables that might be affected by treatment. If no relationship was suggested by loess fits that ignore the repeated measures nature of the dataset, further investigation is unwarranted. However, relationships evident in the rapid visualisation approach warrant further testing.

I examined reach, year, habitat type, depth, velocity, substrate and electroshocker voltage for an effect on the estimate of first pass catchability. For depth and velocity, I used the average of the 15 measurements collected on transects at each site. For substrate, I used the mean substrate size estimate for the wetted site, as these data were consistently recorded through all survey years.

## 3.3 Results

### 3.3.1 Performance of lower Bridge River depletion estimates

Juvenile rainbow trout (*Oncorhynchus mykiss*), coho salmon (*O. kisutch*) and chinook salmon (*O. tshawytscha*) were captured during sampling of 525 lower Bridge River sites between 1996 and 2007 (total captures = 46 141). *O. mykiss*, which may be resident rainbow trout or anadromous steelhead, represented the majority of captures (~66%; n = 30 170) and about 81% of these were age 0+ fish (n = 24 564).

Population estimates for lower Bridge River sites ranged between 1 and 792 rainbow trout fry (median = 38.4, mean = 56.9) and the vast majority of sites contained fewer than 200 fish (Figure 3.2a). Catchability estimates were highly variable (mean = 0.55, median = 0.56, range = 0.14 – 0.87; Figure 3.2b). For most sites, estimates of the change in catchability over depletion passes suggested a 0 to 50% decline (Figure 3.2c). Declines tended to be most pronounced at high initial catchability (Figure 3.2d). Conversely, at low initial catchability, *Model 3* suggested that catchability tended to increase over successive removal passes (Figure 3.2d).

### 3.3.2 Treatment mediated effects on catchability and bias

Graphical analysis of estimated catchability for lower Bridge River sites suggested that catchability has increased over the course of the flow experiment (Figure 3.3). This pattern does not appear to be explained by a parallel shift in abundance (Figure 3.4) or in the change of catchability over successive depletion passes at a given site (Figure 3.5). Trends in increased catchability over time appeared similar between habitat types and between reaches of the lower Bridge River (Figure 3.3).

It did not appear that there are similar trends in catchability as a function of the depth (Figure 3.6), flow (Figure 3.7) or substrate (Figure 3.8) within sites sampled on the lower Bridge River.

## 3.4 Discussion

### 3.4.1 Performance of lower Bridge River depletion estimates

Estimates of catchability and the change

### 3.4.2 Treatment mediated effects on catchability and bias

Exploratory analysis of the lower Bridge River dataset suggests that the only variable with a systematic impact on catchability is the year in which catch is estimated. Capture efficiency has increased over the course of the experiment (Figure 3.9). This pattern does not appear to be simply explained by relationships for abundance or the change in catchability (although estimates of the change in catchability passes at a given site are highly uncertain; Chapter 2). The trend of increase in catchability might be explained by experience, as crews became more familiar with sampling conditions over the course of a long term experiment.

I did not find evidence for differences in catchability between habitat types, or as a function of site depth, flow or substrate character. Rosenburger and Dunham (2005) similarly find inconclusive results for the effect of stream parameters on catchability and estimator bias. In contrast, Peterson et al. (2004) find that catchability is a function of site characteristics including cross-sectional area, bank character and substrate type, and Korman et al. (2009) find differences in catchability between deep and shallow habitats for larger streams.

The time trend in catchability may affect conclusions drawn from the analysis of lower Bridge River sampling data. Bias in depletion estimates of abundance is reduced at higher catchability. This suggests that estimates for lower Bridge River sites became less biased with time. Although small, this change in catchability (Figure 3.9; 1996 median $\hat{q}_1$ = 0.45, 2007 median $\hat{q}_1$ = 0.63) is expected to change the bias of depletion estimates. The magnitude of the change in bias depends on the extent of declines in catchability between successive passes within individual depletion experiments. Changes in

prior distributions for these parameters (Mantyniemi et al. 2005). As a result, priors established on the basis of mark-recapture results are likely to dominate posterior distributions for depletion estimates. This may be acceptable, if mark-recapture surveys indicate high confidence in the priors so established.

A more profitable approach might be to develop a hierarchical Bayesian model (Dorazio et al. 2005; Wyatt 2002; Rivot et al. 2008) appropriate to the lower Bridge River study. Hierarchical models permit information sharing between appropriately similar sites. A hierarchical model assuming constant catchability has been developed for the lower Bridge River (J. Korman, pers. comm.). This should be expanded to consider non-constant catchability models for depletion data.

## 3.5 Conclusions

Depletion estimates for juvenile salmonid abundance for sites sampled on the Lower Bridge River may be subject to substantial bias, but it was difficult to assess the quality of estimates without additional info 0 eloped

(Riley and Fausch 1992; Peterson et al. 2004; Rosenburger and Dunham 2005; Korman et al. 2009; Carrier et al. 2009).

Declining catchability suggested that it was appropriate to apply non-constant catchability models. Under these conditions, abundance estimates for non-constant models are less biased, and confidence intervals more appropriate, than for classic estimators assuming constant catchability (Chapter 2). However, estimates of abundance remain biased, as a function of initial catchability and the decline in catchability. For the lower Bridge River study, bias may be particularly problematic if there are differences between treatments. Although estimates of catchability and the decline in catchability are confounded, I examined trends in catchability as a function of variables that may have changed with experimental treatment. My results suggested that catchability has increased over the course of the experiment, which would result in a decrease in bias. There was no apparent effect of other habitat variables.

Further investigation, in the form of paired mark-recapture and depletion experiments, may be warranted to independently estimate catchability and decline in catchability for lower Bridge River sites. However, application of results to historical lower Bridge River data, in the form of prior distributions for catchability parameters, may remain problematic because non-constant catchability models are sensitive to these prior distributions. An alternative is to develop hierarchical models, which permit information sharing between appropriate sites to improve estimates (Dorazio et al. 2005; Wyatt 2002; Rivot et al. 2008).

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# TABLES

**Table 2.1:** Non-informative and informative prior distributions simulated for Bayesian depletion models. Shape parameters for informative Beta priors ( α , β ) defined from true simulation parameters (Equation 2.8).

| | **Non-informative priors** | **Informative priors** |
|---|---|---|
| ***Model 1*** | $\log(N) \sim \text{Uniform}(0, 10)$<br>$q_1 \sim \text{Beta}(1.1, 1.1)$ | $\log(N) \sim \text{Uniform}(T_k, 10)$<br>$q_1 \sim \text{Beta}(\alpha, \beta)$ |
| ***Model 2*** | $\log(N) \sim \text{Uniform}(0, 10)$<br>$q_1 \sim \text{Beta}(1.1, 1.1)$<br>$q' \sim \text{Beta}(1.1, 1.1)$ | $\log(N) \sim \text{Uniform}(T_k, 10)$<br>$q_1 \sim \text{Beta}(\alpha, \beta)$<br>$q' \sim \text{Beta}(1.1, 1.1)$ |
| ***Model 3*** | $\log(N) \sim \text{Uniform}(0, 10)$<br>$q_1 \sim \text{Beta}(1.1, 1.1)$<br>$q'' \sim \text{Beta}(1.1, 1.1)$<br>$a \sim \text{Beta}(1.1, 1.1)$ | $\log(N) \sim \text{Uniform}(T_k, 10)$<br>$q_1 \sim \text{Beta}(\alpha, \beta)$<br>$q'' \sim \text{Beta}(1.1, 1.1)$<br>$a \sim \text{Beta}(1.1, 1.1)$ |
| ***Model 4*** | $\log(N) \sim \text{Uniform}(0, 10)$<br>$\log(ɖ) \sim \text{Uniform}(0, 10)$<br>$\varepsilon \sim \text{Beta}(1.1, 1.1)$ | $\log(N) \sim \text{Uniform}(T_k, 10)$<br>$\log(ɖ) \sim \text{Uniform}(0, 10)$<br>$\varepsilon \sim \text{Beta}(\alpha, \beta)$ |

**Table 2.2:** Variables systematically tested in simulation study of depletion methods.

| **Variable** | **Meaning** | **Range tested64.6442 0 Tt l7m-34.(1** |
|---|---|---|

**Table 2.3:** Estimation failure rate (%) aggregated over all catchability scenarios.

| ***N*** | ***k*** | ***Model 1*** | ***Model 2*** | ***Model 3*** | ***Model 4*** |
|---|---|---:|---:|---:|---:|
| 25 | 3 | 8.0 | 0.1 | 0.0 | 13.5 |
| 25 | 4 | 4.9 | 0.1 | 0.0 | 8.2 |
| | | | | | |
| 100 | 3 | 2.8 | 0.4 | 0.1 | 4.7 |
| 100 | 4 | 1.5 | 0.6 | 0.4 | 3.5 |

**Table 2.4:** Results of 500 Monte Carlo simulations of depletion estimates for *N* ( $N = 100$, $k = 4$ ). Simulations were run by sequentially increasing the rate of decline in catchability (*r*) and initial catchability ($q_0$). Non-informative priors were applied (Table 2.1). 'MPE' is the mean percent difference between true and estimated *N*; '$CV_{sim}$' is the standard deviation of estimates expressed as a percent of *N*; 'CI cov' is confidence interval coverage; 'P( $\rho > 1$ )' is the probability that confidence interval width > *N*.

| | | ***Total catch*** | | ***Model 1*** | | ***Model 2*** | ***Model 3*** | ***Model 4*** |
|---|---|---|---|---|---|---|---|---|
| $q_0$ | $r$ | **MPE** | $CV_{sim}$ | **MPE** | $CV_{sim}$ | | | |

**Table 2.5:** Results of 500 Monte Carlo simulations of depletion estimates for $N$ ( $N$ = 100, $k$

**Table 2.6:** Results of 500 Monte Carlo simulations of depletion estimates for *N* ( $N = 100$, $k = 8$ ). Simulations were run by sequentially increasing the rate of decline in catchability ($r$) and initial catchability ($q_0$). Non-informative priors were applied (Table 2.1). **Bold** represents improvements (reductions in bias, variance and P(ρ>1), or confidence interval coverage closer to 95%) relative to analogous estimates for $k = 4$ (*cf*. Table 2.4).

| | | ***Total catch*** | | ***Model 1*** | ***Model 2*** | ***Model 3*** | ***Model 4*** |
|---|---|---|---|---|---|---|---|
| $q_0$ | $r$ | **MPE** | **CV$_{sim}$** | | | | |

**Table 2.7:** Results of 500 Monte Carlo simulations of depletion estimates for *N* ( $N = 100$, $k = 3$ ). Simulations were run by sequentially increasing the rate of decline in catchability (*r*) and initial catchability ($q_0$). Non-informative priors were applied (Table 2.1). **Bold** represents improvements (reductions in bias, variance and P(ρ>1), or confidence interval coverage closer to 95%) relative to analogous estimates for $k = 4$ (*cf.* Table 2.4).

| | | ***Total catch*** | | ***Model 1*** | | | | ***Model 2*** | | | | ***Model 3*** | | | | ***Model 4*** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $q_0$ | *r* | **MPE** | **$CV_{sim}$** | **MPE** | **$CV_{sim}$** | **CI cov** | **P(ρ>1)** | **MPE** | **$CV_{sim}$** | **CI cov** | **P(ρ>1)** | **MPE** | **$CV_{sim}$** | **CI cov** | **P(ρ>1)** | **MPE** | **$CV_{sim}$** | **CI cov** | **P(ρ>1)** |
| **0.2** | **1.0** | -50.8 | 5.0 | 25.7 | 40.7 | **95.8** | 86.7 | -5.5 | **26.5** | **95.6** | 86.0 | -10.4 | 21.4 | 98.4 | 85.0 | **43.6** | 32.7 | 100.0 | 99.5 |
| | **1.2** | -57.2 | **4.9** | **-7.2** | 38.3 | **82.5** | 65.7 | -27.3 | **17.6** | **89.2** | 66.4 | -31.6 | **13.7** | **91.4** | 56.6 | 17.3 | 38.8 | 98.1 | 94.0 |
| | **1.4** | -61.6 | **4.7** | **-27.8** | 34.5 | **63.3** | 43.6 | **-39.5** | 14.1 | **75.6** | 48.8 | -43.2 | 10.8 | **73.6** | 28.2 | **-7.1** | 35.5 | **92.8** | 85.2 |
| | **1.6** | -64.6 | **4.7** | **-45.5** | 24.1 | **34.1** | 22.0 | **-48.0** | 11.3 | **59.9** | 32.9 | -51.1 | **8.4** | **45.2** | 9.6 | **-28.2** | 31.0 | **79.2** | 64.9 |
| | **1.8** | -66.6 | **4.5** | **-54.2** | 17.3 | **20.2** | 13.2 | **-53.3** | | | | | | | | | | | |

**Table 2.8:** Results of 500 Monte Carlo simulations of depletion estimates for $N$ ( $N$ = 25, $k$ = 4 ). Simulations were run by sequentially increasing the rate of decline in catchability ($r$) and initial catchability ($q_0$). Non-informative priors were applied (Table 2.1). **Bold** represents improvements (reductions in bias, variance and P(ρ>1), or confidence interval coverage closer to 95%) relative to analogous estimates for $N$ = 100, $k$ = 4 (

**Table 2.10:** Results of 500 Monte Carlo simulations of depletion estimates for final pass catchability $q_4$ ( $N$ = 100, $k$ = 4 ). Simulations were run by sequentially increasing the rate of decline in catchability ($r$) and initial catchability ($q_0$). Non-informative priors were applied (Table 2.1). '$\hat{q}_4$' is the estimate of first pass catchability, 'MPE' is the mean percent difference between $q_4$ and $\hat{q}_4$; 'CV$_{sim}$' is the standard deviation of estimates expressed as a percent of $q_4$.

| | | | ***Model 1*** | | | ***Model 2*** | | | ***Model 3*** | | | ***Model 4*** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $q_0$ | $r$ | **True $q_4$** | $\hat{q}_4$ | **MPE** | **CV$_{sim}$** | $\hat{q}_4$ | **MPE** | **CV$_{sim}$** | $\hat{q}_4$ | **MPE** | **CV$_{sim}$** | $\hat{q}_4$ | **MPE** | **CV$_{sim}$** |
| **0.2** | **1.0** | 0.20 | 0.24 | 19.3 | 28.4 | 0.27 | 35.8 | 40.5 | 0.32 | 60.0 | 39.2 | 0.22 | 9.0 | 20.9 |
| | **1.2** | 0.12 | 0.31 | 167.0 | 65.9 | 0.33 | 184.0 | 86.6 | 0.36 | 211.9 | 73.3 | 0.26 | 123.1 | 50.5 |
| | **1.4** | 0.07 | 0.39 | 433.8 | 115.5 | 0.37 | 410.5 | 141.0 | 0.39 | 434.9 | 111.0 | 0.31 | 326.9 | 92.4 |
| | **1.6** | 0.05 | 0.45 | 818.9 | 184.9 | 0.42 | 752.2 | 235.0 | 0.43 | 777.2 | 185.1 | 0.36 | 634.9 | 156.6 |
| | **1.8** | 0.03 | 0.50 | 1357.9 | 249.2 | 0.45 | 1212.6 | 374.5 | 0.43 | 1156.3 | 263.9 | 0.40 | 1073.2 | 228.4 |
| | **2.0** | 0.03 | 0.54 | 2048.8 | 332.3 | 0.46 | 1734.4 | 501.4 | 0.45 | 1681.9 | 370.8 | 0.43 | 1609.6 | 310.3 |
| **0.4** | **1.0** | 0.40 | 0.40 | -1.0 | 16.0 | 0.39 | -3.6 | 23.9 | 0.41 | 1.3 | 22.2 | 0.33 | -18.0 | 13.9 |
| | **1.2** | 0.23 | 0.45 | 96.0 | 27.6 | 0.40 | 73.1 | 43.5 | 0.41 | 77.3 | 39.8 | 0.36 | 54.1 | 27.4 |
| | **1.4** | 0.15 | 0.51 | 252.9 | 44.2 | 0.44 | 202.6 | 73.0 | 0.42 | 190.1 | 62.4 | 0.40 | 177.3 | 48.5 |
| | **1.6** | 0.10 | 0.56 | 473.8 | 63.5 | 0.47 | 379.1 | 117.2 | 0.43 | 344.2 | 101.2 | 0.44 | 350.8 | 82.1 |
| | **1.8** | 0.07 | 0.60 | 767.7 | 94.5 | 0.48 | 605.2 | 180.1 | 0.45 | 554.2 | 143.3 | 0.46 | 576.4 | 123.0 |
| | **2.0** | 0.05 | 0.63 | 1168.2 | 114.9 | 0.50 | 902.5 | 250.9 | 0.46 | 822.3 | 199.9 | 0.49 | 882.7 | 165.4 |
| **0.6** | **1.0** | 0.60 | 0.59 | -1.5 | 8.2 | 0.57 | -5.5 | 16.8 | 0.52 | -14.1 | 17.6 | 0.51 | -15.8 | 12.4 |
| | **1.2** | 0.35 | 0.61 | 75.1 | 13.6 | 0.51 | 47.3 | 31.3 | 0.46 | 32.1 | 29.5 | 0.48 | 36.9 | 24.6 |
| | **1.4** | 0.22 | 0.64 | 192.0 | 21.9 | 0.51 | 131.5 | 53.3 | 0.44 | 103.4 | 47.2 | 0.48 | 120.1 | 44.3 |
| | **1.6** | 0.15 | 0.67 | 357.1 | 33.7 | 0.51 | 250.6 | 78.4 | 0.45 | 208.5 | 69.6 | 0.50 | 239.9 | 66.6 |
| | **1.8** | 0.10 | 0.70 | 581.6 | 47.2 | 0.52 | 407.9 | 119.6 | 0.45 | 337.5 | 102.2 | 0.51 | 399.3 | 99.2 |
| | **2.0** | 0.08 | 0.72 | 866.3 | 64.4 | 0.54 | 614.4 | 161.4 | 0.46 | 511.8 | 138.1 | 0.53 | 609.1 | 135.0 |
| **0.8** | **1.0** | 0.80 | 0.79 | -1.6 | 4.4 | 0.72 | -10.1 | 11.7 | 0.61 | -23.85 | 13.42 | 0.68 | -14.7 | 9.3 |
| | **1.2** | 0.46 | 0.78 | 68.6 | 8.8 | 0.60 | 30.0 | 27.4 | 0.49 | 5.66 | 25.72 | 0.58 | 25.2 | 25.8 |
| | **1.4** | 0.29 | 0.79 | 169.8 | 14.0 | 0.55 | 89.3 | 45.4 | 0.46 | 57.42 | 37.10 | 0.54 | 85.4 | 43.6 |
| | **1.6** | 0.20 | 0.81 | 313.9 | 20.4 | 0.54 | 174.5 | 75.8 | 0.44 | 124.26 | 54.21 | 0.54 | 174.9 | 69.1 |
| | **1.8** | 0.14 | 0.82 | 497.2 | 30.2 | 0.52 | 279.3 | 102.5 | 0.44 | 219.23 | 81.27 | 0.53 | 286.6 | 95.6 |
| | **2.0** | 0.10 | 0.84 | 737.6 | 41.0 | 0.53 | 426.4 | 147.3 | 0.44 | 340.39 | 107.93 | 0.55 | 452.3 | 134.7 |

**Table 2.11:** Results of 500 Monte Carlo simulations of depletion estimates for change in catchability ( $q_4$ - $q_{1;}$ $N$ = 100, $k$ = 4 ). Simulations were run by sequentially increasing the rate of decline in catchability ($r$) and initial catchability ($q_0$). Non-informative priors were applied (Table 2.1). ‘ $\Delta\hat{q}$ ’ is the difference between estimated catchability for pass 4 and pass 1 ( $\hat{q}_4$ - $\hat{q}_1$ ); ‘MPE $\Delta\hat{q}$ ’ is the mean perc07 Tw is th.00ean perc .958were run by sequent’ is the meuent

**Table 3.1:** Simulation-based change in expected bias (MPE) of abundance estimates for *Model 3*, for a change in initial catchability from $q_0 = 0.4$ to $q_0 = 0.6$, assuming that the reduction in catchability by pass ($r$) remains constant, for $N = \{25, 100\}$ and $k$

# FIGURES

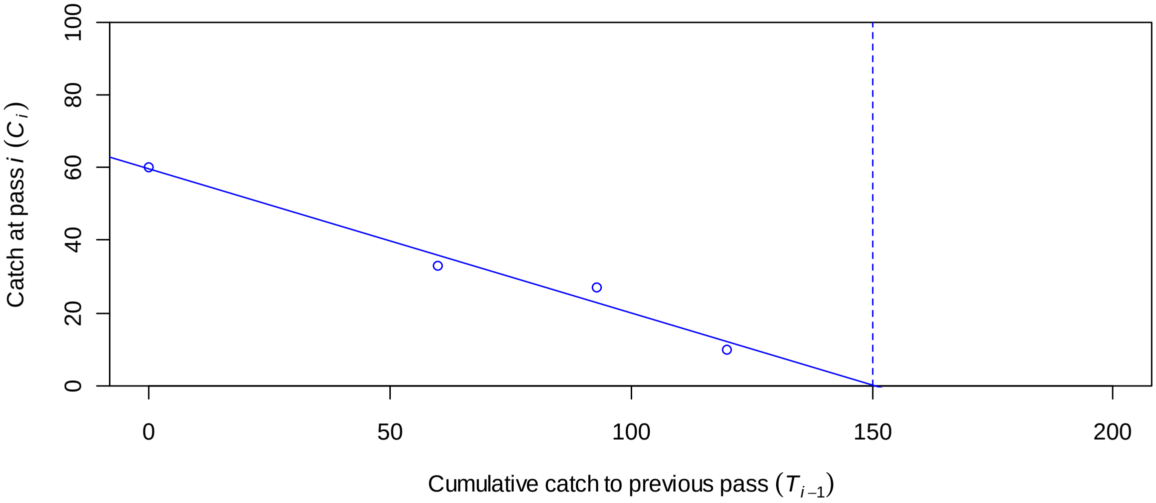
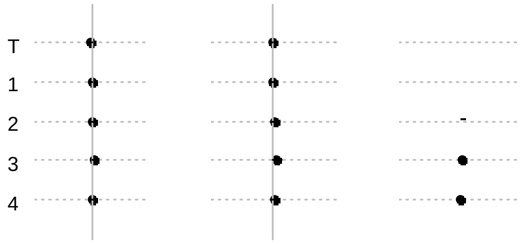


**Figure 2.1:** Graphical depiction of depletion method, assuming constant catchability. The regression method of estimation is illustrated, although this is inappropriate because catches are not independent. Estimation using a depletion model is therefore required.


T
1
2
3
4

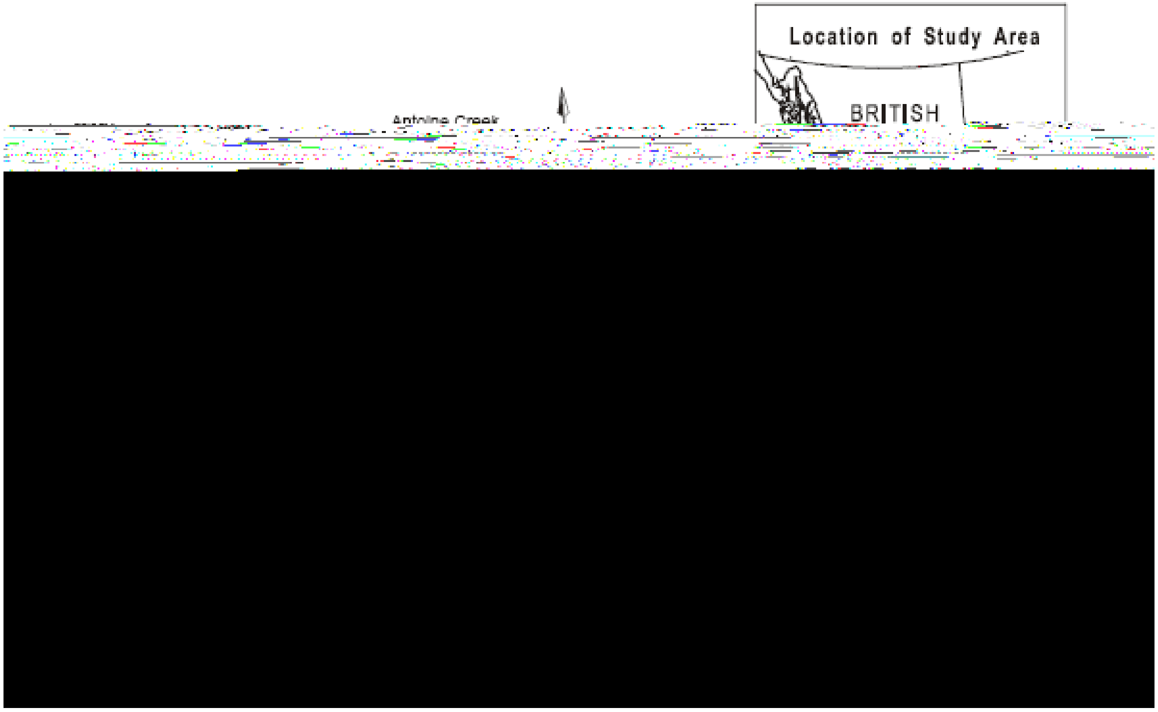
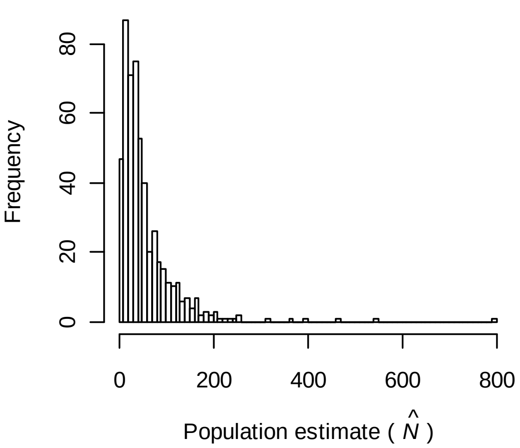
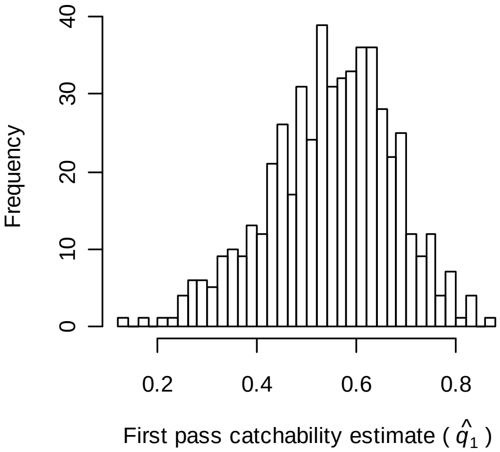
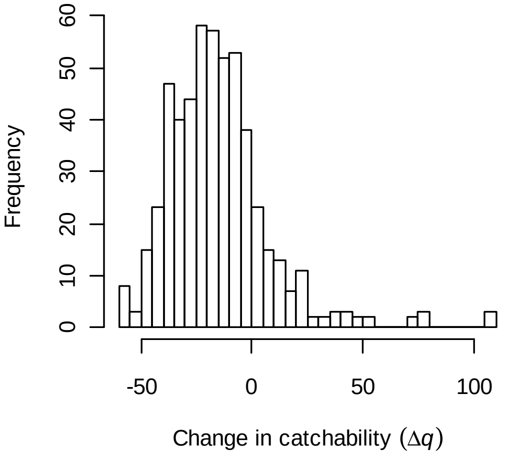
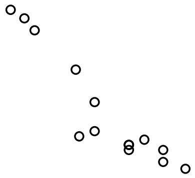


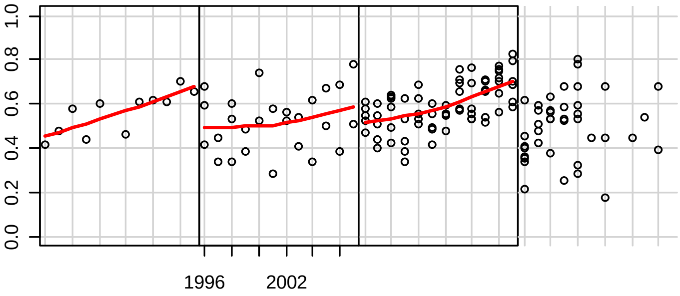
**Figure 3.1:** Lower Bridge River study area**,** reproduced from Sneep (2005).

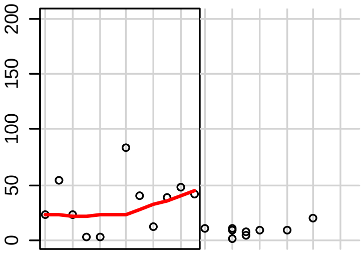

Frequency
0
20
40
60
80
0
200
400
600
800
Population estimate ( $\hat{N}$ )

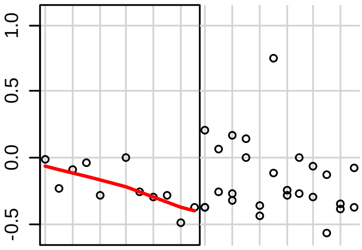

Frequency
0
10
20
30
40
0.2
0.4
0.6
0.8
First pass catchability estimate ( $\hat{q}_1$ )


Frequency
0
10
20
30
40
50
60
-50
0
50
100
Change in catchability ($\Delta q$)




1.0
0.8
0.6
0.4
0.2
0.0
1996
2002


0
50
100
150
200


1.0
0.5
0.0
-0.5

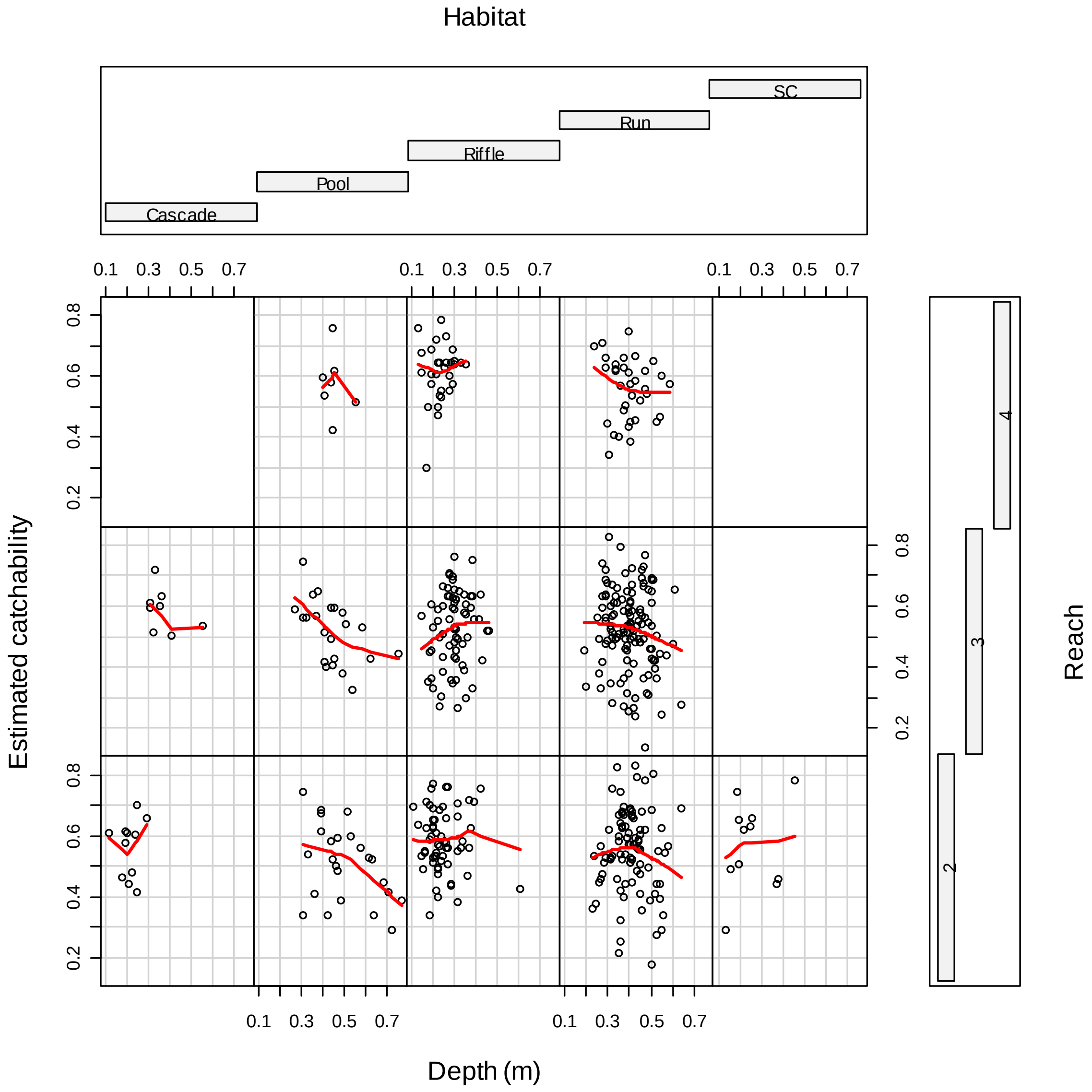
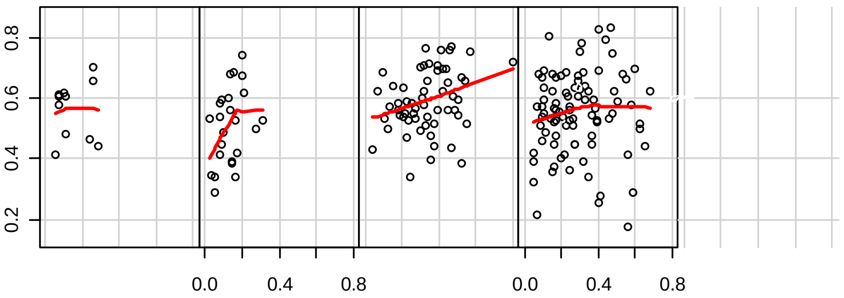
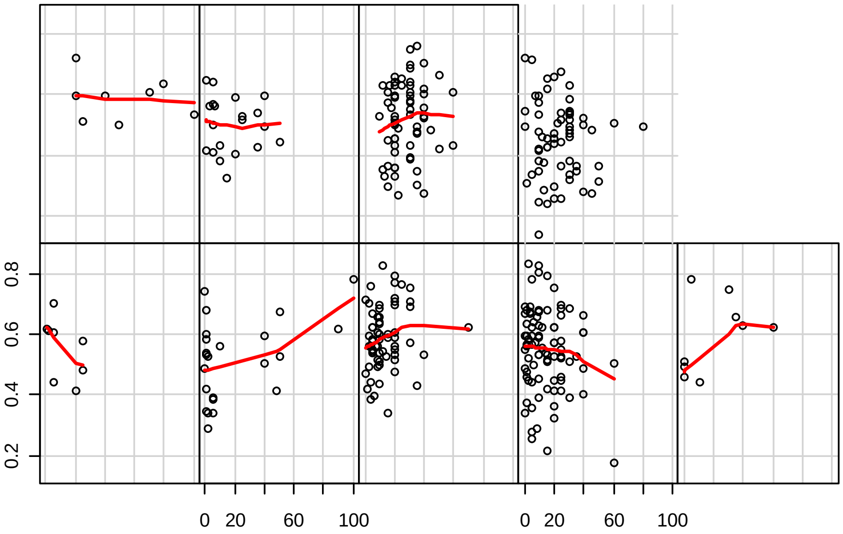


**Figure 3.6:** Conditioning plot of first pass catchability estimates from *Model 3*, for rainbow trout fry sampled at 525 lower Bridge River sites between 1996 and 2007. Catchability estimates are presented as a function of mean site depth (m), reach and habitat type. Indicated fits are locally weighted regression (loess) smoothes.


0.2
0.4
0.6
0.8
0.0
0.4
0.8
0.0
0.4
0.8


0.2
0.4
0.6
0.8
0
20
60
100
0
20
60
100

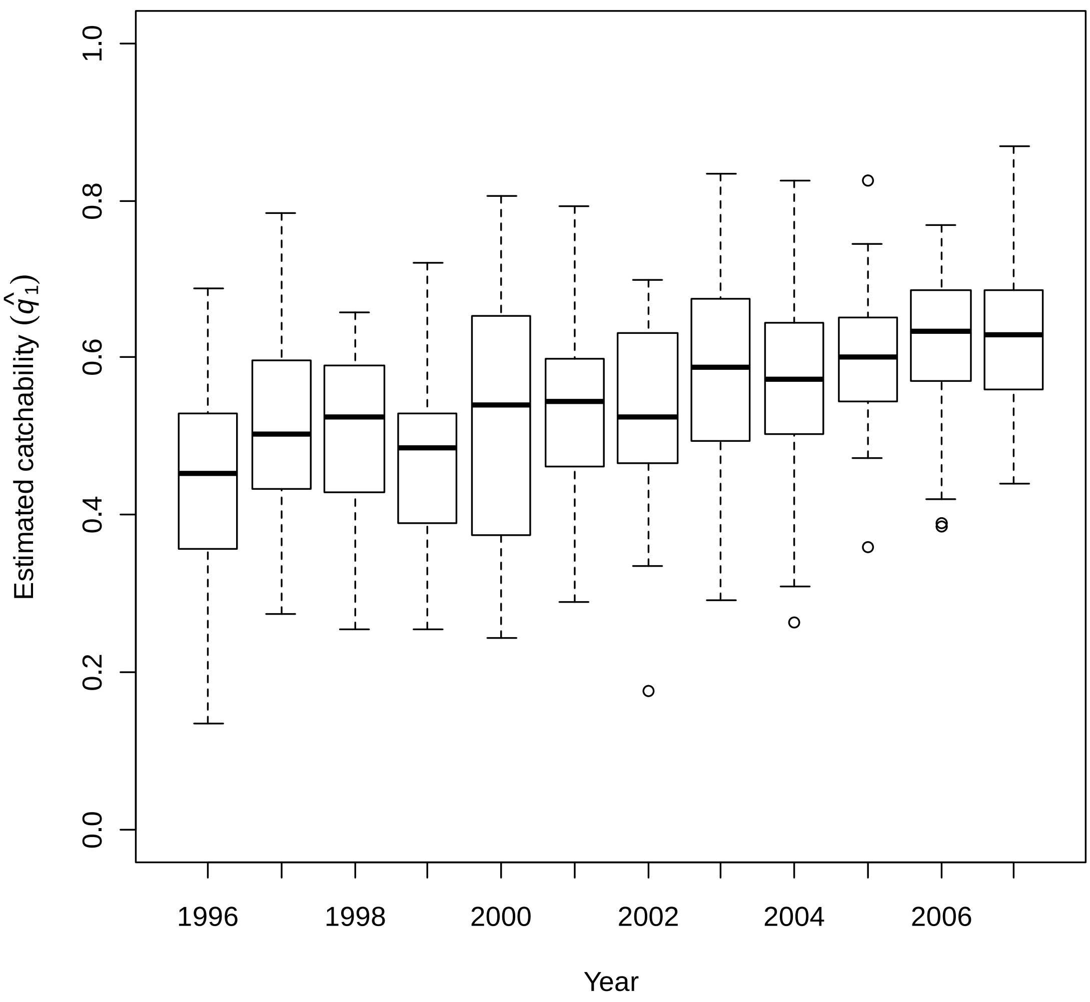


**Figure 3.9:** Trend in first pass catchability estimates from *Model 3*, for rainbow trout fry sampled at 525 lower Bridge River sites between 1996 and 2007. Boxes represent the first and third quartiles, with the median indicated. Whiskers extend to extreme values, with outliers indicated by open circles.

# APPENDICES

## Appendix A: Maximum likelihood parameter estimation

Maximum likelihood methods are often used to estimate values for unknown parameters in depletion models (Schnute 1983). My simulation results suggest that Bayesian methods are preferred, both because estimates are less biased, for declining catchability cases, and because confidence intervals are more likely to include the true

The log of the binomial likelihood (Equation 2.2) can be written with $q$ expressed in terms of the predicted catch by pass $\hat{C}_i$ and predicted total catch $\hat{T}_k$ (Schnute 1983):

$$
\begin{aligned}
&-\mathbf{l}\left(N, q \middle| C_1, \ldots, C_k\right) = \\
&N \log(N) - T_k \log(T_k) - (N - T_k) \log\left(N - \hat{T}_k\right) - \log \genfrac{}{}{0pt}{}{N}{T_k} + \sum_{i=1}^{k} C_i \log \frac{C_i}{\hat{C}_i} + c
\end{aligned}
\tag{A.2}
$$

where $c$ is a constant that can be ignored. The minimum of the log-likelihood occurs where the first partial derivative of the log-likelihood with respect to each parameter is zero. For the constant catchability case, the partial derivative with respect to $q_1$ can be solved to define the conditional maximum likelihood for $q$, given $N$ (Moran 1951):

$$
q_1(N) = \frac{T_k}{kN - \sum_{i=1}^{k} T_i} . \tag{A.3}
$$

Substituting Equation A.3 into the model predicting catches (Equation A.1) gives the conditional maximum likelihood estimate (MLE) of $N$ given the MLE for q, and means that maximum likelihood estimation for *Model 1* catchability may increase or decrease after the first pass. The three parameters, $N$, $q_1$ and $q'$ are required to model the predicted catch:

To obtain maximum likelihood estimates for *N*, I used the R function *optim* to minimise the negative log-likelihood for the binomial removal model (Equation A.2) as a four parameter problem (*N*, $q_1$, $q''$, and *a*), using Equation A.6 to define the objective function. If *optim* failed to converge, I used the slower but more robust *rgenoud* package, which combines evolutionary algorithm methods with a derivative based method (Mebane and Sekhon 2009). I used a likelihood ratio test to define a 95% confidence interval for *N*.

***Model 4:*** **individual catchability model (Mäntyniemi et al. 2005)**

*Model 4* assumes that mean catchability declines over passes, and is described by a parametric function analogous to the Schnute (1983) models:

$$q_i = \frac{\mu\eta}{\eta + i - 1}, \quad i = 1, \ldots, k \qquad \text{(A.7)}$$

where μ is the mean catchability over all fish, and ɋ is a measure of the relative variation of catchability:

$$\eta = \frac{\mu(1-\mu) - \sigma^2}{\sigma^2}. \qquad \text{(A.8)}$$

Large values of $\eta$ indicate low variation in catchability ($\eta \to \infty$ as $\sigma^2 \to 0$). Estimates are required for the three parameters *N*, $\mu$ and $\eta$. Mäntyniemi et al. (2005) use Bayesian methods to estimate parameters (see main report). I minimised the negative log-likelihood for the binomial removal model (Equation A.2) using Equation A.7 to define the objective function. I found that the R package *optim* was highly sensitive to the selection of initial values when optimising over the three parameters *N*, $\mu$ and $\eta$.. I therefore fit the likelihood profile for values of *N* over the interval between the total catch

distributions/likelihood profiles for *N* for depletion models with declining catchability tend to be biased low but skewed right (Appendix D), the mean of these distributions will tend to be less biased than the mode.

**Table A.1:** Results of 500 Monte Carlo simulations of maximum likelihood depletion estimates for $N$ (

**Table A.1 (continued):**

| | | *Model 4 - MLE* | | | | *Model 5 - MLE* | | | |
|---|---|---|---|---|---|---|---|---|---|
| ***$q_0$*** | ***r*** | **MPE** | **$CV_{sim}$** | **CI cov** | **P(ρ>1)** | **MPE** | **$CV_{sim}$** | **CI cov** | **P(ρ>1)** |
| **0.2** | **1.0** | 0.8 | 29.1 | 100.0 | 100.0 | -1.7 | 29.3 | 92.8 | 74.3 |
| | **1.2** | -34.8 | 17.2 | 98.8 | 97.5 | -36.5 | 15.6 | 57.7 | 31.3 |
| | **1.4** | -49-49 | | | | | | | |

## Appendix B: Mäntyniemi et al. (2005) model

Mäntyniemi et al. (2005) assume that catchability might be a characteristic of each individual fish, but derive a simple expression for mean catchability by pass. Their parametric function is analogous to the expression used by Schnute (1983). This appendix follows the methods section of Mäntyniemi et al. (2005) in describing the catchability model used in *Models 6*, *7* and *8*.

Assume that, prior to the first depletion pass, each fish in an enclosed site can be characterised by an individual catchability ($p_n$) considered an independent and random draw from the distribution:

$$f\left(p_n \middle| \mu, \sigma\right),\ n = 1, \ldots, N, \tag{B.9}$$

where $\mu$ and ů are the mean and standard deviation, respectively. Conditionally on $p_n$, let $z_n$ be a Bernoulli-distributed indicator variable that takes the value 1 if individual $n$ is captured on Pass 1, and the value 0 if the individual escapes, i.e.,

$$P\left(z_n \middle| p_n\right) = p_n^{z_n}\left(1 - p_n\right)^{1 - z_n},\ n = 1, \ldots, N, \tag{B.10}$$

Define $\mu$ as the expected value of $p_n$. The conditional distribution of $z_n$ given $\mu$ and ů is:

$$P\left(z_n \middle| \mu, \sigma\right) = \mu^{z_n}\left(1 - \mu\right)^{1 - z_n},\ n = 1, \ldots, N, \tag{B.11}$$

Assuming that fish respond independently to sampling (i.e., values of $z_n$ are conditionally independent, given $\mu$), the catch on the first removal pass ($C_1$) is binomially distributed, i.e.,

$$C_1 = \sum_{n=1}^{N} z_n \middle| N, \mu \sim Binomial\left(N, \mu\right). \tag{B.12}$$

Only the mean catchability, $\mu$, is required to model the catch.

After the removal of this first catch (generally, those fish easiest to catch), the distribution of catchabilities is no longer $f\left(p_n \middle| \mu,\sigma\right)$. Using Bayes rule, i.e., Because the mean $\mu$ and standard deviation *ů* of a Beta distribution are not independent ($\sigma < \sqrt{\mu(1-\mu)}$), introduce the parameter *ɖ* as a measure of the relative variation of catchability:

$$\eta \quad \frac{\mu( \quad \mu) \quad \sigma}{\sigma} \quad \alpha \quad \beta$$

## Appendix C: WinBUGS code for depletion models

### *Model 1: constant catchability*

```
model1{
        for( j in 1:k ){
                x[ j ] ~  dbin  (q1, n[ j ] )
                n[ j+1 ] <- n[ j ] - x[ j ]
        }
        u ~ dunif ( 0, 10 )
        n[ 1 ] <- exp( u )
        q1 ~ dbeta( 1.1, 1.1 )
}
```

### *Model 2: two catchability*

```
model2{
        for( j in 1:k ){
                q[ j ] <- step( 1 - j ) * q1 + ( 1- step( 1 - j )) * q2
                x[ j ] ~  dbin (q[ j ], n[ j ])
                n[ j+1 ] <- n[ j ] - x[ j ]
        }
        u ~ dunif ( 0, 10 )
        n[ 1 ] <- exp( u )
        q1 ~ dbeta( 1.1, 1.1 )
        q2 ~ dbeta( 1.1, 1.1 )
}
```

### *Model 3: declining catchability*

```
model3{
        for( j in 1:k ){
                q[ j ] <- q1 + ( q0 - q1 )*( 1 - pow( a,( j-1 ) ) )
                x[ j ] ~  dbin ( q[ j ], n[ j ] )
                n[ j+1 ] <- n[ j ] -x[ j ]
        }
        u ~ dunif( 0, 10 )
        n[ 1 ] <- exp( u )
        q1 ~ dbeta( 1.1, 1.1 )
        q0 ~ dbeta( 1.1, 1.1 )
        a  ~ dbeta( 1.1, 1.1 )
}
```

### *Model 4: declining catchability*

```
model4{
	for( j in 1:k ){
		q[ j ] <- mu * ( eta / ( eta + j – 1 ) )
		n[ j+1 ] <- n[ j ] –x [ j ]
	}
	u ~ dunif ( 0, 10 )
	n[ 1 ] <- exp( u )
	log.eta ~ dunif( 0, 10 )
	eta <- exp( log.eta )
	mu ~ dbeta( 1.1, 1.1 )
}
```

## Appendix D: Point estimates for Bayesian depletion methods

Bayesian methods using MCMC produce posterior distributions for parameters of interest. In order to compare results of Bayesian estimators within a simulation context, median of the posterior MCMC sample. Results presented are for four pass depletion series with $N = 100$.

If true catchability is constant, the median is less biased than the mean, for almost all scenarios (the exceptions are *Models 2* and *3* at very low catchability; Table D.1). Because the posterior distribution has a long right-hand tail, the mean is biased high relative to the median (Figure D.1). This bias can be substantial, particularly at low catchability (+47% for *Model 4*, $q_0 = 0.2$). Under these conditions, there are substantial differences between the mean and the median of the posterior distribution as point estimates for $\hat{N}$ (Table D.1). The median is also less variable than the mean for *Models 2, 3* and *4*. For *Model 1*, the variance of the mean and the median are similar.

If true catchability declines, the catch series suggests a smaller population than is actually present; as the mean is weighted by the right-hand tail of the posterior distribution, it provides the more accurate point estimate for $\hat{N}$. However, the median is more precise. When Pass 1 catchability is modest or high, there is little difference in bias between the mean and the median as point estimates for $\hat{N}$; for modest catchability, the median tends to be more precise.

The choice of an appropriate point estimate for $\hat{N}$, for comparisons between different depletion models, is driven by differences at low constant catchability. Because the mean is more accurate than the median under most of the scenarios I simulated, I selected the mean as the appropriate point estimate of $\hat{N}$. Researchers applying these models to low, constant catchability situations, and desiring point estimates might consider the trade-off between precision and accuracy differently than I have done.

The posterior distributions for parameters describing the decline in catchability ( $\hat{q}''$, $\hat{a}$ in this example for

**Table D.1:** Results of 500 Monte Carlo simulations of depletion estimates for $N$ ( $N = 100$, $k = 4$ ). Simulations were run by sequentially increasing the rate of decline in catchability ($r$) and initial catchability ($q_0$). The ‘median’ and ‘mean’ of posterior distributions for $\hat{N}$ are presented. MPE refers to