

**AN EVALUATION OF THE BROWNIE TAG-RECAPTURE MODEL USING
SIMULATION-ESTIMATION PROCEDURES, WITH APPLICATION TO
BRITISH COLUMBIA SABLEFISH (*Anoplopoma fimbria*)**

by

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ABSTRACT

The Brownie tag-recapture model analyses multi-year tag recovery data to derive estimates of natural and fishing mortality that can be used to estimate population abundance. However, it makes several assumptions about the behaviour of tagged fish, tagging-induced mortality, tag retention, emigration, tag reporting, and timing of the fishery. I evaluate performance of the Brownie model when individual assumptions are violated, using Monte Carlo simulations over a suite of scenarios with known “true” parameter values chosen to mimic British Columbia sablefish (*Anoplopoma fimbria*). Bias and precision are quantified by comparing parameter estimates with their known “true” values and by the spread in estimates from 500 Monte Carlo trials, respectively. Assumptions about uniform mixing, timing of the fishery, and emigration had the greatest effects on bias of estimates of fishing mortality and abundance. Combining fishery-independent survey CPUE data with tag recovery data did not substantially improve bias or precision of parameter estimates.

Keywords: Brownie model; tag-recapture; sablefish; maximum likelihood estimation; bias; Monte Carlo simulation; survey CPUE; tag reporting rate

Subject Terms: Animal populations – Mathematical models; Fish stock assessment – Mathematical models; Ecology – Mathematical models; Animal marking; Monte Carlo method; Fishes – British Columbia

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1 INTRODUCTION

Estimates of fish population abundance are critical for effective management of fisheries, yet reliable estimates are extremely difficult to obtain. A variety of tagging methods have been developed over the last 200 years to address this problem (Manly et al. 2005). These methods involve the capture and marking of animals at one time and the subsequent recapture of tagged and untagged animals at future times. Analysis of tag release and recovery data can provide estimates of mortality rates and abundance for the population. However, such analyses require relatively strong assumptions about the behaviour and availability of tagged animals, mortality impacts due to tagging, tag loss, and reporting of recaptures. Violating any of these assumptions may increase bias and/or decrease precision of abundance estimates from tagging experiments.

In this paper, I develop a simulation-estimation approach for evaluating the statistical properties of estimates of fishing mortality, natural mortality, and abundance derived from tagging studies that violate several important assumptions. Although the approach I describe intends to mimic tagging studies for British Columbia (BC) sablefish (*Anoplopoma fimbria*), both the simulation and estimation frameworks can be generalized to other tag-recapture programs where a time series of tag recovery data is available.

Sablefish is a long-lived, deep-dwelling groundfish species that is harvested commercially along the west coast of North America (Heifetz and Fujioka 1991; Hanselman et al. 2005). It is one of the most economically important species fished in

British Columbia, with landings of 3800 metric tonnes valued at CAD\$29 million in 2000 (DFO 2005). The fishery is co-managed by Fisheries and Oceans Canada (DFO) and the Canadian Sablefish Association (CSA), which is an industry association of license holders in the sablefish longline trap and longline hook fisheries (CSA 2006). Through a collaborative agreement with the DFO, the CSA makes significant contributions towards fishery management by sponsoring fishery-independent survey monitoring, an extensive coast-wide tagging program, scientific stock assessments, and enforcement. DFO and CSA-contracted scientists collaboratively develop annual scientific assessments of sablefish stock status using both commercial and fishery-independent data (Haist et al. 2004; Haist et al. 2005). Fishery managers consider these results along with social and economic factors when setting total allowable catch (TAC) quotas each year (DFO 2006).

The data sources typically available for sablefish stock assessments include: (1) fishery-independent survey catch-per-unit-effort (CPUE), measured as the average number of fish or total mass (kg) of fish caught per trap; (2) tag releases and recoveries since the sablefish tagging program began in 1991; (3) dockside landings from commercial fisheries; and (4) geo-referenced commercial catch and effort from vessel logbooks (Wyeth and Kronlund 2003; Haist et al. 2005). Data required to calculate the CPUE index are collected annually during the fishery-independent trap survey at the same time that sablefish are tagged and released (Wyeth and Kronlund 2003). This standardized trap survey (1990 – present) is conducted for research and assessment of sablefish each fall (October-November) at nine fixed localities along the BC coast (the ninth locality was added in 1994) (Wyeth and Kronlund 2003; Haist et al. 2004). Each year, the number of fish caught per trap is averaged over all localities, producing a coast-

wide CPUE index of relative abundance (Wyeth and Kronlund 2003), hereafter referred to as “survey CPUE”.

Tag releases and recoveries comprise a central part of the BC sablefish stock assessment program. An average of 5673 fish of fork-length greater than 60 cm were tagged and released from the offshore survey localities each year from 1991 to 2004 (Haist et al. 2004; Haist et al. 2005). Sablefish are tagged with T-bar anchor tags (Floy tags) inserted at the base of the first dorsal fin (Wyeth and Kronlund 2003). Tagged fish are recovered throughout the year by directed sablefish fishing and by the trawl gear sector, which is allocated 8.75% of the commercial quota (DFO 2006). Other recoveries of tagged fish may occur from various hook and line fisheries where sablefish are intercepted as bycatch (DFO 2006). Numerous reward incentives are in place to encourage tag reporting from all sectors (Haist et al. 2004). Analysis of the tagging data to estimate abundance has formed the core of many BC sablefish stock assessments in recent years (e.g., Haist and Hilborn 2000; Haist et al. 2001; Kronlund et al. 2002; Wyeth and Kronlund 2003; Haist et al. 2004; Haist et al. 2005). In this paper, I evaluate the performance of a stock assessment model that uses these data to estimate abundance and fishing mortality.

One possible way to use the tag recovery and commercial catch data to estimate sablefish abundance (A_j) in year j is to employ the well-known relationship between catch (C_j) and exploitation rate (u_j):

$$(1) \quad \hat{A}_j = C_j / \hat{u}_j ,$$

where the carat symbol “^” represents an estimated quantity. The exploitation rate, u_j , is defined as the fraction of fish alive at the beginning of year j that is harvested during the year. Assuming that all catch is taken instantaneously at the beginning of the year, u_j can be estimated from the instantaneous rate of fishing mortality (F_j) as

$$(2) \quad \hat{u}_j = 1 - \exp(-F_j) .$$

The “Brownie” tag-recapture model provides a way to estimate the annual fishing mortality rate (F_j) along with a combined natural mortality-emigration parameter (M^*) and an average tag reporting rate (λ) from observed tag recovery data (Seber 1970; Youngs and Robson 1975; Brownie et al. 1985; Pine et al. 2003; Hoenig et al. 2005). This model has been the primary method for analysing tag recovery data to estimate total mortality rates in wildlife studies (Taylor et al. 2006). Annual estimates of abundance A_j can then be derived by substituting the Brownie estimates of F_j into equation 2 and the estimated value of u_j into equation 1.

The Brownie model is applicable to capture-recapture programs in which there is only one recovery event because the animal is harvested upon its first recapture (Pollock et al. 1994). The Brownie model estimates annual total mortality rates for each release cohort from an $I \times J$ matrix of observed tags recoveries, where I is the number of release cohorts and J is the number of recovery years (Pollock 1991). Table 1 shows an example of such a tag recovery matrix for three years of releases and recoveries ($I = J = 3$). Total mortality is estimated from the rate at which tags from successive annual tag release

cohorts disappear from the observed recoveries (Pollock et al. 2001; Hoenig et al. 2005; Polacheck et al. 2006). For example, suppose that an equal number of tags are released in two successive years, $i = 1$ and $i = 2$. The number of tags released in year 1 and recovered in a subsequent recovery year j , r_{1j} , is less than r_{2j} because the fish tagged in year 1 were subject to an additional year of mortality not experienced by fish tagged in year 2. If information on the seasonal pattern of fishing effort is available in addition to the tag recovery matrix, then the Brownie estimate of total mortality can be subdivided into its fishing mortality (F) and natural mortality (M) components (Hoenig et al. 1998a). In addition, tag reporting rates can also be estimated directly from the matrix of tag recovery data, although Hoenig et al. (1998a) found that the Brownie model did not estimate these reliably. In their analysis, they fit the Brownie model to 10 years of tag recovery data for lake trout in Cayuga Lake, New York. They repeated their analysis using all possible subsets of the data consisting of three or more consecutive years of tag recoveries. Their estimates of λ varied widely depending on which subset of years of tag recovery data they used to fit the model (Hoenig et al. 1998a).

A challenge of applying the Brownie model to estimate fishing and natural mortality rates for BC sablefish is that the capture-recapture design for this fishery likely violates most assumptions of the model. These assumptions include (e.g., Pollock et al. 1994; Brooks et al. 1998; Latour et al. 2001a; Pollock et al. 2001; Pollock et al. 2002; Hoenig et al. 2005; Leigh et al. 2006):

1. The tagged sample is representative of the population (i.e., tagged and untagged fish are uniformly mixed);
2. Tags are not lost;
3. Tagging does not affect survival rates (i.e., no tag-induced mortality);

4. Tags are reported in the year that they are recovered;
5. The fate of each tagged fish is independent of other fish (i.e., fish do not clump or aggregate);
6. There is no emigration; and
7. All tagged fish within a release cohort have the same annual survival and recovery probabilities (i.e., there is no age- or size-selectivity).

Assumption 6 is not usually cited as an assumption of the Brownie model, but it is implicitly assumed because emigration is not distinguished from natural mortality.

Finally, the implementation of the Brownie model investigated in this study also requires the assumption that:

8. All catch is taken instantaneously at the beginning of the year.

Assumption 8 arises because estimates of exploitation rates (\hat{u}_j) are derived from estimates of fishing mortality using equation 2, which makes this assumption. However, Hoenig et al. (1998a) present two alternative formulations of u_j that can be used instead of equation 2 if assumption 8 does not hold and if information is available on the seasonal timing of the fishery.

Violations of any Brownie model assumptions may degrade the performance of the estimator in terms of bias and precision of parameter estimates, which can ultimately have implications for fisheries management advice. Although several researchers have developed structural modifications to the Brownie model to relax various assumptions (e.g., Leigh et al. 2006; Latour et al. 2001b; Brooks et al. 1998; Hoenig et al. 1998b), to my knowledge, the effect of violations of the individual assumptions on the performance of the estimator has yet to be quantified using simulations. Results from such simulation-

estimation trials would better inform analysts and fishery managers of the potential pitfalls of the Brownie model.

Although the Brownie model requires only tag recovery data to estimate mortality rates, Hoenig et al. (1998*a*) speculated that it might be possible to combine an index of abundance as well as catch-at-age data with the model. Indeed, Polacheck et al. (2006) did the latter and showed that incorporating catch-at-age data with the Brownie model decreased bias in estimates of natural mortality and improved precision in estimates of annual fishing mortality. However, to my knowledge, combining an index of relative abundance with a Brownie capture-recapture model has not yet been evaluated via simulations. Therefore, in this study I fit the Brownie model to simulated tag recovery data for BC sablefish, and quantify the potential improvements in bias and precision of parameter estimates by combining the tag recovery data with an index of relative abundance for the species. This is a useful approach because (1) it provides insights on the integration of an index of abundance with the Brownie model, and (2) it evaluates a novel way of analysing two important data sources in the BC sablefish fishery – tagging data and survey CPUE data. Although these two data sources have been combined in tag recovery models for sablefish over the past several years (e.g., Haist et al. 2004; Haist et al. 2005), the statistical properties of the past models have not been evaluated. In addition, the Brownie model has not been previously applied to BC sablefish data.

Given empirical evidence for sablefish movement into BC waters (Heifetz and Fujioka 1991; Kimura et al. 1997; Haist et al. 2001), the Brownie model may confer an advantage over the closed-population Petersen-type tag recovery models that have previously been applied to BC sablefish (e.g., Haist and Hilborn 2000; Haist et al. 2001).

This is because immigration does not bias mortality estimates from the Brownie model, since total mortality is estimated using only the observed tag recovery data and there is no term for abundance in this model.

A major challenge facing stock assessment scientists in the past has been the unknown properties of parameter estimators because true abundances and parameter values are unknown. However, in the last decade, numerous researchers have illustrated the evaluation of stock assessment models using simulated data with known true parameters before applying the models to actual data (e.g., de la Mare 1996; Butterworth and Punt 1999; Peterman et al. 2000; Punt 2003*b*; Chen et al. 2005; Labelle 2005; Wang et al. 2005). In fact, the evaluation of stock assessment models using simulation methods comprises one component of a full management strategy evaluation (MSE) for fisheries (Punt 1992; de la Mare 1998; Punt 2003*a*). In this study, I perform a preliminary analysis of the feasibility of using the Brownie model for stock assessment as part of ongoing MSE work for BC sablefish. This was achieved by using Monte Carlo simulation-estimation procedures to quantify:

1. The effects of violations of assumptions of the Brownie model on its performance, as measured by bias and precision of estimates of parameters and abundance; and
2. The potential improvement in performance of the Brownie model when an index of relative abundance, namely CPUE data from the sablefish survey, is combined with Brownie tag recovery data.

In the former case, particular attention is given to estimates of population abundance since these quantities are most relevant for fisheries management. Although

the use of simulation trials does not guarantee that all possible behaviours of the model can be accounted for, the methods illustrated in this study represent one way to quantify potential model outcomes over a range of plausible scenarios.

2 METHODS

The Monte Carlo simulation-estimation approach used in this study involved generating simulated data sets with known “true” parameters and then obtaining parameter estimates by fitting the Brownie model to the simulated data. Performance of the estimator was quantified by (i) the bias of the estimates relative to their true values, and (ii) the precision of the estimates from 500 Monte Carlo cycles of simulation and estimation. As much as possible, values of the “true” parameters used to generate the simulated data were based on empirical data for BC sablefish.

2.1 Simulation Model

A model was developed to simulate population dynamics of BC sablefish from 1991 through 2003 (details provided in Appendix A). The model generates three types of simulated data for each set of known “true” input parameters: (1) an observed index of relative abundance (survey CPUE), (2) observed tag recovery data, and (3) commercial catch data. The simulation model has two components, both of which run on monthly time steps. The first is a deterministic population dynamics model for total abundance, i.e., there is no process error. The second is an observation model that includes two sources of observation error, namely, random variability in the recovery of tagged fish and in the generation of survey CPUE.

2.1.1 Population dynamics

The population dynamics model is a discrete-time state space model that calculates the number of fish present in each state at each monthly time step. It includes recruitment, natural mortality, fishing mortality, emigration, tagging, tag shedding, and exchange of fish between vulnerable and invulnerable sub-populations. All fish exist in one of two vulnerability states, vulnerable (V) and invulnerable (V'). At each time step, a proportion ($\theta^{V \rightarrow V'}$) of vulnerable fish transfer to the invulnerable state and another proportion ($\theta^{V' \rightarrow V}$) of invulnerable fish transfer to the vulnerable state. An example of this exchange process is a case in which a fish spends some of its time inhabiting steep-sided canyons which are not fished effectively by trap gear (i.e., invulnerable state), and some time making forays into flat plateaus where trap gear is typically deployed (i.e., vulnerable state). Parameters $\{\theta^{V \rightarrow V'}, \theta^{V' \rightarrow V}\}$ thus represent transition probabilities for moving between these two states.

All fish in the population dynamics model are either tagged (G) or untagged (G'). There are no age-structure dynamics, so fish of all ages are subject to the same population dynamics and exploitation rates at each time step. Additionally, a certain proportion of fish, κ , emigrate from the population at each time step. The simulation model does not incorporate a relationship between spawning stock and recruitment mainly because stock productivity is irrelevant to evaluating the Brownie capture-recapture model. Instead, population production is controlled by estimates of annual production derived by Haist et al. (2005) which are supplied as inputs to the population dynamics model. Production inputs are added to the simulated population in the month corresponding to January of each year (i.e., months 1, 13, 25...). No recruits are added in

the other months. The numbers of sablefish in each vulnerability and tagging state are simulated monthly from 1991 through 2003 given these deterministic population dynamics.

2.1.2 Observation model

The observation model generates three types of data: (1) stochastic survey CPUE, (2) stochastic tag recoveries, and (3) commercial catch comprised of both deterministic catches of untagged fish and stochastic tag recoveries.

Let N_{vt}^{ab} represent the number of fish in each vulnerability state a , tagging state b , release month v , and monthly time step t . The vulnerability state a may be either vulnerable or invulnerable: $a \in \{V, V'\}$. The tagging state b may be either tagged or untagged: $b \in \{G, G'\}$. The lower case subscripts v and t refer to the absolute month of tag release and to the current month, respectively. They range from 1 through 156, representing absolute indices for each month from January 1991 through December 2003. Note that the value 0 is used as a placeholder for the tag release month v when fish are untagged (i.e., when $b = G'$). A dot (\cdot) in the place of any index represents summation over all possible states for that index. Also, let the lower case subscripts i and j refer to the absolute year of tag release and to the current year, respectively. They range from 1 through 13, corresponding to the years 1991 through 2003, and are related to the month indices v and t as follows: $i = \lceil v/12 \rceil$ and $j = \lceil t/12 \rceil$.

Although the simulation model runs on monthly time steps from month $t = 1$ (January 1991) through month $t = 156$ (December 2003), survey CPUE data are only generated in October of each year. Thus, the survey CPUE index in year j (Y_j) is

calculated by multiplying a catchability coefficient q by the total number of fish alive in October of year j ($N_{t,j}$, where t is the absolute index of month 10 of year j). Observation error in the survey CPUE is introduced by applying lognormal residuals $\exp(\eta_j)$ to the expected linear relationship between CPUE and abundance (Schnute and Richards 1995):

$$(3) \quad Y_j = qN_{t,j} \exp(\eta_j); \quad \eta_j \sim N(0, \sqrt{\ln(1 + CV/100)^2}) .$$

The coefficient of variation (CV) for the survey CPUE is set to 30% in equation 3, which corresponds to the value typically assumed in sablefish stock assessments (e.g., Haist et al. 2004; Haist et al. 2005), and represents the effects of both within-year trap-to-trap variation and year-to-year variation in the number of fish caught per trap. The simulated survey index Y_j is calculated in October of each year because this is the month in which the standardized sablefish survey is usually conducted (Wyeth and Kronlund 2003; Haist et al. 2005). For example, from 1992 through 2003, the earliest start date for the sablefish survey was September 24, 1998 and the latest end date was November 11, 2000 (Wyeth and Kronlund 2003).

The second type of simulated data is tag recoveries. These are generated each month by applying a fixed monthly exploitation rate, u_t , to the number of vulnerable tagged fish alive in month t , $N_{t,j}^{VG}$. Values used for u_t were input to the simulation model as driving variables, and were set equal to Haist et al.'s (2005) monthly estimates of exploitation rates for BC sablefish. Since Haist et al. (2005) began their estimates of exploitation rates in 1992, I set monthly u_t values for 1991 equal to the 1992 estimates derived by Haist et al. (2005).

I considered two alternative forms of observation error for the tag recoveries: binomial and overdispersed binomial. I used the binomial distribution because it is the simplest distribution describing the two potential fates of a tagged fish in response to a monthly fishing event: either it is caught, or it escapes capture. Thus, I assumed that each tagged fish has a capture probability equal to the monthly exploitation rate, namely

$$(4) \quad C_{vt}^G \sim \text{Bin}(u_t, N_{vt}^{VG}) ,$$

where C_{vt}^G is the number of tagged fish caught in month t that were released in month v , and N_{vt}^{VG} is the total number of vulnerable tagged fish present in month t that were released in month v .

Overdispersed binomial tag recoveries represent a case where the probability of catching a vulnerable tagged fish in month t (u_t) is a stochastic random variable. Overdispersion arises when random variables (e.g., tag recovery data) exhibit more variability than expected from the underlying distribution (Kitada et al. 1994; Polacheck et al. 2006). An example of a situation in which tag recoveries might be overdispersed rather than strictly binomial could arise as follows. Suppose a vessel fishes the same fishing grounds in two consecutive months. The probability of capturing a vulnerable tagged fish in the second month may be less than in the first month if a substantial fraction of the tagged cohort migrates away from the fishing grounds. Overdispersion could reflect a violation of assumptions 5 and/or 7 of the Brownie model (Table 2).

To implement overdispersion, u_t was modelled as a random variable drawn from a beta distribution, which is the natural distribution of the binomial parameter u_t :

$$(5) \quad u_t^* \sim \text{Beta}(\alpha_t, \beta),$$

where u_t^* denotes a random draw from the beta distribution with shape parameters α and β . The mean (μ) of the beta distribution (Hogg et al. 2005 pg. 155) is

$$(6) \quad \mu = \frac{\alpha}{\alpha + \beta}.$$

Monthly α_t values were calculated using equation 7 that define a beta distribution with mean equal to u_t by solving equation 6 for α and substituting u_t for μ :

$$(7) \quad \alpha_t = \frac{u_t \beta}{1 - u_t}.$$

The average of the monthly exploitation rates (u_t) input to the simulation model over all 156 years was 0.008. I searched for a “reasonable” value of β using trial and error and found that $\beta = 800$ resulted in approximately 90% of the random draws of u_t^* from equation 5 to lie between 0.006 and 0.010, which I deemed reasonable. I substituted u_t^* for u_t in equation 4 to generate the “simulated” number of overdispersed binomial tag recoveries. These steps generated the number of tagged fish that were released in month v and caught in month t (C_{vt}^G) for both the binomial (equation 4) and overdispersed binomial (equations 4 through 7) error distributions.

The number of reported tag recoveries was calculated by multiplying the number of “true” tagged recoveries, C_{vt}^G , by an average reporting rate λ :

$$(8) \quad X_{vt}^G = \lambda C_{vt}^G ,$$

where X_{vt}^G is the reported number of tagged fish that were released in month v and recovered in month t . The reported tag recoveries X_{vt}^G form the tag recovery matrix that is input as observed data to the Brownie model (e.g., Table 1, “Observed Recoveries”). The “true” simulated tag reporting rate, λ , is fixed at 0.8 in all simulated scenarios. Note that I treated λ as deterministic rather than as stochastic, as it really is.

The last type of simulated data is commercial catch. Deterministic fishery catches of untagged fish in month t , $C_t^{G'}$, were generated by multiplying the monthly exploitation rate, u_t , by the number of vulnerable untagged fish present in month t , $N_t^{VG'}$:

$$(9) \quad C_t^{G'} = u_t N_t^{VG'} .$$

The total commercial catch each month, C_t^* , is the sum of the tagged and untagged catches calculated in equations 4 and 9:

$$(10) \quad C_t^* = C_t^G + C_t^{G'} .$$

2.1.3 Scenarios

I simulated data sets consisting of survey CPUE, tag recovery, and catch data for the eight scenarios listed in Table 2. These include a base case where the data satisfied all assumptions of the Brownie model (scenario 1), six scenarios that each violate a particular assumption of the Brownie model (scenarios 2 – 7), and a “realistic” scenario (scenario 8) that violates all assumptions except 4 and 7, which I did not test. As much as possible, I chose simulation parameter values to correspond with their estimates for BC

sablefish data. I inferred reasonable values for simulation parameters for which no sablefish data were available. In all scenarios, the number of tags released was set to the actual number of BC sablefish tag releases in each historical year.

Scenario 2 violates assumption 8, that all catch occurs instantaneously at the beginning of the year, i.e., the fishery is an annual pulse fishery. The BC sablefish fishery violates this assumption because it is open year-round and catches are taken throughout the year, though a large component of the catch is taken during the winter (November – March) (Haist et al. 2004). I approximated such a fishery in scenario 2 by applying Haist et al.'s (2005) estimates of monthly exploitation rates in month t to the vulnerable population in month t using equation 9. In the remainder of the scenarios meeting assumption 8, I summed Haist et al.'s (2005) estimates of monthly exploitation rates to obtain annual exploitation rates for each year j (u_j), and applied these annual exploitation rates to the vulnerable population in the month after tagging to generate simulated data for the year. Thus, in both the monthly and annual cases, I applied the same total exploitation rate over the course of the year. However, the catches obtained from the monthly fishery were less than from the annual fishery because in the monthly case, the exploitation rate was applied to a population that had already been reduced by natural mortality over the course of the year.

Scenario 3 violates assumption 1 of the Brownie model, that the tagged sample is representative of the population (Table 2). This assumption is violated if tags are not distributed evenly across the region and do not mix uniformly with untagged fish (Pollock et al. 1994). I implemented this by simulating subpopulations of sablefish that are either vulnerable (V) or invulnerable (V') to the trap fishery. In this case, only

vulnerable fish can be harvested or tagged, so the tagged sample is not representative of the population because there are no invulnerable fish in the sample. In scenario 3, the proportional rates of exchange between vulnerable and invulnerable states were set to $\theta^{V \rightarrow V'} = 0.1$ and $\theta^{V' \rightarrow V} = 0.9$. With these exchange probabilities, approximately 4.4% of the population is invulnerable when the two vulnerability states are in unfished equilibrium with each other (Appendix B), representing a case of incomplete mixing and thus a violation of assumption 1. In all other scenarios the assumption of a fully mixed population is met by setting $\theta^{V \rightarrow V'} = 0.00001$ and $\theta^{V' \rightarrow V} = 0.99999$, so only a negligible 8.7×10^{-5} % of the total population is invulnerable at equilibrium (Appendix B).

Scenarios 4 and 5 violate Brownie assumptions 2 and 3, that there is no tag loss and no tag-induced mortality, respectively (Table 2). Haist and Hilborn (2000) estimated an instantaneous annual rate of tag loss of 0.0366. The corresponding proportion of fish losing tags each month is 0.003, which I applied each month to simulate tag loss in scenario 4 (Table 2). In scenario 5, I simulated initial tag-induced mortality by applying an initial tag survival-retention rate of 0.856 to newly tagged fish. This value was inferred by Haist et al. (2005) based on estimates of the rates of initial and subsequent tag loss estimated by Haist and Hilborn (2000). In all other scenarios where the assumptions of no tag loss and no tag-induced mortality were met, I used 0 for both the monthly tag loss rate and for the initial tag survival-retention rate.

Scenario 6 violates assumption 6 of the Brownie model, that there is no emigration. British Columbia sablefish may not meet this assumption because analyses of tagging data provide evidence of migration of tagged sablefish from northern BC to Alaska (Beamish and McFarlane 1988; Haist et al. 2001). Thus, the simulation model

implements emigration in scenario 6 by removing a constant proportion (0.03) of fish from the population each month. I chose this value arbitrarily because there is no guidance in the literature for total emigration rates from BC. The corresponding instantaneous annual rate of emigration is: $-12 \log_e(1 - 0.03) = 0.37$. In all other scenarios where the assumption of no emigration is met, the monthly proportion of fish emigrating is set to 0.

Tag recoveries in scenario 7 follow an overdispersed binomial error structure; in all other scenarios they follow a binomial error structure as described in Section 2.1.2.

Finally, scenario 8 describes a “realistic case” in which all assumptions of the Brownie model are violated except 4 and 7 (Table 2). The patterns of simulated catch and survey CPUE in scenario 8 are compared with the actual observed BC sablefish catch and survey CPUE patterns in Figure 1 (Haist et al. 2005). This figure shows that the observation model is a reasonable vehicle for examining the expected performance of the Brownie model because it is capable of generating data that are consistent with the actual temporal pattern of observed data for BC sablefish.

2.2 Stock Assessment Model

Section 2.1 described the model used to simulate the dynamics of the sablefish population and tag release cohorts. In this section, I describe the stock assessment model, which attempts to recover the true parameters from the simulated data. The model takes as inputs the survey CPUE (Y_t), reported number of tag recoveries (X_{vt}^G), and the total catch (C_t^*) generated by the simulator, and provides as outputs maximum likelihood estimates of fishing, natural mortality, and reporting rate parameters.

I used maximum likelihood estimation (e.g., Hilborn and Mangel 1997) to estimate the following 15 parameters of the simulated data: an average tag reporting rate λ , a combined natural mortality–emigration parameter M^* , and 13 annual fishing mortality parameters F_j for $j = 1991, \dots, 2003$. This involved maximizing an objective function composed of independent likelihood functions for both the observed tag recoveries and observed survey CPUE data. The objective function measures the agreement between simulated observations and predictions of the stock assessment model so that the maximum likelihood estimates (MLEs) of the parameters are those parameter values that generate predictions that best fit the observed data (Hilborn and Mangel 1997). Maximum likelihood estimation is one method for estimating parameters that allows the inclusion of different hypotheses about statistical error for the observed data. In this study, a multinomial error distribution was assumed for tag recovery data and a lognormal error distribution was assumed for survey CPUE data. I assumed these error distributions because they have previously been applied to these types of data in the literature (e.g., Hoenig et. al. 1998a; Schnute and Richards 1995).

2.2.1 Brownie model

The Brownie model predicts tag recoveries by calculating the probability P_{ij} of recovering a tagged fish in year j that was released in some previous year i , and then multiplying P_{ij} by the number of tags released in year i . The probability P_{ij} is calculated as:

$$(11) \quad P_{ij} = \begin{cases} \phi \lambda u_j & i = j \\ \phi \lambda u_j \prod_{h=i}^{j-1} S_h & j > i \end{cases} ,$$

where ϕ is the probability of surviving initial tag shedding and tagging-induced mortality, S_h is the annual survival rate in year h , and λ and u_j are the average tag reporting rate and annual exploitation rate as already defined (Hoenig et al. 1998a). The product of the S_h terms in equation 11 accounts for the total survival probability to year $j-1$. The annual survival rate in year j is modelled as a function of a combined natural mortality-emigration rate M^* and fishing mortality F_j :

$$(12) \quad S_j = \exp(-M^* - F_j) .$$

Natural mortality and emigration are combined because these are not individually estimable based on observed recoveries alone. The expected number of tags recovered in year j that were released in year i (R_{ij}) is then

$$(13) \quad E[R_{ij}] = \mathfrak{R}_i P_{ij} ,$$

where \mathfrak{R}_i is the number of tags released in year i .

Predicted recoveries R_{ij} for each cohort of fish tagged in year i (row i of the tag recovery matrix) are assumed to follow a multinomial error structure that is independent of recoveries from all other tag release cohorts (Brooks et al. 1998; Hoenig et al. 1998a). The multinomial distribution is a generalization of the binomial, describing an experiment in which there is more than one possible outcome (Hilborn and Mangel 1997; Brooks et al. 1998). In the context of the Brownie model, the data falling into the

multinomial categories for any given tag release cohort i are the number of tags recovered in year $j = i, j = i + 1, j = i + 2, \dots, j = J$. Thus, there are $J - i + 1$ possible outcomes for each tag cohort released in year i , corresponding to the possible years in which fish from this release cohort could be recaptured. The multinomial negative log-likelihood of the tag recovery data ℓ_T is

$$(14) \quad \ell_T = -\sum_{i=1}^J \left[(\mathfrak{R}_i - r_{iJ}^*) \log_e P_{iJ}^* + \sum_{j=i}^J r_{ij} \log_e P_{ij} \right],$$

where $P_{iJ}^* (= 1 - \sum_j P_{ij})$ is the probability that a fish tagged in year i is not recovered by the last recovery year J and $r_{iJ}^* (= \sum_j r_{ij})$ is the total number of fish recovered from the initial cohort tagged in year i (Hoenig et al. 1998a). The summation in each term represents the overall probability of recovery for fish released in year i for all recovery years j and therefore does not sum to 1. The subscript “ T ” denotes that the likelihood component defined in equation 14 pertains to the tag recovery data only, to distinguish it from subsequent contributions to the likelihood for the overall objective function described below.

Hoenig et al. (1998a) present a general definition of u_j , the exploitation rate in year j , as a function of F_j , M_j , and the seasonal distribution of fishing effort over the year, ε_{jk} :

$$(15) \quad u_j = f(F_j, M_j, \varepsilon_{jk}) = \sum_{k=1}^K a_{jk} b_{jk} c_{jk}.$$

Here, ε_{jk} is the fraction of the total fishing effort that is applied in each period k of year j , for $k = 1, 2, \dots, K$, where year j is divided into K periods. Thus ε_{jk} denotes the distribution of fishing effort over the year (Hoenig et. al. 1998a). The fraction of the population surviving to the beginning of period k in year j , a_{jk} , is

$$(16) \quad a_{jk} = \exp(-M_j(k-1)\Delta t - F_j \sum_{h=0}^{k-1} \varepsilon_{jh}) \quad k > 1.$$

When there is only one fishing period ($k = 1$), $a_{j1} = 1$ since all fish survive to the beginning of period k . The fraction of fish dying in period k of year j , b_{jk} , is

$$(17) \quad b_{jk} = 1 - \exp(-M_j\Delta t - F_j\varepsilon_{jk}),$$

and the proportion of total catch taken in period k of year j , c_{jk} , is

$$(18) \quad c_{jk} = \frac{F_j\varepsilon_{jk}}{F_j\varepsilon_{jk} + M_j\Delta t}.$$

If fishing effort is constant over the year, equation 15 reduces to the standard Baranov catch equation, and when all fishing takes place instantaneously at the beginning of the year, equation 15 reduces to equation 2 (Hoenig et. al 1998a). This study assumes a pulse fishery so it uses equation 2, but if data on the seasonal timing of the fishery were available, then the Baranov catch equation or equation 15 could be used as an alternative formulation.

The annual parameter M^* differs from standard definitions of M because it represents the additive effects of instantaneous emigration and natural mortality. These parameters are confounded in the estimation procedure because the Brownie model cannot resolve the two sources of loss given only the data in the tag recovery matrix. Furthermore, I assumed that the rates of natural mortality and emigration were constant over time, so I estimated a single parameter M^* rather than a time-dependent parameter M_j^* . The “true” simulated value of M^* in all eight scenarios is

$$(19) \quad M^* = -12[\log_e(S) + \log_e(1 - \kappa)] ,$$

where S is the proportion of fish surviving natural mortality each month, κ is the proportion of fish emigrating each month, and the multiplier 12 converts the monthly S and κ values to an annual M^* . The value of S was set to 0.993 in all eight scenarios while $\kappa = 0.03$ in scenarios 6 and 8 and $\kappa = 0$ in all other scenarios.

Assuming that there was no initial tag shedding or tagging-induced mortality, I considered $\phi = 1.0$ to be a fixed parameter in the Brownie model. I tested the effect of this assumption in scenario 5, where I simulated a scenario that included initial tag shedding and tagging-induced mortality.

I extended the Brownie model to derive estimates of abundance at the time of tagging by applying the familiar relationship between catch and exploitation rate given by equation 1. The estimated exploitation rate in year j (\hat{u}_j) was derived from equation 2 using estimates of F_j obtained from the Brownie model. By comparing abundance estimates with their known “true” values from the simulations, I was able to quantify the

bias and precision involved in using Brownie estimates of fishing mortality parameters (F_j) to estimate abundance.

2.2.2 Index of relative abundance model

One aim of my research was to determine whether combining an index of abundance, such as the survey CPUE, with the tag recovery data would reduce bias and improve precision of parameter estimates. This was achieved by developing a model with likelihood components for both tag recovery and survey CPUE data using a method analogous to that of Polacheck et al. (2006), who integrated catch-at-age data with the Brownie model.

I assumed that a lognormal distribution characterized the random variability around each simulated survey CPUE observation because:

(1) this distribution takes on only positive values (Limpert et al. 2001), constraining the observed survey CPUE values Y_j to be positive; and

(2) this distribution is asymmetrical and skewed (Limpert et al. 2001) so there is a high frequency of low numbers of fish caught per trap, which diminishes quickly in the long tail of the distribution, corresponding to low frequencies of bigger numbers of fish caught per trap. Thus, the “observed” survey CPUE values Y_j ($1992 \leq j \leq 2003$) were:

$$(20) \quad Y_j = \hat{Y}_j \exp(\eta_j), \quad \eta_j \sim N(0, \sigma) .$$

The predicted survey CPUE values \hat{Y}_j are equal to a catchability coefficient q multiplied by the predicted number of fish in October of year j , \hat{N}_j :

$$(21) \quad \hat{Y}_j = q\hat{N}_j .$$

Solving equation 20 for η_j and substituting equation 21 for \hat{Y}_j , the lognormal residuals can be expressed as:

$$(22) \quad \eta_j = \log_e \left(Y_j / \hat{N}_j \right) - \log_e q .$$

The corresponding negative log-likelihood function (ℓ_s) for the lognormally-distributed residuals defined in equation 22 for J years of data is (Schnute and Richards 1995; Hilborn and Mangel 1997):

$$(23) \quad \ell_s = \frac{J}{2} \log_e (2\pi\sigma^2) + \frac{1}{2\sigma^2} \sum_j \eta_j^2 .$$

One complexity in minimizing ℓ_s is the choice of values for q and σ^2 . These are considered nuisance parameters because they are not of direct interest, but are necessary for the analysis. Conditional maximum likelihood estimates of $\log_e q$ and σ^2 can be obtained analytically by minimizing the negative log-likelihood (equation 23) with respect to these parameters (Walters and Ludwig 1994). Substituting the conditional MLE for $\log q$ into equation 22 and for σ^2 into equation 23 and ignoring additive constants (which do not affect the parameter values that give the minimum), the overall survey negative log-likelihood is

$$(24) \quad \ell_s = \frac{J}{2} \log_e \left(\sum_i \eta_i^2 \right).$$

2.2.3 Overall objective function

In section 2.2.1, I estimated the suite of 15 parameters using the Brownie model alone, which used only the tag recovery data. In that case, the overall objective function for parameter estimation is given by equation 14.

In section 2.2.2, I estimated the same suite of 15 parameters using both the tag recovery and the survey CPUE data. The standard method of combining likelihoods for two or more independent sources of data is to multiply them or to add their negative log-likelihoods (e.g., Hilborn and Mangel 1997, Schnute and Richards 1995, Polacheck et al. 2006). Thus, the overall objective function (ℓ) that I minimized when combining the tag recovery and survey CPUE data was:

$$(25) \quad \ell = \ell_T + \ell_s .$$

I implemented the parameter estimation model using the AD-Model Builder (ADMB) software package (Otter Research 1999). This package calculates exact analytical derivatives of the objective function using automatic differentiation and provides very efficient function minimization (Otter Research 1999). The ADMB package uses a pre-compiled C++ library called AUTODIF, which provides very efficient and stable function minimization because (1) it has pre-compiled derivatives for the commonly used array and matrix operations, and (2) it uses automatic differentiation, rather than the finite difference approximation, to calculate derivatives of other functions (Maunder 2004).

2.3 Simulation Framework

For each scenario listed in Table 2, I conducted a Monte Carlo experiment with 500 simulation-estimation trials. Each experiment involved the following four steps:

1. Simulate 500 sets of tag recovery, survey CPUE, and catch data with known parameters appropriate to the scenario;
2. Fit the parameter estimation model to each of the 500 simulated data sets to obtain estimates of $F_{1991} - F_{2003}$, M^* , and λ (15 parameters in total) using (a) the tag-recapture data and the Brownie model (equation 14), and (b) the tag-recapture plus survey CPUE data and the integrated model (equation 25);
3. Apply equations 1 and 2 to calculate 13 abundance estimates from 1991 through 2003 using the values of F_{1991} through F_{2003} estimated in step 2;
4. Compute the relative percentage bias for each of the 15 parameter estimates and 13 abundance estimates:

$$(26) \quad \%bias = \left(\frac{estimate - true}{true} \right) \times 100\% .$$

2.4 Performance Measures

I used median percentage bias and inter-quartile range of percentage bias to summarize the bias and precision, respectively, of parameter estimates obtained from the 500 Monte Carlo trials. The inter-quartile range is bounded by the 25th and 75th percentiles of the distribution of parameter estimates. I used rank statistics such as median and inter-quartile range as measures of bias and precision to reduce sensitivity of the results to outliers.

For each estimated quantity Q , the improvement in the median value of percentage bias from including the survey CPUE data (b^*) was computed using

$$(27) \quad b^* = |b^T| - |b^{TS}|,$$

where b^T is the median percentage bias of Q estimated using the tag recovery data only, and b^{TS} is the median percentage bias of Q estimated using both the tag recovery data and the survey CPUE data. A positive value for b^* indicates that including the survey CPUE data decreased the median value of the parameter estimate, resulting in a reduction in bias. Similarly, I computed the improvement in precision of estimates of each quantity Q (p^*) obtained by including the survey CPUE data as:

$$(28) \quad p^* = p^T - p^{TS}.$$

In equation 28, p^T is the inter-quartile range of parameter Q estimated using the tag recovery data only, and p^{TS} is the inter-quartile range of parameter Q estimated using both the tag recovery and survey CPUE data.

3 RESULTS

3.1 Base Case and Realistic Case

When all assumptions of the Brownie model were met (scenario 1; Table 2), all parameters were estimated extremely well (Figure 2a) with median percentage biases from 500 Monte Carlo trials within 1% of true values. The median estimated abundance also matched very closely with the simulated numbers of fish (Figure 2b); biases of the median abundance ranged from -1.3% in 2003 to -0.01% in 1995. The precision of abundance estimates as measured by the inter-quartile range improved as the number of years of data increased (Figure 2b).

In the “realistic” scenario in which all assumptions were violated (scenario 8; Table 2), medians of the estimates of annual F parameters were biased low by 1.5% to 7.1% in all years except 2002, when the median estimate of F_{2002} was biased high by 6.2% (Figure 3a). The average tag reporting rate parameter λ was underestimated by 37%, and the combined natural mortality-emigration rate parameter M^* was overestimated by 4.6%. However, the inter-quartile range for all parameters overlapped the 0% bias reference line (Figure 3a). Abundances were estimated surprisingly well for the realistic case given that no assumptions (except 4 and 7) were met: the median of abundance estimates ranged from an underestimate of 25% in 1994 to an overestimate of 48% in 1997 (Figure 3b). Additionally, the “true” abundance was within the inter-quartile range of abundance estimates every year except 1997 (Figure 3b). The median of the

abundance estimates was biased high in 4 years out of 13, and was biased low in the remaining 9 years (Figure 3b).

3.2 Parameter Estimates

The largest bias in parameter estimates occurred when the following two assumptions were violated: (1) all catch is taken instantaneously at the beginning of the year (assumption 8, violated in scenario 2) and (2) the fish are completely mixed and the tagged sample is representative of the population (assumption 1, violated in scenario 3). In scenarios 2 and 3, estimates of F_{1999} through F_{2001} were mostly biased low by about 2-6% and 10%, respectively (Figure 4a).

Most parameters were estimated to within 2.2% of their true values for scenarios 4 through 7 (Figure 4a). Tag loss (scenario 4) resulted in approximately the same bias as the base case for most parameters except M^* , which was overestimated by 42% and is off-scale of Figure 4a. Tagging-induced mortality (scenario 5) resulted in consistent overestimates of annual F parameters by about 1%, while λ and M^* were underestimated by 15% (again, off-scale of the figure) and 1%, respectively. Emigration (scenario 6) also resulted in patterns similar to the base case, except the estimate of λ , which was biased low by about 4%. Overdispersed binomial tag recoveries (scenario 7) yielded a pattern opposite to that observed for tag-induced mortality. In this case, annual F parameters were all underestimated by about 1%, while λ and M^* were overestimated.

Precision of parameter estimates for scenarios 2-7 was similar to that of the base case for all scenarios except scenario 6 (emigration) and scenario 7 (overdispersed binomial tag recoveries) (Figure 4b). In these latter two scenarios, the inter-quartile

range statistics were on average 1.5 and 2 times greater than the base case, respectively (Figure 4b). The precision of annual fishing mortality parameters was greatest for years in the middle of the time series; i.e., for $F_{1996} - F_{1998}$, and grew worse towards the earliest and latest years in the time series (Figure 4b). Note that M^* was estimated with unusually high precision (inter-quartile range = 8%) for the emigration scenario (Figure 4b); this parameter was also estimated with very little bias (-0.1%) under that scenario (Figure 4a).

3.3 Abundance Estimates

Annual abundance from 1991 to 2003 was estimated to within about 6% of the “true” simulated abundance for all scenarios (Figure 5a). The bias of abundance estimates was most affected in scenarios 2 (monthly exploitation) and 6 (emigration) (Figure 5a). In most years in scenario 2, abundances alternated between being overestimated and being underestimated from year to year after 1994 (Figure 5a). In general, abundance was more often underestimated than overestimated (9 out of 13 years) (Figure 5a).

The precision of abundance estimates from 1991 to 2003 (Figure 5b) followed closely the pattern of precision of $F_{1991} - F_{2003}$ estimates (Figure 4b) because abundance estimates are derived directly from estimates of fishing mortality using equations 1 and 2.

3.4 Effect of Adding Survey CPUE Data

Combining the survey CPUE with the tagging data did not generally affect the bias or precision of parameters in either direction by more than 1% and 2% respectively, across scenarios 2 through 7 (Figure 6). Similar results were obtained for abundance

estimates; adding the survey CPUE data showed little or no consistent improvement in bias or precision when single Brownie assumptions were violated at a time (Figure 7a, Figure 7b). However, in the “realistic” case (scenario 8), including the survey CPUE data increased the bias (Figure 6a) but reduced the precision (Figure 6b) of estimated parameters.

4 DISCUSSION

4.1 Major Conclusions

4.1.1 Objective 1: Violations of individual Brownie assumptions

The objective of this study was to assess the feasibility of using the Brownie model as a stock assessment tool for BC sablefish. Specifically, my first aim was to quantify the effects of violations of the individual Brownie model assumptions on parameter estimates by sequentially violating each of the assumptions in scenarios 2 through 7 (Table 1). I found that the biases observed in parameter estimates for the “realistic” scenario (scenario 8) were dominated by violations of Brownie assumptions 1 and 8: that the tagged sample is representative of the population (i.e., tagged and untagged fish are completely mixed), and that the catch is taken instantaneously at the beginning of the year. This is because violations of assumptions 1 and 8 (in scenarios 3 and 2) resulted in the greatest underestimates of fishing mortality (Figure 4a). These underestimates could have arisen because fewer tagged fish are available to the fishery when these two assumptions are violated as compared to when they are met. For example, when tagged and untagged fish are incompletely mixed (violation of assumption 1), some tagged fish are invulnerable to the fishery. Similarly, when not all the catch is taken at the beginning of the year (violation of assumption 8), fewer tagged fish are available to the fishery each month because of natural losses of tagged fish over the course of the year. In either case, fewer tagged fish available to the fishery means

that fewer tag recoveries are observed in the tag recovery matrix, resulting in underestimates of the actual fishing mortality.

However, additional scenarios are needed to confirm that assumptions 1 and 8 also have the greatest effect on bias of parameter estimates when all assumptions are violated simultaneously. It appears that interactions can result in violations of certain assumptions amplifying or compensating for others when producing the net overall bias in parameter estimates. This is because the biases in estimates for scenarios that violate individual assumptions do not sum to the biases observed in the realistic scenario 8, as would be expected if the biases were independent and additive (compare Figures 3a and 4a). Additional scenarios could be used to determine which combinations of assumptions have the most effect on biases in the realistic scenario. For example, if biases from a scenario violating all assumptions except assumption 1 were compared with the biases in scenario 8, the effects of incomplete mixing could be quantified under the presence of potential interactions. If this procedure were repeated for each Brownie assumption, the rank order of the relative importance of the assumptions could be more fully diagnosed.

4.1.2 Objective 2: Incorporation of survey CPUE data

A second aim of my research was to quantify the potential reduction in bias and increase in precision of parameter estimates when survey CPUE data are combined with tag recovery data in the Brownie model. I found that inclusion of the survey CPUE did not substantially change the bias or precision of parameter or abundance estimates in scenarios 2 – 7 (Figure 6; Figure 7). This is counter-intuitive because even in trials when the survey CPUE data showed a strong trend and might indeed have been a better index of the true population dynamics than the tagging data (as was the case in several of the

simulated Monte Carlo trials), it had little effect on the overall bias or precision of parameter estimates.

To diagnose this problem, I drew profiles of the negative log likelihood functions for both the tagging and survey CPUE data (Figure 8). Figure 8 was generated using the data set from the first Monte Carlo trial of the base case (scenario 1). Note that the values of the tagging and survey CPUE likelihood functions in this figure are on quite different scales (between 81 000 and 87 000 for the tagging likelihood; between -2.5 and -1.5 for the survey CPUE likelihood). The magnitude of the objective function value for each data source is determined by the number of individual data points contributing to it, as well as the constraints of the particular likelihood distributions assumed (e.g., multinomial distribution for the tag recovery data). The overall likelihood is the product of the individual likelihoods over all the data points. Since there are much more tagging data than survey data, the value of the tagging likelihood is far greater than the value of the survey likelihood. This implies that the survey CPUE data implicitly are weighted less than the tagging data in the overall likelihood function (equation 25); thus, inclusion of the survey data had little effect on the overall bias or precision of parameter estimates.

Additionally, Figure 8 shows that the minimum value of the survey CPUE likelihood occurs when $M^* = 0.26$. However, the “true” value of M^* in scenario 1 was 0.084. Thus, the survey model attributes all the residual variation in the data to M^* rather than to the F_j parameters, driving the MLE of M^* away from the “true” simulation value of 0.084 to 0.26. Thus, it appears that the survey CPUE data is not influencing the estimates of F_j parameters at all, and that estimates of fishing mortality parameters are informed by the tagging data alone. This is because estimates of fishing mortality

derived from tagging are used to estimate abundance using equation 1, and these estimates are substituted into the survey model for \hat{N}_j in equation 21. Recall that in section 2.2.2 when the survey likelihood function was developed, there was no explicit population model for the survey CPUE data; the component of the likelihood function due to survey CPUE data simply fit log-normally distributed errors to the “observed” data points (equations 20 – 24). Without an explicit population dynamics model, the survey CPUE likelihood is attempting to estimate 13 F parameters from only 12 years of survey data, resulting in an over-parameterized model.

One possible remedy for this situation might be to specify a population dynamics model to explain the variation in the survey CPUE data independently of the F values derived from tagging. Such a model would generate the predicted number of fish in October of year j , \hat{N}_j . An example of a population dynamics model that could be used to derive \hat{N}_j independently of the tagging data is given in equation 29:

$$(29) \quad \hat{N}_{j+1} = e^{-M^*} (\hat{N}_j - C_j) + \bar{R},$$

where \bar{R} is the average annual recruitment over the time series. In this example, the additional parameters to be estimated in this case are N_0 and \bar{R} . The values of \hat{N}_j derived from this population dynamics model would be substituted into equation 21. The remaining calculations for the survey CPUE likelihood would remain the same. In this formulation, M^* would be the only parameter shared by both the tagging and survey CPUE likelihoods. Note that equation 29 is simply an example of a possible population dynamics model that could be used to derive estimates of \hat{N}_j to be used in equation 21,

but that equation 29 in particular might not adequately describe the residuals in the survey CPUE data because it has only two free parameters (N_0 and \bar{R}). Alternative structural models for deriving \hat{N}_j independently of the tagging data should also be developed and tested.

4.2 Implications of Selected Brownie Assumptions

4.2.1 Assumption 1 - Incomplete mixing

Results obtained for scenario 3 quantitatively verify the assertions of other researchers that complete mixing is a critical assumption for unbiased application of the Brownie model (Hoenig et al. 1998*b*; Latour et al. 2001*b*; Pollock et al. 2001). In scenario 3, where about 4.4% of the total population is invulnerable at equilibrium ($\theta^{V \rightarrow V'} = 0.1$ and $\theta^{V' \rightarrow V} = 0.9$, Appendix B), annual fishing mortality parameters (F_j s) were underestimated by about 10% (Figure 4a). Presumably, these biases will grow even larger as $\theta^{V \rightarrow V'}$ increases and $\theta^{V' \rightarrow V}$ decreases because fewer fish will be available to the trap fishery, resulting in the Brownie model being confronted with fewer observed tag recoveries. Since the Brownie parameter estimates are only applicable to the portion of the population that the observed tag recoveries were caught from, analysts should be aware that when there is incomplete mixing, the Brownie parameter estimates only pertain to the vulnerable substock.

4.2.2 Assumption 8 - Assuming that the timing of the fishery is known correctly and all catch is taken instantaneously at the beginning of the year

I found that annual fishing mortality (F) parameters were generally underestimated when Brownie assumption 8 was violated (Figure 4a). Scenario 2

violates this assumption by taking catches monthly rather than instantaneously at the beginning of the year. The total exploitation rate over the course of the year was held constant whether catches were taken monthly or annually. Fishing mortality was underestimated because in scenario 2 I applied a monthly exploitation rate to the number of fish alive at the start of each month. However, this number is depleted over the course of the year due to fishing and natural mortality in the previous months. Thus, the total number of observed tag recoveries in the tag recovery matrix is less in scenario 2 when compared to the situation where all fishing happens at the beginning of the year, given equal exploitation rates over the course of the entire year. The Brownie model interprets fewer observed tag recoveries in the tag recovery matrix as less fishing pressure on the stock than was actually applied. Hence, the Brownie model underestimates annual fishing mortality when fishing is applied monthly rather than annually.

My result on this point contrasts with Hoenig et al.'s (1998a), who found that estimates of fishing mortality and natural mortality were relatively insensitive to the assumed timing of the fishery for a data set of tag recoveries of lake trout in Lake Cayuga, New York. Subsequent literature on the Brownie model cites their study when claiming that the assumption about timing of the fishery is relatively unimportant to the estimates obtained from the Brownie model (e.g., Hoenig et al. 2005). However, in the BC sablefish case, incorrectly assuming that all fishing takes place at the beginning of the year introduced bias in parameter and abundance estimates. Iterating over 500 potential sets of simulated tag recoveries, I estimated that the bias in parameter estimates introduced by failing to meet the pulse fishery assumption is 2 – 6%, whereas Hoenig et al. (1998a) could only conclude that parameter estimates for their one data set were

insensitive to the assumptions about timing of the fishery. They were not able to quantify bias because their study used field data for which the true parameter values were unknown. Biases of 2 – 6% may or may not be important for fishery management, and closed-loop simulation studies including the full decision making, biological, and scientific assessment components of the fishery system (e.g., de la Mare 1998) can be used to investigate the effects of these estimation biases on the attainment of management objectives for the fishery. In any case, my results show that assumptions about the timing of the fishery might introduce biases in parameter estimates that analysts should be aware of. Thus, the effects of this assumption should not be dismissed, but rather, evaluated on a case-by-case basis.

I could not estimate abundance using equations 1 and 2 when the data did not meet assumption 8 because equation 2 assumes that all catch is taken instantaneously at the beginning of the year. Because scenario 2 violated this assumption, it was not valid to apply equation 2 in this case. As a result, abundance estimates for scenario 2 appear to alternate somewhat erratically from one year to the next (Figure 5a). Perhaps the easiest way of dealing with the implications of violating assumption 8 might be to provide the Brownie model with additional data on the timing of the fishery, and apply Hoenig et al.'s (1998a) general definition of u_j as a function of F_j , M_j , and the seasonal distribution of fishing effort over the year.

4.2.3 Assumptions 2 and 3 - Tag loss and tagging-induced mortality

Overall, violations of the tag loss and tagging-induced mortality assumptions were relatively unimportant in terms of bias of parameter and abundance estimates, since

the Brownie model always estimated parameters to within about 1% of their true values when these assumptions were violated (scenarios 4 and 5). However, M^* was substantially overestimated (by 42%) in scenario 4, which violated the assumption of no tag loss. This bias occurred because the Brownie model has no way to distinguish among causes of fewer observed tag recoveries (tag loss, natural mortality, or emigration). All three of these factors are manifested as fewer tags than would otherwise be expected in the tag recovery matrix. Accounting for tag loss and tag-induced mortality in the Brownie model is relatively simple, since Hoenig et al.'s (1998a) formulation of the Brownie model allows the tag retention-survival rate ϕ to be set lower than 1.0. Independent estimates of tag loss and tagging-induced mortality are available for BC sablefish (Haist et al. 2005), and can be substituted for ϕ in the Brownie model as appropriate. Doing so would most likely account for most of the bias observed in scenarios 4 and 5. Alternatively, ϕ could be estimated as long as it is not confounded with the other estimated parameters.

4.3 Estimation of Tag Reporting Rates

Estimates of tag reporting rates are necessary when tagging data are used to estimate abundance (Pine et al. 2003). This is because if reporting rates are less than 100%, then fewer tags will appear in the tag recovery matrix than expected, resulting in underestimates of fishing mortality. Since fishing mortality and abundance are inversely proportional (equation 1), abundance will be overestimated when fishing mortality is underestimated. This bias can be accounted for if estimates of tag reporting rates are available. However, reporting rates for externally applied tags are difficult to estimate precisely (Pollock et al. 2001). Methods involving high-reward tags (Pollock et al. 2001;

Taylor et. al 2006), fishery observers (Pollock et al. 2002), planted tags (Hearn et al. 2003), and catch from multi-component fisheries (Taylor et. al 2006) have all been used for obtaining independent estimates of tag reporting rates (Pine et al. 2003; Hoenig et al. 2005).

The bias caused by imperfect tag reporting can also be accounted for if fish are tagged using recent technological innovations that allow tag detection rates to be close to 100%. For example, passive integrated transponder (PIT) tags (e.g., Pengilly and Watson 1994; Gibbons and Andrews 2004), coded-wire tags (e.g., Jefferts et al. 1963), and genetic tagging methods (Palsboll 1999) greatly reduce the problems associated with estimation of tag reporting rates because tags are detected electronically or via genetic analysis. Thus, tag detection does not depend on accurate reports of tag recaptures by fish harvesters.

In this study, I was able to directly estimate an average tag reporting rate parameter (λ) from the observed tag recovery data. This involved estimating λ simultaneously with the other estimated parameters using the Brownie model. Hoenig et al. (1998a) concluded that information on reporting rates in the tag recovery data is weak, because they could not find stable estimates of tag reporting rates from the recovery data when they fit the model to fewer years of recoveries than in their full data set. However, my simulation studies yielded relatively precise estimates of λ . In fact, I found that the precision of estimates of λ (as measured by the inter-quartile range of λ estimates) was better than the precision of estimates of F_j and M^* in some scenarios (Figure 4b). It should be noted that the “true” tag reporting rate in my simulations was 0.8, while Hoenig et al. (1998a) assumed a true reporting rate of 0.18. Many more tags were

observed with a true reporting rate of 0.8, thereby reducing the variance of the observed tag recovery data. This could explain why Hoenig et al. (1998a) and I found different results regarding the precision of reporting rate estimates: my routine was able to converge because the simulated tag recovery data showed less variance than did Hoenig et al.'s (1998a) lake trout data. Indeed, their estimates of reporting rate stabilized when they added simulated returns of high-reward tags, thus increasing their average tag reporting rate and number of observed recoveries (Hoenig et al. 1998a).

In a subsequent analysis, I attempted to break λ up into a set of annual reporting rate parameters λ_i , and estimate these simultaneously with annual F_i and M^* parameters. This resulted in over-parameterization of the Brownie model (more parameters than necessary to fit the model to the data), resulting in the model chasing noise rather than describing the general trends in the data. Consequently, the estimation routine did not converge.

4.4 Recommendations to Scientists and Managers

For the Brownie model to be successfully applied as a stock assessment tool for BC sablefish, the assumptions that have the greatest effects on estimates of abundance should be addressed. Based on my results, research efforts should be directed towards taking both the true timing of the fishery and emigration into account, since these two assumptions resulted in the greatest underestimates of abundance (Figure 5a). It is relatively straightforward to relax the pulse fishery assumption and use data on the true timing of the fishery because intensive spatio-temporal catch and effort sampling has been conducted since the beginning of the sablefish tagging program. These catch and

effort data can be used to implement the general definition for u_j (equation 15) provided by Hoenig et al. (1998a) that makes no additional assumptions about the timing of the fishery. However, potential gains and tradeoffs in bias and precision of abundance estimates from using this definition of u_j should still be quantified using simulation studies. Accounting for sablefish emigration from BC may be more challenging since there are uncertainties concerning sablefish movement patterns (e.g., Beamish and McFarlane 1988; Heifetz and Fujioka 1991). However, emigration rates from BC could be estimated by examining recoveries of BC-tagged fish in Gulf of Alaska and continental U.S. waters.

Additionally, the incomplete mixing problem (assumption 1) must be addressed, because incomplete mixing has the greatest effect on parameter estimates (Figure 4a). Aggregation and incomplete mixing phenomena appear to affect the population dynamics of marine fishes such as tuna, anchoveta, herring, and mackerel (Clark and Mangel 1979). If, like these species, sablefish exhibit vulnerability exchange dynamics as I have generally defined above, this could make the Brownie model inappropriate for stock assessment of BC sablefish unless this assumption is accounted for. Therefore, as a start, I recommend using Hoenig et al.'s (1998b) modifications to the Brownie model that explicitly incorporate non-mixing of newly tagged fish. However, since their model refers specifically to newly tagged fish, further modifications will be necessary to take into account exchanges of tagged and untagged fish between vulnerable and invulnerable states in each time step.

4.5 Contributions of this Research

This research contributes to two major topics: theoretical research in combining data sources, and science and management of BC sablefish.

4.5.1 Theoretical research in combining data sources

This paper provides insights into some complexities of combining two independent data sources, namely the tag recovery and survey CPUE data, in a fisheries estimation problem. Although past studies have successfully combined independent indices (e.g., Polacheck et al. 2006), my research shows that combining data sources in an objective function is not trivial, especially when the values of the objective function for the various sources of data are on entirely different scales. This is because different scales for the values of the objective function from the two data sources imply that the data sources are implicitly being given different weights in the overall objective function. I recommend further investigations of statistical methods and alternative model structures for combining the two data sources, as described below in section 4.6.

4.5.2 Science and management of BC sablefish

The Monte Carlo methods illustrated in this study are valuable given current research in the development of management procedures for BC sablefish. In particular, by evaluating the Brownie model in a Monte Carlo framework, this study is a building block for an in-depth analysis of the BC sablefish fishery in the context of a holistic analysis of management strategies (de la Mare 1998). The simulation model I have developed can be used as an operating model for evaluating assessment models and harvest rules over a range of scenarios against objectives for the BC sablefish fishery, and

thus represents a useful tool for analysing this system. In addition, this study represents the first formal simulation-based analysis of the estimation properties of a potential stock assessment method for BC sablefish.

4.6 Future Directions

The results of this paper, as well as the contributions identified in section 4.5, suggest two major issues for future research stemming from this project. These issues relate to (i) resolving how to best include survey or fishery CPUE data with tagging data in the objective function, and (ii) evaluating the consequences of violating the Brownie assumptions in a management procedure simulation.

4.6.1 Resolve issues of combining survey CPUE with tagging data

I recommend focusing future work on determining how to best combine survey CPUE and tag recovery data in the objective function. In particular, it should be determined what conditions are necessary for inclusion of the survey data to improve the bias and precision of parameter estimates obtained from the Brownie model. It appears that an investigation of alternative structural models for fitting the survey CPUE data is appropriate. As a start, I suggest implementing a population dynamics model for the survey CPUE data, such as the one specified in equation 29. This will allow the model for lognormal survey errors (equations 20 – 24) to be fit to the survey CPUE data, without using estimates of annual F parameters from the tagging model to derive \hat{N}_j values used in equation 21.

It is reasonable to expect that including the survey CPUE data will reduce bias and increase precision of parameter estimates, at least in those Monte Carlo trials

showing a strong trend with low residual variation in survey CPUE data. If this does not occur, then the model is not specified correctly, and/or survey CPUE data are not weighted appropriately with tagging data in the overall likelihood. One way to ensure that the tag recovery data are not implicitly given undue weight due to the number of tag recovery data points is to modify the Brownie multinomial likelihood for the tagging data (equation 14). The multinomial likelihood is quite restrictive since: (1) it only accounts for observation error in the tag recoveries and thus ignores possible overdispersion in the tag recovery data; (2) there might be correlations among tag release cohorts; and (3) the multinomial requires that the sum of the probabilities for recovering tags released in year i sums to 1.0 over all recovery years j . The multinomial likelihood for tagging data could be relaxed in the following ways:

- modify the tagging likelihood to account for overdispersion in the observed data;
- use a negative binomial likelihood for the tag recoveries rather than the multinomial likelihood. The negative binomial distribution includes a variance parameter related to process error, which would also be estimated.

In addition, it would be useful to evaluate the effects on parameter estimates of situations in which the survey CPUE and tagging data indicate contradictory trends in the underlying population dynamics. Such data may arise in situations such as the following:

- A situation in which the population is declining while tags are deliberately being under-reported by fishermen at a rate proportional to abundance. In this case, the survey CPUE would show a declining pattern (assuming it correctly reflected the population), and there may be grounds for lowering the TAC. However, if fishermen detect the declining abundance (perhaps because they observe declining commercial fishery

CPUE), and deliberately choose to under-report tag recoveries in proportion to this decline, then the tagging data may incorrectly show no trend or increasing abundance over time because fishing mortality would be underestimated. Note that this is different from a situation in which reporting rates decrease at higher abundance due to large catches creating difficulties with processing all the tags on-deck before the fish are headed because of the sheer volume of catch to be processed. To simulate under-reporting, the tag reporting rate parameter in the simulator should be set to a value less than 1.0. If reliable estimates of the tag reporting rate are available, then under-reporting can be accounted for in the estimation phase.

- Another example would be a situation in which the population is declining, fish are incompletely mixed, and effort is shifting away from tag release sites. The fixed tag release localities for BC sablefish are at regions of historically high catches. However, under a scenario of decreasing abundance, local populations may decline, forcing effort to shift away from these tag release sites. If effort shifted to areas with low densities of tagged fish, then the number of tag recoveries would decrease, fishing mortality would be underestimated, and abundance would be overestimated. Thus, under this scenario the tagging data would show an increasing abundance trend, while the survey CPUE data would show a declining trend provided that the survey correctly indexed abundance. A spatially-explicit model for fishing effort could be used to generate simulated data for this scenario.

4.6.2 Evaluate costs of violating Brownie assumptions in a management context

I also recommend that the costs of violating assumptions of the Brownie model be evaluated in the context of the full fishery management system for BC sablefish. This

involves running closed-loop simulations of all components of the fishery, including a decision making process, actions taken by the fishery, population dynamics, data collection (including observation error), stock assessment, and inputs to the decision making process (de la Mare 1998). Fishery objectives are an essential component of such a framework, because costs of violating assumptions of the Brownie model should be measured relative to the objectives specified for the fishery. For example, if assumptions of the Brownie model are not met, then there may be less chance of meeting fishery objectives, resulting in costs of over-fishing, lost fishing opportunities, or other monetary costs. Fishery objectives should be developed through a collaborative process involving members of the Canadian Sablefish Association, management, and other stakeholders (Cox and Martell 2005). Performance measures need to be calculated over the course of the simulation and judged against fishery objectives to evaluate the extent to which objectives are met under the various scenarios.

Once such a modeling framework is developed, it can be used as a tool to investigate questions raised in this paper such as:

- What is an acceptable level of bias in parameter estimates for meeting management objectives for the fishery? Are biases of 2-6%, as observed in scenarios 2 and 6 (Figure 4a; Figure 5a), important in terms of our ability to meet management objectives for the fishery? If these biases do thwart the achievement of management objectives, then research efforts directed towards reducing them can be justified.
- Violations of which of the Brownie assumptions have the greatest effects on the achievement of management objectives when more than one assumption is violated simultaneously? Research and management efforts should be directed towards taking

these assumptions into account. These assumptions can be identified by quantifying the rank order of importance of assumptions using additional scenarios that simultaneously violate various combinations of assumptions as described in section 4.1.

- What is the effect of uncertainty in the values of simulation parameters driving the scenarios on the ability to meet management objectives? For example, fishing mortality parameters were estimated to within 2% in the emigration scenario (scenario 6 – Figure 4a). I assumed a constant emigration rate (3% per month) in this scenario. If a range of emigration rates were tested, at what threshold rate would management objectives be seriously compromised? Is that threshold rate plausible for sablefish? Investigation of these questions will indicate whether the observed biases were due to violations of particular assumptions or to the specific parameter values used in Table 2, and whether these simulation parameter values are important from a management standpoint.
- What is the value of information gained by incorporating different indices, and how does this offset the costs of data collection for each of these indices? The value of information gained by including the survey CPUE index can be quantified by measuring the increased extent to which management objectives are met when the survey CPUE data are included, as compared to when only the Brownie tag recovery data are used. If management objectives have been specified in such a way that the value of information can be quantified in monetary terms, then it can be compared with the costs of collecting the survey CPUE data.

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APPENDIX A – DETAILS OF THE SIMULATION MODEL

The purpose of this appendix is to specify in detail the dynamics of the simulation model. The notation used is as follows. Vulnerability states are “vulnerable” (V) and “invulnerable” (V'). Tagging states are “tagged” (G) and “untagged” (G'). Indices relating to vulnerability and tag state are superscripted, while time-related indices (month of tag release ν and current month t) are subscripted. The release month ν is set to 0 for untagged fish.

A.1 Initialization

The number of fish in each vulnerability and tagging state at the start of the simulation are defined in equations A.1 through A.6. Let $N_{\nu t}^{ab}$ represent the number of fish in each vulnerability state a , tagging state b , release month ν , and monthly time step t . At the first time step (month $t = 1$), the total number of fish, $N_{\cdot 1}^{\cdot}$, is initialized to a deterministic unfished equilibrium among stock production, natural mortality, and emigration:

$$(A.1) \quad N_{\cdot 1}^{\cdot} = \frac{\bar{\rho}}{1 - S + \kappa} ,$$

where $\bar{\rho}$ is average number of new fish added each month (“production”), S is the proportion of fish surviving natural mortality each month, and κ is the proportion of fish emigrating each month.

$N_{.1}^{..}$ is divided between the vulnerable and invulnerable states according to an unfished equilibrium between the two vulnerability states, where P^V is the proportion of total fish that is vulnerable:

$$(A.2) \quad N_{.1}^{V\cdot} = P^V N_{.1}^{..}.$$

The value of P^V is determined by the proportional rates of exchange between the two vulnerability states ($\theta^{V \rightarrow V'}$ and $\theta^{V' \rightarrow V}$) (see Appendix B). The remaining fish are allocated to the invulnerable state (N_{01}^{VG}) in equation A.3. Note that all invulnerable fish are initially untagged:

$$(A.3) \quad N_{01}^{VG} = N_{.1}^{..} - N_{.1}^{V\cdot}.$$

Equation A.4 makes it explicit that there are no invulnerable tagged fish at time $t = 1$

(N_{11}^{VG}):

$$(A.4) \quad N_{11}^{VG} = 0.$$

The initial number of vulnerable tagged fish for a tagging cohort released in month $v = 1$ (N_{11}^{VG}) is the number of tagged fish released in month $v = 1$ (\mathfrak{R}_1) that remain after some proportion γ is lost to initial tag shedding and tagging-induced mortality:

$$(A.5) \quad N_{11}^{VG} = \mathfrak{R}_1 \gamma.$$

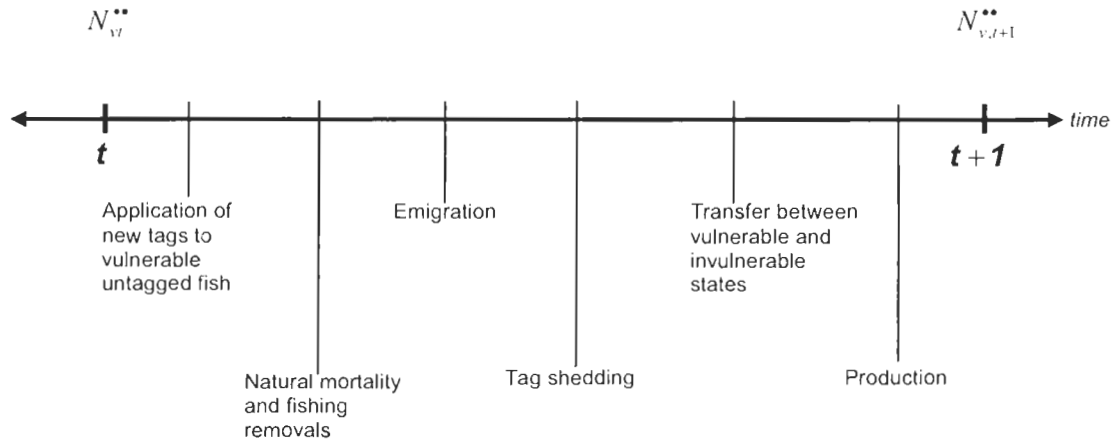
Finally, the vulnerable fish left after tagging are allocated to the vulnerable untagged state (N_{01}^{VG}):

$$(A.6) \quad N_{01}^{VG} = N_{.1}^{V\cdot} - N_{11}^{VG}.$$

A.2 State Dynamics ($2 \leq t \leq T, 1 \leq v \leq t-1$)

I simulated population dynamics to generate the number of fish in each vulnerability and tagging state for each month t from $t = 2$ to $t = T$, where T was set to 156 to represent the simulated population for 13 years from 1991 through 2003. The number of new fish (ρ_t) in each month t of the simulation were pre-specified as input parameters to the simulation model, and were set equal to monthly production estimates from Haist et al. (2005). The following processes comprise the population dynamics in each month t : the release of newly tagged fish, natural mortality, fishing mortality, emigration, tag shedding, exchange between vulnerable and invulnerable states, and stock production (addition of new fish to the population) (Figure A.1).

Figure A.1: Assumed timeline and order of processes taking place in each time step t .



Equations A.7 through A.10 describe the number fish present at the beginning of month t in each of the following states, respectively: invulnerable untagged (N_{0t}^{VG}), vulnerable untagged (N_{0t}^{VG}), invulnerable tagged (N_{jt}^{VG}), and vulnerable tagged (N_{jt}^{VG}).

These numbers are calculated sequentially by applying the processes shown in Figure A.1. Equations A.7 and A.8 describe the monthly state dynamics of untagged fish ($g = G'$), while equations A.9 and A.10 describe the dynamics of tagged fish ($g = G$).

$$(A.7) \quad N_{0t}^{V'G'} = (1 - \theta^{V' \rightarrow V'}) N_{0t-1}^{V'G'} S(1 - \kappa) + \theta^{V' \rightarrow V'} (1 - u_{t-1}) (N_{0t-1}^{V'G'} - \mathfrak{R}_{t-1}) S(1 - \kappa) + P^V I_{t-1} + \rho_{t-1}$$

$$(A.8) \quad N_{0t}^{VG'} = \theta^{V' \rightarrow V} N_{0t-1}^{V'G'} S(1 - \kappa) + (1 - \theta^{V' \rightarrow V'}) (1 - u_{t-1}) (N_{0t-1}^{V'G'} - \mathfrak{R}_{t-1}) S(1 - \kappa) + (1 - P^V) I_{t-1}$$

$$(A.9) \quad N_{vt}^{V'G} = (1 - \theta^{V' \rightarrow V'}) N_{vt-1}^{V'G} S(1 - \kappa) \delta + \theta^{V' \rightarrow V'} (1 - u_{t-1}) N_{vt-1}^{V'G} S(1 - \kappa) \delta$$

$$(A.10) \quad N_{vt}^{VG} = \theta^{V' \rightarrow V} N_{vt-1}^{V'G} S(1 - \kappa) \delta + (1 - \theta^{V' \rightarrow V'}) (1 - u_{t-1}) N_{vt-1}^{V'G} S(1 - \kappa) \delta.$$

The additional symbols in these equations are: u_t , the exploitation rate in month t ; \mathfrak{R}_t , the number of tags released in month t ; and δ , the fraction of fish retaining tags each month.

Not all of the processes shown in Figure A.1 are applicable to all states of fish in every month. For example, new fish (ρ) are only added to the invulnerable untagged state (equation A.7). I specified all stock production to be added in January of each year by setting $\rho_t = 0$ for all months where t was not January. New fish join the population as invulnerable, untagged individuals (equation A.7); thus, I assume that all new fish are invulnerable. For example, they might be small enough to squeeze through the escape rings in sablefish traps, thus being invulnerable to trap gear. New fish ultimately become vulnerable through exchange between the vulnerable and invulnerable states.

Tag shedding reduces the number of fish in the tagged state according to δ , the proportion of fish retaining tags each month (equations A.9 and A.10). I assumed that the number of fish that lose tags and rejoin the untagged state is negligible with respect to the

size of the untagged population. Thus, equation 10 does not include any terms for the contribution of untagged fish that were previously tagged but became untagged through the tag shedding process.

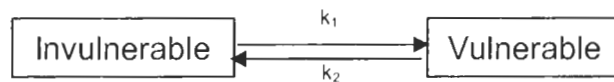
Fish that are newly tagged in the current month $v = t$ (\mathfrak{R}_t) are added to the tagged population according to equation A.11:

$$(A.11) \begin{bmatrix} N_{vt}^{VG} \\ N_{vt}^{VG} \end{bmatrix} = \begin{bmatrix} 0 \\ \mathfrak{R}_t \gamma \end{bmatrix}.$$

The model assumes that all newly tagged fish are vulnerable, so N_{jt}^{VG} is assigned 0. The number of newly tagged fish that remain after initial tag shedding and tagging-induced mortality (γ) is assigned to N_{jt}^{VG} . The processes depicted in Figure A.1 are applied to newly tagged fish in the next time period, in equations A.9 and A.10. Thus, I assume that newly tagged fish do not experience natural mortality, emigration, transfer between vulnerability states, or fishing mortality in the time period that they are tagged.

APPENDIX B – ASSUMPTION OF EQUILIBRIUM BETWEEN VULNERABLE AND INVULNERABLE STATES

The purpose of this appendix is to derive an equilibrium between the vulnerable and invulnerable states. Assume a dynamic system composed of fish that are either vulnerable to fishing gear or invulnerable to it. Let invulnerable fish become vulnerable at an instantaneous rate k_1 , and let vulnerable fish become invulnerable at an instantaneous rate k_2 .



At equilibrium, the rates of change between the two states are equal. That is,

$$(B.1) \quad N^{I'} k_1 = N^V k_2,$$

where $N^{I'}$ and N^V are the total number of invulnerable and vulnerable fish, respectively.

Since N , the total number of fish in the population, is

$$(B.2) \quad N = N^{I'} + N^V,$$

we can rewrite B.1 as

$$(B.3) \quad (N - N^V) k_1 = N^V k_2.$$

Solving for N^V ,

$$(B.4) \quad N^V = \frac{k_1}{k_1 + k_2} N.$$

Thus, the proportion of total fish, N , that are vulnerable to the fishery (P^V) is:

$$(B.5) \quad P^V = \frac{k_1}{k_1 + k_2}.$$

The monthly proportions of invulnerable fish becoming vulnerable ($\theta^{V' \rightarrow V}$) and of vulnerable fish becoming invulnerable ($\theta^{V \rightarrow V'}$) can be expressed in terms of the instantaneous rates k_1 and k_2 using equations B.6 and B.7:

$$(B.6) \quad \theta^{V' \rightarrow V} = 1 - e^{-k_1};$$

$$(B.7) \quad \theta^{V \rightarrow V'} = 1 - e^{-k_2}.$$

Solving for k_1 and k_2 ,

$$(B.8) \quad k_1 = -\ln(1 - \theta^{V' \rightarrow V}) \text{ and}$$

$$(B.9) \quad k_2 = -\ln(1 - \theta^{V \rightarrow V'}).$$

Substituting B.8 and B.9 into B.5 and dividing by -1, the proportion of vulnerable fish is

$$(B.10) \quad P^V = \frac{\ln(1 - \theta^{V' \rightarrow V})}{\ln(1 - \theta^{V' \rightarrow V}) + \ln(1 - \theta^{V \rightarrow V'})}.$$

The proportion of invulnerable fish $P^{V'}$ is

$$(B.11) \quad P^{V'} = 1 - P^V.$$

In scenario 3, when $\theta^{V' \rightarrow V} = 0.9$ and $\theta^{V \rightarrow V'} = 0.1$ (Table 2), $P^V = 0.956$ and $P^{V'} = 0.044$.

In all other scenarios, $\theta^{V' \rightarrow V} = 0.99999$ and $\theta^{V \rightarrow V'} = 0.00001$ (Table 2). Accordingly,

$$P^V = 0.9999991 \text{ and } P^{V'} = 8.69 \times 10^{-7}.$$

Table 1: Number of tag recoveries, grouped by release year, in a three-year tagging experiment. In this example, there are $I = 3$ years of releases and $J = 3$ years of recoveries. The expected recoveries are those predicted by the Brownie model, given the observed recoveries that are input to the model. Symbols are: \mathfrak{R}_i , number of fish tagged in year i ; ϕ , survival-tag retention rate for newly tagged fish; λ , average tag reporting rate; u_j , exploitation rate in year j ; S_j , total annual survival rate in year j ; and r_{ij} , the observed number of tags recovered in year j ($j = i, i+1, \dots, J$) that were released in year i . S_j is defined as $S_j = \exp(-F_j - M^*)$, while u_j is defined in equation 2 as $u_j = 1 - \exp(-F_j)$.

Release year i	Recovery year j		
	1	2	3
Expected recoveries			
1	\mathfrak{R}_1	$\mathfrak{R}_1 \phi \lambda u_1$	$\mathfrak{R}_1 \phi \lambda u_2 S_1$
2	\mathfrak{R}_2	$\mathfrak{R}_2 \phi \lambda u_2$	$\mathfrak{R}_2 \phi \lambda u_3 S_2$
3	\mathfrak{R}_3		$\mathfrak{R}_3 \phi \lambda u_3$
Observed recoveries			
1	\mathfrak{R}_1	r_{11}	r_{12}
2	\mathfrak{R}_2		r_{22}
3	\mathfrak{R}_3		r_{33}

Table 2: Simulated scenarios.

Each row corresponds to a simulated scenario, and lists the Brownie assumption it corresponds to, as well as the values of parameters used to simulate that scenario; changes from the base case are shown in boldface. Parameter values for BC sablefish are used whenever they are available; see the “Source” column. Symbols are: $\theta^{V \rightarrow I}$, monthly proportion of fish moving from the invulnerable to the vulnerable state; $\theta^{I \rightarrow V}$, monthly proportion moving from the vulnerable to the invulnerable state; and β , the overdispersion shape parameter for the beta distribution for errors in tag recoveries.

Scenario	Description	Violated Brownie assumptions	Timing of fishery	Mixing	Tag loss	Tag-induced mortality	Emigration	Over-dispersion	Source
1	Base case - All assumptions met		first month	$\theta^{I \rightarrow V} = 0.99999$ $\theta^{V \rightarrow I} = 0.00001$	0	0	0	0	
2	Monthly exploitation	8	all 12 months	$\theta^{I \rightarrow V} = 0.99999$ $\theta^{V \rightarrow I} = 0.00001$	0	0	0	0	Haist et al. (2005)
3	Incomplete mixing	1	first month	$\theta^{I \rightarrow V} = \mathbf{0.9}$ $\theta^{V \rightarrow I} = \mathbf{0.1}$	0	0	0	0	
4	Tag loss	2	first month	$\theta^{I \rightarrow V} = 0.99999$ $\theta^{V \rightarrow I} = 0.00001$	0.3% per month	0	0	0	Haist et al. (2005)
5	Tagging-induced mortality	3	first month	$\theta^{I \rightarrow V} = 0.99999$ $\theta^{V \rightarrow I} = 0.00001$	0	“Survival-retention” rate = 0.856	0	0	Haist et al. (2005)
6	Emigration	6	first month	$\theta^{I \rightarrow V} = 0.99999$ $\theta^{V \rightarrow I} = 0.00001$	0	0	3% of fish emigrate per month	0	Haist et al. (2005)
7	Overdispersion in tag recoveries	5	first month	$\theta^{I \rightarrow V} = 0.99999$ $\theta^{V \rightarrow I} = 0.00001$	0	0	0	$\beta = 800$	
8	“Realistic” case – All assumptions violated (except 4, 7)	1, 2, 3, 5, 6, 8	all 12 months	$\theta^{I \rightarrow V} = \mathbf{0.9}$ $\theta^{V \rightarrow I} = \mathbf{0.1}$	0.3% per month	“Survival-retention” rate = 0.856	3% of fish emigrate per month	$\beta = 800$	

Figure 1: Simulated data from 500 Monte Carlo simulations of a “realistic” scenario (scenario 8) in which no assumptions of the Brownie model are met (except 4 and 7) (box plots), plotted along with (a) true BC sablefish landings (open circles), and (b) survey CPUE data (open circles) reported by Haist et al. (2005).

Box plots of simulated catch are extremely narrow because stochastic catches of tagged fish come from a binomial distribution with very large N and thus have a low variance (equation 4), and catches of untagged fish are deterministic in the simulator. The bottom and top of the boxes indicate the first and third quartiles of the estimates over 500 trials, while the heavy central lines indicate the median estimate. The whiskers extend 1.5 times the inter-quartile range.

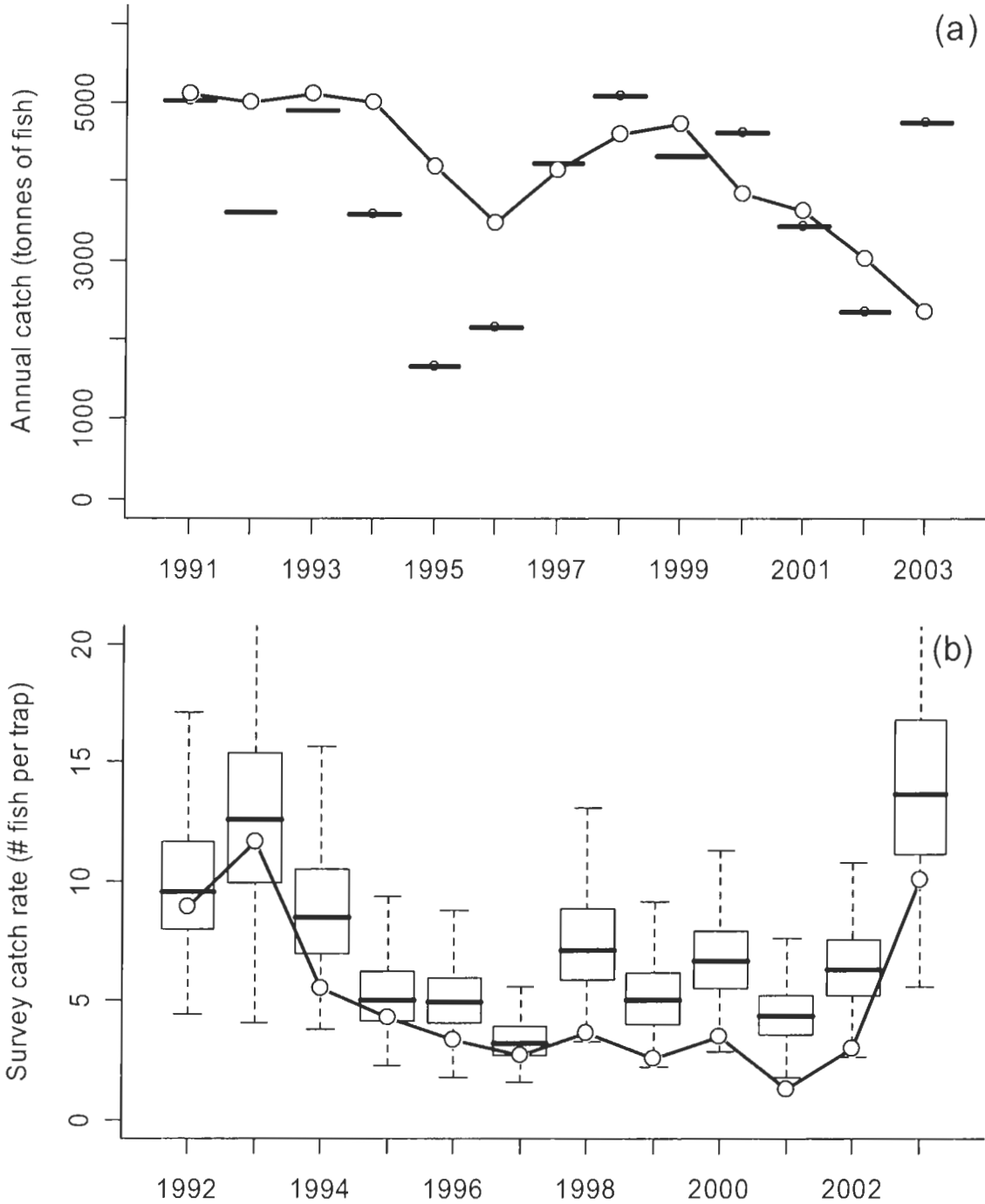


Figure 2: Parameter and abundance estimates for the base case (scenario 1) over 500 Monte Carlo trials.

(a) Box plots of the percentage bias in estimates of annual fishing mortality from 1991 – 2003 (F_{91} - F_{03}), average tag reporting rate (λ), and a combined instantaneous natural mortality-emigration parameter (M^*). (b) Box plots of estimated abundance, plotted with the “true” simulated abundance in the month of tagging (large open circles). In both (a) and (b), the bottom and top of the boxes indicate the first and third quartiles of the estimates over 500 trials, while the heavy central lines indicate the median estimate. Whiskers extend 1.5 times the inter-quartile range. Small open circles show outliers.

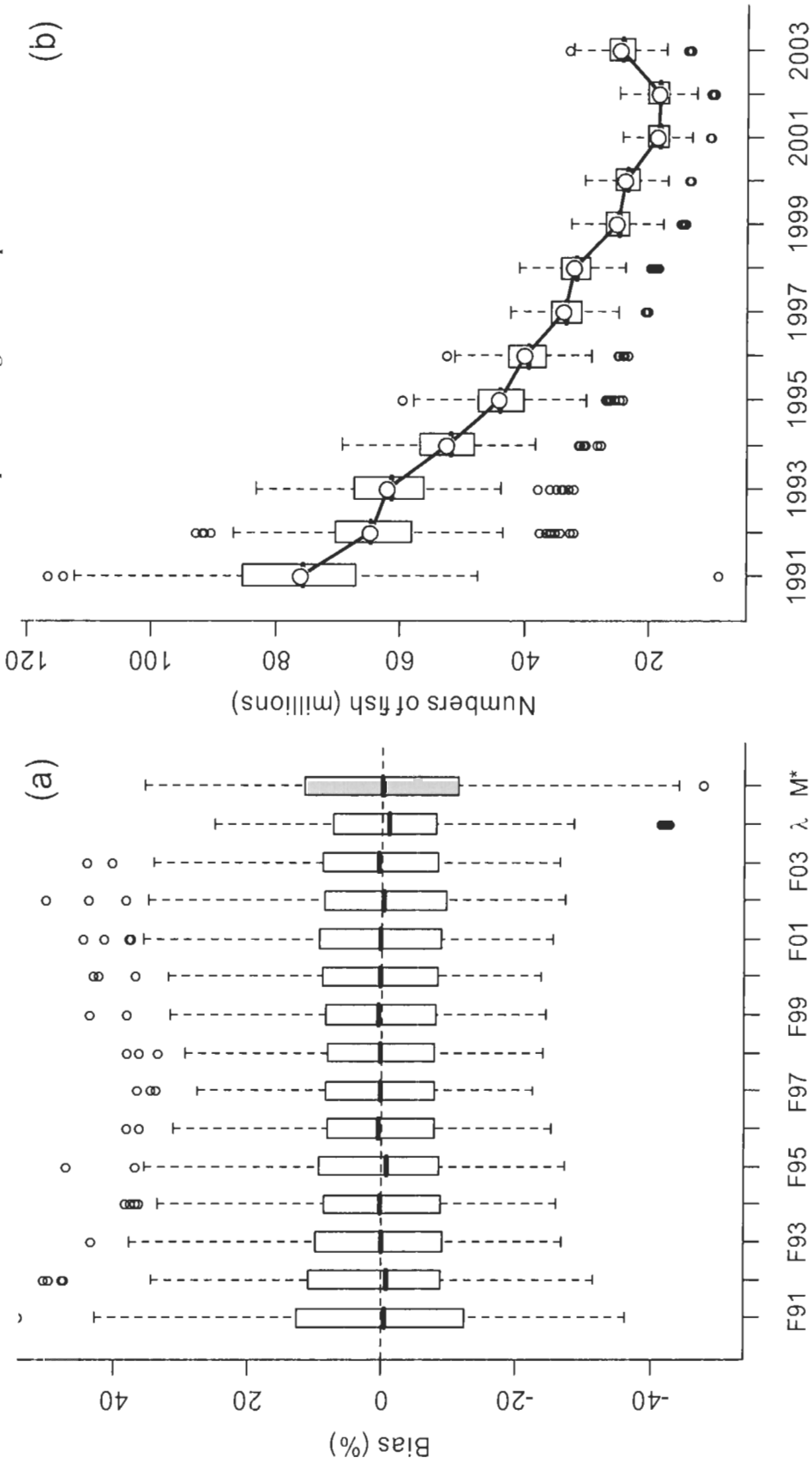


Figure 3: Same as Figure 2 except for a “realistic” case (scenario 8) over 500 Monte Carlo trials. Percentages at the top of each whisker in panel (b) reflect the percentage bias of the median abundance estimate in each year.

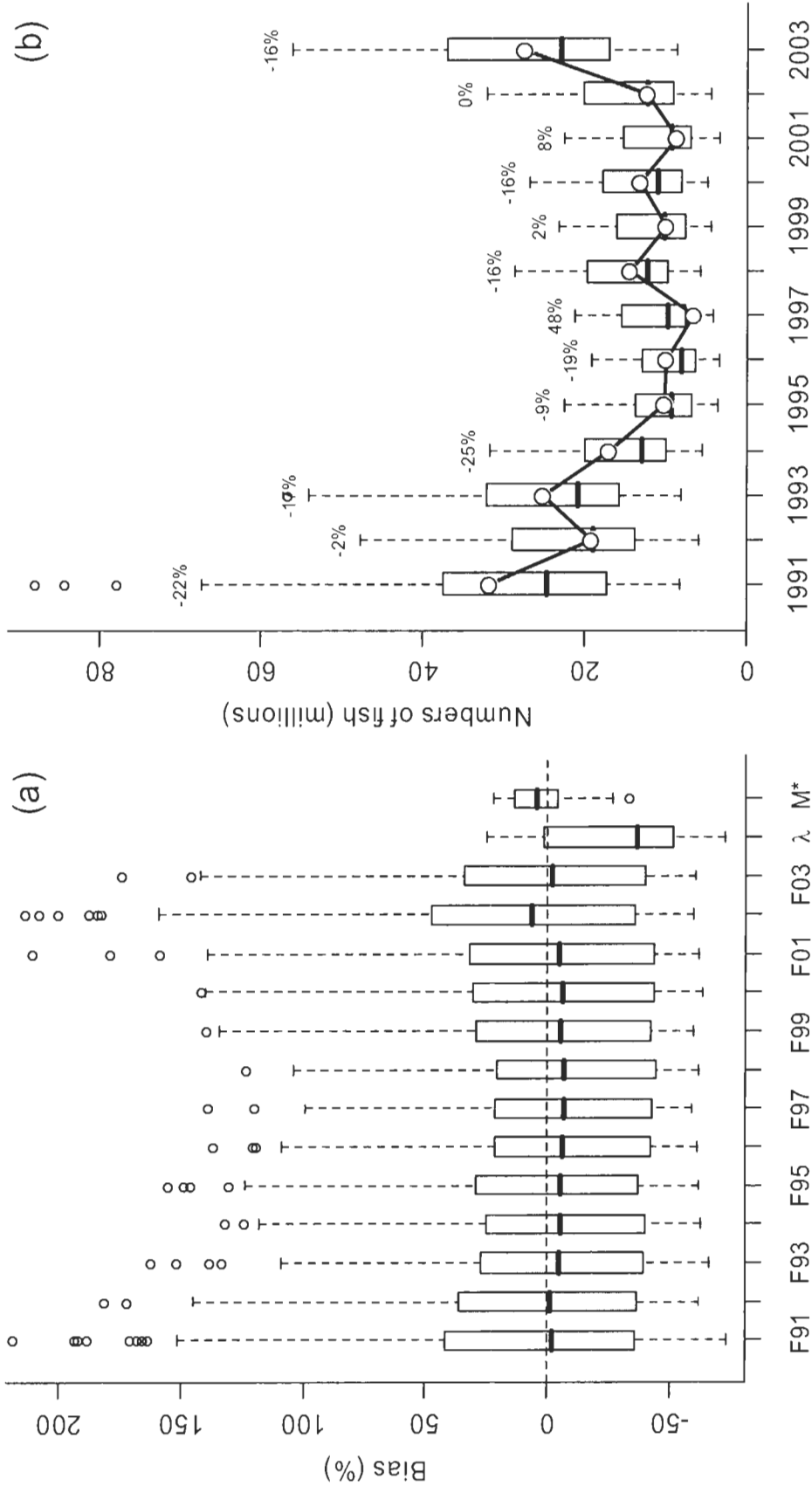


Figure 4: Parameter estimates over 500 Monte Carlo trials for scenarios 2-7.

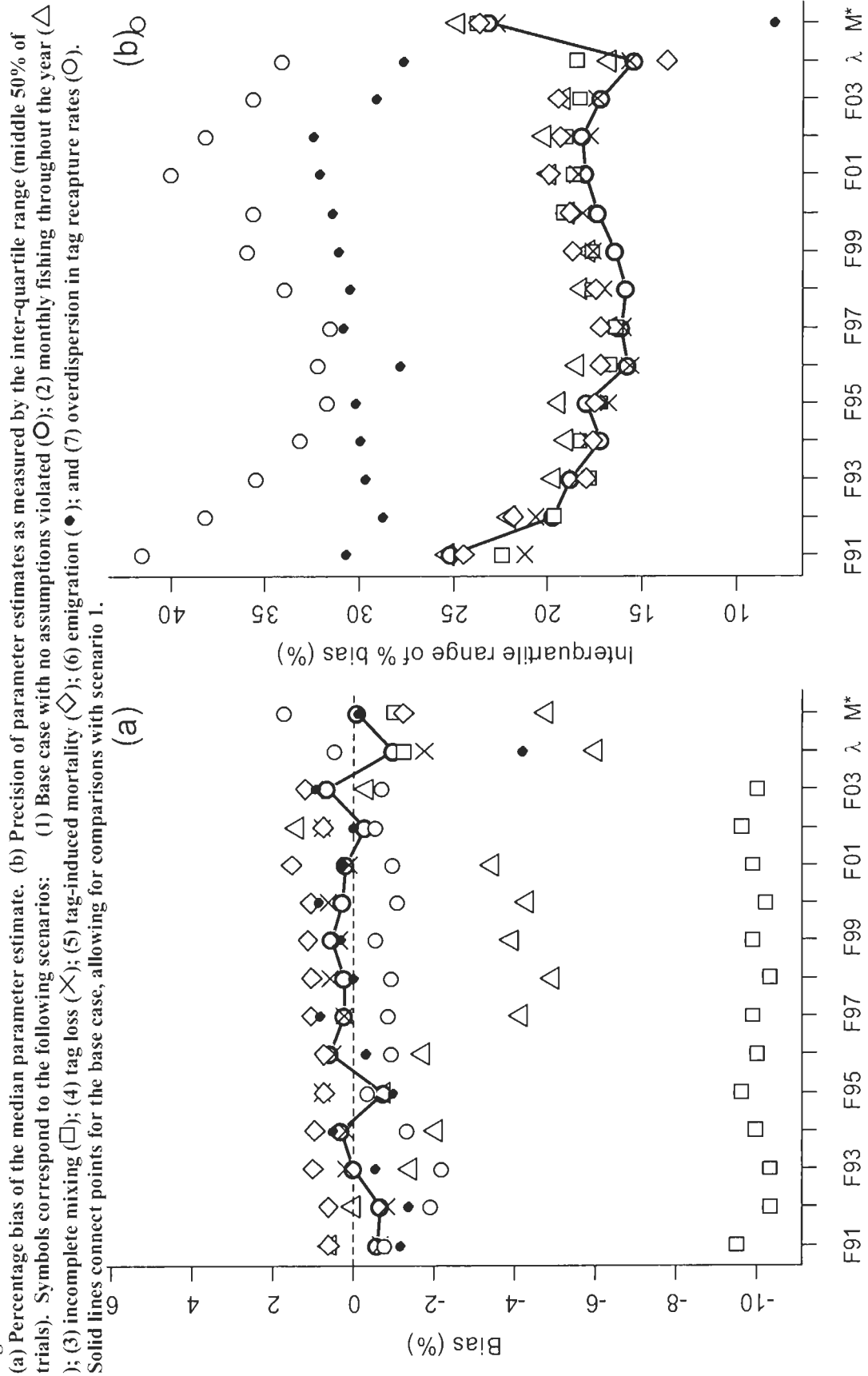


Figure 5: Abundance estimates from 1991 through 2003 over 500 Monte Carlo trials for scenarios 2-7. (a) Percentage bias of the median abundance estimate. (b) Precision of abundance estimates as measured by the inter-quartile range (middle 50% of trials). The symbols are as in Figure 4.

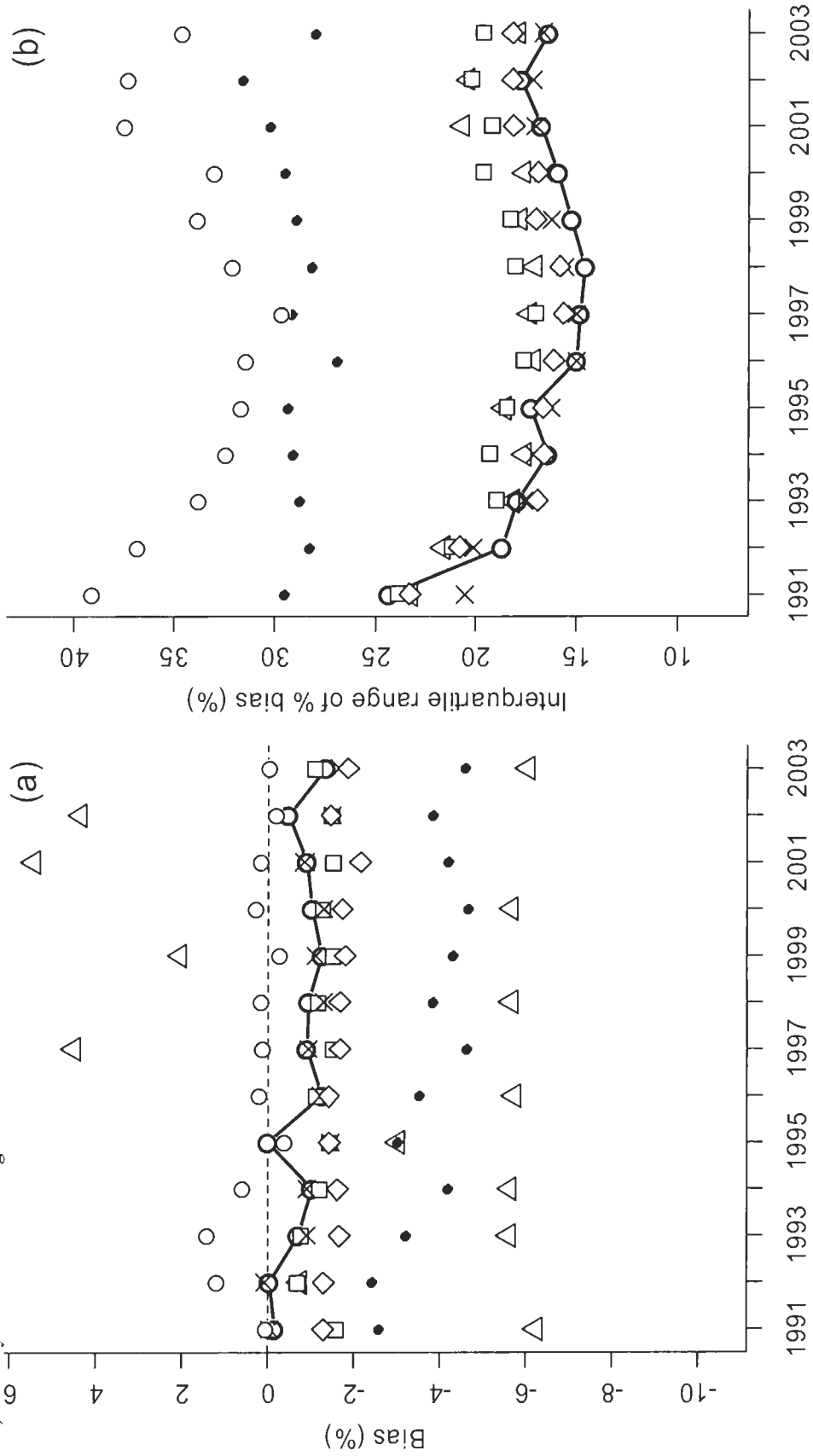


Figure 6: Parameter estimates: Improvement in (a) median percentage bias and (b) precision of parameter estimates by combining the survey CPUE with tag recovery data over 500 Monte Carlo trials. In both panels, positive values show improvement and negative values show deterioration in the magnitude of bias/precision from including the survey CPUE data. Symbols are as in Figure 4, except for (*), which represents scenario 8 (realistic scenario).

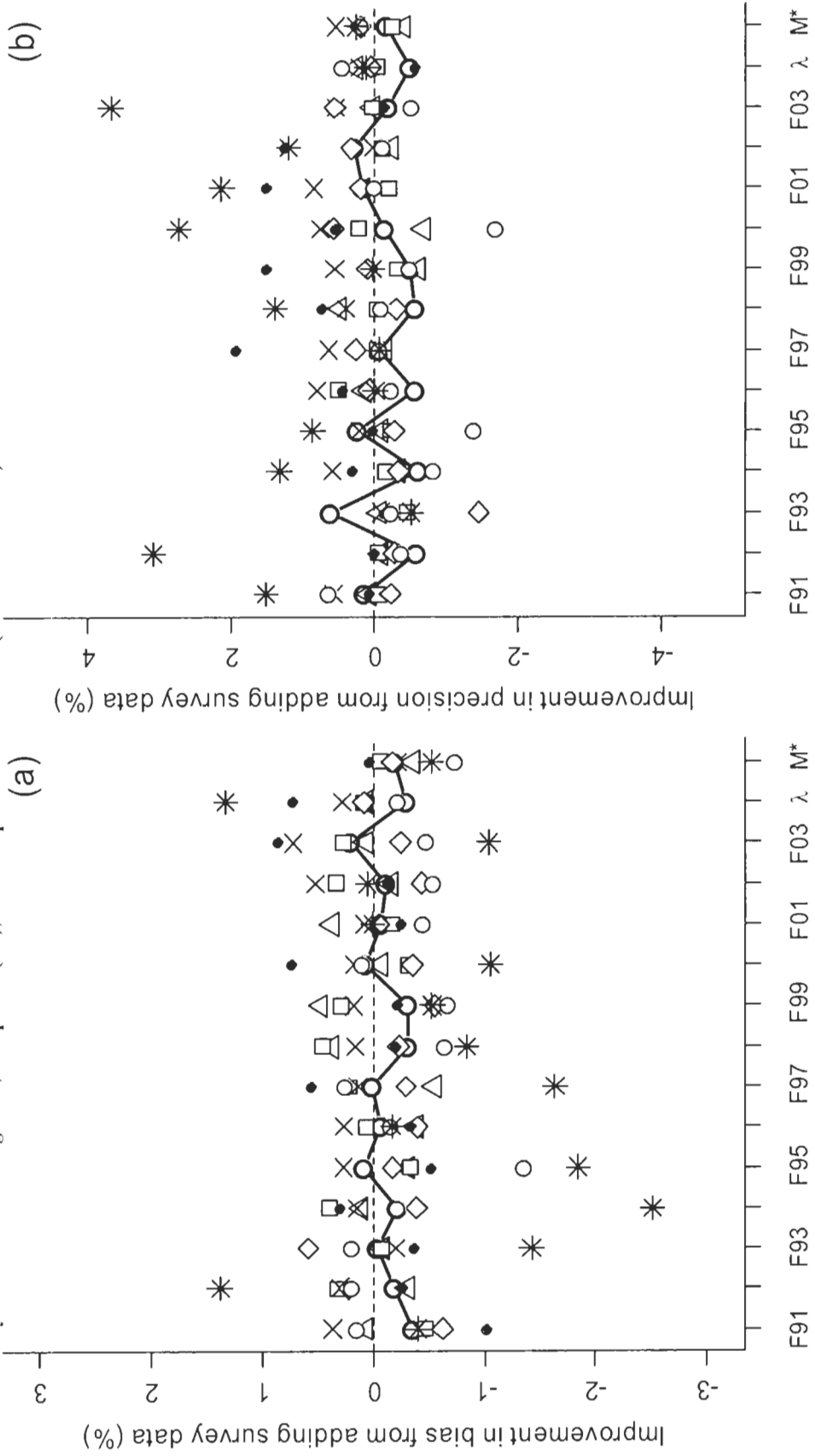


Figure 7: Abundance estimates: Improvement in (a) median percentage bias and (b) precision of abundance estimates by combining the survey CPUE with tag recovery data over 500 Monte Carlo trials. In both panels, positive values show improvement and negative values show deterioration in the magnitude of bias/precision from including the survey CPUE data. Symbols are as in Figure 4, except for (*), which represents scenario 8 (realistic scenario).

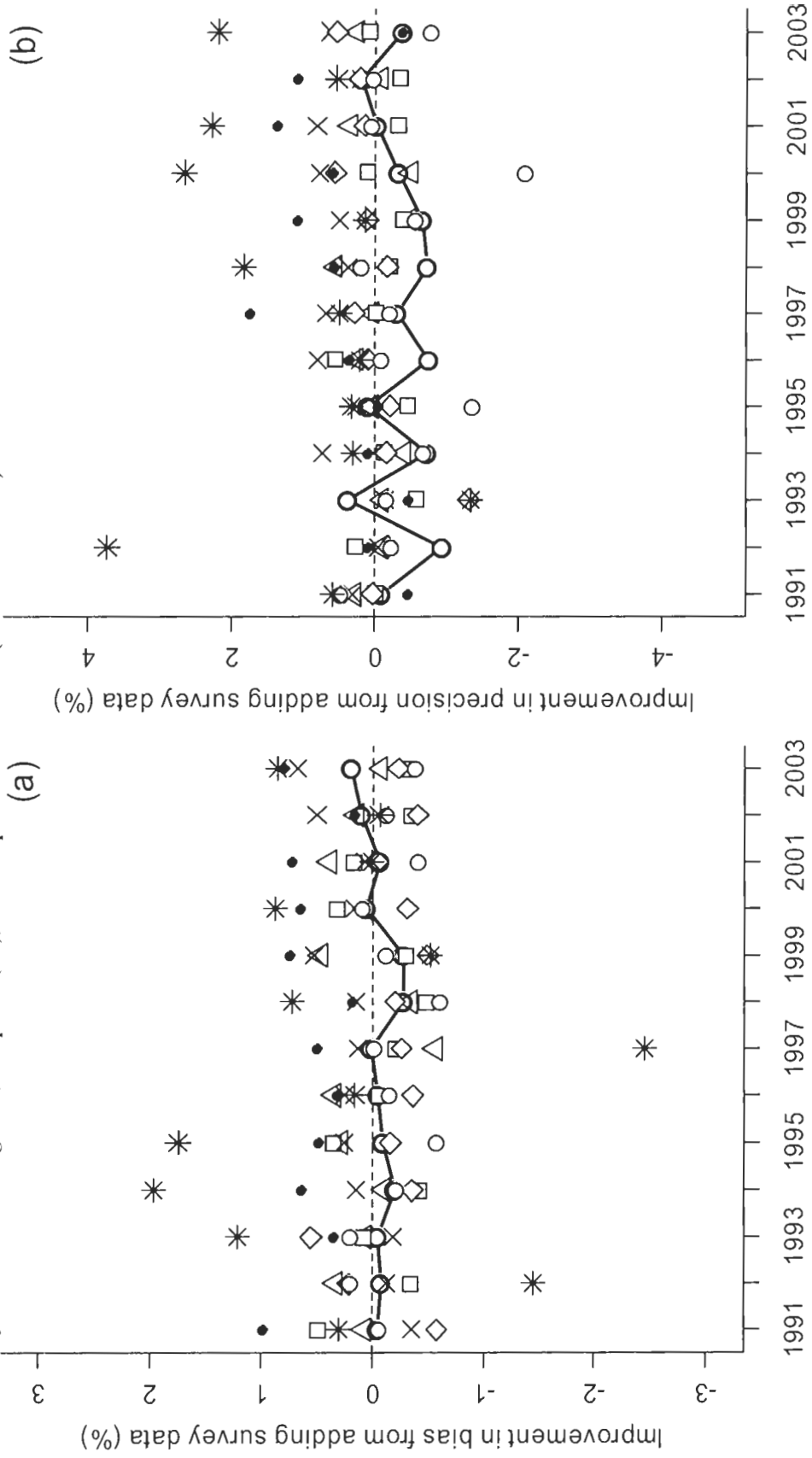


Figure 8: Likelihood profiles for the tagging and survey CPUE negative log likelihood functions. These plots show the value of the likelihood for a particular value of M^* when all other estimated parameters are at their MLE values. The likelihoods were fit to the first simulated Monte Carlo data set from the Base Case scenario (scenario 1).

