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Unbiased Methods for Calculating Mortality in Mark-Selective Fisheries Models for Ocean Salmon

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ARTICLE

Unbiased Methods for Calculating Mortality in Mark-Selective Fisheries Models for Ocean Salmon

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Abstract
Mark-selective fisheries (MSF) are increasingly being used as a strategy for managing fisheries for Coho Salmon *Oncorhynchus kisutch* and Chinook Salmon *O. tshawytscha* on the west coast of North America. Mark-selective fisheries allow anglers to keep legal-size Coho Salmon or Chinook Salmon with a missing adipose fin (typically hatchery fish) and require the release of those with an adipose fin (unmarked fish, which are usually wild fish). The objective of MSF is to provide meaningful fisheries on abundant stocks of hatchery salmon while reducing the impact on wild (unmarked) salmon stocks. As has been previously shown, the model currently used in the Pacific Fishery Management Council's preseason planning process to project mortalities for proposed Coho Salmon and Chinook Salmon fisheries underestimates the number of unmarked salmon mortalities occurring in MSF and concurrent nonselective fisheries. We propose equations that provide unbiased estimates of salmon mortalities that occur in these fisheries due to the release of fish. The performance of the proposed methods is evaluated and compared to the current methods using a simulation model. The methods are shown to provide unbiased calculations of total mortalities for unmarked salmon in both mark-selective and concurrent nonselective fisheries. The unbiased methods are able to incorporate different release-mortality and mark-recognition rates for the fisheries modeled.

In 1998, the State of Washington introduced mark-selective fisheries (MSF) as a salmon *Oncorhynchus* spp. fisheries management tool (PFMC 1999). Regulations for MSF permit anglers to retain legal-size Coho Salmon *O. kisutch* or Chinook Salmon *O. tshawytscha* that have had their adipose fin removed (marked) and require the release of all Coho or Chinook Salmon with an adipose fin (unmarked). The objective of these fisheries is to provide meaningful fisheries on abundant (generally marked) hatchery salmon while reducing the impact on wild (unmarked) salmon. The annual harvest of marked Coho Salmon by MSF off the coast of Washington State has ranged from 28 to 249 thousand fish (Figure 1A; PFMC 2011). Mark-selective fisheries for Chinook Salmon in Washington have been conducted in the inner marine waters of the Strait of Juan de Fuca and Puget Sound since 2003 (WDFW 2008a, 2008b) while MSF for Chinook Salmon were conducted in Washington coastal marine waters for the first time in 2010 (WDFW 2011). The harvest of marked Chinook Salmon in Washington's marine waters has increased greatly since the inception of MSF and reached a total of about 25 thousand fish annually in recent years (Figure 1B).

The Fishery Regulation Assessment Model (FRAM) is used annually by the Pacific Fishery Management Council ([PFMC] 2008a) to evaluate the potential impact to major stocks of Coho and Chinook salmons from a proposed set

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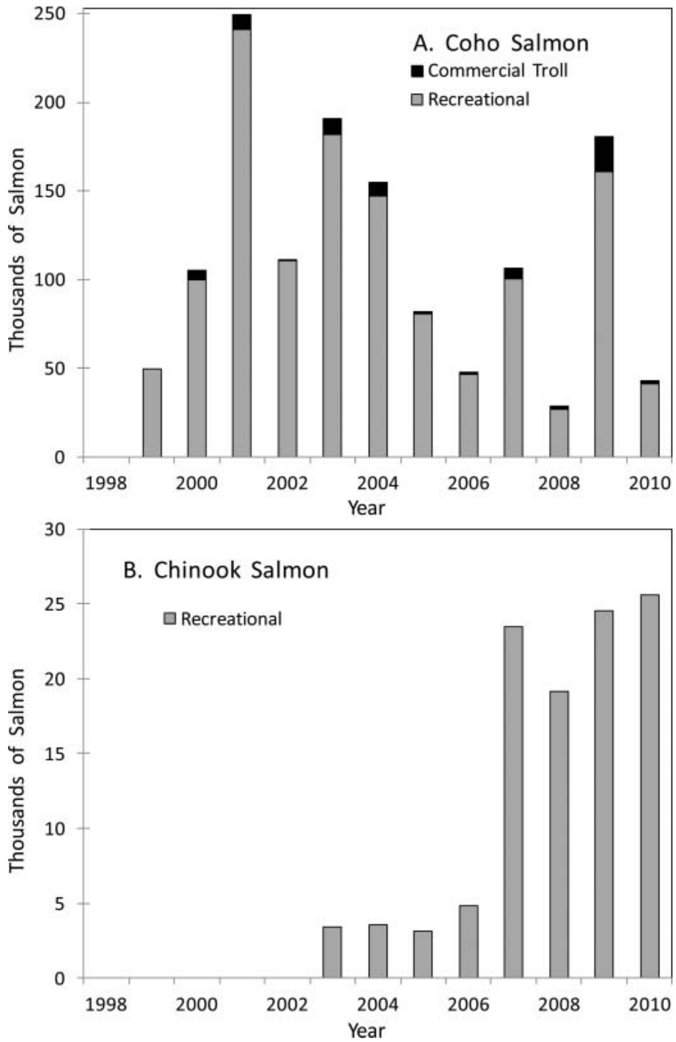

FIGURE 1. Annual catches of marked salmon by mark-selective fisheries conducted in the marine waters of Washington State for **(A)** Coho Salmon caught by recreational and commercial troll fisheries and **(B)** Chinook Salmon caught by recreational fisheries.

of fishery regulations for a management season. Based upon FRAM projections, proposed fishery regulations are adjusted to achieve escapement goals or stay below exploitation rate targets for stocks of concern (often stocks listed under the U.S. Endangered Species Act). The FRAM is a single-pool, deterministic model with discrete time periods varying in length from 1 to 7 months (PFMC 2008a). All fisheries during a modeled time period are assumed to operate simultaneously on a single pool of fish. The pool consists of all major stocks that have been caught historically in the fishery as estimated from coded wire tag (CWT) recoveries (Nandor et al. 2010). Exploitation rates estimated from CWTs recovered during a base period when salmon abundances were relatively high and fisheries were widely distributed in both time and area are the basis for the predictions of fishery mortalities by stock (PSC 2005). Details for the methods and algorithms used in the FRAM are presented in PFMC (2008b). Descriptions of the base-period data used for the Coho and Chinook Salmon FRAMs are provided in Packer and Cook-Tabor (2007) and PFMC (2008c), respectively. Models similar to the FRAM are used for salmon management in other forums such as the Chinook Model by the Pacific Salmon Commission (JCTC 2012) and the Klamath Harvest Rate Model (Prager and Mohr 2001).

Prior to the implementation of MSF, a key assumption in these models was that the exploitation rates for specific coded-wire-tagged salmon stocks (often called indicator stocks) were representative of the exploitation rates for wild and hatchery stocks (typically from the same watershed) with similar life histories and ocean distributions. However, with the advent of MSF this basic assumption was violated because in MSF unmarked fish are released while the corresponding marked hatchery stocks are retained and removed from the population. These models were built with the assumption that there was no release of legal-sized fish caught during the base period used to estimate average fishery-specific exploitation rates for each stock. A time-period-specific exploitation rate is, therefore, assumed to represent the encounter rate of a stock in a fishery. The models were restructured with the advent of MSF. The time-period-specific exploitation rates were still used to estimate the exploitation rates on the marked stocks, but these same rates were used as surrogates for the encounter rates for the unmarked stocks (PFMC 2008b). These encounter rates are used to produce stock-specific estimates of the number of encounters with unmarked fish in a mark-selective fishery, which, combined with an estimate of the release-mortality rate, provide estimates of the mortalities due to the catch and release of unmarked fish. In these models, the exploitation rate on the unmarked stock component in a mark-selective fishery is a linear function of the time-period-specific average exploitation rate from the base period ($\bar{\mu}^{Base}$), a scalar that relates current year expected effort to base period effort, and a release mortality rate (δ). The "simple" exploitation rates for the marked and unmarked cohorts in a mark-selective fishery (μ^M and μ^U, respectively) are calculated as

$$\mu^M = \bar{\mu}^{Base} \cdot scalar$$

and

$$\mu^U = \bar{\mu}^{Base} \cdot scalar \cdot \delta,$$

where $\bar{\mu}^{Base}$ is the same for the marked and unmarked components of a specific stock.

Lawson and Sampson (1996) demonstrated that in a mark-selective fishery, the actual mortality rate for unmarked fish is an increasing function of the time-period-specific exploitation rate. This causes the total number of unmarked mortalities in MSF to be underestimated by models relying on the linear relationship between exploitation rate and release-mortality rate. Yuen and Conrad (2011) demonstrated that this bias (underestimation of unmarked mortalities) also occurs in any modeled nonselective fisheries (NSF) that take place during the same model time period as the MSF. These biases are the result of approximating the nonlinear Baranov catch equation with a linear model. When MSF operate during a modeled time period, unmarked mortalities are underestimated because released fish that survive may encounter the fishing gear more than once during the time period and the unmarked-to-marked fish ratio for all fish in the pool increases as a result of the selective removal of marked fish in MSF. Neither of these processes is currently captured by the algorithms used to calculate unmarked mortalities when MSF are operating during a modeled time period.

In most current management models, time period and fishery-specific exploitation rates that are derived from base period data and adjusted for current year fishery projections are (1) equivalent to mortality rates for a marked cohort in MSF and NSF and (2) equivalent to encounter rates for an unmarked cohort in MSF and mortality rates in NSF. Mortalities in fisheries are typically projected using either quotas or exploitation rate scalars. For a quota fishery, a total catch for the fishery (summed across all stocks) is specified. Fishery effort or season length needed to achieve that quota is then projected using $\bar{\mu}^{Base}$. For an exploitation rate scalar fishery, the exploitation rate in the fishery is scaled relative to $\bar{\mu}^{Base}$ using a user-defined scalar. The most common scaling mechanism is fishing effort relative to the average level during the base period (PFMC 2008b). In this paper we describe unbiased methods for calculating total mortalities for marked and unmarked fish when MSF are modeled using either scalars or quotas. We also describe unbiased methods for both allocating total fishery-related mortalities in a modeled time period to each fishery and calculating the number of mortalities in each fishery attributed to landed and nonlanded catch (e.g., mortalities due to intentional release or mark-recognition error).

METHODS

We first developed equations that provide unbiased calculations for the number of unmarked mortalities when there are multiple MSF and a nonselective fishery operating concurrently during a time period. Because most of the management models using equations of this type are accounting models that provide calculations of catch, total mortalities, and exploitations rates for specific stocks of interest by fishery and time period, we choose not to refer to them as estimates but as calculations. Many of the model inputs are assumed (such as natural mortality rates and release mortality rates) and there are currently no methods incorporated into the models to provide estimates of the uncertainty associated with any model output.

The simulation model and methods used to evaluate the performance of the proposed unbiased methods are also briefly described. Finally, we describe how the proposed unbiased methods would be implemented in the FRAM.

Basic unbiased equations.—Table 1 defines the notation used in the development of the equations and parameters of the simulation model. Following the notation of Lawson and Sampson (1996), but with separate mark-recognition rates for marked (γ) and unmarked (ζ) fish and setting the parameters related to drop-off mortality to zero, the probability of a marked fish dying (p_M) in a mark-selective fishery during time span t is

$$p_M(t) = 1 - \exp\{-\lambda \cdot t \cdot [\gamma + (1 - \gamma) \cdot \delta]\} \tag{1}$$

and the probability of an unmarked fish dying (p_U) during time span t is

$$p_U(t) = 1 - \exp\{-\lambda \cdot t \cdot [(\delta \cdot \zeta) + (1 - \zeta)]\}, \tag{2}$$

where λ is the instantaneous encounter rate of a fish with the gear.

During a single, discrete time period, if the recognition rate for marked fish (γ) is 100%, equation (1) simplifies to

$$p_M = 1 - \exp(-\lambda) = \mu^M \tag{3a}$$

or

$$\exp(-\lambda) = 1 - \mu^M. \tag{3b}$$

In this equation, p_M is equivalent to an exploitation rate for the marked cohort (μ^M) in a fishery during the time period. When p_M is multiplied by the number of marked fish (N^M) present at the beginning of the time period (but after natural mortality) it provides the number of marked fish encountered by the gear and landed in the fishery.

Similarly, when the recognition rate for unmarked fish (ζ) is 100% equation (2) simplifies to

$$p_U = 1 - \exp(-\lambda \cdot \delta). \tag{4}$$

By substituting the right side of equation (3b) into equation (4) for exp(–λ), the exploitation rate for an unmarked cohort ($\hat{\mu}^U$) becomes

$$\hat{\mu}^U = 1 - (1 - \mu^M)^\delta. \tag{5}$$

Equation (5) provides an unbiased method for calculating the total exploitation rate for an unmarked cohort when the only fishery in the time period is a mark-selective fishery with a release mortality rate of δ (superscript ˆ indicates an unbiased exploitation rate calculation).

As demonstrated by Yuen and Conrad (2011), additional complexities are introduced when multiple mark-selective and nonselective fisheries impact an unmarked cohort during the same time period in a single-pool model (i.e., all fisheries impact a cohort simultaneously). As they demonstrated, even when assuming a constant δ in each mark-selective fishery

$$\left[\sum_i \left(1 - \left(1 - \mu_i^M\right)^\delta\right)\right] < 1 - \left[1 - \left(\mu_1^M + \mu_2^M + \cdots \mu_i^M\right)\right]^\delta, \tag{6}$$

TABLE 1. Definitions of parameters used in equations.

Parameter	Definition
N^j	Initial number of marked ($j = M$) or unmarked ($j = U$) fish after natural mortality has occurred in a time step.
N_S^j	Initial number of marked ($j = M$) or unmarked ($j = U$) fish from stock s after natural mortality has occurred in a time step.
λ	Instantaneous encounter rate of a fish with the gear.
δ_i	Release-mortality rate: probability that a fish that is caught and released dies due to the encounter in fishery i.
δ_{ji}	Overall release mortality rate for marked ($j = M$) or unmarked ($j = U$) fish that accounts for mark-recognition error in fishery i.
δ_{jI}^W	Weighted release mortality rate for marked ($j = M$) or unmarked ($j = U$) fish calculated across all fisheries in a modeled time step.
γ_i	Recognition rate for marked fish: the probability that a caught marked fish is properly identified as a marked fish and retained in fishery i.
ζ_i	Recognition rate for unmarked fish: the probability that a caught unmarked fish is properly identified as unmarked and released in fishery i.
$\bar{\mu}^{Base}$	Exploitation rate for a cohort estimated as an average of base period exploitation rates defined as the total number of fishery mortalities divided by the cohort size at the beginning of a time period.
μ_i^M	Exploitation rate for the marked cohort: the total number of marked fish mortalities occurring in fishery i divided by the marked fish cohort size at the beginning of a time period (N^M).
$\tilde{\mu}_i^M$ and $\hat{\mu}_i^M$	Biased and unbiased calculations, respectively, of the exploitation rate on a marked cohort in fishery i.
μ_i^U	Exploitation rate for the unmarked cohort: the total number of unmarked fish mortalities occurring in fishery i divided by the unmarked fish cohort size at the beginning of a time period (N^U).
$\tilde{\mu}_i^U$ and $\hat{\mu}_i^U$	Biased and unbiased calculations, respectively, of the exploitation rate on an unmarked cohort in fishery i.
π_i	Proportion of total unmarked fish mortalities in all fisheries during a time period that occurred in fishery i.
D_i^j	Total number of marked ($j = M$) or unmarked ($j = U$) fish mortalities in fishery i.
D_{Li}^j	Number of marked ($j = M$) or unmarked ($j = U$) fish mortalities in fishery i that were landed catch.
D_{Ni}^j	Number of marked ($j = M$) or unmarked ($j = U$) fish mortalities in fishery i that were nonlanded mortalities.
D_{LSi}^j	Number of marked ($j = M$) or unmarked ($j = U$) fish mortalities from stock s that were landed catch in fishery i.

where μ_i^M is the exploitation rate for the marked component of a stock in fishery i during the time period and is a surrogate for the encounter rate for the unmarked component of the stock. The sum of the individual fishery unbiased calculations (the left side of the equation) will always be less than the right side of equation (6) because of the nonlinearity resulting from the quantities inside the parentheses being raised to the δ power. This is an important distinction, because initial bias correction attempts were performed separately on each fishery and then summed over all fisheries in a time step (left side of equation 6). These bias-adjusted calculations worked well within the FRAM's computational structure and did not necessitate finding a solution for δ when multiple fisheries with different release mortality occurred in a time step. This initial method, however, underestimated the true exploitation rate on the unmarked cohort.

The right side of equation (6) correctly calculates the total exploitation rate on an unmarked cohort for a single-pool model when δ is constant across all fisheries:

$$\hat{\mu}_I = 1 - \left(1 - \sum_i \mu_i^M\right)^{\delta}. \tag{7}$$

However, the proper δ for equation (7) when multiple MSF (with different release mortality rates) and NSF operate concurrently during a modeled time period must be determined. This is described in the next section.

Weighted release mortality rate equations.—As described previously, the release of salmon is the source of the bias in the exploitation rate calculations unless there is 100% release mortality. The release of a fish can be a consequence of fisheries regulations or mark-recognition error. Many stocks are subject to a mixture of nonselective and mark-selective fisheries, as well as mark-recognition error, during the same time step. To accurately compute exploitation rates on these stocks, a weighted release mortality rate is needed. Nonselective fisheries can be viewed as MSF with $\delta = 1.0$, i.e., a fishery with a 100% release mortality rate. Recognition errors for marked fish in MSF (i.e., when γ is <1.0) reduce the exploitation rate on a marked cohort (because some marked fish are released and survive) and introduce bias into the exploitation rate calculation for the marked component of a stock. Similarly, recognition errors for unmarked fish in MSF (i.e., when ζ is <1.0) increase the exploitation rate on an unmarked cohort (because some unmarked fish are kept). An overall release mortality rate in fishery i that accounts for mark-recognition error for a marked cohort (δ_{Mi}) is defined by

$$\delta_{Mi} = \gamma_i + [(1 - \gamma_i) \cdot \delta_i]. \tag{8}$$

Similarly, for the unmarked cohort

$$\delta_{Ui} = (1 - \zeta_i) + (\zeta_i \cdot \delta_i). \tag{9}$$

Weighted release mortality rates across all fisheries in the modeled time period for marked and unmarked cohorts (δ_{MI}^{W} and δ_{UI}^{W}, respectively) can be calculated using fishery-specific release mortality rates and μ_i^M to weight each rate. Specifically, for the marked cohort

$$\begin{aligned}\delta_{MI}^{W} &= \sum_i^I \left(\frac{\mu_i^M}{\sum_i^I \mu_i^M} \cdot \delta_{Mi} \right) \\ &= \frac{\sum_i^I \left[\mu_i^M \cdot \{\gamma_i + ((1 - \gamma_i) \cdot \delta_i)\} \right]}{\sum_i^I \mu_i^M} = \frac{\tilde{\mu}_I^M}{\mu_I^M}\end{aligned} \tag{10}$$

and for the unmarked cohort

$$\begin{aligned}\delta_{UI}^{W} &= \sum_i^I \left(\frac{\mu_i^M}{\sum_i^I \mu_i^M} \cdot \delta_{Ui} \right) \\ &= \frac{\sum_i^I \left[\mu_i^M \cdot \{(1 - \zeta_i) + (\zeta_i \cdot \delta_i)\} \right]}{\sum_i^I \mu_i^M} = \frac{\tilde{\mu}_I^U}{\mu_I^M}\end{aligned} \tag{11}$$

when there are I total fisheries in the modeled time period (subscript I indicates summed across all fisheries and superscript $\sim$ indicates a biased exploitation rate calculation). The weighted release mortality rates are simply the ratio of the sum of the biased exploitation rate calculations, which account for release mortalities (either $\tilde{\mu}_I^M$ or $\tilde{\mu}_I^U$) and the sum of the μ_i^M. These weighted release mortality rates are needed to provide unbiased calculations of marked and unmarked exploitation rates when fish are released due to mark-recognition error or MSF.

Calculating total marked and unmarked fishery mortalities.—When there is perfect mark recognition of marked fish in MSF ($\gamma = 1.0$), the total exploitation rate for a marked cohort in a modeled time period is calculated as

$$\hat{\mu}_I^M = 1 - \left(1 - \sum_i^I \mu_i^M \right)^1 = \sum_i^I \mu_i^M \tag{12}$$

and the total exploitation rate for an unmarked cohort when ζ is 1.0 as

$$\hat{\mu}_I^U = 1 - \left(1 - \sum_i^I \mu_i^M \right)^{\delta_{UI}^{W}}. \tag{13}$$

When there is imperfect mark recognition for marked fish in MSF ($\gamma < 1.0$), additional complexities are introduced because μ_i^M no longer provides an unbiased estimate of either the exploitation rate or encounter rate for the marked cohort due to the release of marked fish (some of which will die upon release). Note that $\gamma < 1.0$ can also be used to account for legal-sized marked fish that are released intentionally by anglers. The marked cohort exploitation rate is now subject to the same bias as the unmarked cohort but it is usually much smaller because recognition rates for marked fish are typically high ($\geq$0.90). When there is error in identifying marked fish, an unbiased calculation of the total exploitation rate for the marked cohort is provided by

$$\hat{\mu}_I^M = 1 - \left(1 - \sum_i^I \mu_i^M \right)^{\delta_{MI}^{W}}. \tag{14}$$

When equation (14) is solved for μ_I^M the result is

$$\mu_I^M = 1 - \left(1 - \hat{\mu}_I^M\right)^{1/\delta_{MI}^{W}}. \tag{15}$$

This definition of μ_I^M can be substituted back into equation (13) to define the unbiased exploitation rate for the unmarked cohort relative to the unbiased exploitation rate on the marked cohort:

$$\hat{\mu}_I^U = 1 - \left(1 - \hat{\mu}_I^M\right)^{\delta_{UI}^{W}/\delta_{MI}^{W}}. \tag{16}$$

Equations (13) and (16) are the key equations needed to provide unbiased calculations of unmarked exploitation rates and mortalities when there are MSF and NSF operating concurrently during a modeled time step and there is mark-recognition error in the MSF. Equations (12) and (14) are the analogous equations needed to provide unbiased calculations of marked exploitation rates and mortalities.

Allocating total mortalities to fisheries and sources of mortality.—For management purposes, the total number of unmarked mortalities that are projected to occur in all fisheries ($N^U \cdot \hat{\mu}_I^U$) must be apportioned to each fishery in the time period. The proportional contribution of a cohort's "simple" (biased) exploitation rate for each fishery to the sum of the individual "simple" exploitation rates for all fisheries in the time period can be used to apportion total mortalities to each fishery:

$$\hat{D}_i^U = \left(N^U \cdot \hat{\mu}_I^U\right) \cdot \pi_i \ \textit{with}\ \pi_i = \frac{\mu_i^M \cdot \delta_{Ui}}{\sum_i^I \left(\mu_i^M \cdot \delta_{Ui}\right)} = \frac{\tilde{\mu}_i^U}{\sum_i^I \tilde{\mu}_i^U}, \tag{17}$$

where $\hat{D}_i^U$ is the total number of unmarked mortalities occurring in fishery i and the sum of the proportions of unmarked mortalities occurring in each fishery will equal 1 ($\Sigma \pi_i = 1$). This is equivalent to the unbiased exploitation rate for the unmarked cohort in fishery i being

$$\hat{\mu}_i^U = \hat{\mu}_I^U \cdot \pi_i. \quad (18)$$

A similar procedure can be used to apportion total marked mortalities to fisheries.

Once total mortalities for a fishery have been calculated ($\hat{D}_i^U$), they can be apportioned to landed (catch) and nonlanded mortalities using methods similar to those used above to apportion total mortalities to fisheries. For an unmarked cohort, landed catch for fishery i ($\hat{D}_{Li}^U$) is calculated as

$$\hat{D}_{Li}^U = \hat{D}_i^U \cdot \frac{1-\zeta_i}{(1-\zeta_i)+(\zeta_i \cdot \delta_i)} \quad (19)$$

and nonlanded mortality ($\hat{D}_{Ni}^U$) is calculated as

$$\hat{D}_{Ni}^U = \hat{D}_i^U \cdot \frac{(\zeta_i \cdot \delta_i)}{(1-\zeta_i)+(\zeta_i \cdot \delta_i)}. \quad (20)$$

Similarly for a marked cohort

$$\hat{D}_{Li}^M = \hat{D}_i^M \cdot \frac{\gamma_i}{\gamma_i + [(1-\gamma_i)\cdot \delta_i]} \quad (21)$$

and nonlanded mortality ($\hat{D}_{Ni}^M$) is calculated as

$$\hat{D}_{Ni}^M = \hat{D}_i^M \cdot \frac{(1-\gamma_i)\cdot \delta_i}{\gamma_i + [(1-\gamma_i)\cdot \delta_i]}. \quad (22)$$

Simulation model description.—The simulation model we used was very similar to the individual-based simulation model described by Yuen and Conrad (2011). There were three fisheries simulated, two MSF with different release-mortality rates and one nonselective fishery. One difference between the models was that the catch target for the nonselective fishery was based on a number of marked fish landed in our simulations and not the combined landed catch of marked and unmarked fish (Yuen and Conrad 2011). A target landed catch of marked fish for each fishery modeled was established using μ_i^M.

Starting sizes for the marked and unmarked cohorts were always 200,000 fish each. Performance of the unbiased methods was evaluated using simulations in which we varied three main categories of parameters as follows:

- μ_I^M for the marked cohort (ranging from 0.08 to 0.80);
- combinations of mark-recognition rates (γ_i and ζ_i):
  - 100% mark recognition for the unmarked and marked cohorts,
  - 90% mark recognition for the unmarked cohort and 100% for the marked cohort,
  - 100% mark recognition for the unmarked cohort and 90% for the marked cohort,
  - 90% for both the unmarked and marked cohorts,
  - 90% mark recognition for the unmarked cohort and 95% for the marked cohort, and
  - 95% mark recognition for the unmarked cohort and 90% for the marked cohort; and
- proportions of the total exploitation rate of the marked cohort occurring in MSF:
  - scenario 1 = about 25% of μ_I^M for the marked cohort in MSF,
  - scenario 2 = about 43% of μ_I^M for the marked cohort in MSF, and
  - scenario 3 = about 75% of μ_I^M for the marked cohort in MSF.

A total of 72 different simulations were run for these analyses (6 combinations of mark-recognition rates for the unmarked and marked cohorts × 3 different proportions of the total exploitation rate on the marked cohort occurring in MSF × 4 different levels of μ_I^M at each combination of the previous factors). The simulations conducted for this study did not include any increase in the release-mortality rate with successive encounters.

For the unmarked cohort, we calculated mean relative bias as the difference between the exploitation rates calculated using the equations described above and simulation (model) exploitation rates expressed relative to the model result:

$$relative\ bias = \frac{\sum\left(\frac{\mu_{EQ}^U - \mu_{model}^U}{\mu_{model}^U}\right)}{n}, \quad (23)$$

where n = number of replications of a simulation (100 for all evaluations reported here) and the equations are either the simple biased equation (for each fishery or summed over all three fisheries) or the unbiased versions of the equations (13 and 16). Relative bias was calculated similarly for the marked cohort.

Application to the FRAM.—In the FRAM, as long as fisheries are modeled as rates, the solutions for computing unbiased exploitation rates for the unmarked cohort presented here work well and produce results that match expectations. The FRAM output deviates from expectations for scenarios where MSF are modeled as quotas and recognition of the mark status of captured fish is imperfect, e.g., a proportion of the marked fish encountered are released or a portion of the unmarked fish encountered are retained. In the FRAM, mark-selective quotas are modeled as the landed catch of marked and unmarked fish. The unmarked landed catch is the result of anglers mistakenly retaining a portion of the unmarked fish encountered during MSF. All quota fisheries are initially modeled at base period exploitation rates. For a marked cohort, the total landed catch of stock s in fishery i is calculated using the base period exploitation rate and the projected current year abundance of stock s:

$$\tilde{D}_{Lsi}^M = \bar{\mu}_{si}^{Base} \cdot N_s^M \cdot \gamma_i \quad (24)$$

and for an unmarked cohort

$$\tilde{D}^U_{Lsi} = \bar{\mu}^{Base}_{si} \cdot N^U_s \cdot (1 - \zeta_i). \tag{25}$$

The FRAM then sums landed catch over all stocks encountered in a fishery:

$$Base\ Period\ Catch_i = \sum_s \tilde{D}^j_{Lsi}, \tag{26}$$

where $j = M$ or U depending upon the mark status of the cohort. In a final step, the FRAM compares the current year catch quota for the fishery with this base period catch and scales the base period exploitation rate by the ratio of quota catch to base period catch:

$$Scalar_i = \frac{Catch\ Quota\ Fishery_i}{Base\ Period\ Catch_i} \tag{27}$$

and

$$\mu^M_{si} = Scalar_i \cdot \bar{\mu}^{Base}_{si}. \tag{28}$$

The resulting stock-specific exploitation rate for fishery i (μ^M_{si}) can then be used to compute the unbiased exploitation rate for the unmarked component of stock s. Even though the unbiased equations are used to calculate the unmarked exploitation rate, this rate can be biased because the computation of μ^M_{si} may be biased if there is imperfect mark recognition.

This problem cannot be addressed solely on the stock level, since a fishery quota is made up of the catch of many stocks. However, an iterative solution can be found, where the quota is first modeled using base period exploitation rates. Finding the correct $\hat{\mu}^M_{si}$ for a quota fishery can be accomplished by using the unbiased calculations presented earlier in this paper:

$$\hat{\mu}^M_{si} = \left[1 - \left(1 - \sum_i^I \mu^M_{si}\right)^{\delta^W}\right] \cdot \pi_{si}, \tag{29}$$

where μ^M_{si} for quota fishery i is the base period exploitation rate for stock s ($\bar{\mu}^{Base}_{si}$). Then the landed catch of marked fish is

$$\tilde{D}^M_{Lsi} = \hat{\mu}^M_{si} \cdot N^M_s \cdot \frac{\gamma_i}{\gamma_i + [(1 - \gamma_i) \cdot \delta_i]} \tag{30}$$

and the landed catch of unmarked fish

$$\tilde{D}^U_{Lsi} = \hat{\mu}^U_{si} \cdot N^U_s \cdot \frac{1 - \zeta_i}{(1 - \zeta_i) + (\zeta_i \cdot \delta_i)}, \tag{31}$$

where $\hat{\mu}^U_{si}$ is calculated using equations (13) or (16).

Total catch and a scalar are then computed as in equations (26) and (27) using these new estimates of landed catch. The scalar is applied to the base period exploitation rate and the iterative loop (equations 29, 30, and 31 and the computation of total catch and a new scalar) is repeated. Iterations are continued until the newly computed value is within a predetermined number of fish of the target quota.

RESULTS

Because the calculation of fishery-specific exploitation rates for the unmarked cohort is a two-step process using the proposed unbiased methods (first estimate the total exploitation rate and then partition this rate to the contributing fisheries), the results are presented in two sections. First, we compare the calculations of the total exploitation rate for the unmarked cohort by the biased and unbiased methods to simulation results. We then examine fishery-specific calculations for subsets of the simulation results to compare results of the two calculation methods

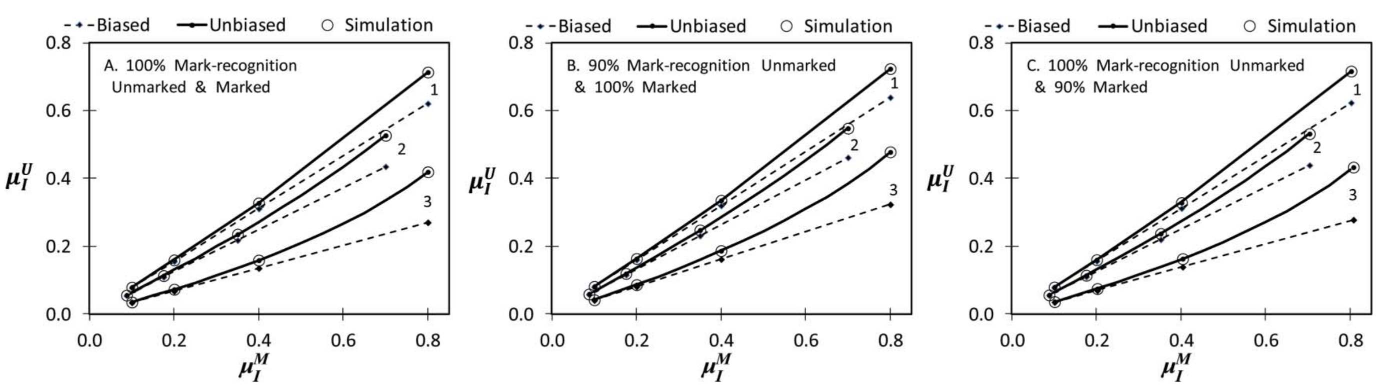

FIGURE 2. Total exploitation rates on the unmarked cohort (μ^U_I) as a function of μ^M_I for the biased and unbiased calculations compared with the simulation results. Three different scenarios for the proportion of μ^M_I occurring in mark-selective fisheries (1) 25%, (2) 43%, and (3) 75% are examined (numbers to the right indicate the scenario). Mark-recognition rates of (**A**) 100% for both unmarked and marked salmon, (**B**) 90% for unmarked and 100% for marked salmon, and (**C**) 100% for unmarked and 90% for marked salmon.

to the simulation results, illustrate common trends, and demonstrate that the unbiased methods perform well across the range of fishery parameters explored.

Estimation of Total Exploitation Rate for the Unmarked Cohort

There was strong agreement between total exploitation rates on the unmarked cohort calculated using the unbiased methods and the simulation results. Relative biases for the unbiased calculations were between −0.5% and 0.5% for all simulations. For comparison, relative biases for the biased calculations were between −1.1% and −35.8%.

The differences between the biased calculations and simulation results increased as μ_I^M increased and also increased as the proportion of μ_I^M in MSF increased (Figure 2). For a given μ_I^M, increasing the proportion occurring in MSF is mathematically equivalent to decreasing the weighted release mortality rate which has been shown to increase bias. The unbiased calculations of the total exploitation rate on the unmarked cohort were essentially the same as the simulation results (Figure 2). By comparing Figures 2A, 2B, and 2C it can be seen that a low level of mark-recognition error (10%) for either the unmarked (Figure 2B) or marked (Figure 2C) cohorts has little effect on the results when total exploitation rate is examined.

As has been previously demonstrated by Lawson and Sampson (1996) and Yuen and Conrad (2011), for a fixed set of release mortality rates, relative bias in the calculation of total exploitation rate on the unmarked cohort increases as the exploitation rate increases on the marked cohort (Figure 3). The effect of increasing the proportion of the total exploitation rate on the marked cohort in MSF is seen by comparing Figures 3A, 3B, and 3C. Noting that the three panels have different scales for the *y*-axis, maximum relative bias increased from about 12% (Figure 3A) to nearly 35% (Figure 3C) for $\mu_I^M = 0.80$. Relative bias decreases slightly as the recognition rate for unmarked fish decreases because a lower mark-recognition rate for the unmarked cohort in MSF reduces the number of unmarked fish released and available for recapture. Relative bias for the unbiased calculations is zero or nearly zero in every instance (Figure 3).

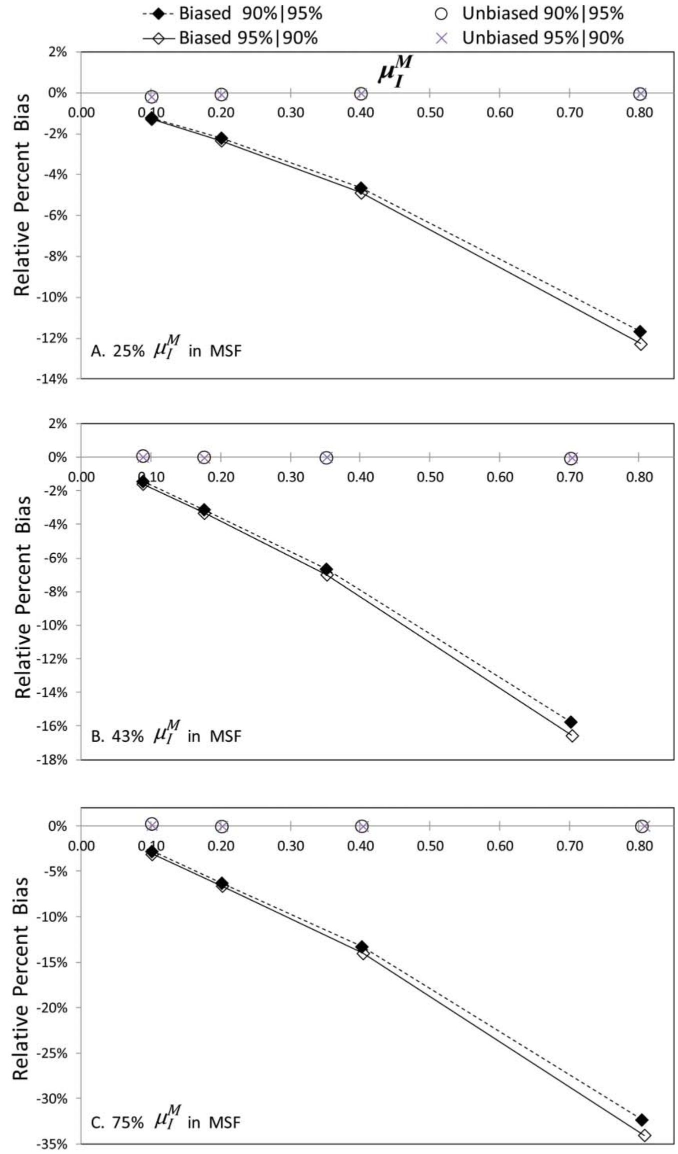

FIGURE 3. Comparison of bias (relative to simulation results) for biased and unbiased calculations of μ_I^U over a range of μ_I^M, two different scenarios for marked and unmarked recognition rates (% unmarked | % marked), and three different scenarios for the proportion of μ_I^M occurring in mark-selective fisheries (**A**) 25%, (**B**) 43%, and (**C**) 75%.

Estimation of Fishery-specific Exploitations Rates for the Unmarked Cohort

Agreement between fishery-specific exploitation rates on the unmarked cohort calculated using the unbiased methods and the simulation results was very good. For the two MSF simulated, relative biases for the unbiased calculations were between −1.2% and 1.6% for all simulations. This is an improvement as the relative biases for the biased calculations were between −0.1% and −35.9% (Table 2). The relative biases that were furthest from zero for the unbiased calculations, and the relative biases that were closest to zero for the biased calculations, all occurred for the simulations with the lowest μ_I^M exploitation rates (<0.20) and smallest proportions of μ_I^M occurring in MSF (<50%). At low levels of exploitation in MSF, the simulation results are more variable than at higher exploitation rates. The higher relative biases for the fishery-specific unbiased calculations of exploitation rates on the unmarked cohort are a result of random variation in the simulation results. At higher levels of exploitation in MSF, the relative biases for the unbiased calculations of fishery-specific exploitation rates are in the same range as those for the unbiased calculations for the total unmarked cohort exploitation rate discussed in the previous section, i.e., $< \pm 1\%$.

TABLE 2. Summary of the relative bias in fishery-specific exploitation rate calculations for the unmarked cohort by the biased and unbiased methods compared with simulation results. Summarized for each level of the percentage of the total marked cohort exploitation rate (μ_I^M) occurring in MSF and across the six combinations of mark-recognition rates for the unmarked and marked cohorts and four different values of μ_I^M used in the simulations. There are a total of 24 observations in each level summarized.

		Biased calculations			Unbiased calculation		
% of μ_I^M in MSF	Summary statistic	MSF #1	MSF #2	NSF	MSF #1	MSF #2	NSF
25%	Mean	−5.2%	−4.9%	−5.1%	−0.1%	0.2%	−0.1%
	Median	−3.5%	−3.6%	−3.5%	0.0%	0.1%	0.0%
	Minimum	−13.0%	−12.9%	−13.0%	−1.2%	−0.4%	−0.2%
	Maximum	−1.0%	−0.1%	−1.2%	1.4%	0.9%	0.1%
43%	Mean	−6.9%	−7.1%	−7.0%	0.2%	−0.1%	0.0%
	Median	−5.0%	−5.3%	−5.1%	0.0%	−0.1%	0.0%
	Minimum	−17.4%	−17.6%	−17.5%	−0.7%	−0.4%	−0.1%
	Maximum	−0.5%	−1.2%	−1.4%	1.6%	0.3%	0.2%
75%	Mean	−14.3%	−14.5%	−14.2%	0.0%	−0.2%	0.1%
	Median	−10.1%	−10.3%	−10.0%	0.1%	−0.2%	0.1%
	Minimum	−35.8%	−35.9%	−35.8%	−0.7%	−0.3%	0.0%
	Maximum	−2.9%	−3.0%	−2.6%	0.5%	0.1%	0.5%

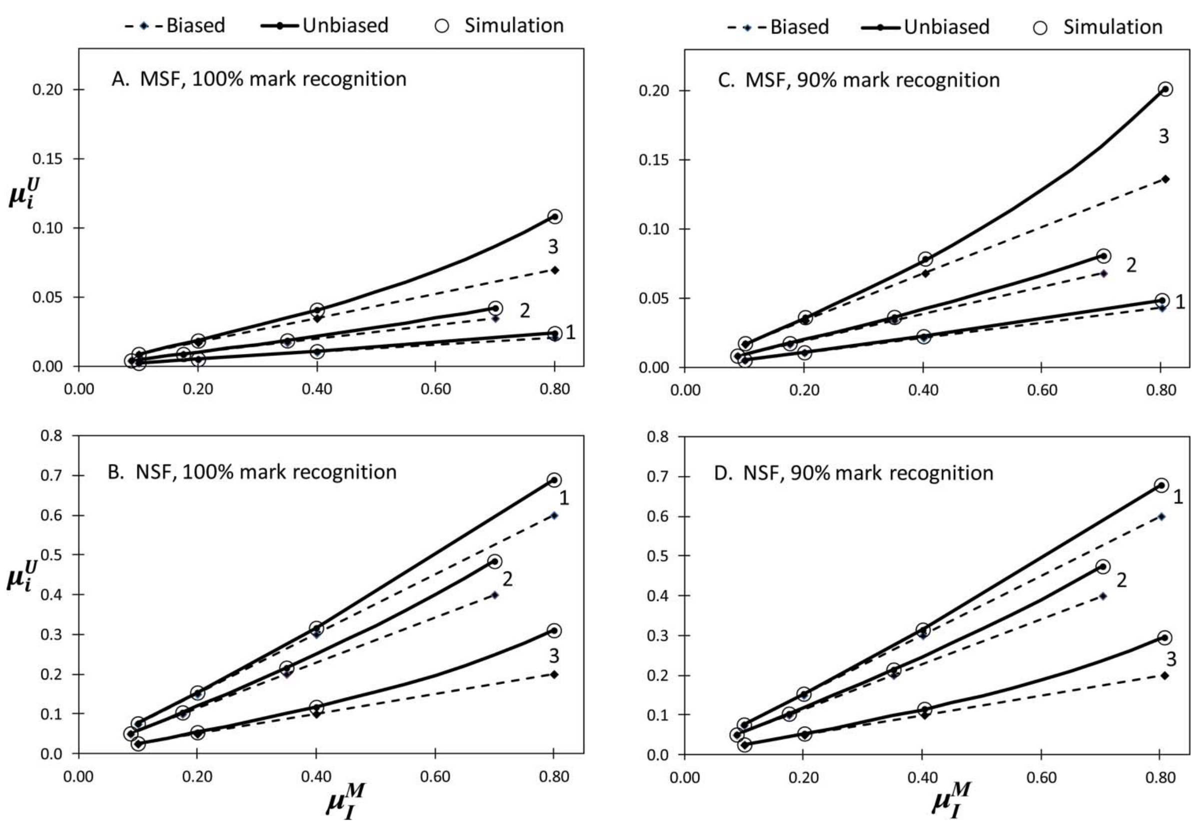

FIGURE 4. Exploitation rates on the unmarked cohort as a function of μ_I^M in MSF (combined) and NSF for the biased and unbiased calculations compared to the simulation results. Three different scenarios for the proportion of μ_I^M occurring in MSF (1) 25%, (2) 43%, and (3) 75% are examined (numbers to the right indicate the scenario). Panels (**A**) and (**B**) show MSF with 100% mark recognition, and panels (**C**) and (**D**) show MSF with 90% mark recognition (mark-recognition rates specified are for both marked and unmarked fish).

As was shown previously for all fisheries combined (Figure 2), the bias in the calculated exploitation rate on the unmarked cohort in each fishery increases with μ_I^M (Figure 4). For a specific μ_I^M, the bias also increases as the proportion of μ_I^M in MSF increases for both the mark-selective and nonselective fisheries. The unbiased calculations of exploitation rates on the unmarked cohort were essentially the same as the simulation results for both the MSF and NSF (Figure 4). Mark-recognition error in MSF increased the exploitation rate on the unmarked cohort in the MSF but had little effect on relative bias. This increase in the exploitation rate on the unmarked cohort in MSF due to mark-recognition error is due to the following:

- unmarked fish being mistakenly landed instead of released, and
- the fishery sorting through more marked fish (compared with the same fishery with $\gamma = 1.0$) to reach the target for landed marked fish because marked fish are being mistakenly released.

Figure 5 compares fishery-specific relative bias for different scenarios when the mark-recognition rate for unmarked fish is 90% and 100% for marked fish. Relative bias is the same in each of the mark-selective fisheries and the nonselective fishery for a given μ_I^M and proportion of μ_I^M in MSF (Figure 5). As shown previously, bias increases with μ_I^M. The slightly higher level of bias for the unbiased calculations ($\pm 1.5\%$) at low levels of total exploitation on the marked cohort (≤ 0.10) due to variability of the simulation results is seen in Figure 5. For all other cases, relative bias for the unbiased calculations is not discernable from zero.

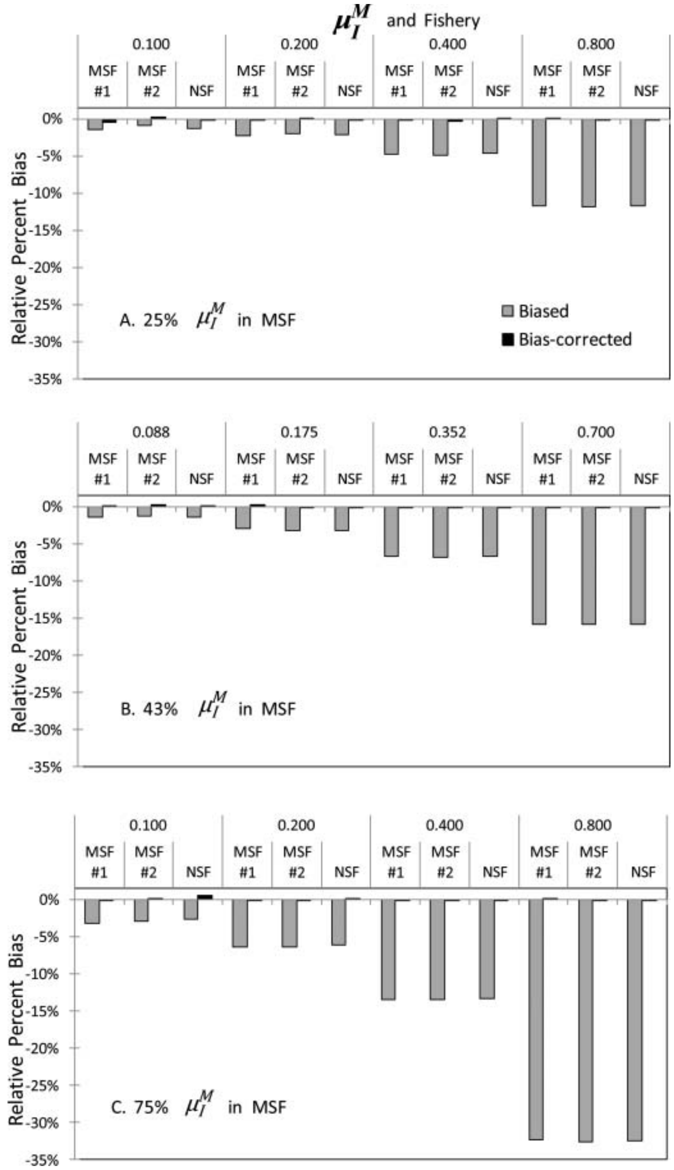

FIGURE 5. Comparison of bias (relative to simulation results) for biased and unbiased calculations of μ_i^U in MSF and NSF over a range of μ_I^M, 90% mark recognition for the unmarked cohort, and three different scenarios for the proportion of μ_I^M occurring in MSF (**A**) 25%, (**B**) 43%, and (**C**) 75%.

DISCUSSION

The relative bias for the simulation model used by Yuen and Conrad (2011) was dependent on the unmarked-to-marked fish ratio for the starting cohorts. This was because their simulation model used the total landed catch of both marked and unmarked fish to establish a stopping rule in NSF (essentially a combined quota for marked and unmarked fish). For the simulation model used for this paper, the stopping rule for both MSF and NSF was based on the landed catch of marked fish (a marked fish only quota). This simplifies the development of unbiased calculations and results in relative bias no longer being dependent on the unmarked-to-marked fish ratio for the starting cohorts. The actual number of unmarked mortalities associated with a given landed catch of marked fish is identical for the two models. The differences between the two simulation models arise because the NSF are ended during the simulations at different numbers of landed marked fish.

Conrad and Hagen-Breaux (2011) examined the relative bias in estimates of exploitation rates on unmarked stocks for the 2009 and 2010 preseason Coho FRAM runs used by the PFMC (2009, 2010). They applied the unbiased methods proposed here to the FRAM output and compared unbiased calculations with original FRAM calculations of exploitation rates for each unmarked stock in the model. Relative bias for total exploitation rate calculations (defined as total fishery mortalities divided by total fishery mortalities plus escapement) across all model time periods was between 0.07% and −3.5% for all stocks and averaged −0.89% and −0.68% in 2009 and 2010, respectively. Applying unbiased methods to the model output resulted in an exploitation rate that exceeded the guidelines for two listed Coho Salmon stocks. For one listed stock, fisheries were structured to fish up to the exploitation rate guideline; thus, after accounting for bias the exploitation rate for this stock exceeded the guideline in both years (Conrad and Hagen-Breaux 2011).

Several current salmon fishery management models, used for both preseason planning and postseason assessment of fisheries, calculate mortalities for unmarked cohorts in MSF using methods that rely on a linear relationship between a base period exploitation rate ($\bar{\mu}^{Base}$) and a release-mortality rate. Previous research has demonstrated that the single-pool paradigm that most of these models rely on results in an underestimate of the unmarked mortalities occurring in MSF (Lawson and Sampson 1996) and any concurrent NSF (Yuen and Conrad 2011). We have proposed methods that correct for this bias and demonstrated through simulation that they provide unbiased calculations of the unmarked mortalities in both MSF and NSF.

A key assumption of these single-pool models is that all salmon of the species of interest are randomly mixed throughout all fishery areas during the time period being modeled. In our simulations, this process is modeled by allowing an unmarked fish encountered and released by a mark-selective fishery to be immediately available for recapture by the same fishery or any other fisheries in the same time period (as long as the marked fish quota for a fishery has not been met). This assumption is not met in reality as, for example, a fish released in Puget Sound cannot be immediately available for recapture by a fishery in northern California.

But this assumption is necessary as alternatives to the single-pool model require detailed information on the migration routes and migration timing for a large number of hatchery and wild stocks that is currently not available. The large number of stocks involved in some of the management models (e.g., 123 Coho Salmon stocks and 38 Chinook Salmon stocks for the management models used by the PFMC) presents a daunting challenge for the collection of the data needed to parameterize these models. Zhou (2004) describes a pipeline model that provides estimates of unmarked mortalities in MSF using change-in-ratio methods similar to those used to estimate animal abundance (Seber 1982). Two important assumptions of his model are that the marked and unmarked stocks migrate together through a series of mark-selective and nonselective fisheries in a known sequence (the pipeline) and that the fisheries are of sufficiently short duration so that they maintain a constant ratio of unmarked to marked fish in the catch. Zhou's equations do not allow for parallel or concurrent fisheries or for multiple encounters in MSF. Given the large number of stocks and fisheries involved in the FRAM, it is not possible to specify migration pipelines with currently available migration information. Given its assumptions and requirement for additional migration information, it is not clear that this model offers any advantages over the current single-pool model once unbiased methods have been implemented.

Models using continuous equations to project population growth have a long history of use in population dynamics and harvest management (e.g., Malthusian growth model, Baranov's catch equation). While these calculations are very useful in the realm of fisheries management, their application is not limited to this field. Any discipline dealing with instantaneous rates of change, such as economics or population biology, is familiar with the basic concepts presented here. This paper adapts the basic equation to specifically deal with problems commonly encountered in fisheries management, such as multiple sources of gear-related mortalities and complex regulatory regimes. Mark-selective fisheries are becoming increasingly popular in response to ESA listings and conservation concerns. When applied in the FRAM, the equations in this paper use historical exploitation rate data from retention fisheries to estimate mortalities on populations exposed to a sophisticated regime of retention and MSF. Mark-selective fisheries require the release of unmarked salmon, subjecting populations to a range of values for surviving gear encounters that are a function of release rates (intentional and unintentional) as well as release mortality rates. The algorithms presented here capture these processes by using a weighted release mortality rate in conjunction with the basic exponential algorithm.

The FRAM is the main model used to estimate salmon mortalities in marine MSF under the jurisdiction of the PFMC. The Coho FRAM is currently being modified to incorporate the methods described in this paper to account for the bias introduced by MSF for Coho Salmon. Other salmon fishery management models are also subject to the bias described in this paper. Spreadsheet-based models, for instance, are commonly used to evaluate the impacts of recreational and commercial MSF on salmon in terminal freshwater systems (e.g., in Puget Sound and the Columbia River). Bias in these fisheries can arise due to inconsistencies between the idealized continuous mortality process and a combination of temporal and spatial model resolution effects. More broadly, any model used to evaluate total fishery impacts when there is a significant nonretention component (e.g., trout catch-and-release fisheries, fisheries with mandatory release of nontarget species, or release due to minimum size limits) is subject to the biases described in this paper. For salmon, this includes the Pacific Salmon Commission's exploitation rate analysis (JCTC 2012), which accounts for landed and nonretention fishery mortalities in a variety of U.S. and Canadian fisheries, and the Klamath Ocean Harvest Model, which accounts for landed and nonretention mortalities in Chinook Salmon fisheries off Oregon and California (M. Mohr, National Marine Fisheries Service, personal communication). Although we are not intimately familiar with planning models used beyond the salmon arena, we suspect the issues addressed in this paper are germane to a variety of other exploited fish and shellfish species.

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