Spatial Heterogeneity, Variable Rewards, Tag Loss, and Tagging Mortality Affect the Performance of Mark–Recapture Designs to Estimate Exploitation: an Example using Red Snapper in the Northern Gulf of Mexico

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Spatial Heterogeneity, Variable Rewards, Tag Loss, and Tagging Mortality Affect the Performance of Mark–Recapture Designs to Estimate Exploitation: an Example using Red Snapper in the Northern Gulf of Mexico

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Abstract
Accurate estimates of exploitation rate are essential to the management of exploited fisheries. Tagging studies are often used to estimate exploitation rates, but the performance of these approaches depends strongly on study design characteristics and the magnitude of assumption violations. We simulated a suite of candidate study designs for 1-year high-reward and variable-reward tagging studies, exploring a range of sample sizes (number of tagged fish), exploitation rates, tagging mortality rates, tag loss rates, proportions of double-tagged fish, and spatial variation in fish density, tag releases, and fishing effort. We calculated the uncertainty, biases, and reward costs of these candidate study designs to determine the most cost-effective approach to accurately estimate exploitation rate for Red Snapper *Lutjanus campechanus* in Alabama waters of the Gulf of Mexico. We also investigated how incorrectly assuming a 100% reporting rate would affect these study results. Our simulations demonstrated that using all high-reward tags provided more accurate and precise exploitation rate estimates than the variable-reward approach but only if 100% reporting could be safely assumed. Further, distributing tags uniformly over the study area when the true spatial distribution of the population and fishing pressure varied over that area drastically biased exploitation rate estimates, suggesting that prior knowledge of the population's true spatial distribution over the study area is needed to ensure accurate estimates of exploitation rate. The most cost-effective study design involved tagging between 400 and 1,600 fish with high-reward tags, with 40% of the fish double-tagged, and the tags spatially distributed in the same proportion as the population. However, violation of the 100% reporting rate assumption resulted in a proportional downward bias in the estimated exploitation rate. Simulation studies such as this are critical to ensure that cost-effective study designs produce accurate and precise estimates of exploitation rate, particularly for high-value species such as Red Snapper.

Designing tagging studies to estimate fishing mortality of exploited stocks requires an understanding of the underlying assumptions and structure of the study design and how these factors affect the accuracy, precision, and costs of the study. For instance, an important assumption researchers often make when conducting tagging studies is that tagged fish and untagged fish are equally vulnerable to harvest (Ricker 1975; Pollock et al. 2001; Miranda et al. 2002; Meyer and Schill 2014). However, if the distribution of the population and exploitation rates are spatially varied over the study area and if tagged fish are not distributed according to these spatial variations (e.g., accurately in proportion to the population), this assumption would be violated without fully understanding how the violation may have affected study results. In addition, tagging studies will often either assume a tag loss rate or estimate it simultaneously by double-tagging fish (Pollock et al. 2001; Miranda et al. 2002). However, uncertainty remains on the impact of assuming an incorrect tag loss rate or knowing the appropriate proportion of double-tagged fish needed to accurately estimate the tag loss rate. Further,

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researchers have often assumed that using all high-reward tags would require a large monetary investment, making this type of study cost prohibitive (Miranda et al. 2002; Meyer and Schill 2014). However, others have disputed this assumption, stating that there is little evidence to support such a claim and that high-reward tagging studies should not be so readily dismissed (Pollock et al. 2001; Walters and Martell 2004; Meyer and Schill 2014). To our knowledge, no studies have examined the extent to which the trade-offs associated with variable-reward versus high-reward tagging studies (e.g., costs, reporting rates, and tagging effort; Pollock et al. 2001) may compromise the accuracy and precision of study results. Researchers have stated the importance of this knowledge (Pine et al. 2003), but few have specifically demonstrated how and by what degree these assumptions and factors impact study outcomes using several scenarios where underlying assumptions are violated through model simulation (Minta and Mangel 1989). Further, none to our knowledge have reported the sample sizes (number of tagged fish) and monetary costs of these scenarios to determine the best and most cost-effective approach to determine exploitation rate.

The fishery for Red Snapper *Lutjanus campechanus* is arguably the most controversial fishery in the northern Gulf of Mexico (Hood et al. 2007; Cowan et al. 2011). Statistical catch-at-age models have historically been used to estimate exploitation rates of Red Snapper. These state-of-the-art models are highly complex, inferring exploitation rates from harvest, age or size composition, and survey catch rate data. However, the estimates from these assessments have been contentious due to uncertainty in the data, debates about model formulation, and a lack of understanding of the methods by stakeholders. Tensions have heightened further in recent years, as increasingly restrictive regulatory actions have been taken to curtail exploitation rates to achieve federal stock-rebuilding goals. For instance, the duration of the recreational harvest season has steadily declined, reaching a historical low of 9 d in 2014, which was viewed unfavorably by recreational anglers and businesses that depend on that fishery. The short recreational season has been particularly controversial in Alabama, where recreational harvest makes up approximately 95% of the total Red Snapper harvest (Alabama Department of Conservation and Natural Resources [ALDCNR], personal communication).

Given the economic and social importance of the Gulf of Mexico fishery for Red Snapper, its current status as overfished, and the current contention between fishery managers and stakeholders, innovative approaches for assessing the status of the stock are warranted and of critical importance (Cowan et al. 2011). Alternative assessment methods for Red Snapper, such as a reward tagging study, could complement the National Marine Fisheries Service's (NMFS) catch-at-age model (SEDAR 2013). Indeed, a recent push by Alabama Senator Richard Shelby to examine the management of Red Snapper in the Gulf of Mexico has resulted in \$10,000,000 being allocated to examine alternative approaches to data collection and analysis, which could include reward tagging studies (U.S. House of Representatives 2016; U.S. Senate 2016). The first and most essential step in performing a reward tagging study, however, should be to evaluate the performance of candidate study designs via simulation to ensure that the resulting estimates of exploitation rate are accurate and precise.

We estimated the performance and costs of several candidate study designs for a 1-year reward tagging study to estimate directed Red Snapper recreational fishing mortality in Alabama waters. Specifically, we were interested in (1) where and how many fish to tag; (2) how the spatial variation in fish abundance, tag distribution, fishing effort, and tagging mortality affects the reliability of exploitation rate estimates and project costs; (3) what proportion of tagged fish should be double-tagged to estimate tag loss rates; (4) how incorrectly assuming a 100% reporting rate for high-reward tags would affect study results; and (5) the relative performance and costs of high-reward and variable-reward tagging approaches.

METHODS

Approach.—We evaluated reward tagging designs for a 1-year study to estimate directed (i.e., open season only) recreational fishing mortality of Red Snapper in Alabama waters by simulating the release of tagged fish into the population immediately prior to the opening of the recreational fishing season. Reward tagging studies rely on anglers to report the capture of tagged fish, for which they receive a monetary reward. Because of the short duration of the recreational fishing season (<50 d in 2010–2014), commercial harvest (only making up approximately 5% of the total annual harvest in Alabama waters; ALDCNR, personal communication) was assumed negligible. Red Snapper natural mortality (M) was also assumed negligible over this short time period. This assumption holds for Red Snapper because of the estimated low annual M of 0.1, which equates to a daily rate of 0.00027 (SEDAR 2013). Over a period of 50 d, this rate would only contribute 0.01 to total mortality and little if any change in exploitation rate estimates. For example, using a true fishing mortality rate (F) of 0.2 that is assumed to occur only within the 50-d fishing season, the exploitation rate would be estimated at 0.18 over 50 d (using $F/[F + M \times 50/365] \times [1 - \mathrm{EXP}\{-F - M \times 50/365\}]$) regardless of whether M is set at 0.0 or 0.1 year^{-1}. For species with higher M values of 0.2 and 0.3, natural mortality would still only contribute 0.03–0.04 to total mortality rates over 50 d. The exploitation rate (i.e., proportion of the stock harvested; fishing mortality) could therefore be estimated as the proportion of tagged Red Snapper that are harvested and reported by recreational anglers during the fishing season after accounting for tag loss, tagging mortality, and angler reporting rate. Tag loss was estimated simultaneously by double-tagging the fish and estimating the tag loss rate from the proportion of double-tagged fish that were reported as having a single tag. We assumed that tagging mortality was known from auxiliary studies (Campbell et al. 2014), and angler reporting rates were assumed to be 100% due to the high-dollar reward. In a subset of simulations, we also investigated the impact of incorrectly assuming a 100% reporting rate.

We divided our conceptual Red Snapper population into shallow (>30-m), intermediate (30–60-m), and deep (<60-m) depth strata (*d*; Figure 1) because the spatial distribution of Red Snapper is not uniform with depth (Mitchell et al. 2004) and because postrelease mortality is positively related to depth due to barotrauma (Gitschlag and Renaud 1994; Rummer and Bennett 2005). Similar depth ranges have been used to stratify Red Snapper abundance and catch distributions in other studies (Mitchell et al. 2004; SEDAR 2013). We simulated 10 scenarios that differed in terms of the true proportional distribution of Red Snapper abundance across depth strata (D_d), the proportional allocation of tags across strata (P_d), the true exploitation rate across strata (U_d), the tagging mortality rate across strata (Campbell et al. 2014), the study type (high reward versus variable reward), the true rate of tag loss (TLR; 0.1, 0.2, or 0.3), and the proportion of fish that were double-tagged to estimate the tag loss rate (0.2 or 0.4; see the Supplement available in the online version of this article).

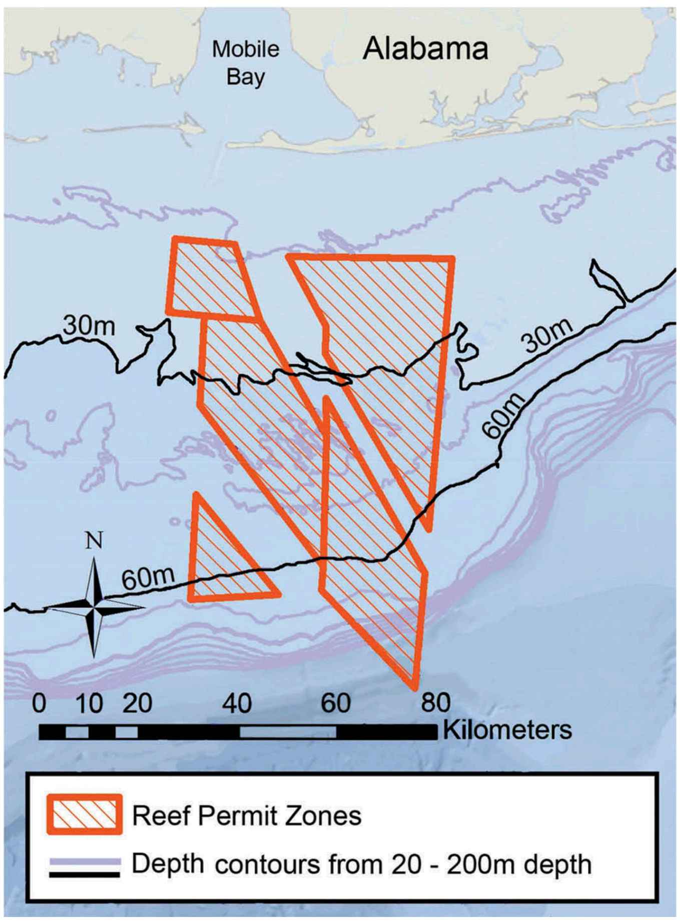

FIGURE 1. Hypothetical tagging study location in Alabama waters of the Gulf of Mexico for model simulations of Red Snapper. Three areas were delineated by depth for each simulated scenario: <30-m, 30–60-m, and >60-m depth (indicated by black contour lines). The reef permit zones (indicated by orange lines) are areas with artificial reefs and constitute the primary Red Snapper fishing locations in Alabama waters.

For those characteristics that were varied by depth, each was either uniform across depth strata or varied with depth to reasonably reflect the distribution of these factors for Red Snapper in the northern Gulf of Mexico off the coast of Alabama (Table 1). For instance, for scenarios in which relative abundance varied across depth strata, we assumed that 20% of the population was located in shallow water (<30 m), 30% was located in intermediate depths (30–60 m), and 50% was located in deeper water (>60 m). These values were estimated using mean proportional relative abundance data collected from the vertical line commercial fleet during 2007–2009 and 2011–2013 (SEDAR 2013; Nicholas Ducharme-Barth, University of Florida, personal communication). Previous research has also suggested that tagging mortality rates of captured Red Snapper varied by depth, with shallow depths having the lowest rate (0.1), intermediate depths having an intermediate rate (0.2), and deeper depths have the highest tagging mortality rate (0.4; Table 1; Campbell et al. 2014). The proportional distribution of Alabama Red Snapper exploitation (i.e., fishing effort) across depth strata was assumed based on input from 50 local boat captains and enforcement officers (John Mareska, ALDCNR, personal communication) and was 50% at shallower depths, 40% at intermediate depths, and 10% at the deepest stratum (Table 1).

A reward payment of $250 per tag was assumed to elicit a 100% reporting rate (Table 1). We based this assumption on previous studies (Nichols et al. 1991; Denson et al. 2002; Taylor et al. 2006). First, a study on banded ducks from 1988 showed that a reward of $100 resulted in a 100% reporting rate by hunters (Nichols et al. 1991). This amount was also found sufficient to produce 100% reporting in a 2002 mark–recapture study on Red Drum *Sciaenops ocellatus* by Denson et al. (2002). To ensure a 100% reporting rate, we adjusted the $100 reward for inflation by using the consumer price index inflation factor for 1988–2016 from the Bureau of Labor Statistics (2015). This correction for inflation resulted in a reward amount of approximately $200. To further guard against nonreporting, we adjusted this reward amount upward to $250 to account for unanticipated demographic or socioeconomic differences between Red Snapper anglers and anglers/hunters in previous studies. Studies have also found tag reporting rates for low-value tags, demonstrating that $5 tags resulted in an approximate 20% reporting rate (Taylor et al. 2006) and that $10 and $20 tags (adjusted for inflation) resulted in reporting rates of approximately 40% and 50% (Nichols et al. 1991). These values were used to construct a

TABLE 1. Ten tagging simulation scenarios in which various parameters were either held uniform across depth strata (normal text) or varied to reflect the distribution expected for Red Snapper in Gulf of Mexico waters off Alabama (bold italic text). Sample sizes (*N*), true exploitation rates, tagging mortality rates (multiplied by 0.5, 1.0, or 1.5), and tag loss rates (0.1, 0.2, or 0.3) were varied in each scenario to examine the sensitivity of each scenario to these factors. For variable-reward scenarios, the proportion of tagged fish at each reward level was inversely proportional to the tag reporting rate (see Figure 2). All scenarios were run with two different percentages of double-tagged fish (20% and 40%) for estimating tag loss.

Scenario	Depth stratum	Proportional fish distribution	Proportional tag distribution	Tagging mortality rate	Proportion tagged at reward level	Reporting rate at reward level	True exploitation rate multiplier
1	Shallow	0.33	0.33	0.30	1 ($250)	1 ($250)	1.0
	Intermediate	0.33	0.33	0.30	1 ($250)	1 ($250)	1.0
	Deep	0.33	0.33	0.30	1 ($250)	1 ($250)	1.0
2	Shallow	***0.20***	0.33	0.30	1 ($250)	1 ($250)	1.0
	Intermediate	***0.30***	0.33	0.30	1 ($250)	1 ($250)	1.0
	Deep	***0.50***	0.33	0.30	1 ($250)	1 ($250)	1.0
3	Shallow	0.33	***0.20***	0.30	1 ($250)	1 ($250)	1.0
	Intermediate	0.33	***0.30***	0.30	1 ($250)	1 ($250)	1.0
	Deep	0.33	***0.50***	0.30	1 ($250)	1 ($250)	1.0
4	Shallow	0.33	0.33	***0.10***	1 ($250)	1 ($250)	1.0
	Intermediate	0.33	0.33	***0.20***	1 ($250)	1 ($250)	1.0
	Deep	0.33	0.33	***0.40***	1 ($250)	1 ($250)	1.0
5	Shallow	0.33	0.33	0.30	1 ($250)	1 ($250)	***1.0***
	Intermediate	0.33	0.33	0.30	1 ($250)	1 ($250)	***0.8***
	Deep	0.33	0.33	0.30	1 ($250)	1 ($250)	***0.2***
6	Shallow	0.33	0.33	***0.10***	1 ($250)	1 ($250)	***1.0***
	Intermediate	0.33	0.33	***0.20***	1 ($250)	1 ($250)	***0.8***
	Deep	0.33	0.33	***0.40***	1 ($250)	1 ($250)	***0.2***
7	Shallow	***0.20***	0.33	***0.10***	1 ($250)	1 ($250)	***1.0***
	Intermediate	***0.30***	0.33	***0.20***	1 ($250)	1 ($250)	***0.8***
	Deep	***0.50***	0.33	***0.40***	1 ($250)	1 ($250)	***0.2***
8	Shallow	***0.20***	***0.20***	***0.10***	1 ($250)	1 ($250)	***1.0***
	Intermediate	***0.30***	***0.30***	***0.20***	1 ($250)	1 ($250)	***0.8***
	Deep	***0.50***	***0.50***	***0.40***	1 ($250)	1 ($250)	***0.2***
9	Shallow	0.33	0.33	0.30	See Figure 2	See Figure 2	1.0
	Intermediate	0.33	0.33	0.30	See Figure 2	See Figure 2	1.0
	Deep	0.33	0.33	0.30	See Figure 2	See Figure 2	1.0
10	Shallow	***0.20***	***0.20***	***0.10***	See Figure 2	See Figure 2	***1.0***
	Intermediate	***0.30***	***0.30***	***0.20***	See Figure 2	See Figure 2	***0.8***
	Deep	***0.50***	***0.50***	***0.40***	See Figure 2	See Figure 2	***0.2***

tag reward–reporting rate relationship for high-reward (scenarios 1–8; described below) and variable-reward (scenarios 9 and 10) model simulation scenarios (Table 1; Figure 2). Further, the proportion of tagged fish per reward level was inversely proportional to the reporting rate estimated from previous research at each reward amount for variable-reward scenarios (Figure 2; Nichols et al. 1991; Denson et al. 2002; Taylor et al. 2006; Bureau of Labor Statistics 2015).

Simulation model.—We simulated a population of tagged Red Snapper ($N_{d,r,t}$) in each depth stratum *d*, reward level *r*, and number of tags applied *t* (i.e., $t = 1$, single tagged; $t = 2$, double-tagged) by multiplying the total number of fish tagged (*n*) by a proportional allocation of tags to each stratum (P_d = depth allocation; P_r = reward level allocation; P_t = proportion single-tagged or double-tagged). For variable-reward scenarios, tagged Red Snapper were apportioned to reward levels inversely proportional to the assumed true angler reporting rate (λ_r). For high-reward scenarios, λ_r was assumed to equal 1.0, and only one reward level stratum was simulated; the exception was the scenario in which the reporting rate was incorrectly assumed to be 100%, where λ_r was set at 0.9 and again at 0.6. We simulated the number of tagged fish reported ($R_{d,r,t,i}$) as having one of three fates (*i*; reported with two tags attached, reported with one tag attached, or not reported) by drawing random deviates from a multinomial distribution with the number of trials $N_{d,r,t}$ and fate-specific probabilities calculated as follows:

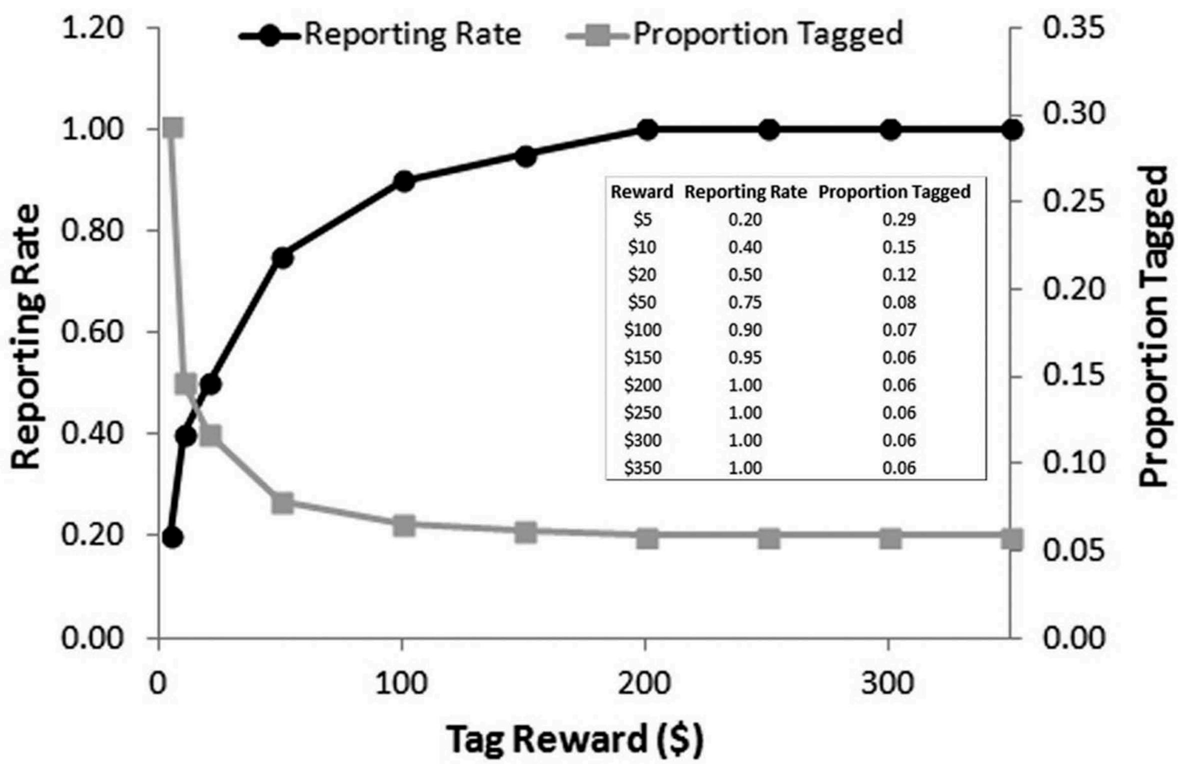

FIGURE 2. Assumed relationship between reward per tag and the tag reporting rate. This relationship was based on previous research (Nichols et al. 1991; Denson et al. 2002; Taylor et al. 2006), with adjustments to monetary rewards based on inflation from the time of those studies (e.g., a $100 reward in 1988 was equivalent to $200 in 2015). For simulation scenarios with variable reward levels, the proportion of tagged Red Snapper per reward level was inversely proportional to the reporting rate.

$$P_{d,r,t,i} = \begin{cases} \left[(1-m_d)(1-\mathrm{TLR})^2 U_d \lambda_r\right]^{t-1} & \text{for } i=1 \text{ (reported with two tags)} \\ t(1-m_d)\mathrm{TLR}^{t-1}(1-\mathrm{TLR})U_d\lambda_r & \text{for } i=2 \text{ (reported with one tag)} \\ 1-\sum_{i=1}^{2} P_{d,r,t,i} & \text{for } i=3 \text{ (not reported)} \end{cases} \tag{1}$$

where m_d is the depth-specific tagging mortality rate, which was assumed known without error (Campbell et al. 2014), TLR is the finite rate of tag loss, and U_d is the depth-stratum-specific exploitation rate. We presumed that m_d would be obtained external to the tagging model via tagging mortality field trials. Reward costs were calculated as the product of $R_{d,r,t,i}$ and the per-tag reward amount(s). We were primarily interested in estimating the average exploitation rate across depth strata. The true average exploitation rate was obtained by taking a weighted average of the exploitation rates in each depth stratum, weighted by the true proportion of the population in each stratum.

*Estimation model.—*The estimation model was identical to the simulation model and thus was stratified by depth; separate exploitation rate parameters were estimated for each depth stratum from the releases and returns from each stratum. Angler reporting rate (λ_r) was assumed to be 1.0 for all high-reward scenarios. For variable-reward scenarios, $\hat{\lambda}_r$ was estimated as a two-parameter logistic function (see the Supplement). The TLR was estimated for all scenarios. Tagging mortality (m_d) was assumed to be known without error. The estimation was simple and used a maximum likelihood approach to compute the negative log likelihood of the tag returns in each stratum ($R_{d,r,t,i}$) from a multinomial probability mass function, with number of trials $N_{d,r,t}$ and fate-specific probabilities computed in a manner identical to that used for the simulation model (equation 1 above). The negative log likelihood was then minimized using the nonlinear search function "optim()" in R software (R Core Team 2015). The SEs of parameter estimates were obtained by inverting the Hessian matrix, and coefficients of variation (CVs) were estimated by dividing the SEs by the parameter point estimates. We then estimated the overall exploitation rate for the population as the weighted average of the stratum-specific estimated exploitation rates, weighted by the assumed proportional distribution of Red Snapper across depth strata, which was assumed known without error in some scenarios and was assumed incorrectly in other scenarios (Table 1). The weighted average SE of the overall exploitation rate was also computed.

Simulation scenarios.—We configured a total of 10 scenarios (Table 1):

- Scenario 1 represented a high-reward study for the "simplest" situation in which Red Snapper were distributed evenly across depth strata, exploitation rates were constant across strata, and tagging mortality rates did not vary with depth.
- In scenario 2, Red Snapper abundance varied with depth (i.e., D_d) to reflect the more reasonable distribution of the Red Snapper population in the northern Gulf of Mexico (20% of the population in waters > 30 m, 30% in waters 30–60 m, and 50% in waters > 60 m).
- In scenario 3, the true population was evenly distributed across depth strata, but the analyst assumed an uneven distribution with depth and therefore allocated tagged fish to depth strata accordingly (Table 1). This scenario was formulated to evaluate the consequences of being incorrect on the assumed distribution of the population but under equal exploitation rates across strata.
- In scenario 4, only the tagging mortality rate varied across strata, while all other factors were uniform. The rate of tagging mortality by area impacts the number of tagged fish that are alive and available for recapture in each area.
- In scenario 5, only the true exploitation rate varied across strata, while all other factors were uniform.
- In scenario 6, both the true exploitation rates and the release mortality rates were set to vary across strata, while the proportional distributions of fish density and tags were kept uniform (Table 1).
- Scenario 7 represented a realistic situation in terms of the proportional distribution of fish density, tagging mortality, and true exploitation rates across depth strata for the Red Snapper population; however, the fish were tagged uniformly across depth strata (Table 1).
- Scenario 8 was intended to be our "best" approximation of the most realistic situation in which Red Snapper distribution, exploitation rates, and tagging mortality rates varied with depth, and the analyst made a correct assumption about the depth distribution of fish and tagged accordingly (Table 1). This scenario was run three times: (1) correctly assuming a 100% reporting rate, (2) incorrectly assuming a 100% reporting rate when the true rate was 90%, and (3) incorrectly assuming a 100% reporting rate when the true rate was 60%.
- Scenarios 9 and 10 were identical to scenarios 1 and 8, respectively, but with a variable-reward program (Figure 2).

For each scenario, we examined how input parameter specifications for sample size (number of tagged fish), the magnitude of the true exploitation rate, the magnitude of the tagging mortality rates, the magnitude of tag loss, and the proportion of double-tagged fish influenced parameter estimates. We ran 500 stochastic iterations for all possible combinations of the following input parameter specifications: (1) a range of sample sizes in increments of 100 from 500 to 5,000; (2) true exploitation rates in increments of 0.05 from 0.05 to 0.50; (3) three tagging mortality rates that varied from a base value by a multiplier of 0.5, 1.0, and 1.5; (4) three tag loss rates (0.1, 0.2, and 0.3); and (5) two proportions of double-tagged fish (0.2 and 0.4).

Comparing model output.—First, we examined the percentage of the 500 iterations that failed to converge for each combination of parameter specifications and scenarios. This evaluation helped to determine the likelihood that a particular scenario or input parameter specification would result in too few tag returns to estimate the exploitation rate. Uncertainty in parameter estimates was calculated as the median (of 500 iterations) CV for each input parameter specification and scenario (e.g., see Figure 3). Biases in estimated exploitation rates and tag loss rates were calculated by taking the median (of 500 iterations) of the percent relative bias (MPRB; [estimated exploitation rates for each area – true exploitation rates for each area]/true exploitation rates for each area × 100) for each input parameter specification (i.e., sample sizes, true exploitation rates, tagging mortality rates, tag loss rates, proportion of double-tagged fish) in each scenario. The median (of 500 iterations) costs for reward payouts were also reported for each input parameter specification and scenario. These median values for CV, MPRB, and reward costs for sample sizes, true exploitation rates, tagging mortality rates, tag loss rates, and the two proportions of double-tagged fish were also averaged for each scenario to compare the values among scenarios.

Cost-effective sampling.—To identify the most cost-effective sample size for each scenario, we first narrowed our results to include only those scenarios associated with published tagging mortality rates (using the base values of 0.1, 0.2, and 0.4 across depth strata; Campbell et al. 2014), two reasonable true exploitation rates (0.1 and 0.2; SEDAR 2013), and where 40% of fish were double-tagged. We then selected the smallest sample size for each scenario for which the median CV was below 0.1, 0.2, or 0.3 and for which the MPRB of exploitation and tag loss rate estimates did not exceed 2%. These levels of parameter bias and precision have been used previously as levels that provide confidence in model results (Pollock et al. 2001; SEDAR 2013). If the smallest sample size that satisfied our criteria was 500 tags (i.e., the lowest number we simulated), we ran additional simulations at lower sample sizes to ensure that we selected the minimum sample size possible to meet

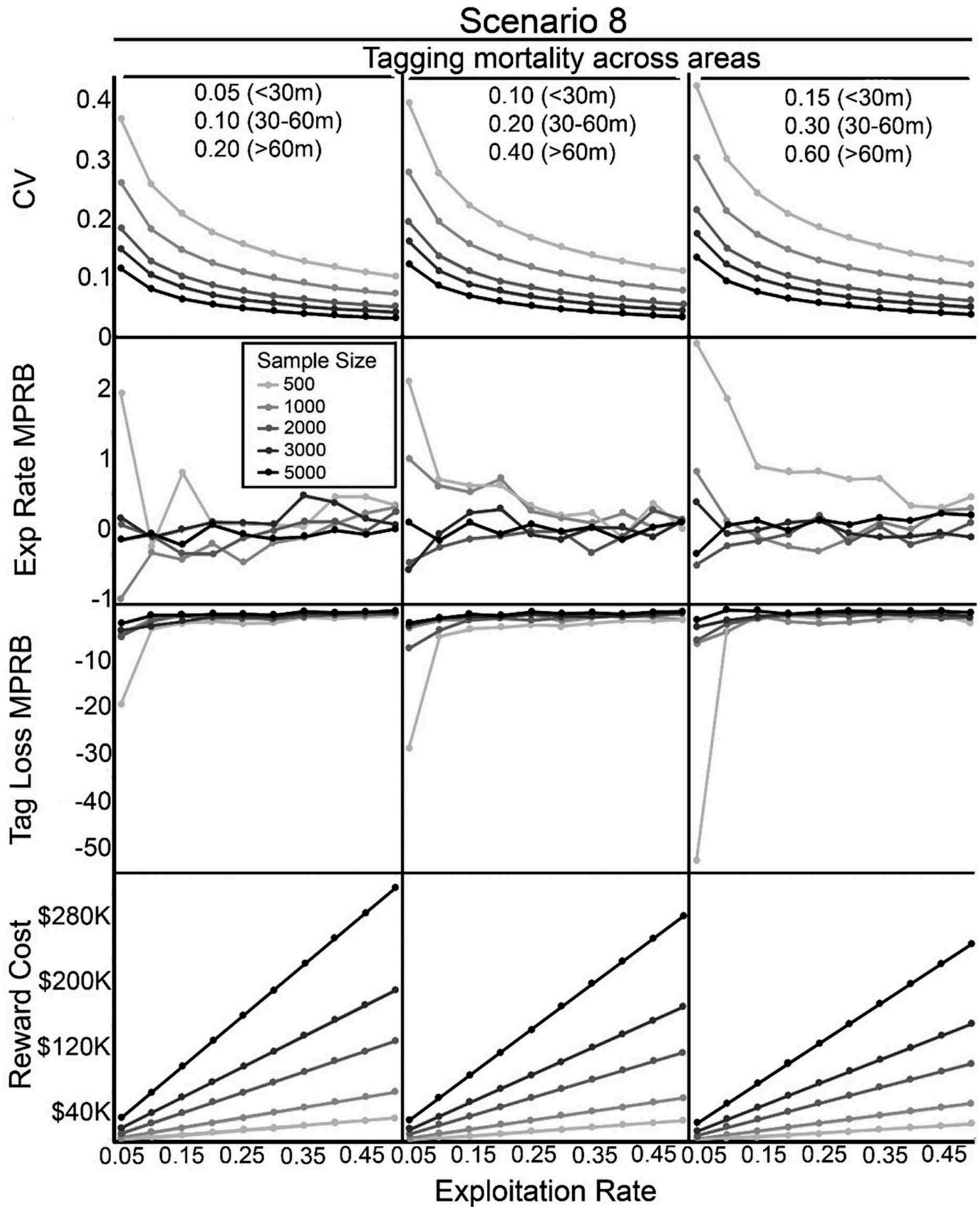

FIGURE 3. The influence of Red Snapper sample size, true exploitation rate, and tagging mortality rate on model output: coefficient of variation (CV; i.e., parameter uncertainty), median percent relative bias (MPRB) in exploitation rate estimates, MPRB in tag loss rate estimates, and reward cost. Each point represents the median value of 500 iterations for scenario 8, in which all parameters were set to reflect the Red Snapper population in Gulf of Mexico waters off Alabama. The gradient in line color represents the smallest (500; lightest gray color) to largest (5,000; black) sample sizes shown.

these criteria. The reward costs for the sample sizes that met the criteria were then compared. These estimates of error and costs helped to determine the best input parameter specifications (e.g., sample size) for each scenario and the best overall scenario to estimate Red Snapper recreational exploitation rate within state waters.

All analyses were conducted using R software (R Core Team 2015).

RESULTS

Parameter Influence on Model Output

Among all scenarios, uncertainty (CV) and bias (MPRB) in exploitation and tag loss rates improved with increasing sample size and true exploitation rates and worsened with higher tagging mortality rates (e.g., Figure 3). The cost of tag rewards also increased with increased sample sizes and exploitation rates while also declining with higher tagging mortality rates. These results were expected, as increasing the sample size and true exploitation rate would result in a higher number of recaptured and reported fish for use in estimating exploitation rate and for which to pay out tag rewards, while a higher tagging mortality rate would decrease the number of fish available to recapture and report. Similar results were obtained across simulated tag loss rates (0.1, 0.2, and 0.3). For instance, uncertainty estimates were lower but costs were higher under low simulated tag loss rates (e.g., Figure 4). However, bias in tag loss rate estimates increased under low simulated tag loss rates. This result was due to low returns of double-tagged fish with a single tag under low tag loss rates, leaving a very small sample size for estimation of tag loss rate. Mean estimates of tag loss rate improved when 40% of fish were double-tagged (MPRB = –0.64%) rather than just 20% of fish (MPRB = –1.64%). The bias in exploitation rate estimates improved when 40% of fish were double-tagged (MPRB = 0.74%) rather than 20% of fish (MPRB = 1.85%). However, the percentage of 500 iterations that failed to converge was similar when 40% (mean failure rate = 0.10%; range = 0.0–21.4%) and 20% (mean failure rate = 0.13%; range = 0.0–23.2%) of fish were double-tagged.

Comparing Scenarios

Of the high-reward scenarios where either all parameters remained uniform across areas or only a single parameter varied across areas (scenarios 1–5), scenario 5 had the highest level of parameter uncertainty (Table 1; Figure 5). Only exploitation rate varied across strata in scenario 5, with lower rates in deeper strata, which would lower the number of fish being recaptured and thus reported relative to scenarios 1–4 (Table 1). In addition, scenarios 1–4, where (1) all parameters were spatially uniform, (2) only the population distribution was spatially varied, (3) only the tag distribution was spatially varied, or (4) only the tagging mortality was spatially varied, had very similar low levels of overall parameter uncertainty. Overall mean MPRB in exploitation rate estimates among these scenarios remained low (<1%), very slightly underestimating the exploitation rate. Tag loss rates were also underestimated on average in each of these scenarios. However, only for scenario 5, in which the exploitation rate alone was spatially varied, did the mean MPRB in tag loss rate estimates exceed –1%. Parameter uncertainty across all scenarios was very strongly linked with the number of returned tags: more tag returns resulted in less parameter uncertainty, and fewer tag returns resulted in more parameter uncertainty. Similar to this trend, the overall reward cost among scenarios was also directly related to the estimated number of returned tags for each scenario. The more tags that were returned, the higher the reward costs. Thus, scenarios 1–4, with only high rewards and multiple parameters treated as uniform across areas, had the highest reward costs (Figure 5).

For high-reward scenarios 6 and 7, the exploitation rate and tagging mortality rate varied across strata, while tags were distributed evenly across strata (Figure 5). For scenario 6, however, the true population was evenly distributed, while for scenario 7 the true population was not evenly distributed across strata (Table 1). Despite this difference, the level of parameter uncertainty did not change (Figure 5), although exploitation rate estimates for scenario 7 were overestimated by 23.4% on average. For scenario 8, which varied all parameters in the same fashion as scenario 7 with the exception that the tag distribution matched the population across strata, parameter uncertainty was slightly higher; the mean MPRB of the tag loss rate was marginally more negative for scenario 8, but exploitation rate estimates were within 1% of the true value (Table 1; Figure 5). Additionally, in comparing scenario 8 (with 40% of fish double-tagged) when 100% reporting was assumed correctly relative to when 100% reporting was assumed but only 90% or 60% reporting occurred, levels of parameter uncertainty (100% reporting: 0.09 ± 0.05 [mean ± SD]; 90% reporting: 0.09 ± 0.06; 60% reporting: 0.11 ± 0.07) and tag loss MPRB (100% reporting: –0.6 ± 2.2%; 90% reporting: –0.7 ± 3.1%; 60% reporting: –1.3 ± 5.4%) were very similar. However, the MPRB (mean ± SD) for exploitation rate was –10.0 ± 0.56% when the reporting rate was 90% and –40.0 ± 0.49% when the reporting rate was 60% under an incorrectly assumed 100% reporting rate. When the reporting rate was correctly assumed to be 100%, the MPRB was 0.03 ± 0.56%.

For all high-reward scenarios (1–8), of the 500 iterations for each sample size (50), true exploitation rate (10), tagging mortality rate (3), tag loss rate (3), and proportion of double-tagged fish (2; a total of 4,500,000 model runs for each scenario), none failed to converge. This was not the case for variable-reward scenarios. For scenario 9, where all parameters were spatially uniform, the percentage of the 500 iterations that failed to converge ranged from 0.0% to 17.2% among the tested sample sizes, exploitation rates, tagging mortality rates, tag loss rates, and proportions of double-tagged fish (Figure 6). The average percent failure among these parameters was 0.4%. For scenario 10, where all factors were spatially varied, the percentage of the 500 iterations that failed to converge ranged from 0.0% to 23.2%, and the

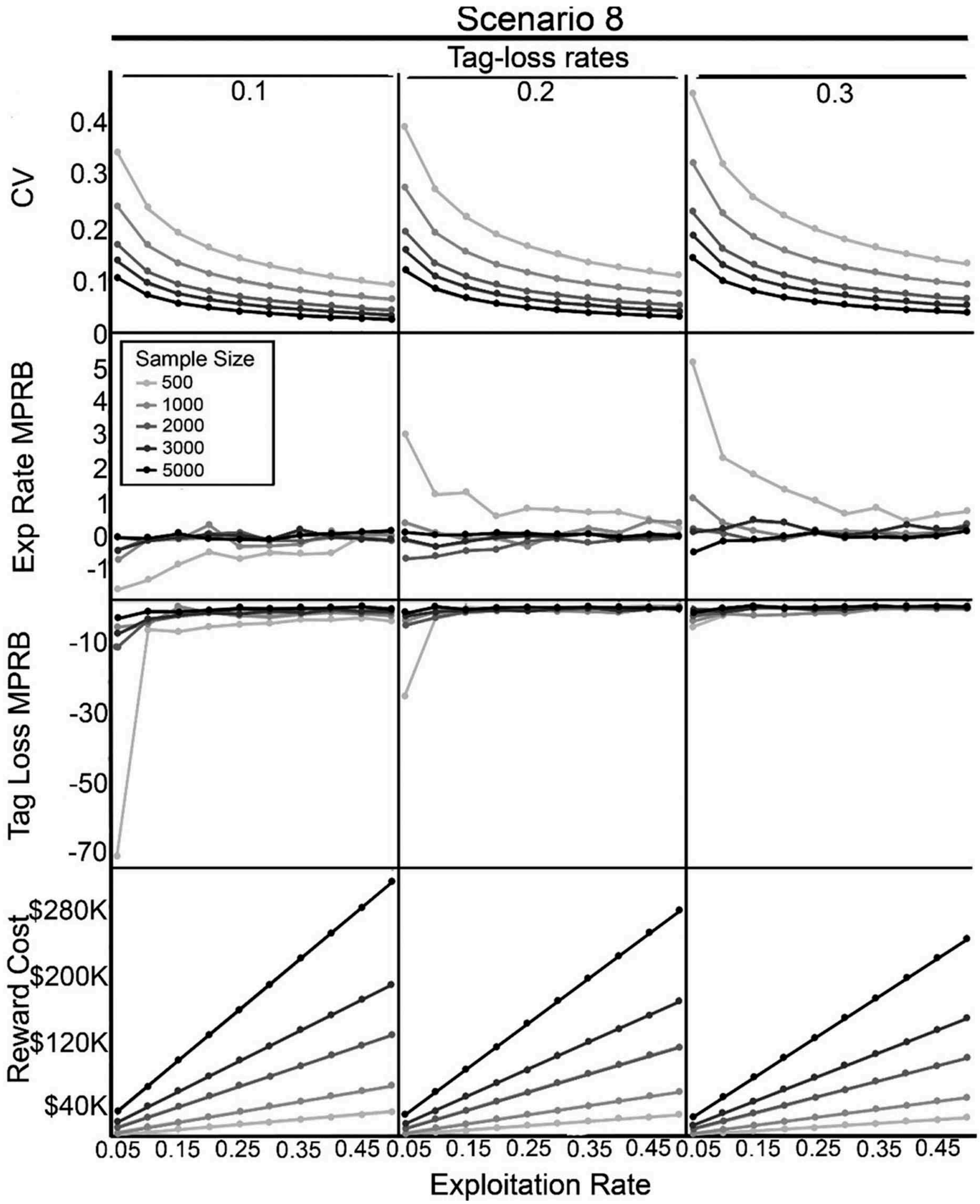

FIGURE 4. The influence of Red Snapper sample size, true tag loss rate, and tagging mortality rate on model output: coefficient of variation (CV; i.e., parameter uncertainty), median percent relative bias (MPRB) in exploitation rate estimates, MPRB in tag loss rate estimates, and reward cost. Each point represents the median value of 500 iterations for scenario 8, where all parameters were set to reflect the Red Snapper population in Alabama waters of the Gulf of Mexico. The gradient in line color represents the smallest (500; lightest gray color) to largest (5,000; black) sample sizes shown.

average percent failure rate was higher at 0.8%. The highest percentage of failures was observed when true exploitation rates and sample sizes were lower and when tagging mortality rates were higher, resulting in too few returned tags to estimate exploitation rate (Figure 6). Indeed, even some of the highest sample sizes (5,000 tagged fish) had a nonzero chance

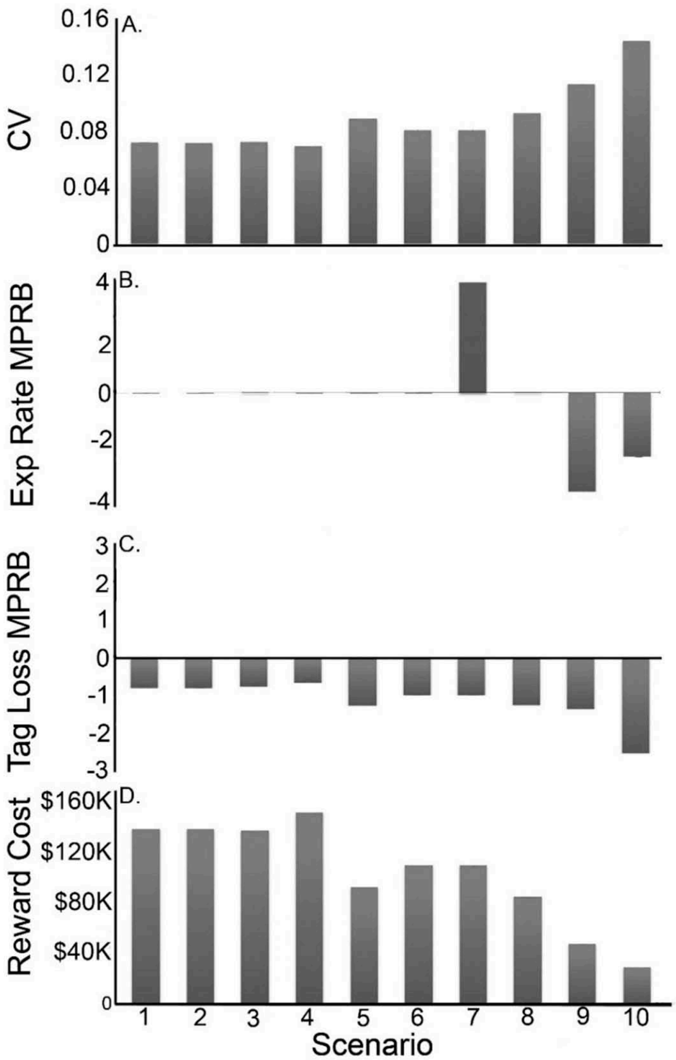

FIGURE 5. **(A)** Median coefficient of variation (CV), **(B)** median percent relative bias (MPRB) in exploitation rate, **(C)** MPRB in tag loss rate, and **(D)** median reward cost of 500 iterations averaged across tested sample sizes (50), exploitation rates (10), tagging mortality rates (3), tag loss rates (3), and percentages of double-tagged fish (2) by model simulation scenario (see Table 1) for Red Snapper. The maximum value for the MPRB in exploitation rate was set to 4% (*x*-axis) to allow smaller values to be visible. However, the MPRB for scenario 7 (23.4%) exceeded this maximum. It should also be noted that all scenarios were treated the same for comparisons and that because values represent a large range in sample sizes (i.e., 500–5,000) and other parameters, the importance of these results lies in the comparison among scenarios rather than in the specific values shown.

of failure (0.0–1.6% of 500 iterations) when exploitation rate was low (and vice versa) for the variable-reward scenarios (Table 1; Figure 6). Overall parameter uncertainty (e.g., uncertainty in the exploitation rate estimates) among scenarios was highest for variable-reward scenarios 9 and 10 (Figure 5). Additionally, parameter uncertainties for these scenarios were likely underestimated, as many low sample sizes and true exploitation rates failed to converge (Figure 6) and thus also failed to produce a CV; if they had converged, the CVs would have been high (Figure 3). In addition, variable-reward scenarios 9 and 10 underestimated the exploitation rate by 3.1% and 2.0% on average, and the mean MPRB in tag loss rate estimates exceeded –1%, demonstrating less accurate results than nearly all other scenarios (Figure 5). However, because much fewer tags would be returned using these variable-reward scenarios, they offered the lowest average reward costs (Figure 5).

Cost-Effective Sample Sizes

For each scenario, the smallest sample sizes and associated reward costs that met the parameter uncertainty criterion (CV < 0.3, 0.2, or 0.1) and the exploitation and tag loss rate bias criteria (MPRB within 2% of zero) were determined for two reasonable true exploitation rates (0.1 and 0.2) for Red Snapper in waters off Alabama (SEDAR 2013; Tables 2, 3). These results assumed tagging mortality rates of 0.1, 0.2, and 0.4 across depth strata (Campbell et al. 2014) and a tag loss rate of 0.2. For these scenarios, we set the proportion of double-tagged fish at 40%. We choose 40% because this approach reduced bias in tag loss and exploitation rate estimates and, in nearly every case, reduced cost. For example, the most cost-effective approach for scenario 8, with a CV below 0.2 and a true exploitation rate of 0.1, was tagging 1,200 fish with 20% double-tagged (cost = $12,250) or tagging 1,000 fish with 40% double-tagged (cost = $12,000). Although double-tagging at 40% appeared to perform better than 20%, we do not suggest that 40% is optimal. Our goal was to identify cost-effective sample sizes while holding the percentage of fish double-tagged constant rather than to conduct a detailed analysis of the relationship between percent double-tagged and cost efficiency.

For high-reward scenario 1 (i.e., all parameters were spatially uniform), the smallest sample sizes that met our most lenient (CV < 0.3) and intermediate (CV < 0.2) parameter uncertainty criteria included 500 tagged fish when the exploitation rate was 0.1 and 400 tagged fish when the exploitation rate was 0.2 (Tables 2, 3). The estimated reward costs for this scenario at these sample sizes were $9,750 and $15,500, respectively (Tables 2, 3). However, to lower the CV to below 0.1, the number of tagged fish would need to increase to 1,900 if the true exploitation rate was 0.1 and to 1,000 if the true exploitation rate was 0.2, with associated reward costs of $36,750 and $39,000 (Table 2). For high-reward scenario 8, which used the most likely true spatial distributions of the population, tags, and tagging mortality and two reasonable assumed true exploitation rates (0.1 and 0.2) across the study area for Alabama (Mitchell et al. 2004; SEDAR 2013; Campbell et al. 2014; Nicholas Ducharme-Barth, University of Florida, personal communication; John Mareska, ALDCNR, personal

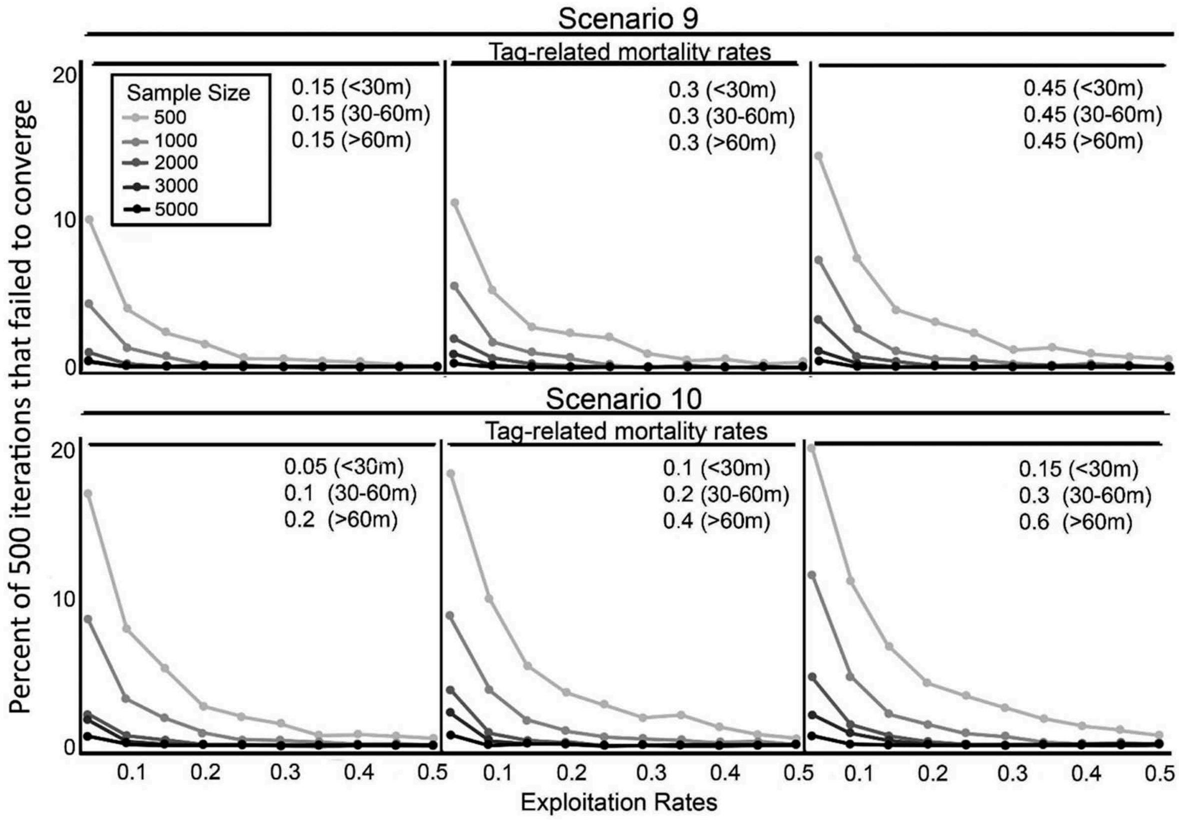

FIGURE 6. The influence of Red Snapper sample size, tagging mortality rate, and true exploitation rate on the mean percentage of 500 iterations that failed to produce an exploitation rate (i.e., failed to converge) for variable-reward scenarios 9 and 10 (see Table 1). The gradient in line color represents the smallest (500; lightest gray color) to largest (5,000; black) sample sizes shown.

communication), the smallest sample sizes that could produce a CV below 0.3 were 800 tagged fish at a true exploitation rate of 0.1 and 400 tagged fish at a true exploitation rate of 0.2 (Tables 2, 3; Figure 3). The associated reward costs for this scenario and these sample sizes were \$9,500 and \$9,750. To produce a CV below 0.2, the sample size and the associated costs would increase to 1,000 tagged fish and \$12,000 at a true exploitation rate of 0.1 and would remain the same at a true exploitation rate of 0.2 (Tables 2, 3). The smallest sample sizes and reward costs that resulted in a CV below 0.1 were 3,200 tagged fish at \$38,500, an unreasonable sample size for the hypothetical study suggested here, and 1,600 tagged fish at \$38,500 (Tables 2, 3). None of the tested sample sizes for scenario 7 met our parameter uncertainty and bias criteria. Scenarios 9 and 10 also showed no tested sample sizes that met our lowest parameter uncertainty (CV < 0.1) and bias criteria. However, for these two variable-reward scenarios, there were sample sizes that met higher parameter uncertainty criteria (Tables 2, 3), although the sample sizes required to meet the criteria were generally much higher than those for high-reward scenarios with the same parameter specifications (comparing scenarios 1 and 9 and scenarios 8 and 10; Tables 2, 3). Lastly, there were no sample sizes that met our parameter uncertainty and bias criteria for scenario 8 when the reporting rate was 60% or 90% and wrongly assumed to be 100%.

DISCUSSION

High-Reward versus Variable-Reward Approach

There are numerous tradeoffs to using either a high-reward or variable-reward tagging approach. For instance, high-reward tagging methods often simplify models by assuming that the high reward will result in 100% of captured tags being reported by anglers. As a result, this method has been used in many fisheries and wildlife studies (Henny and Burnham 1976; Conroy and Blandin 1984; Murphy and Taylor 1991; Nichols et al. 1991; Pollock et al. 2001; Denson et al. 2002). However, this method does not allow the researcher to investigate angler reporting behavior, as can be done using a variable-reward approach. Variable-reward studies often facilitate estimation of the asymptote in the tag reward–reporting rate relationship, where a higher reward amount does not cause any additional

TABLE 2. For each scenario, we present the smallest sample sizes and associated reward costs at which the following parameter uncertainty and estimation bias criteria were met: (1) the median coefficient of variation (CV) for the model was below 0.3, 0.2, or 0.1; and (2) the median percent relative bias (MPRB) in exploitation rate or tag loss rate estimates was within 2% of the true value. For these comparisons, the true exploitation rate was set at 0.1 (SEDAR 2013); the tagging mortality rates across areas were set at 0.1 (depth < 30 m), 0.2 (30–60 m), and 0.4 (>60 m; Campbell et al. 2014); tag loss was set at 20%; and the proportion of double-tagged fish was set at 40%. None of the sample sizes for scenario 7 met the criteria.

Scenario	Sample size	CV	MPRB, exploitation rate	MPRB, tag loss rate	Reward cost ($)
			CV < 0.3, true exploitation rate = 0.1		
1	500	0.20	0.74	−1.88	9,750
2	500	0.20	0.74	−1.88	9,750
3	300	0.26	0.28	−1.46	5,750
4	300	0.25	0.67	0.91	6,250
5	400	0.28	0.63	−1.43	5,000
6	300	0.29	1.22	−1.74	4,500
8	800	0.20	0.32	−1.47	9,500
9	1,100	0.21	−1.03	0.46	7,398
10	1,400	0.24	1.33	0.68	5,820
			CV < 0.2, true exploitation rate = 0.1		
1	500	0.20	0.74	−1.88	9,750
2	500	0.20	0.74	−1.88	9,750
3	500	0.20	1.23	−1.61	9,750
4	500	0.19	1.19	−1.48	10,750
5	800	0.19	0.86	−0.34	10,500
6	700	0.19	−0.13	−0.44	10,750
8	1,000	0.18	0.74	−0.25	12,000
9	1,200	0.20	0.56	1.45	8,238
10	2,100	0.19	−0.40	0.12	8,668
			CV < 0.1, true exploitation rate = 0.1		
1	1,900	0.10	−0.95	−0.73	36,750
2	1,900	0.10	−0.95	−0.73	36,750
3	1,900	0.10	−0.09	−0.09	37,000
4	1,800	0.10	−0.54	0.64	38,250
5	2,900	0.10	−0.49	−0.29	37,500
6	2,500	0.10	−0.59	0.21	38,500
8	3,200	0.10	−0.44	0.86	38,500

increase in the reporting rate, and then assume that the asymptote represents the cost needed to elicit 100% reporting (Pollock et al. 2001). Therefore, use of only high-reward tags means that a tag reward–reporting rate relationship cannot be estimated and that the reward amount used must be assumed to represent that asymptote. There is no guarantee that 100% reporting actually occurs at the asymptote found in a variable-reward study or at the asymptote assumed in a high-reward study. A variable-reward approach cannot rule out the possibility that some subset of anglers would require a much higher reward than feasible (higher than the highest variable-reward level tested; e.g., $10,000) to report a tag (Pollock et al. 2001). Our analysis suggests that an incorrect assumption of 100% reporting can have important impacts on study results due to an inverse proportional relationship between the bias in the assumed reporting rate and the bias in the estimated exploitation rate.

Using all high-reward tags is thought to be much more expensive than using both lower- and higher-reward tags together. Our results generally supported this claim when sample sizes were the same for the high-reward and variable-reward scenarios. However, due to lower reporting rates on low-dollar tags, the variable-reward scenarios often required a much higher number of tags to be released for results to be as dependable as the high-reward scenarios. As such, scenarios using only high-reward tags proved to be much more reliable (lower parameter uncertainty) and provided the best estimates of the exploitation rate and tag loss rate (lower MPRB) compared to the same scenarios using variable-reward tags. In addition, the possibility that a variable-reward tagging study could result in insufficient data to estimate exploitation rate makes this approach less practical, particularly if the study species has a low exploitation rate. Increasing the sample size

TABLE 3. For each scenario, we present the smallest sample sizes and associated reward costs at which the following parameter uncertainty and estimation bias criteria were met: (1) the median coefficient of variation (CV) for the model was below 0.3, 0.2, or 0.1; and (2) the median percent relative bias (MPRB) in exploitation rate and tag loss rate estimates was within 2% of the true value. For these comparisons, the true exploitation rate was set at 0.2 (SEDAR 2013); the tagging mortality rates across areas were set at 0.1 (depth < 30 m), 0.2 (30–60 m), and 0.4 (>60 m; Campbell et al. 2014); tag loss was set at 20%; and the proportion of double-tagged fish was set at 40%. None of the sample sizes for scenario 7 met the criteria.

Scenario	Sample size	CV	MPRB, exploitation rate	MPRB, tag loss rate	Reward cost ($)
			CV < 0.3, true exploitation rate = 0.2		
1	400	0.15	0.21	−0.01	15,500
2	400	0.15	0.21	−0.01	15,500
3	200	0.21	0.44	0.89	7,750
4	200	0.21	−0.07	1.58	8,500
5	200	0.27	0.14	−1.14	5,250
6	300	0.20	0.01	1.36	9,250
8	400	0.20	1.12	1.22	9,750
9	400	0.24	1.63	−1.31	5,253
10	800	0.21	0.83	−1.33	6,853
			CV < 0.2, true exploitation rate = 0.2		
1	400	0.15	0.21	−0.01	15,500
2	400	0.15	0.21	−0.01	15,500
3	400	0.15	0.24	0.11	15,750
4	300	0.17	0.48	−0.08	12,750
5	400	0.19	0.14	0.59	10,250
6	300	0.20	0.01	1.36	9,250
8	400	0.20	1.12	1.22	9,750
9	700	0.18	−0.89	−1.76	9,618
10	1,400	0.16	−1.06	0.40	11,643
			CV < 0.1, true exploitation rate = 0.2		
1	1,000	0.09	−0.28	−0.93	39,000
2	1,000	0.09	−0.28	−0.93	39,000
3	900	0.10	−0.36	−0.78	35,000
4	900	0.10	−0.38	−0.91	38,500
5	1,400	0.10	0.15	−1.00	36,250
6	1,200	0.10	−0.04	−1.17	37,000
8	1,600	0.10	0.13	−1.48	38,500

did not compensate for these shortcomings when the more strict level of parameter uncertainty (CV < 0.1) was used, as none of the tested sample sizes was large enough (maximum sample size tested = 5,000) for the variable-reward scenarios to meet these criteria (CV < 0.1; MPRB within 2% of the true value). Lastly, comparing scenarios 8 and 10 directly demonstrated that using a variable-reward scenario versus a high-reward scenario only reduced the cost of rewards by $3,680 to $3,333 (true exploitation rate = 0.1) or by $2,898 (true exploitation rate = 0.2) and even increased the cost (by $1,893) when the exploitation rate was 0.2 and the parameter uncertainty criterion was a CV less than 0.2.

Additional sources of error that accompany variable-reward tagging studies were not accounted for in our models but have been discussed by others (Pollock et al. 2001). For example, low-reward tags may be collected and unreported by fishers until a higher reward tag is caught, at which time all of the tags are then reported, thus violating the assumptions that returned tags are independent and that the time of recapture and reporting is correct (Pollock et al. 2001). Therefore, while it is useful to have numerous tags at various reward levels to inform a tag reward–reporting rate relationship (e.g., Taylor et al. 2006), to better understand fisher reporting behavior, and to lower the overall costs of a tag–recapture project, other attributes—including the higher chance of failure, higher parameter uncertainty, higher bias in exploitation rate estimates, and additional possible sources of error (Pollock et al. 2001)—often make this approach less desirable than a study that uses all high-reward tags. As such, using only high-reward tags would be preferable if a priori information on angler reporting rates exists or if reporting can be estimated directly external to the tagging model. An example of such an approach would be a telemetry array in which angler harvest can be inferred from fish detection patterns (Topping and Szedlmayer 2013). However, if these estimates are unavailable and if a goal of the project is to better understand fisher reporting behavior, a variable-reward approach would be best although it would likely be more expensive, would require the researcher to tolerate less-precise estimates of exploitation rate, and would likely require substantially greater effort to tag more fish. Further, because the reliability of high-reward and variable-reward tagging results depends upon correctly assuming 100% reporting of tagged fish, the reward must be sufficient to ensure 100% reporting or to reach the asymptote in the tag reward–reporting rate relationship. A publicity campaign could be conducted to ensure that fishers know to look for tags to avoid violating these reporting assumptions. Additionally, researchers could investigate whether fishers are aware of the tagging study through a phone or dockside survey conducted prior to the start of the study. However, even with these measures, in a high-dollar fishery such as the Red Snapper fishery, with recreational expenses upwards of $500 in gas or $250 on a charter boat and an antagonistic relationship between and among management agencies and user groups, anglers may assume that not reporting their tags would eventually result in longer fishing seasons (Brown and Wilkins 1978). Thus, it may be necessary to use much higher dollar amounts (e.g., $500 to $1,000) to elicit 100% reporting in a fishery such as this. An alternative approach may be to conservatively estimate a lower reporting rate (e.g., 90%) in models, assuming that some portion of the fishery will refuse to report tags. This would, however, run the risk of overestimating the exploitation rate. Further, while using and advertising high-dollar rewards could hypothetically lead to increased fishing effort, asking whether fishers would have been fishing regardless of the chance to catch a tagged fish could help to estimate any increase in effort. In addition, in a fishery that requires such a large monetary investment to fish, it is unlikely that effort would drastically increase at the chance of catching a tagged fish.

Impact of Spatial Variability

Often, the most important spatial consideration made in planning a tagging study is to ensure that the tagged population is well mixed with the untagged population because a modest amount of nonmixing could cause a substantial bias in mortality estimates (Hoenig et al. 1998). The solution to this potential problem is often to distribute tags at various locations throughout the study area without considering the distribution of the exploited population or the variability in fishing effort throughout the study area (Pollock et al. 2001). As such, few studies have simultaneously considered the impact of spatial heterogeneity in abundance, fishing effort, and tagging mortality rates in the context of fishery-dependent tagging studies to estimate exploitation (Pollock et al. 2001; Pine et al. 2003). Therefore, since the impact of nonmixing on study results had already been established, here our models focused on these other spatial considerations and assumed that the tagged fish were well mixed within each of our depth strata. Results showed that assuming a uniform distribution of Red Snapper across depth strata (and distributing tags accordingly) when the population and exploitation rate varied across strata caused substantial bias in estimates of exploitation rate (mean overestimate = 23%). The likely explanation for this result is that tagged fish and the untagged population were not equally vulnerable to harvest, and the assumed weighting factor in computing the weighted average exploitation rate would be incorrect. For instance, in this particular case, there was a higher proportion of tagged fish versus untagged fish in shallower areas (e.g., 33% versus 20% of the population across strata), where exploitation rates were higher (e.g., 50%). Further supporting this explanation, when the depth distribution of Red Snapper was correctly assumed—and thus tags were distributed in the same proportion as the population—under otherwise identical circumstances, the mean bias in exploitation rate estimates was low (–0.38%). However, when true exploitation rates were uniform across the study area, the spatial distribution of tags did not affect estimation bias, even when that distribution did not match the spatial distribution of the fish population, because tag return probabilities were equal across strata.

These results highlight the need for prior knowledge of the spatial distribution of the population and the importance of considering the spatial distribution of fishing effort (i.e., exploitation) across a study area before conducting a fishery-dependent tagging study. Thus, prior estimates of these quantities would be necessary to reduce bias in exploitation rate estimates. This prior information could be obtained from spatially stratified creel surveys to inform fishing effort distribution and catch rate data and from fishery-independent surveys to inform fish abundance distributions. For Red Snapper in Alabama waters, for example, fishery-independent surveys to enumerate benthic structure densities and associated Red Snapper catch rates have been developed in recent years by the Dauphin Island Sea Laboratory and Auburn University. These estimates could be used to inform fish spatial distributions. Another option to ensure that tagged fish are distributed proportionally to fish abundance would be to apply equal fishing effort across spatial strata if it is reasonable to assume equal catchability across strata.

It is also important to note that parameter uncertainties among input parameter specifications and scenarios were closely tied to the estimated number of returned tags. For instance, models that estimated more returned tags (i.e., due to a higher exploitation rate, lower tagging mortality rate, or higher sample size) had lower parameter uncertainty. This rule applied among scenarios as well: scenarios that resulted in more returned tags (e.g., spatially uniform fishing pressure versus scenarios with lower fishing pressure in deeper areas) had lower levels of parameter uncertainty.

Most Cost-Effective Approach

Under the most realistic scenario we simulated (scenario 8; spatial heterogeneity in abundance, tagging mortality, and exploitation rates), our analysis suggested that between 400 and 1,600 high-reward tags would need to be released in proportion to abundance to achieve reasonably precise and unbiased exploitation rate estimates if 40% of the fish were double-tagged. The reward costs to such a project would be between $9,500 and $38,500 and would depend on (1) the level of parameter uncertainty that is acceptable for the study and (2) the true exploitation rate of the fishery. One way to potentially improve parameter precision without increasing sample size and reward costs would be to lower the tagging mortality rates. Tagging mortality rates can be adjusted using specially designed techniques to minimize barotrauma. Some of these techniques include venting the gas bladder after capture (decompression) or fish recompression by lowering and releasing the fish at depth using cages, weighted hooks, or specialized release hooks and pressure-activated lip-grips (SeaQualizer; Gitschlag and Renaud 1994; SEDAR 2013; Drumhiller et al. 2014; Harrison 2015). Notably, some studies have found that venting the gas bladder actually increases release mortality rates for individuals caught in deeper waters (Wilde 2009). However, much of the harm caused by venting can be attributed to angler inexperience with the proper venting techniques (Harrison 2015). Additionally, when proper venting and recompression techniques were compared, recompression alone or a combination of venting and recompression produced higher survival rates than venting alone (Drumhiller et al. 2014; Harrison 2015). Regardless of the tagging method, it will be important to obtain reliable estimates of tagging mortality rates either from the literature or from concurrent in situ studies.

State natural resource management agencies along the Gulf of Mexico coast have expressed interest in more localized (i.e., state) control over Red Snapper management (e.g., ALDCNR 2014, 2015). However, a more localized management strategy requires a better understanding of movement rates into and out of state waters (Pine et al. 2003; Schroepfer and Szedlmayer 2006). Although the study we describe here was not designed to investigate movement rates, a reward-tagging study in state waters could provide insight on Red Snapper emigration rates because fish would only be tagged in state waters, whereas they could be recaptured by fishers throughout the Gulf of Mexico (McGarvey and Feenstra 2002; Cowen et al. 2009). However, making sense of tag returns from out of state would require an understanding of the spatial distribution of fishing effort in these areas. Results could also provide estimates on the proportion of Red Snapper from state waters that are harvested by out-of-state fishers. Further, this reward-tagging approach could also be used to estimate the vulnerability of different sizes of Red Snapper to harvest, providing information on the size selectivity of the fishery (Pine et al. 2003; Bacheler et al. 2010). Lastly, combining tagging data with harvest surveys could be used to directly estimate catchability (Pine et al. 2003).

Management Recommendations

While no simulation or set of models can fully represent the complexity of an exploited population in the natural environment, these methods can be used to illuminate the assumption violations that may cause serious problems in study design and to provide the most cost-effective approach for meeting study objectives. Our simulations demonstrated that using all high-reward tags was more effective than using variable-reward tags when the primary goal was to estimate exploitation rate. However, a serious effort should be made to ensure that the high reward selected represents a 100% reporting rate unless direct estimates (e.g., telemetry) are available. Furthermore, distributing tags uniformly over a study area when the true spatial distributions of the population and of exploitation vary over that area can have a drastic impact on estimates of exploitation rate. Thus, we suggest that some prior knowledge of the spatial distribution of the population be used to estimate the proportional distribution of the tagged fish unless it is feasible to tag fish in proportion to abundance. We also suggest that double-tagging 40% of all tagged individuals should result in more reliable and cost-effective estimates of tag loss. These findings should assist in study design planning for future efforts toward fishery-dependent tagging approaches for Red Snapper in the northern Gulf of Mexico and other areas. This approach can also be used as a template for future tag–recapture studies to ensure that the most cost-effective approach is used to produce reliable and accurate estimates of exploitation rate.

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