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ARTICLE

Estimating Exploitation Rates in the Alabama Red Snapper Fishery Using a High-Reward Tag–Recapture Approach

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Abstract
Accurate estimates of exploitation are essential to managing an exploited fishery. However, these estimates are often dependent on the area and vulnerable sizes of fish considered in a study. High-reward tagging studies offer a simple and direct approach to estimating exploitation rates at these various scales and in examining how model parameters impact exploitation rate estimates. These methods can ultimately provide a better understanding of the spatial dynamics of exploitation at smaller local and regional scales within a fishery—a measure often needed for more site-attached species, such as the Red Snapper *Lutjanus campechanus*. We used this approach to tag 724 Red Snapper during 2016 in the Alabama Artificial Reef Zone within the northern Gulf of Mexico to estimate recreational exploitation rates in Alabama waters. We fitted a series of tag return models, analyzed using maximum likelihood, to examine how release depth, movement between depth strata, fish length, and the rate at which anglers released fish impacted estimates of exploitation rate under a range of assumed natural and tagging mortality rates. Our model results suggested higher fishing mortality in the shallower depth stratum than in the deep stratum, constant movement rates with release depth, and constant release rates across fish lengths. Exploitation rate for the aggregate tagged population across the entire sample area was estimated at 0.14. Exploitation rates estimated for each depth stratum were 0.20 (shallow stratum: <36.5 m) and 0.06 (deep stratum: 36.5–61.0 m). In addition, length-based vulnerability to harvest was dome-shaped, with peak exploitation rates of 0.37 (shallow stratum) and 0.12 (deep stratum) occurring at 600–700 mm TL. Although previous studies have suggested higher exploitation rates in shallower waters compared to deeper waters, few estimates exist at these smaller spatial scales.

Accurate estimates of exploitation rate are essential to managing an exploited fishery, as these estimates will have drastic impacts on the health of the fishery, the local economy, and stakeholder livelihoods (SEDAR 2013). One difficulty in estimating exploitation is that estimates are dependent on the area and vulnerable sizes considered

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in a study (Patterson 2007; Saillant et al. 2010; Karnauskas et al. 2017). For instance, a smaller, more heavily fished region or the most vulnerable sizes of fish within a population will generally have higher exploitation rates than those areas and fish sizes with lower fishing effort or different vulnerability dynamics. Additionally, while estimates of exploitation on these more regional or local scales do not represent the entire fishery, they do offer information on the spatial variation of exploitation and are essential to inform local management strategies for more site-attached species with relatively low levels of adult movement. The Red Snapper *Lutjanus campechanus* in the northern Gulf of Mexico is one such species with low estimated levels of adult movement that may require regional estimates of exploitation to inform local management and balance biological and economic goals (Karnauskas et al. 2017).

The current statistical catch-at-age assessment model for the Red Snapper fishery was developed by the National Marine Fisheries Service and does not provide fine enough spatial resolution to inform regional management (SEDAR 2013). These models use commercial and recreational landings, discards, age composition observations, and abundance indices from two large spatial strata (east and west) that are roughly separated by the Mississippi River. Exploitation rate for the entire fishery is described in the stock assessment model as the catch expressed as a fraction of the abundance estimate, accounting for discards, from both areas and is used as a proxy for annual fishing mortality, which was most recently estimated at 0.054 for the entire northern Gulf of Mexico (SEDAR 2013). Therefore, this estimate may not represent exploitation rates occurring at regional spatial scales because of spatial differences in fishing effort and fish size or age structure throughout the northern Gulf of Mexico (e.g., Alabama Artificial Reef Zone [AARZ]; Szedlmayer and Shipp 1994; Minton and Heath 1998; Patterson et al. 2001b). Localized estimates would be valuable for management of this site-attached species with low adult movement rates (Patterson 2007; Saillant et al. 2010; Karnauskas et al. 2017). In particular, estimates of exploitation rates from more heavily fished areas may help direct local management efforts (Patterson 2007). One approach to obtain these estimates is a high-reward tagging study (Cowan et al. 2011; Sackett et al. 2017).

High-reward tag–recapture studies offer a direct approach to estimate exploitation rates and may serve as a complement to catch-at-age models. Agreement among these independent approaches can increase confidence in model estimates or highlight assumptions that may need to be addressed. In addition, tag–recapture studies may provide additional insights into the fishery, as the fishers provide information directly to the researcher about their catch (e.g., depth and habitat type; Hood et al. 2007; Cowan et al. 2011). Lastly, this type of study has the potential to increase stakeholder engagement because it provides an opportunity for anglers to become directly involved in the research that supports the assessment process while receiving a monetary reward for their participation (Jentoft and McCay 1995; Coffey 2005; Pita et al. 2010). This type of engagement would be particularly beneficial for the Red Snapper fishery, which is currently considered one of the most controversial in the northern Gulf of Mexico (Hood et al. 2007; Cowan et al. 2011). Increasingly restrictive regulations enacted in recent years to meet federal stock rebuilding goals have led to controversy regarding the management process and the stock assessment models on which quotas are based (Sargeant 2017). Federal recreational fishery regulations have been particularly contentious in Alabama, where recreational harvest currently comprises approximately 95% of the total Red Snapper harvest (Alabama Department of Conservation and Natural Resources, personal communication). As such, the state of Alabama enacted a state-regulated recreational Red Snapper season for waters off Alabama that was 66 d (May 27–July 31) in 2016 and extended beyond the 11-d (June 1–11) private boat season and 46-d (June 1–July 16) charter boat opening. The implementation of state-level management strategies such as this requires the estimation of stock status and mortality at similar spatial scales.

Therefore, our specific objectives were to (1) conduct a high-reward Red Snapper tag–recapture study in the Gulf of Mexico off the coast of Alabama to estimate open-season recreational exploitation rates on artificial reefs in Alabama waters, particularly the AARZ; (2) examine how release depth, movement, fish length, and angler release rate impact estimates of exploitation rate; and (3) examine the sensitivity of estimated exploitation rates under a range of assumed natural, tagging, and angler release mortality rates.

METHODS

Approach.— We estimated exploitation rates for Red Snapper that were captured, tagged, and released in waters less than 61 m (200 ft) deep within the AARZ. Red Snapper were not tagged in deeper water (i.e., >61 m) because of higher tagging mortality rates associated with fish captured from these depths (Gitschlag and Renaud 1994; Rummer and Bennett 2005), monetary and time constraints, and low anticipated tag returns, as approximately 10% of recreational fishing effort is thought to occur in these deeper areas (Karnauskas et al. 2017; Sackett and Catalano 2017). We stratified the AARZ into a shallow depth stratum (<36.5 m [<120 ft]) and a deep stratum (36.5–61.0 m) because Red Snapper abundance and recreational fishing effort vary systematically with depth and distance from shore (Sackett and Catalano 2017). Similar depth ranges have been used to stratify Red

Snapper abundance and catch distributions by the Alabama Marine Resources Division and other researchers (Mitchell et al. 2004; SEDAR 2013).

We captured, tagged, and released Red Snapper into each depth stratum in proportion to an estimate of the relative population size in each. We estimated the relative population sizes by multiplying an estimate of the number of reefs (artificial or natural) previously mapped and identified using side-scan sonar in each depth stratum by the average catch rate from vertical longline surveys conducted at these reefs. The most up-to-date information was used for these estimates and included data from the period 2012–2016. For more details on these methods, see Gregalis et al. (2012) and Karnauskas et al. (2017). The analysis indicated that the shallow depth stratum contained 60% of the population, with the remaining 40% occurring in the deep stratum.

To tag Red Snapper in proportion to their relative abundance, we randomly selected 150 reef sites within the AARZ: 60% in the shallow depth stratum and 40% in the deep stratum. We tagged no more than five fish per site to reduce dependence of the fates of Red Snapper released at the same site. As such, we tagged 724 Red Snapper, with 65% of fish tagged in the shallow depth stratum and 35% tagged in the deep stratum, very close to the proportional distribution of the population (Figure 1A). Fish were tagged from April 25 to May 26, 2016, just prior to the opening of the recreational fishing season (June 1, 2016). At each site, we used hook-and-line sampling to capture Red Snapper. Two different types of bottom tackle, referred to as "sow" and "double-drop" rigs, were used to incorporate a wider range of Red Snapper sizes into the tagged population. The sow rig was a single-hook rig with a slip lead, 1 m of 36.29-kg-test (80-lb-test) monofilament, and a 10/0 circle hook. The double drop was a two-hook rig with a bank sinker and an 8/0 circle hook. Rigs were baited with either cut squid *Loligo* spp. or Gulf Menhaden *Brevoortia patronus.*

At the surface, fish were measured (mm TL) prior to insertion of a Hallprint PDAT nylon dart-style tag into the musculature at the base of the spiny dorsal fin by using a 4-mm, stainless-steel needle. Tagged fish were included in the study only if they appeared to be in good health at the surface and the tag barb was firmly anchored between the pterygiophore bones. Every third fish received two tags to facilitate estimation of tag loss rates. Tagged fish were released unvented by using a SeaQualizer descending recompression device (Drumhiller et al. 2014; Harrison 2015).

Fish release condition was assessed by attaching a GoPro Hero4 camera to the release line 1.75 m above the SeaQualizer to record the fish's behavior just after release at depth. A release condition index was assigned for each fish based on its behavior. The release condition index values were as follows: 0 = unknown (due to a bad camera angle, murky water, or the camera being reeled up too soon), 1 = good (the fish swam away during descent before the SeaQualizer weight hit the seafloor), 2 = fair (fish swam away after the descent was over and the weight hit the seafloor), 3 = poor (fish was belly up or otherwise showing little sign of life; e.g., lying on its side with little to no movement of the operculum), and 4 = presumed dead (fish showed no signs of life after release).

Anglers were paid a reward of US$250 per tag for reporting recaptured fish, with double-tagged fish worth $500 (i.e., two $250 tags). The reward amount was printed on each tag and was assumed to elicit 100% reporting (Sackett and Catalano 2017). The study was advertised through flyers distributed to local fishing communities, bait shops, and fishery-related businesses. We also advertised through radio, newspaper, and social media. As was shown in our advertisements and displayed on the tag, fishers were asked to report the recapture of tagged fish and to fill out a survey by either e-mail or a toll-free phone number and return the tag to us for a reward (see Supplemental Figure S1 available separately online). The survey asked fishers for information to identify the fish and to distinguish our tags from those used in other Red Snapper tagging programs in the northern Gulf of Mexico (tag number and color); whether the fish was kept or released; whether the tagged fish was caught commercially or recreationally through a private boat or a charter (for-hire) boat; the date of the capture; and, if the fisher had a fishing license, which state it was from. We also asked for information on the location of the capture (state waters, depth stratum, specific depth of capture, type of reef [e.g., published or unpublished, natural or artificial], latitude, and longitude), the size of the fish, and the port of departure and return. We also used simple linear regression and ANOVA to evaluate fisher responses where appropriate. Specifically, regression was used to examine the relationships between recapture locations over time and fish size with the time the fish was at large and the distance the fish moved, whereas ANOVA was used to determine the differences in mean fish size between depth strata and fishing sectors. It is important to note that the fish size used for these analyses was the TL of the fish when tagged because of the short duration of the season and because the fish sizes reported upon recapture by fishers were not always reliable.

Estimation model.— We used a multinomial maximum likelihood model to estimate depth-specific capture rates ($F0'_d$), parameters describing length- and depth-specific vulnerability to harvest ($L50_d$, σ; equation 7, below), the tag loss rate (*Tag Loss*), fish voluntary release rate (r_l), and rates of movement from release depth stratum d to recapture depth stratum d' ($\Psi_{dd'}$; sensu Williams et al. 2001; Table 1). The recapture depth stratum was not always reported by anglers, and follow-up attempts to contact anglers to obtain this information were unsuccessful in some cases. To ensure that these tag returns were included in the model, we

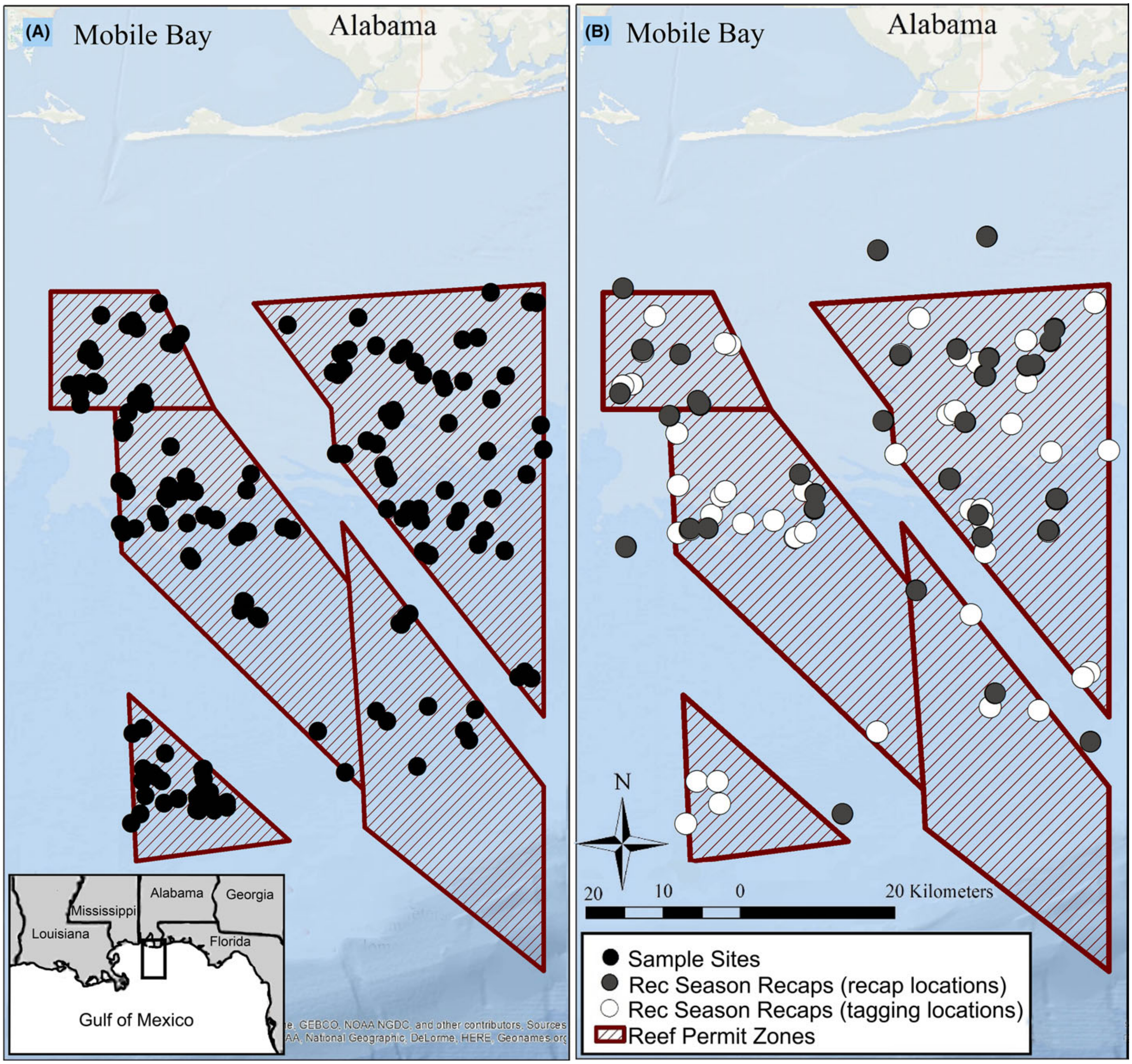

FIGURE 1. **(A)** Red Snapper sampling sites (tagging locations of all fish; black circles) in the Alabama Artificial Reef Zone within the Gulf of Mexico; and **(B)** recapture locations of Red Snapper reported with GPS coordinates (gray circles) and tagging locations of individuals that were recaptured during the Alabama state recreational (rec) fishing season (May 27–July 31, 2016; white circles).

estimated an additional parameter (φ) that represented the probability that the recapture depth was known and reported by the angler. We estimated the average growth of recaptured Red Snapper over the recreational season using the von Bertalanffy growth function with constants from Patterson et al. (2001a; asymptotic length L_∞ = 969 mm, growth coefficient k = 0.19, theoretical age at zero length t_0 = 0.02) and the number of days at large for each individual Red Snapper. Thus, Red Snapper recaptured during the Alabama state recreational fishing season were estimated to have grown 23.2 ± 8.8 mm on average (±SD) over this time (range = 1.5–40.0 mm). As such, we used 100-mm length-bins to stratify fish length at tagging to encompass any growth that might have occurred between release and recapture over this relatively short season. The model then predicted the tag return probabilities ($P_{dd'tt'lj}$)

TABLE 1. Parameters and modeled quantities of the maximum likelihood model along with their descriptions.

Parameter	Description
d	Release depth stratum (shallow or deep)
d'	Recapture depth stratum (shallow, deep, or unreported)
t	Number of tags at release (one or two)
t'	Number of tags remaining upon recapture (one or two)
l	TL interval (100 mm)
j	Catch-and-release status (harvested or released)
$P_{dd'tt'lj}$	Probability of a released fish being reported as recaptured
$\gamma_{tt'}$	Probability of tag retention (probability that a fish released with t tags is recaptured with t' tags)
Tag Loss	Probability of tag loss per individual tag
m_d	Postrelease mortality rate
U'_{dlj}	Finite annual capture rate (fraction of tagged fish that are removed from the population by anglers)
U_{dl}	Finite annual exploitation rate (fraction dead due to fishing-related causes; i.e., harvest and postrelease mortality)
$\Psi_{dd'}$	Probability of movement
$F0'_d$	Instantaneous capture rate of fully vulnerable fish
F'_{dlj}	Instantaneous capture rate
F_{dl}	Instantaneous fishing mortality rate
Fcr_{dl}	Instantaneous fishing mortality rate attributable to angler catch and release
Fh_{dl}	Instantaneous fishing mortality rate attributable to harvest
Z'_{dlj}	Instantaneous total decay rate of tagged fish in the population; includes natural mortality and tag removal by anglers
Z_{dl}	Instantaneous total mortality rate of tagged fish in the population; includes natural, harvest, and angler catch-and-release mortality
M	Instantaneous natural mortality rate
ν_{dl}	Vulnerability to capture by anglers
$L50_d$	Length (TL, mm) at maximum vulnerability
σ	SD of the Gaussian vulnerability curve
r_l	Voluntary release rate (proportion of fish captured and released by anglers)
B_0	Intercept of the logistic model to predict voluntary release rate as a function of fish length
B_1	Slope of the logistic model to predict voluntary release rate as a function of fish length
δ	Fraction of angler-released fish that die

for fish that were tagged and released in depth stratum d (shallow or deep) and recaptured in stratum d' (shallow, deep, or unknown/unreported); tagged with t tags (one or two) and recaptured with t' tags remaining attached (one or two); with fate j (harvested or released); and in 100-mm length interval l:

$$P_{dd'tt'lj} = \begin{cases} \gamma_{tt'}(1-m_d)U'_{d'lj}\Psi_{dd'}\varphi & \text{for known recapture depth } d' \\ \gamma_{tt'}(1-m_d)[U'_{d'lj}\Psi_{dd'} + U'_{dlj}(1-\Psi_{dd'})](1-\varphi) & \text{for unknown } d' \end{cases}, \tag{1}$$

where $\gamma_{tt'}$ is the probability of tag retention (one or two tags retained); m_d is an assumed literature-based, depth-specific tagging mortality rate; U'_{dlj} is the depth-, length-, and fate-specific finite capture rate at the depth stratum of release (i.e., fish did not move; $d' = d$); $U'_{d'lj}$ is the capture rate at the nonrelease depth stratum (i.e., fish moved; $d' \neq d$); $\Psi_{dd'}$ is the estimated probability of movement between the release and recapture depth strata; and φ is the probability that anglers reported the recapture depth stratum. Movement probability was assumed to be one-way and linear between the time of tagging and recapture. Tagging mortality rates m_d were assumed to be 0.1 in the shallow depth stratum and 0.2 in the deep stratum (Campbell et al. 2014). The probability that a fish of length interval l released at depth stratum d with t tags went unrecovered was calculated as $1 - \sum_{d'}\sum_{t'}\sum_{j} P_{dd'tt'lj}$. The tag retention probabilities $\gamma_{tt'}$ were calculated as

$$\gamma_{tt'} = \begin{cases} 1 - \textit{Tag Loss} & \text{for } t = 1 \text{ and } t' = 1 \text{ (single tagged; tag retained)} \\ (1 - \textit{Tag Loss})^2 & \text{for } t = 2 \text{ and } t' = 2 \text{ (double tagged; both tags retained)} \\ 2(\textit{Tag Loss})(1 - \textit{Tag Loss}) & \text{for } t = 2 \text{ and } t' = 1 \text{ (double tagged; one tag lost)} \end{cases}, \tag{2}$$

where *Tag Loss* is the estimated tag loss rate (i.e., proportion of tags lost after release). Our approach assumed that the loss of individual tags from the same fish were independent events. We did not allow for long-term tag loss as a function of time at large due to the short duration of the fishing season. Movement ($\Psi_{dd'}$) was assumed to occur prior to the time of capture. When $d \neq d'$, the quantity $\Psi_{dd'}$ represents the probability of Red Snapper movement between depth strata. The sum of the $\Psi_{dd'}$ for fish released into stratum d must equal 1.0; thus, it follows that the probability of not moving ($\Psi_{dd'}$; i.e., $d = d'$) is equal to 1 minus the probability of movement. The finite capture rate for stratum d, length-bin l, and fate j (released versus harvested; i.e., the exploitation rate on tags) was modeled via

$$U'_{dlj} = \frac{F'_{dlj}}{Z'_{dl}}\left(1 - e^{Z'_{dl}}\right), \tag{3}$$

where F'_{dlj} is the depth-, length-, and fate- (harvest or release) specific instantaneous capture rate; and Z'_{dl} is the instantaneous total rate of loss of tagged fish from the population due to angler captures. The instantaneous capture rate was modeled as

$$F'_{dlj} = \begin{cases} F0'_d \nu_{dl} r_l & \text{for fate } j = 1 \text{ (fish was released voluntarily)} \\ F0'_d \nu_{dl}(1 - r_l) & \text{for fate } j = 2 \text{ (fish was harvested)} \end{cases}, \tag{4}$$

where $F0'_d$ is the depth-specific instantaneous capture rate for fully vulnerable fish, and ν_{dl} is the depth- and length-specific vulnerability to capture. The instantaneous total mortality rate of tagged fish was modeled as

$$Z'_{dl} = M + \sum_j F'_{dlj}, \tag{5}$$

where M is the assumed instantaneous natural mortality rate. The M-value was assumed to be 0.1 year^{-1} (SEDAR 2013) but was multiplied by 0.13 (i.e., 47/365 d) in the model to account for the average (±SE) of 47 ± 2 d at-large for recovered tags. The instantaneous rate formulation was used to permit evaluation of the sensitivity of exploitation rate estimates to the assumed M (see *Sensitivity* below). The voluntary release rate r_l was modeled as a logistic function of fish length that was constant between depth strata:

$$r_l = \frac{e^{B_0 + B_1 l}}{1 + e^{B_0 + B_1 l}}, \tag{6}$$

where B_0 and B_1 are as defined in Table 1. Length- and recapture depth-specific vulnerability to capture (ν_{dl}) was modeled using a Gaussian function,

$$\nu_{dl} = e^{\frac{-(l - L50_d)^2}{2\sigma^2}}, \tag{7}$$

where $L50_d$ is the estimated depth-specific length at maximum vulnerability (i.e., vulnerability = 1.0) and σ is the estimated SD of vulnerability across lengths.

Finite exploitation rates of Red Snapper (U_{dl}; proportion that died due to harvest or catch-and-release mortality) were modeled via

$$U_{dl} = \frac{F_{dl}}{Z_{dl}}(1 - e^{-Z_{dl}}), \tag{8}$$

where F_{dl} is the instantaneous mortality rate of Red Snapper due to fishing-related causes and Z_{dl} is the total instantaneous mortality rate of Red Snapper. The F_{dl} were obtained by summing the harvest mortality rates (Fh_{dl}) and catch-and-release mortality rates (Fcr_{dl}), which were obtained as follows:

$$Fcr_{dl} = F'_{dlj=1}\delta \tag{9}$$

$$Fh_{dl} = F'_{dlj=2}, \tag{10}$$

where δ is the assumed postrelease mortality rate (probability of mortality after release) for angler-caught fish and F'_{dlj} is as defined for equation (3). We assumed tagging and angler release mortality rates of 0.1 for the shallow depth stratum and 0.2 for the deep stratum. These values were calculated from a meta-analysis of Red Snapper release mortality rates for the recreational fishery (Campbell et al. 2014). Thus, the values were averaged to encompass each depth stratum tested here. The Z_{dl} were obtained via

$$Z_{dl} = Fcr_{dl} + Fh_{dl} + M. \tag{11}$$

We evaluated 24 candidate models in which fishing mortality and movement rates were either constant or varied between depth strata and in which vulnerability was either constant or varied with fish length and depth stratum (Table 2). Candidate models were compared using Akaike's information criterion corrected for small sample sizes (AIC$_c$) and associated model weights (w_i), and

TABLE 2. Seven of 24 weighted candidate models ranked with Akaike's information criterion corrected for small sample sizes (AIC$_c$; Burnham and Anderson 1998) to estimate the exploitation rate of Red Snapper tagged in the Alabama Artificial Reef Zone (see Figure 1; K = number of parameters; w_i = model probability weight [a measure of relative strength]; F = fishing mortality; ν = vulnerability; Ψ = movement probability; r = angler release rate). Parenthetical terms represent whether the factor was varied with depth (d; shallow stratum: <36.5 m; deep stratum = 36.5–61.0 m), was varied with fish TL (l), or was held constant (.).

Model				K	AIC$_c$	w_i
$F(d)$	$\nu(., l)$	$\Psi(.)$	$r(.)$	8	686.51	0.32
$F(d)$	$\nu(d, l)$	$\Psi(.)$	$r(.)$	9	687.44	0.20
$F(d)$	$\nu(., l)$	$\Psi(.)$	$r(l)$	9	688.08	0.15
$F(d)$	$\nu(., l)$	$\Psi(d)$	$r(.)$	9	688.79	0.10
$F(d)$	$\nu(d, l)$	$\Psi(.)$	$r(l)$	10	689.01	0.09
$F(d)$	$\nu(., l)$	$\Psi(d)$	$r(l)$	10	689.51	0.07
$F(d)$	$\nu(d, l)$	$\Psi(d)$	$r(.)$	10	689.77	0.06

weighted parameter estimates and their SEs were computed when appropriate (Burnham and Anderson 1998). Furthermore, predictive variable weights (the sum of w_i over all candidate models in which that predictor variable is explicitly included; Burnham and Anderson 1998) were compared to determine the importance of individual predictive variables for model results. The models were fitted by minimizing the negative log likelihood using the "optim()" function in R (Broyden–Fletcher–Goldfarb–Shanno optimization algorithm; R Core Team 2015). Parameter SEs were estimated by inverting the Hessian matrix, which assumes asymptotic normality of the likelihood function at the value of the maximum likelihood estimate. The 95% confidence intervals (CIs) were estimated using the Wald method. Instantaneous fully vulnerable capture rates ($F0'_d$) and vulnerability parameters ($L50_d$, σ) were estimated on the log scale to constrain them to positive values, whereas *Tag Loss* and the probability that the recapture depth was known and reported (φ) were estimated on the logit scale to constrain them between 0.0 and 1.0.

Sensitivity.— We assessed the sensitivity of exploitation rate estimates to the assumed M, tagging mortality rates, and fish movement assumptions. To assess sensitivity to M, we re-ran our minimum-AIC$_c$ model under M-values that ranged from 0.05 to 0.30 year^{-1} by increments of 0.05 year^{-1}. Sensitivity to tagging mortality assumptions was evaluated with two approaches. The first approach involved re-running the minimum-AIC$_c$ model under a range of assumed tagging mortality rates that were half, double, triple, and quadruple the original literature-based assumption of 0.1 in the shallow depth stratum and 0.2 in the deep stratum. The second approach involved running the model on a subset of the data that included only fish with an assessed released condition of 1 or 2 and assuming no tagging mortality. We also tested the sensitivity of angler release mortality to model estimates by using the original literature-based assumption of 0.1 in the shallow depth stratum and 0.2 in the deep stratum, the maximum estimates of release mortality from Campbell et al. (2014) for nonvented Red Snapper (0.25 for the shallow stratum; 0.4 for the deep stratum), and the mean nonvented mortality for each depth stratum from the Campbell et al. (2014) study (0.2 for the shallow stratum; 0.3 for the deep stratum).

RESULTS

Recaptures

Eighty-two recaptured fish were reported by recreational anglers and two recaptures were reported by commercial anglers during the Alabama state recreational fishing season. Of the 724 Red Snapper that were tagged and released, six were recaptured prior to the start of the Alabama recreational season and thus were excluded from the total number of tagged fish available to recapture during the fishing season (i.e., 718; this value was used in our analyses). Recreational recaptures equated to 11% of all tagged fish. The proportions of fish recaptured in each depth stratum were 0.14 for the shallow stratum and 0.07 for the deep stratum. For both charter boat and private boat fishers, the majority of recaptures were from the shallow stratum (74% and 83%) rather than from the deep stratum (26% and 18%). Forty-nine percent of recreational recaptures were from private boats, 41% were from charter or for-hire boats, and 10% of anglers submitting recapture information did not answer this question. Seventy percent of recreational Red Snapper recaptures came from anglers with fishing licenses issued by the state of Alabama, and 22% of recaptures were from fishers that had no fishing license; recaptures were also reported by anglers holding licenses from four other states (Florida: 4% of recaptures; Kentucky: 1%; Mississippi: 1%; and Tennessee: 1%). Thirty-five percent of all recaptured fish were double-tagged (95% binomial CI = 25–47%); this percentage was not significantly different from the percentage of all tagged fish that were double-tagged (33%; 95% binomial CI = 30–37%). In addition, the proportion of double-tagged fish that were recaptured during the Alabama fishing season (0.12; 95% binomial CI = 0.08–0.17%) was similar to the proportion of single-tagged fish that were recaptured during the season (0.11; 95% binomial CI = 0.09–0.14%). Four of 29 recaptured double-tagged fish had lost a tag.

Nearly all 2016 recreational recaptures occurred within the Alabama state recreational season (93%; May 27–July 31), with only 3% occurring just prior to the start of the season and 3% occurring between the end of the fishing season and the end of the year. Ninety-four percent of recaptures from charter boats fell within the federal season for charter boats (June 1–July 16; Figure 2) and within the Alabama state season. Only 60% of recaptures from private boats occurred within the federal season for private boats (June 1–11), although 93% occurred during the Alabama state season. Twelve recaptured fish (15%) were released during the Alabama season: one was recaptured by a charter fisher, and 11 were recaptured by private fishers. The percentage of charter recaptures that were released was 9%, and the percentage of private recaptures released was 18%. In addition, recaptures during the Alabama state season occurred in shallower waters later in the season for all recaptures ($R^2 = 0.19$, $P < 0.01$, $N = 52$; depth = 7,381.61 − [2.07^{-6} × date recaptured]) and for private boat recaptures ($R^2 = 0.32$, $P < 0.01$, $N = 31$; depth = 8,314.35 − [2.33^{-6} × date recaptured]) and charter boat recaptures ($R^2 = 0.29$, $P = 0.01$, $N = 21$; depth = 13,965.22 − [3.93^{-6} × date recaptured]) separately (Figure 2).

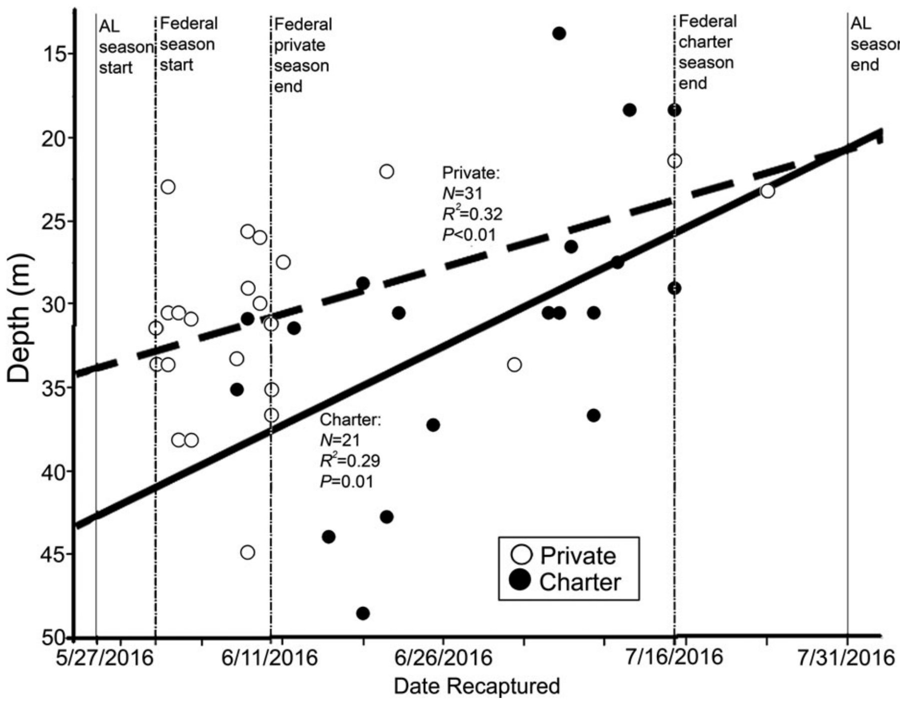

FIGURE 2. Relationship between Red Snapper recapture timing and the depth of recaptures by private boat (dashed angled line) and charter boat (solid angled line) anglers during the Alabama state fishing season (solid vertical lines). The federal private and charter boat seasons are also indicated (dashed vertical lines).

Fish movement averaged 7.9 km and ranged from 0.01 to 42.6 km between tag and recapture locations during the Alabama recreational fishery season. These measurements were based on 41 sets of angler-provided GPS coordinates (latitudes and longitudes) with enough significant digits to ensure precise recapture locations (at least four decimal degrees or degrees, minutes, seconds; Figure 1B). Of these 41 recaptures, and assuming the reported recapture locations were accurate, 78% of the fish moved less than 15 km. There was no relationship between the distance moved and either the size of the fish (P = 0.65) or the time at large (P = 0.13).

The reported locations of recaptured fish were not always in agreement with GPS coordinates provided by fishers. For instance, of those fishers that provided precise GPS coordinates, 17% indicated the survey catch location as inside or outside of the AARZ while providing GPS coordinates that demonstrated the opposite (Figure 1B). There was a slightly lower percent disagreement (15%) between the survey response regarding which depth stratum the fish was recaptured in and the depth stratum suggested by the supplied GPS coordinates. To rectify these differences in our analyses, we used fisher survey responses for location data when GPS coordinates were not provided, and we used GPS coordinates for location data when provided (bathymetry contour data were used to determine the depth stratum). Based on this approach, we estimated that 84% of recaptured fish were located inside of the AARZ. The angler responses to survey questions also suggested that 54% of recaptured fish were from unpublished reefs, 27% of recaptures were from published reefs, and 20% of respondents did not know whether the fish was caught from an unpublished or published reef. Additionally, we found that 60% of recaptured fish were from artificial reefs and 3% were from natural reefs, whereas for 37% of recaptures, the fishers could not distinguish the type of reef from which the fish was recaptured.

The average TL (±SD) of recaptured fish when tagged was 600.7 ± 119 mm (range = 409–889 mm), with larger fish being both tagged (F-ratio = 87.9, P < 0.01) and recaptured in deeper waters (F-ratio = 16.6, P < 0.01; Figure 3). Fish that were caught during the Alabama state season were at large for an average (±SE) of 46.6 ± 2 d (range = 3–81 d).

The proportion of tagged fish that were recaptured during the Alabama state recreational season was examined for each 100-mm length-bin, which provided insight into vulnerable Red Snapper sizes in each depth stratum and between the different recreational fisheries (i.e., private versus charter). For instance, the largest proportion of single-tagged fish that were recaptured from shallow releases was from the 600–700-mm size-bin (0.32; Figure 4A). Similarly, the proportion of single-tagged fish recaptured from deep releases also peaked at 600–700 mm and was 0.11

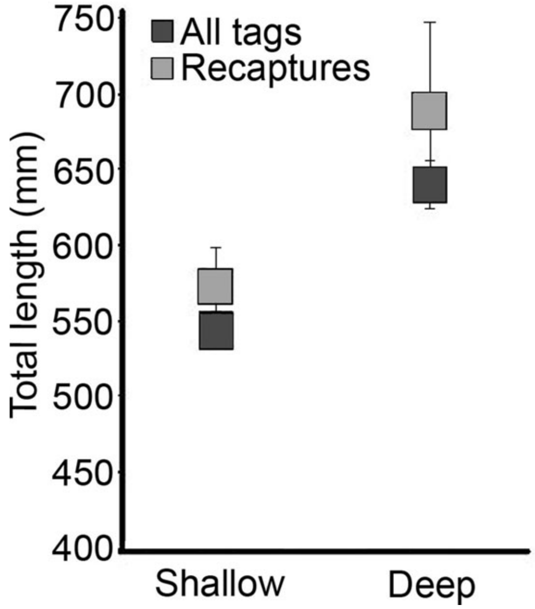

FIGURE 3. Mean TL (±95% confidence interval) of all Red Snapper that were tagged and recaptured in the shallow depth stratum (<36.5 m) and the deep stratum (36.5–61.0 m) of the Alabama Artificial Reef Zone within the Gulf of Mexico. Size for recaptured fish is reported as the TL at tagging.

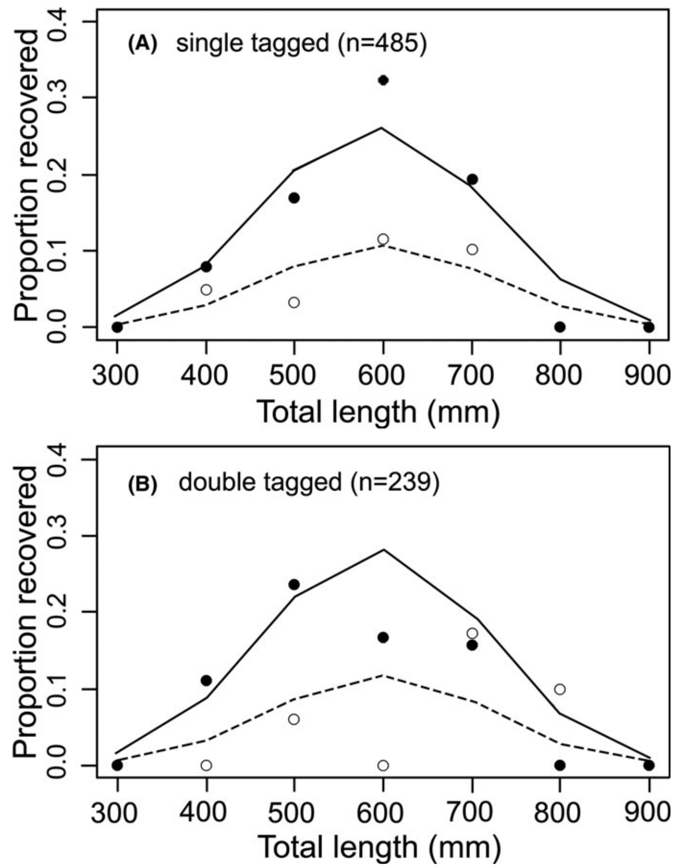

FIGURE 4. Observed (circles) and model-predicted (lines) proportions of tagged Red Snapper in 100-mm TL size-bins that were reported as recaptured by anglers for fish released in the shallow stratum (<36.5 m; solid circles and solid line) and deep stratum (36.5–61.0 m; open circles and dashed line) of the Alabama Artificial Reef Zone within the Gulf of Mexico. **(A)** shows the data and model fits to the single-tagged fish releases, and **(B)** depicts the double-tagged releases. The number of fish tagged is indicated in each panel.

(Figure 4). The proportion of double-tagged fish that were recaptured was more variable with respect to fish length, reflecting the smaller sample sizes (Figure 4B). Dividing recreational recaptures into those from charter boats and private boats demonstrated that Red Snapper across two length-bins (600–800 mm) had the largest proportion of recaptures for the charter boat fishery (0.08), whereas Red Snapper between 500 and 600 mm had the largest proportion of recaptures for private fishers (0.10).

Estimating Exploitation

Of the 24 models that were fitted to the tag return data, seven had model weights (the probability that the model is the best of those tested) greater than 0.01 (Burnham and Anderson 1998; Table 2). In each of the seven models, fishing mortality varied with depth, and vulnerability varied with fish length (Table 2). As such, these two factors had predictive variable weights of 1.0, demonstrating their presence in all of the top models (Table 3). Models that incorporated vulnerability and movement held constant with depth had predictive variable weights of 0.73 and 0.76 (Table 3). Angler release rate held constant with fish length had a much higher parameter weight than angler release rate that varied with fish length. Thus, the minimum-AIC$_c$ model, with a model weight of 0.32, included fishing mortality that varied with depth, vulnerability that varied with fish length, movement and vulnerability that were constant across depth strata, and angler release rate that was constant with fish length. The most vulnerable size-class averaged across models was 600–700 mm (Figure 4). Model-averaged exploitation (U_{dl}) for this fully vulnerable size-class was estimated to be 0.37 ± 0.071 (mean ± SE; instantaneous fishing mortality [F_{dl}] = 0.47 year^{-1}) in the shallow depth stratum and 0.12 ± 0.035 (F = 0.13 year^{-1}) in the deep stratum. The tag loss rate (*Tag Loss*) was estimated to be 0.08 ± 0.038 over the Alabama recreational fishing season. Movement between both depth strata ($\Psi_{dd'}$) was estimated to be 0.14 ± 0.061. Angler release rate (r_l) was estimated to be 0.19 ± 0.16 and was constant with fish length. Accounting for the vulnerability of each size-class as determined by the weighted average estimates, we calculated the exploitation rate for the tagged population in each depth stratum and a weighted average for the aggregate tagged population. These exploitation estimates were 0.20 (F = 0.25 year^{-1})

TABLE 3. Predictive variable weights (i.e., the sum of model weights that included the given predictive variable; Burnham and Anderson 1998; see Table 2; F = fishing mortality; ν = vulnerability; Ψ = movement probability; r = angler release rate). Parenthetical terms represent whether the predictive variable was varied with depth (d; shallow stratum: <36.5 m; deep stratum = 36.5–61.0 m), was varied with fish TL (l), or was held constant (.).

Predictive variable	Predictive variable weight
$F(d)$	1.00
$F(.)$	0.00
$\nu(l)$	1.00
$\nu(.)$	0.00
$\nu(d)$	0.27
$\nu(.)$	0.73
$\Psi(d)$	0.24
$\Psi(.)$	0.76
$r(l)$	0.31
$r(.)$	0.69

in the shallow depth stratum, 0.06 (F = 0.07 year^{-1}) in the deep stratum, and 0.14 (F = 0.18 year^{-1}) for the aggregate tagged population.

Sensitivity

Although the estimate of exploitation rate from our minimum-AIC$_c$ model was not sensitive to changes in the M (Figure 5A) or angler release mortality (Figure 5B) used in the model, it was sensitive to changes in the tagging mortality rate (Figure 5C). When our assumed tagging mortality rates for this model (shallow stratum: 0.1; deep stratum: 0.2) were halved (shallow stratum: 0.05; deep stratum: 0.1), the exploitation rate estimated for the most vulnerable size-class of Red Snapper decreased by 14% for the shallow stratum and by 17% for the deep stratum compared to our original estimates. Exploitation rate estimates increased by 5% for the shallow stratum and by 17% for the deep stratum when tagging mortality was doubled. When tagging mortality was tripled, the estimated exploitation rate for shallow and deep strata increased by 24% and 67%, respectively; when tagging mortality was quadrupled, the exploitation rate increased by 43% and 217%, respectively. In addition, when data were limited to include only those fish that were tagged and released in the best condition (release condition 1 or 2), assuming a tagging mortality rate of zero, the exploitation rate estimates were 25% lower for the deep stratum and 3% lower for the shallow stratum (Figure 5C).

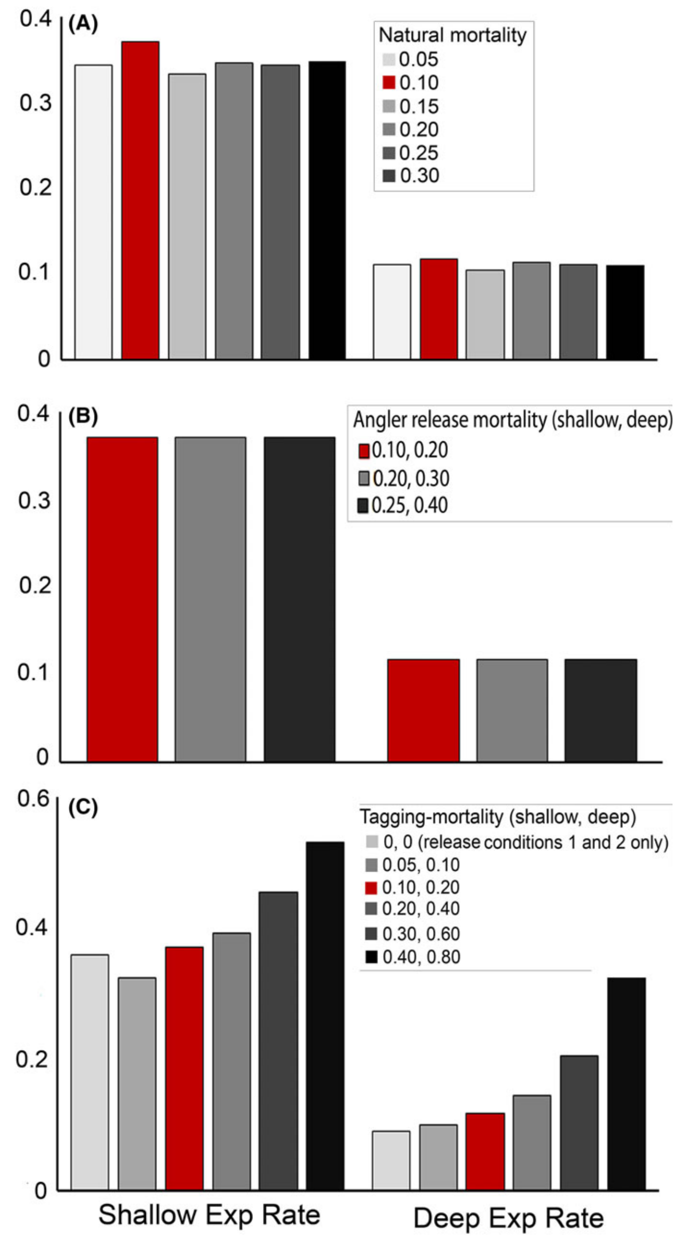

FIGURE 5. Sensitivity of the highest-ranked model (the model with the lowest Akaike's information criterion corrected for small sample sizes; Burnham and Anderson 1998; see Table 2) to different values of **(A)** natural mortality rate, **(B)** angler release mortality, and **(C)** tagging mortality rate of Red Snapper in the shallow stratum (<36.5 m) and deep stratum (36.5–61.0 m) of the Alabama Artificial Reef Zone within the Gulf of Mexico. Exploitation (exp) rate estimates are for the most vulnerable size-class (600–700 mm). In each panel, the red bars represent the values assumed in the original model.

DISCUSSION

Using a tag–recapture approach in the AARZ off the Alabama coast, we found strong empirical support for higher fishing mortality in the shallower depth stratum than in the deep stratum, a dome-shaped relationship between vulnerability and fish length, constant movement rates with release depth, and constant release rates across fish lengths. Model-averaged results agreed with the estimates from the minimum-AIC$_c$ model, which estimated the exploitation rate across the entire sample area and tagged population as 0.14. The stratum-specific exploitation rate estimates were 0.20 for the shallow depth stratum and 0.06 for the deep stratum. Although previous studies have suggested higher exploitation rates in shallower waters compared to deeper waters, few specific estimates exist at these smaller spatial scales (Topping and Szedlmayer 2013: $F = 0.27$, 95% CI = 0.11–0.54; Karnauskas et al. 2017; Sackett and Catalano 2017). Furthermore, the importance of spatial variability to Red Snapper ecology, fishing mortality, and removals—and thus management—suggests a need for exploitation estimates at finer spatial and biological scales than those used to generate the estimates presently available (Karnauskas et al. 2017). Future studies examining exploitation rates for Red Snapper should account for these spatial and size-related differences. Currently, in the federal stock assessment, the spatial variability of exploitation results is only very broadly considered in the fishery, which is divided into two large spatial strata (east and west of the Mississippi River; SEDAR 2013).

Our analysis suggests that the vulnerability of tagged Red Snapper to the recreational fishery in and around the AARZ was dome-shaped, with the most vulnerable fish being those between 600 and 700 mm. The exploitation rate for this size-class was 0.37 in the shallow depth stratum and 0.12 in the deep stratum. Thus, exploitation estimates for the most vulnerable size-class in the shallow stratum were over double those of the entire tagged population in the AARZ. Raw recapture data from our study also suggested that vulnerability may have varied with fishing type (for-hire charter versus private). The raw data suggested that smaller fish were more vulnerable to private fishers (500–600 mm) in comparison with for-hire headboat or charter boat fishers (600–800 mm). There are several possible explanations for the differences in recaptured fish sizes between these fishery sectors, including differences in terminal gear type, fisher experience, fisher knowledge of the area and habitat, and the rate and size of frequented fishing grounds that may deplete larger fish.

Site fidelity of Red Snapper has been estimated by numerous researchers to examine the importance of reefs and other habitats to the life history of Red Snapper, to assess whether reefs produce or attract Red Snapper, and to help determine the value of more localized management strategies (Bohnsack 1989; Patterson et al. 2001b; Patterson and Cowan 2003; Szedlmayer and Schroepfer 2005; Schroepfer and Szedlmayer 2006; McCawley and Cowan 2007). Some of these estimates have suggested that Red Snapper in the AARZ have high site fidelity to artificial reef structures, with approximately 76–97% of tagged fish remaining at or very near tagging locations (≤2 km, with many <200 m) for extended periods of time (e.g., ~120 d; Szedlmayer and Shipp 1994; Szedlmayer and Schroepfer 2005; Schroepfer and Szedlmayer 2006). Others have estimated site fidelity to be more intermediate, with approximately 36–50% remaining at or very near (≤2 km) their original tagging location for an extended period of time (i.e., 180 d; Patterson et al. 2001b; Patterson and Cowan 2003; Strelcheck et al. 2007). Indeed, studies by Schroepfer and Szedlmayer (2006) and Topping and Szedlmayer (2011) estimated a 50–72% per year rate of site fidelity to artificial reefs for ultrasonically tagged adult Red Snapper in waters off Alabama across numerous years. Here, recaptured Red Snapper tagged within the AARZ were estimated to move 7.85 km on average between tagging and recapture locations, with 78% remaining within 15 km of tagging sites. Our site fidelity results were consistent with movement rates seen by Schroepfer and Szedlmayer (2006) and were still similar to the intermediate site fidelity seen by others as well due to the short duration of our study (Patterson et al. 2001b; Patterson and Cowan 2003; Strelcheck et al. 2007). However, it is important to note that our movement analysis was not equivalent to the telemetry results discussed above because of the limited location data (tag and recapture) and the reliance on fishers to recapture tags. Varying estimates of site fidelity and movement among studies are likely the result of temporal changes in episodic events (e.g., storm systems and cold fronts; Moseley 1966), prey movements (Bradley and Bryan 1975), changes in habitat quality, and sampling of different Red Snapper subpopulations or size-classes (Wells and Cowan 2007). Lastly, it is important to note that none of the fish tagged in the AARZ were recaptured and reported from waters off any other state in the northern Gulf of Mexico. This is a surprising result, as the coast of Alabama makes up a very narrow portion of the Gulf of Mexico coastline and a portion of fish in this study moved far enough to have left the waters off Alabama, though they were not recaptured and reported in other waters. Instead, most tagged fish that moved relocated from shallow to deep or from deep to shallow waters rather than longitudinally into other states' waters. These results could be related to the movement of adult Red Snapper to forage; previous studies have suggested that Red Snapper may temporarily move off preferred reef structures to feed on mud/sand-associated prey and pelagic prey before returning to the reef (Bohnsack et al. 1997; McCawley and Cowan 2007; Wells et al. 2008). Another potential explanation could be that there is less fishing effort for Red Snapper in the waters off other Gulf coast states. Although the fish movements seen during our study were dependent on the spatial distribution of fishing effort and the accuracy of fisher responses, results do support previous ultrasonic telemetry study conclusions that a large portion of adult Red Snapper likely exhibit site fidelity to artificial reef structures. Furthermore, the site fidelity observed among tagged fish in the AARZ along with the high level of site fidelity to waters off Alabama suggest that the depletion or rebuilding of adult size-classes in local areas like the AARZ is at least partly under local influence, whether positive (e.g., local stock rebuilding) or negative (e.g., overfishing). Thus, understanding exploitation at these smaller spatial scales is warranted to ensure the sustainability of local populations of adult Red Snapper.

The consistency in tag loss rate estimates across tested models (all weighted models had the same tag loss rate estimate) lent confidence to this estimate (0.08) for dart tags in Red Snapper. In addition, the return rates of single-tagged (worth $250) and double-tagged (worth $500) fish were similar, suggesting that any increase in the $250 reward amount would not have increased the reporting rate. Thus, our findings indicate that a reward amount of $250 was adequate to elicit near-100% reporting. This result was further supported by the equivalent proportion of double-tagged fish that were released and returned, showing no bias in the reporting of double-tagged versus single-tagged fish. Assuming that a high reward amount will elicit 100% reporting is a common procedure (Henny and Burnham 1976; Conroy and Blandin 1984; Murphy and Taylor 1991; Nichols et al. 1991; Pollock et al. 2001; Denson et al. 2002) but must be evaluated for each fishery. We cannot rule out that for some fishers, no reasonable reward amount (e.g., $10,000) would elicit a report or that there could be a similar bias in the nonreporting of single- and double-tagged fish. This obstacle is particularly problematic in an expensive fishery, such as that for Red Snapper (e.g., daily fuel costs can exceed $500), as fishers may assume that not returning a tag could eventually result in a longer fishing season (Brown and Wilkins 1978; Pollock et al. 2001). In the present case, if the reporting rate is less than the assumed 100%, our estimates would be underestimated (Sackett and Catalano 2017). Thus, our estimates of exploitation should be viewed as minimum values, which could be biased low if nonreporting rates were nonnegligible.

Our estimates of exploitation rate were sensitive to our assumed tagging mortality rates, with estimates from the shallow depth stratum generally changing more drastically than those from the deep stratum due to a larger portion of exploitation occurring in the shallow depth zone. Limiting data to only those tagged Red Snapper most likely to have survived tagging and assuming a tagging mortality rate of zero resulted in similar exploitation rate estimates compared to the best model. Thus, assuming survival of those fish in good condition may suggest that our assumed tagging mortality values of 10% in the shallow depth stratum and 20% in the deep stratum are close to the actual tagging mortality rates, incorporating fish that expire immediately after release and those that have delayed postrelease mortality. Other researchers have estimated that a 20% catch-and-release mortality rate only applies to fish caught in waters between 20 and 40 m deep (Patterson et al. 2001b; Burns et al. 2004; Rummer 2007), with rates of about 50% in waters at the deepest end of the range used here (60 m; Burns et al. 2002). Southeast Data, Assessment, and Review (SEDAR 2005) estimated Red Snapper catch-and-release mortality to range from 18% to 88% in both the recreational and commercial fisheries. Curtis et al. (2015) found 15% overall immediate release mortality and 13% delayed release mortality for Red Snapper, with higher survival in cooler temperatures and shallower depths and when fish were vented or released by using a descender device. It is important to note that although many of these other estimates included a much wider depth range than used in our study and did not use the same SeaQualizer technique we used, these catch-and-release estimates may apply to the fishery as a whole. Rummer (2007) suggested that in fisheries like the Red Snapper fishery, where catch-and-release mortality can be high and the species demonstrates site fidelity, a spatial management (e.g., marine protected area) approach may be more effective than season closures or size and bag limits, which encourage catch and release and could hamper the recovery of the fishery. In Hawaii, a spatial management approach, including several smaller marine protected areas distributed throughout the range of the species and fishery, proved relatively successful for several deepwater snapper species (Sackett et al. 2014, 2017).

The Red Snapper fishery is the most important recreational and commercial fishery in the northern Gulf of Mexico (Fischer et al. 2004). Thus, knowledge about the exploitation that Red Snapper subpopulations experience at smaller spatial scales (e.g., at the regional and state level) is important for the future of this fishery (Patterson 2007; Saillant et al. 2010; Karnauskas et al. 2017). Here, we suggest that studies of exploitation at spatial scales relevant for Red Snapper ecology and the distribution of fishing effort be used to better understand the impact of exploitation on the fishery over an area and to support local and regional fishery management efforts (Karnauskas et al. 2017). Our examination of Red Snapper in the AARZ shows that future studies examining exploitation rate for Red Snapper in the northern Gulf of Mexico should account for spatial and size-related differences in exploitation and vulnerability and should obtain direct estimates of tagging mortality to reduce reliance on assumed literature-based values. Our results also showed that because of Red Snapper site fidelity to the AARZ and to the waters off Alabama in general, the depletion or rebuilding of adult Red Snapper may be at least partly dependent on local management influence. Therefore, estimating regional exploitation rates is prudent to guide management of Red Snapper at smaller spatial scales.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.