A meta-analysis of red snapper (*Lutjanus campechanus*) discard mortality in the Gulf of Mexico

Chloe Ramsay, Julie Vecchio, Dominque Lazarre, Beverly Sauls

SEDAR74-AP-01

26 November 2022

Please cite this document as:

Ramsay, Chloe, Julie Vecchio, Dominque Lazarre, Beverly Sauls. 2022. A meta-analysis of red snapper (*Lutjanus campechanus*) discard mortality in the Gulf of Mexico. SEDAR74-AP-01. SEDAR, North Charleston, SC. 25 pp.

A meta-analysis of red snapper (*Lutjanus campechanus*) discard mortality in the Gulf of Mexico

CAMPBELL *et al*. 2014 META-ANALYSIS UPDATE

Chloe Ramsay, Julie Vecchio, Dominque Lazarre, Beverly Sauls

Florida Fish and Wildlife Conservation Commission

Fish and Wildlife Research Institute

100 8th Ave SE

St. Petersburg, FL 33701

October 2022

Table of Contents

I. ABSTRACT

Red Snapper (*Lutjanus campechanus)* is an economically important fishery in the Gulf of Mexico. Red Snapper are subject to discard mortality from barotrauma as this species is physoclistous, demersal, and are often caught in deeper waters. Novel research to address discard mortality since a 2014 meta-analysis on this topic has been extensive, with a focus on also estimating delayed mortality rather than just immediate mortality at the surface (*i.e.,* swim or float). To synthesize research on discard mortality of Red Snapper we conducted a meta-analysis, combining 11 studies, with 84 distinct estimates from 34 years of research. Only studies that assessed both immediate and delayed mortality were included. We assessed if depth, season, release method, or region could significantly predict discard mortality and generate estimates. We found a significant positive relationship between depth and discard mortality and that, in the western Gulf, fishing in the summer significantly increases discard mortality compared to fishing in other seasons. We found no effect of release method or region on discard mortality. Our mortality estimate, including both immediate and delayed mortality measures, is 34% at the average depth studied (45m), which more than doubles the estimate of discard mortality generated by a previous meta-analysis on this topic. Given that this meta-analysis generated estimates from both immediate mortality and delayed mortality from capture, we propose that these updated and higher estimates of discard mortality are likely more representative of the mortality experienced by the fishery.

II. INTRODUCTION

Catch and release has long been accepted as an effective and intuitive conservation tactic (Policansky, 2022). In theory, fish that do not meet a minimum size limit or are not the target species can be released alive, having no negative impact on the fish population (Cooke & Schramm, 2007; Raby et al., 2014). However, in practice, fishing can lead to mortality, and estimating how many untargeted or undersized fish experience mortality from fishing is an important part of effectively managing fisheries. Due to size limits and season closures, over 75% of caught Red Snapper are discarded (NMFS Fisheries Statistical Division, 2022). Therefore, as new data on the discard mortality of this species becomes available, updated estimates should be used to better understand the fishery and support management as they continue to successfully rebuild this fishery (SEDAR 52, 2018).

Early research on discard mortality largely focused on immediate mortality from fishing (*i.e.*, fish dead on release or unable to swim away; Campbell et al., 2014; S. L. Diamond & Campbell, 2009). Immediate mortality is often caused by barotrauma or hooking injures (Bartholomew & Bohnsack, 2005; Burns & Froeschke, 2012; Muoneke & Childress, 1994; Rummer & Bennett, 2005). Hooking injuries such as lacerations to gill, internal viscera, or esophagus can also lead to immediate mortality at the surface and are easily identifiable upon release (Bartholomew & Bohnsack, 2005; Burns & Froeschke, 2012; Render & Wilson, 1994). Barotrauma occurs due to pressure changes fish experience as they are brought to the surface. Common symptoms of barotrauma are bulging eyes, a distended abdominal region, flared opercula, and stomach eversion or prolapse (Rummer & Bennett, 2005). These effects can be particularly problematic for fish who are physoclistous (*i.e.*, do not have a pneumatic duct connecting the swim bladder to the digestive tract, which allows fish to fill or empty their swim bladder rapidly), such as Red Snapper, and therefore cannot acclimate as quickly to changes in depth. Distended swim bladders can lead to fish being unable to easily descend upon release, making them vulnerable to predation from both the sea and air as well as increased stress due to exposure to higher temperatures and sunlight (Rummer & Bennett, 2005; Scyphers et al., 2013; Wilde, 2009). Recent research has focused on the use of descender devices to reduce discard mortality from barotrauma (Ayala, 2020; Bohaboy et al., 2020; Curtis et al., 2015; Diamond et al., 2011; Drumhiller et al., 2014; Runde et al., 2021; Stunz et al., 2017). Descender devices physically bring the fish down to the depth they were caught at, allowing them to be released at the depth and pressure that they are acclimated to.

While hooking injures and barotrauma can be easy for angers to identify, fish that are caught often undergo more subtle physical damage and physiological stressors which can lead to delayed mortality (Raby et al., 2014). For example, barotrauma, handling, and exposure to air can cause changes in heart rate, ventilation rate, blood pressure, reductions in muscle energy stores, and other physiological stress responses. These responses, which may take hours to return to baseline levels, can result in cellular and tissue damage, reduced immunity, and behavioral changes which can all lead to delayed mortality (Davis, 2002; Mohan et al., 2020; Rummer, 2007; Wood et al., 1983). These physiological changes can leave fish too disoriented to avoid predation (Campbell, 2008; Parsons & Eggleston, 2005) and can even cause fish to release chemical cues that attract predators (Dallas et al., 2010; Jenkins et al., 2004). Due to these effects, researchers have been increasingly studying both immediate and delayed mortality when assessing discard mortality. For example, much of the recent research on Red Snapper discard mortality has used either acoustic or passive tags to assess any additional mortality that occurs in fish that appear healthy upon release (Bohaboy et al., 2020; Curtis et al., 2015; Runde et al., 2021; Stunz et al., 2017; Tompkins, 2017; Vecchio et al., 2020).

In 2014, Campbell *et al.* performed a meta-analysis to assess Red Snapper discard mortality rates in the Gulf of Mexico and whether they differed based on common fishing factors such as differences between commercial and recreational fisheries, fishing depth, etc. (Campbell et al., 2014). This model did not exclude mortality estimates that just addressed immediate mortality, however the authors emphasized the need for more research on delayed mortality and stated that using only immediate mortality for estimations should only be done as a last resort (Campbell et al., 2014). Due to the novel research focusing on delayed mortality and descender devices that had as occurred since this meta-analysis was conducted, we are updating this model. We reassess factors that affect discard mortality and estimate mortality rates in the recreational Red Snapper fishery in the Gulf of Mexico using new research and only studies that also include delayed mortality.

III. METHODS

We updated the Campbell *et al.* 2014 meta-analysis by adding data from studies that assessed the discard mortality of Red Snapper in the Gulf of Mexico after 2014 (Table 1). Additionally, we removed data included in the Campbell *et al*. 2014 meta-analysis that only measured immediate mortality upon release due to concerns that these data would underestimate Red Snapper mortality as negative physiological and behavioral effects from being fished can persist (Campbell, 2008; Drumhiller et al., 2014; Raby et al., 2014). After these changes the database included 11 studies, all assessing discard mortality in recreational fisheries. Mortality estimates were separated by depth of catch (m), region (west, east, and central), season (summer and not summer), and release method (no venting, some venting, total venting, and descending device use) when possible. If data was not separatable by one of those factors it was not included in the analysis of that factor. After separation, we had 84 estimates of mortality throughout the Gulf of Mexico.

Of these 11 studies, most used acoustic tags to track fish, with only one study where fish were tagged with conventional plastic-tipped dart tags (Vecchio et al., 2022) and three cage studies (Diamond & Campbell, 2009; Parker, 1985; Render & Wilson, 1996). Six studies were in the Western region (defined as Texas and Louisiana to MRIP statistical zone 13), three studies were conducted at least partially in the central region (defined as the rest of Louisiana, Mississippi, Alabama, and the panhandle of Florida through MRIP statistical zone 7 and Levy county) and only one study assessed discard mortality in the eastern region (defined as peninsular Florida starting at statistical zone 6 and Citrus county and continuing south). Regions defined here stock assessment regions for SEDAR 74(SEDAR 74, 2022). 46 of the 84 estimates occurred during the summer. While many studies reported months that the studies were conducted in, we differentiated seasons as they were defined in the manuscripts. 14 of the estimates were classified as no venting, 22 estimates were from descended fish (not always to the sea floor), and the remaining estimates came from fish where venting procedures were performed. Fish were classified as 'total venting' if all the fish in the treatment group were vented. Fish were classified as 'some venting' if some of the fish from the estimate were vented either through angler discretion (Vecchio et al., 2022) or because mortality estimates were not broken down by venting or not (Render & Wilson, 1996). Depths ranged from 10-85m, with a mean of 45m and a median of 49m. The sample sizes of fish tested to generate our estimates varied widely from three to 6150. Differences in sample sizes were addressed by giving estimates with smaller sample sizes higher variances around their effect sizes (and vice versa) and including this variance in our model, as described below. We attempted to classify by hook type but found that all studies used circle hooks or mixed hooks (including circle hooks) and therefore did not include this classification. All data used in this analysis can be found in Table 1.

Table 1: List of studies used in a meta-analysis of release mortality of red snapper (*Lutjanus campechanus)* in the Gulf of Mexico for which estimates of mortality are categorized in to depth in meters, season grouped as not summer (NS) and summer (S), region grouped as east (E), central (C), and west (W), study type (ST) grouped as caged (C), acoustic tag (AT), and passive tag (PT), and release method (RM) grouped as not vented (NV), some fish vented (SV), all (total) fish vented (TV), and descended (D). The number of fish included in each estimate (n) and the number of "dead" and "alive" fish used to calculate the mortality are also shown.

Mortality	n	dead	alive	Depth	Season	Region	ST	RM	Study
0.21	14	3	11	22	NS		C		Parker et al. 1985
0.197	282	56	226	21	NS	W	C	SV	Render and Wilson 1996
0.11	30	3	27	30	S		C		Parker et al. 1985
0.42	47	20	27	30	S	W	C	TV	Diamond and Campbell 2009
0.13	30	4	26	30	NS	W	C	TV	Diamond and Campbell 2009
0.42	56	24	32	40	S	W	C	TV	Diamond and Campbell 2009
0.34	32	11	21	40	NS	W	C	TV	Diamond and Campbell 2009
0.69	24	17	7	50	S	W	C	SV	Diamond and Campbell 2009
0.44	36	16	20	50	NS	W	C	SV	Diamond and Campbell 2009
0.77	9	7	2	50	S	W	AT	D	Diamond et al. 2011
0.5	4	2	2	50	S	W	AT	TV	Diamond et al. 2011
1	12	12	0	50	S	W	AT	NV	Diamond et al. 2011
0.625	8	5	3	50	NS	W	AT	D	Diamond et al. 2011
0.25	8	2	6	50	NS	W	AT	NV	Diamond et al. 2011
0.778	9	7	2	30	NS	C	AT	NV	Bohaboy et al. 2020
0.37	8	3	5	30	S	C	AT	D	Bohaboy et al. 2020
0.333	18	6	12	30	S	C	AT	NV	Bohaboy et al. 2020
0.227	22	5	17	30	S	C	AT	D	Bohaboy et al. 2020
0.563	16	9	7	50	S	C	AT	NV	Bohaboy et al. 2020
0.35	17	6	11	50	S	C	AT	D	Bohaboy et al. 2020
0.8	10	8	2	50	S	C	AT	NV	Bohaboy et al. 2020
0.571429	14	8	6	50	S	C	AT	D	Bohaboy et al. 2020
0	7	0	7	30	NS	W	AT	D	Curtis et al. 2015

0.25	8	2	6	30	NS	W	AT	NV	Curtis et al. 2015
0.143	7	1	6	30	NS	W	AT	TV	Curtis et al. 2015
0.333	6	2	4	50	NS	W	AT	D	Curtis et al. 2015
0.4	10	4	6	50	NS	W	AT	NV	Curtis et al. 2015
0.4	5	2	3	50	NS	W	AT	TV	Curtis et al. 2015
0.167	6	1	5	50	S	W	AT	D	Curtis et al. 2015
0.867	7	6	1	50	S	W	AT	NV	Curtis et al. 2015
0.25	4	1	3	50	S	W	AT	TV	Curtis et al. 2015
0.333	6	2	4	50	NS	W	AT	D	Curtis et al. 2015
0.222	9	2	7	50	NS	W	AT	NV	Curtis et al. 2015
0.12	8	1	7	40	S	W	AT	D	Stunz et al. 2017
0.33	6	2	4	40	S	W	AT	NV	Stunz et al. 2017
0.43	7	3	4	40	S	W	AT	TV	Stunz et al. 2017
0.67	9	6	3	60	S	W	AT	D	Stunz et al. 2017
0.6	5	3	2	60	S	W	AT	NV	Stunz et al. 2017
0.1	7	1	6	60	S	W	AT	TV	Stunz et al. 2017
0	7	0	7	40	NS	W	AT	D	Stunz et al. 2017
0	10	0	10	40	NS	W	AT	NV	Stunz et al. 2017
0.11	9	1	8	40	NS	W	AT	TV	Stunz et al. 2017
0	8	0	8	60	NS	W	AT	D	Stunz et al. 2017
0.25	8	2	6	60	NS	W	AT	NV	Stunz et al. 2017
0.29	7	2	5	60	NS	W	AT	TV	Stunz et al. 2017
0.13	71	9	62	27.5		C	AT	D	Williams-Grove 2015
0.291	86	25	61	27.5		C	AT	D	Williams-Grove 2015
0.083	36	3	33	37	S		AT	D	Runde et al. 2021
0.14	14	2	12	29	S	W	AT	D	Tompkins 2017
0.42	12	5	7	39	S	W	AT	D	Tompkins 2017
0.5	14	7	7	49	S	W	AT	D	Tompkins 2017
0.58	14	8	6	58	S	W	AT	D	Tompkins 2017
0.86	15	13	2	81	S	W	AT	D	Tompkins 2017
0.15816	49	7.75	41.25	10	NS	C	PT	SV	Vecchio et al. 2022
0.1924	3997	769	3228	25	NS	C	PT	SV	Vecchio et al. 2022
0.22395	6150	1377	4773	35	NS	C	PT	SV	Vecchio et al. 2022
0.23797	1147	273	874.1	45	NS	C	PT	SV	Vecchio et al. 2022
0.26072	382	99.59	282.4	55	NS	C	PT	SV	Vecchio et al. 2022
0.30517	125	38.15	86.85	65	NS	C	PT	SV	Vecchio et al. 2022
0.24338	60	14.6	45.4	75	NS	C	PT	SV	Vecchio et al. 2022
0.34888	33	11.51	21.49	85	NS	C	PT	SV	Vecchio et al. 2022
0.17949	237	42.54	194.5	10	NS	E	PT	SV	Vecchio et al. 2022
0.23728	352	83.52	268.5	25	NS	E	PT	SV	Vecchio et al. 2022
0.29048	962	279.5	682.6	35	NS	E	PT	SV	Vecchio et al. 2022
0.29881	885	264.4	620.6	45	NS	E	PT	SV	Vecchio et al. 2022
0.30808	586	180.5	405.5	55	NS	E	PT	SV	Vecchio et al. 2022
0.31938	151	48.23	102.8	65	NS	E	PT	SV	Vecchio et al. 2022
0.29733	12	3.57	8.43	75	NS	E	PT	SV	Vecchio et al. 2022

0.33844	36	12.18	23.82	85	NS	E	PT	SV	Vecchio et al. 2022
0.1411	31	4.37	26.63	10	S	C	PT	SV	Vecchio et al. 2022
0.19933	1259	251	1008	25	S	C	PT	SV	Vecchio et al. 2022
0.20792	1766	367.2	1399	35	S	C	PT	SV	Vecchio et al. 2022
0.22816	333	75.98	257	45	S	C	PT	SV	Vecchio et al. 2022
0.22802	128	29.19	98.81	55	S	C	PT	SV	Vecchio et al. 2022
0.28217	18	5.08	12.92	65	S	C	PT	SV	Vecchio et al. 2022
0.248	3	0.74	2.26	75	S	C	PT	SV	Vecchio et al. 2022
0.21417	30	6.43	23.57	10	S	E	PT	SV	Vecchio et al. 2022
0.2757	161	44.39	116.6	25	S	E	PT	SV	Vecchio et al. 2022
0.28576	295	84.3	210.7	35	S	E	PT	SV	Vecchio et al. 2022
0.30004	288	86.41	201.6	45	S	E	PT	SV	Vecchio et al. 2022
0.24255	139	33.71	105.3	55	S	E	PT	SV	Vecchio et al. 2022
0.30786	21	6.47	14.53	65	S	E	PT	SV	Vecchio et al. 2022
0.35838	21	7.53	13.47	75	S	E	PT	SV	Vecchio et al. 2022

Analyses were conducted in R using the *metafor* package (R Core Team, 2020; Viechtbauer, 2010). Effect sizes were calculated using the *escalc* function using the frequency of dead fish out of the total number of fish tested. This function also calculates a variance for each effect size from the sample size of the estimate. Mixed effect models were run with the *rma.mv* function. The calculated effect sizes were used as the response variable. Season, region, the interaction between season and region, depth, and release method were used as predictor variables. Study and study type (cage, passive tag, acoustic tag) were included as random effects. Depth was a continuous variable, and the rest of the variables were categorical. Variances from the calculated effect sizes were included in the model. A backward stepwise regression model selection procedure was performed using AICs and BICs and removing release method from the full model generated the best fit. Predicted values and their associated 95% confidence limits were calculated using the *predict* function in *metafor* (Viechtbauer 2010) and converted back to proportions by taking the inverse of the logit-transformed data (see Campbell et al., 2014 for more details). Post-hoc tests were run by separating the analyses into the western and not western (eastern and central regions combined) regions to allow us to generate separate, more accurate predictions across regions, seasons, and depths as the effect of season was only present in the western region. Heterogeneity in the models were tested using Cochran's Q-test and the I^2 index. These are commonly used heterogeneity tests, which allow us to determine if the variability in the meta-analysis indicates 'true' variability or is due to sampling error (Cochran, 1954; Higgins & Thompson, 2022). Graphs were generated using the *ggplot2* package (Wickham et al., 2022).

IV. RESULTS

Summer significantly increased the estimated mortality when compared to non-summer (estimate=0.77, $z_{7,72}$=3.91. p<0.001; Fig. 1A). There was also a significant interaction between region and season and the western region had a significantly higher mortality rate in the summer than in the non-summer. However, this pattern was not true for the other regions, suggesting that these significantly effects of seasonality were driven by the western region (summer*central: estimate=-0.81, $z_{7,72}$=-4.02, p<0.001; summer*eastern: estimate=-0.76, $z_{7,72}$=-3.55, p<0.001; Fig. 1B). There was a significant positive association between depth and mortality rate (estimate=0.012, $z_{7,72}$=7.78, p<0.001; Fig. 2A). We calculated the slope of this positive association for comparison with the estimates generated by Campbell et al. 2014. Our results generated a 3.6% increase in mortality for every 10m increase

in depth, while the Campbell et al. 2014 paper predicted a 3% increase (Fig. 2). Region did not significantly alter estimated mortality rates as a main effect (Region Central: estimate=0.16, $z_{7,72}$=0.41, p=0.68; Region East: estimate=0.44, $z_{7,72}$=1.11, p=0.27; Fig. 3A). Release method also did not significantly affect Red Snapper mortality rate and was not included in the best fitting model (Fig. 3B).

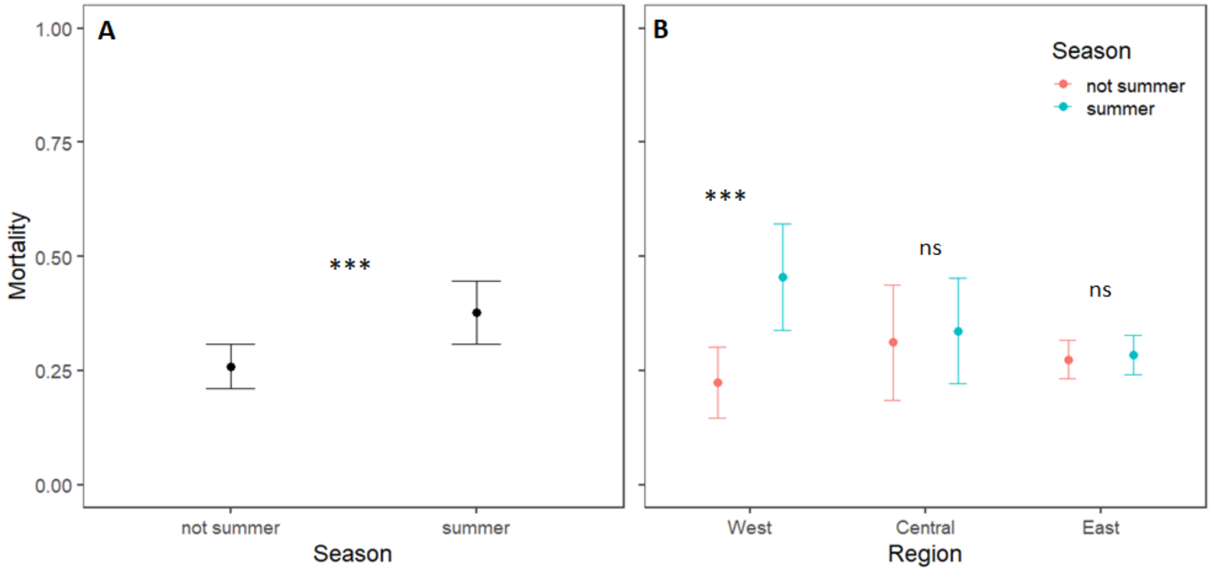

Figure 1: **A)** The proportional discard mortality of Red Snapper (*Lutjanus campechanus)* in the Gulf of Mexico was significantly higher in summer than the non-summer seasonal group (estimate=0.77, $z_{7,72}$=3.91. p<0.001). **B)** The western region had a significantly higher proportional mortality rate in the summer than in non-summer, but this pattern was not true for the other regions (summer*central: estimate=-0.81, $z_{7,72}$=-4.02, p<0.001; summer*eastern: estimate=-0.76, $z_{7,72}$=-3.55, p<0.001). Points represent average proportional mortalities and error bars represent 95% confidence intervals. Asterisks indicate significance level and 'ns' indicate comparisons that were not significant.

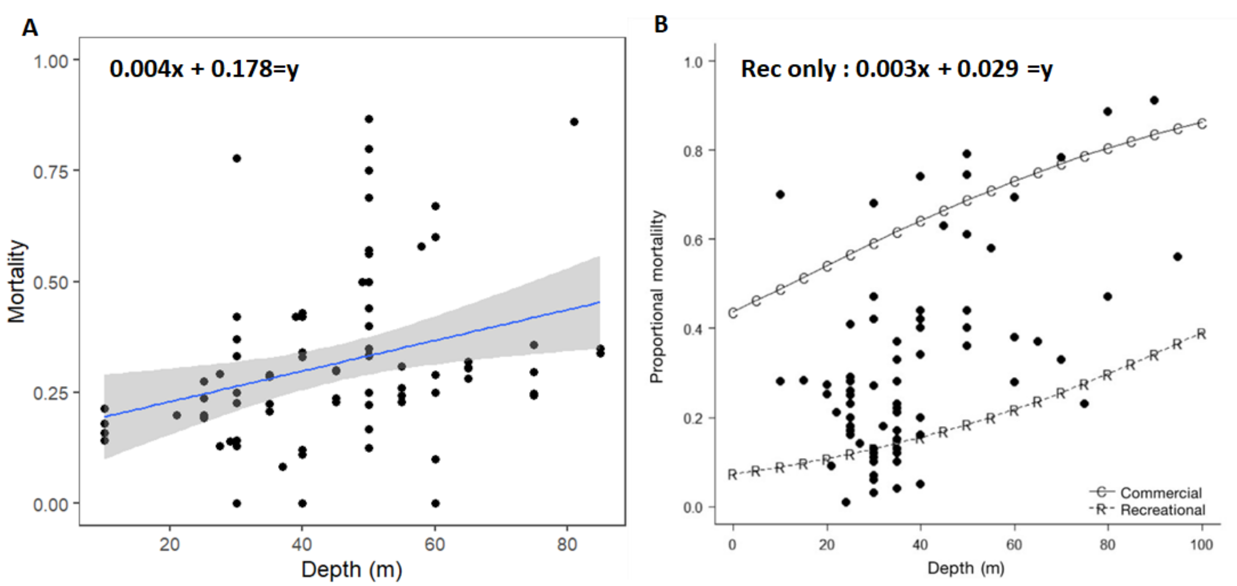

Figure 2: A) The proportional discard mortality of Red Snapper (*Lutjanus campechanus)* in the Gulf of Mexico had a significant positive association with depth (estimate=0.012, $z_{7,72}$=7.78, p<0.001). Shown is the slope of the line, indicating a 3.6% increase in mortality with every 10m. Points are raw mortality estimates from the data, the blue line indicates the predicted mortality by depth from the data and the gray band represents at 95% confidence interval around this prediction. **B)** There was also a significant positive association between depth and proportional mortality in the Campbell et al. 2014 paper. Shown is the slope of the line for the recreational data only (the slope which most closely aligns with our data), indicating a 3% increase in mortality with every 10m. The points are raw mortality estimates and the line indicates the predicted relationship between mortality and depth.

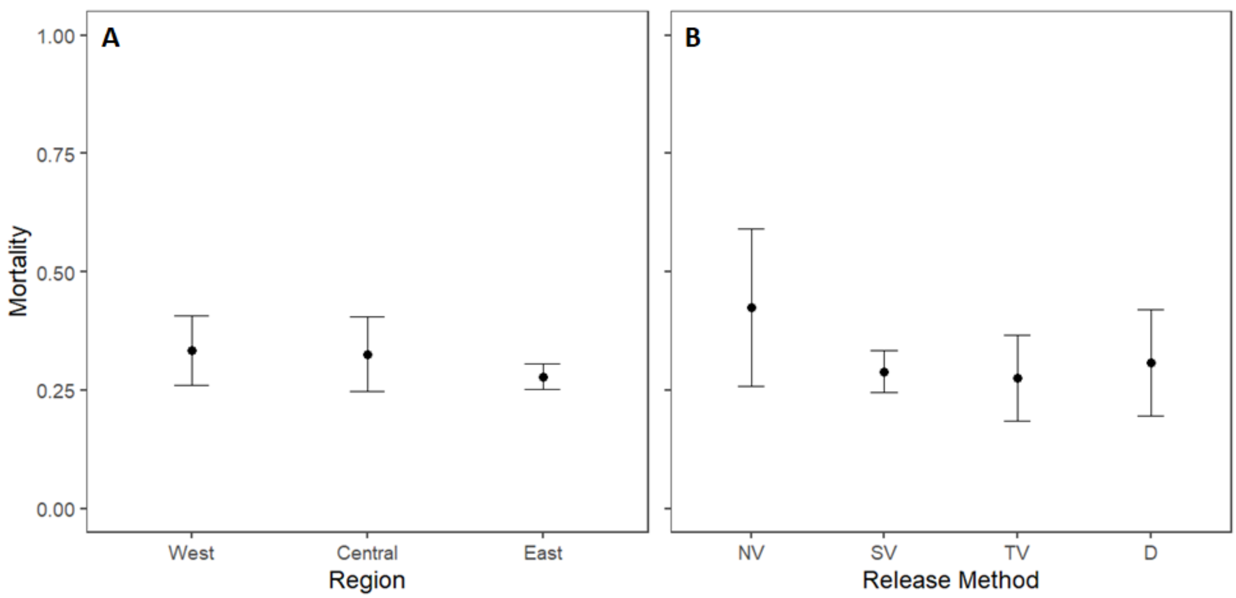

Figure 3: A) The discard mortality of Red Snapper (*Lutjanus campechanus)* in the Gulf of Mexico was not significantly altered by region as a main effect (Region Central: estimate=0.16, $z_{7,72}$=0.39, p=0.68; Region East: estimate=0.44, $z_{7,72}$=1.11, p=0.27). **B)** Release method also did not significantly affect discard mortality rate and was not included in the best fitting model. Points represent average proportional mortalities and error bars represent 95% confidence intervals.

Post-hoc tests addressing the western region separately from the eastern and central regions found similar results. In the western region, summer mortality was significantly higher than non-summer (estimate = 0.74, $z_{2,37}$=3.81, p<0.001), there was a positive association between depth and mortality (estimate=0.04, $z_{2,37}$=4.82, p<0.001; Fig. 4A). In the eastern and central regions, season did not significantly predict mortality (estimate=-0.03, $z_{2,35}$=-0.65, p=0.52), but depth was positively associated with mortality (estimate=0.02, $z_{2,35}$=9.4, p<0.001, Fig.4B). Running these regions separately allows us to generate predicted estimates of mortality by fishing season and depth, as season affects these regions differently.

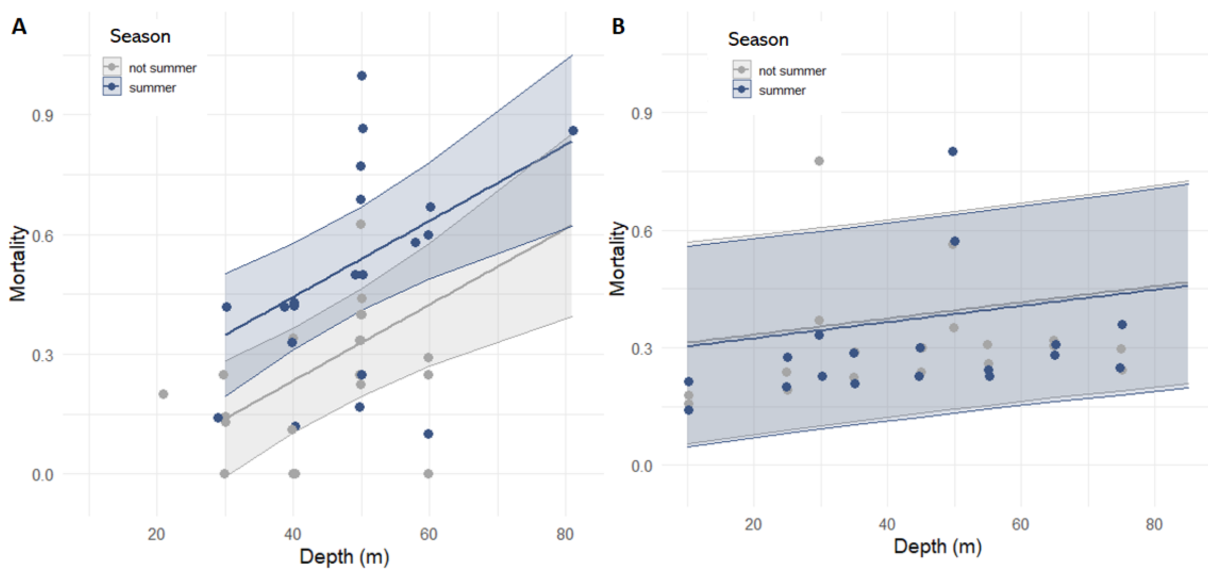

Figure 4: A) In the western region (Texas and Louisiana) of the Gulf of Mexico **t**he proportional discard mortality of Red Snapper (*Lutjanus campechanus)* was significantly positively associated with depth (estimate=0.04, $z_{2,37}$=4.82, p<0.001) and summer led to significantly higher discard mortality than non-summer (estimate = 0.74, $z_{2,37}$=3.81, p<0.001). **B)** In the eastern and central regions (Mississippi, Alabama, and parts of Louisiana and Florida) there was also a significant positive association between depth and mortality (estimate=0.02, $z_{2,35}$=9.4, p<0.001), but season did not affect discard mortality (estimate=-0.03, $z_{2,35}$=-0.65, p=0.52). Points are raw mortality estimates from the data, the lines indicate the predicted mortality by depth from the data and the bands represent the 95% confidence interval around this prediction. Blue and gray lines and bands represent summer and not summer data, respectively.

Mortality estimates ranged from 0-100% with a mean of 33% and a median of 29%. The highest mortality estimate occurred during the summer, in the western region in unvented fish, at 50m (Diamond & Campbell, 2009). Four studies had average mortality estimates between 40-

65% (Bohaboy et al., 2020; Diamond et al., 2011; Diamond & Campbell, 2009; Tompkins, 2017) and two studies had average mortality estimates of less than 20% (Parker, 1985; Runde et al., 2021). Models predicted that the discard mortality at the average fishing depth from the tested studies (45m) would be 34%, which more than doubles the 16.4% mortality estimate from Campbell 2014 at the same depth. When modeling regions separately, models predicted that mortality at the average fishing depth from the tested studies (45m) in the western region in the winter is 33% and that this increases to 51.1% in the summer. Whereas the estimated mortality in the eastern and central regions is 35.5% regardless of season.

When testing for heterogeneity the Cochran's Q-test showed that there was significant variability among the predictors (QM_7=170.40, p<0.001) and a significant amount of residual heterogeneity (QE_{72}=114.06, p=0.0012). Additionally, the calculated I^2 index is 86.58 indicating that 86.58% of the heterogeneity is true heterogeneity and not due to random sampling. These heterogeneity tests suggest that the chosen model predicts the variation in the data well, although remaining residual heterogeneity suggests that the tested predictors do not encompass all the variation in the data.

V. DISCUSSION

Red Snapper is an economically important fishery in the Gulf of Mexico. Seasonal closures and size limits cause over 75% of Red Snapper that are caught to be discarded (NMFS Fisheries Statistical Division, 2022). Updating the discard mortality estimates used in stock assessments with newly available research will help support the successful rebuilding of the Gulf of Mexico Red Snapper fishery (SEDAR 52, 2018). When synthesizing new data on release mortality in the recreational Red Snapper fishery, including only studies which measured both immediate and delayed mortality, we found that depth of capture was positively associated with discard mortality and that discard mortality was higher in the summer than in other seasons in the western gulf. Additionally, we found that the updated model more than doubled the estimated percent discard mortality compared to a previous meta-analysis that did not exclude studies with only immediate discard mortality estimates (Campbell et al., 2014).

We found that depth of capture was significantly positively associated with discard mortality in the Gulf of Mexico (Fig. 2). Studies in this meta-analysis that examined this question also found that depth of capture was positively associated with discard mortality (Curtis et al., 2015; Diamond & Campbell, 2009; Stunz et al., 2017; Tompkins, 2017). Additionally, a positive association between capture depth and fishing mortality has been seen in other fisheries (Alós J., 2008; Bartholomew & Bohnsack, 2005; Campbell et al., 2010; Drumhiller et al., 2014; Hannah et al., 2008; Sauls, 2014). Campbell et al. 2014 found that a 10m increase in depth led to a 3% increase in mortality and we found a similar result of 4%. There is a positive relationship between depth of capture and increased barotrauma (Brown et al., 2010; Ferter et al., 2015; Rummer & Bennett, 2005). Barotrauma can cause extensive physical and behavioral damage to fish that experience it (Raby et al., 2014; Rummer & Bennett, 2005). Managers have been working to mitigate these effects through the use of venting and descending devices. Only 13 of the estimates in this study did not use either venting or a descending device when releasing fish (Table 1) and yet a positive association between depth and mortality still occurred. This suggests that even if venting or descending can reduce discard mortality, catching fish at shallower depths is still the most effective way to lower discard mortality, as it reduces barotrauma. Additionally, there is evidence that mortality may grow exponentially after a certain depth, due to catastrophic barotrauma seen at depths of 50m and above (Stunz et al., 2017; Tompkins, 2017). Catastrophic barotrauma occurs when the swim bladder ruptures and this often leads to mortality (Rummer & Bennett, 2005; Stunz et al., 2017). However, we did not see a steep increase in mortality at depths above 50m in this analysis.

Focusing on studies that included estimates of both immediate and delayed mortality led to a more than two times increase in the estimates of discard mortality of Red Snapper in the Gulf of Mexico (Campbell et al., 2014). At the mean depth from the tested studies (45m), we found that release mortality was 34%, compared to 16.4% as predicted by the Campbell model. As the slope of the positive relationship between depth and mortality remained similar to what was previously reported (Campbell et al., 2014), this over twofold increase in release mortality occurs across all depths of capture. Studies that have analyzed immediate and delayed mortality have also found that immediate mortality estimates approximately doubled (Curtis et al., 2015) or more than doubled (Diamond & Campbell, 2009) with the addition of delayed mortality. We conclude that discard mortality estimates used in assessments should include delayed mortality. In addition to mounting evidence in support of the inclusion of delayed mortality (Curtis et al., 2015; Davis, 2002; Diamond & Campbell, 2009), we show that it can significantly increase the expected discard mortality in a fishery.

We also found that discard mortality in the western region was higher in summer than in non-summer seasons (Fig. 1). This effect has been found in other literature (Bartholomew & Bohnsack, 2005; Diamond & Campbell, 2009; Render & Wilson, 1994), and it is likely due to a steep thermocline that generates in the west during the warmer months (Curtis et al., 2015; Stunz et al., 2017). The change in temperature a fish experiences as it is brought to the surface increases the negative physiological and behavioral affects a fish would experience normally during capture (Boyd et al., 2010; Campbell, 2008; Muoneke & Childress, 1994). Additionally, oxygen stress can lead to discard mortality and higher temperature waters do not hold as much oxygen as cooler waters (Bartholomew & Bohnsack, 2005; Rummer, 2007). This meta-analysis used a generalized metric of 'season' and assumes seasons are associated with changes in water temperature. However, some studies used in the analysis did explicitly test water temperature and confirmed the presence of a strong thermocline in the western region in the months that they categorized as 'summer' (Curtis et al., 2015; Stunz et al., 2017; Tompkins, 2017). While this summer vs. non-summer category allows us to tangentially look at effects of open and closed fishing seasons on discard mortality, we suggest that future research should address this question explicitly. Finally, although we did not find significant differences in discard mortality by stock assessment region (Fig 3A), we did find the effect of season in the western region only (Fig. 1). Therefore, we suggest that stock assessments use separate estimates of discard mortality in the open and closed seasons in the western region. However, models can combine the eastern and central regions and seasons in these regions when generating discard mortality estimates.

While research has found that venting and descending of Red Snapper is an effective method to reduce discard mortality (Ayala, 2020; Drumhiller et al., 2014; Pulver, 2017), including many of the studies used in this analysis (Bohaboy et al., 2020; Curtis et al., 2015; Runde et al., 2021; Stunz et al., 2017; Tompkins, 2017), we did not find a significant effect of release methods on discard mortality (Fig 3B). This could be due to the differences in how venting and descending occurred and were measured across the tested studies. Studies were classified as having descended their catch if they released the fish at depth. However, we classified fish as 'descended' even if they were released at shallower depth than they were caught at, potentially affecting how acclimated fish were during release. However, a previous study found that releasing red snapper at one-third, two-thirds, or at their capture depth did not affect survival (Tompkins, 2017). We also included venting studies that did not report their results of vented and unvented fish separately (Render & Wilson, 1996) or only vented some fish based on angler discretion (Vecchio et al., 2022). While venting at angler discretion is likely a more realistic view of venting discarding mortality, the lack of consistency across studies could have confounded the results. Additionally, the positive effects of descending and venting on discard mortality are not without caveats. For example, one study found that the positive effects from venting and descending fish were much greater in the summer, when the stress from the thermocline is greatest and when the season is open (Curtis et al., 2015). In another study, the use of a descending device in the winter lead to 100% survival at 40 and 60m, but in summer descending actually increased mortality at 40m, but not at 60m (Stunz et al., 2017). These unaccounted-for factors may have confounded any positive main effects of venting or descending we might have seen. However, we did see a nonsignificant decrease in mortality when venting or descending techniques were used compared to no venting (Fig. 3b).

Season and size limits are still in effect as the Red Snapper fishery in the Gulf of Mexico continues to rebuild (SEDAR 52, 2018). Therefore, assessments of the mortality of discarded fish are necessary to continue effectively managing this fishery. Here we provide a model that can be used to estimate mortality in the recreational fishery by fishing depth throughout the Gulf and by season in the western Gulf. Additionally, this model predicts a more than twofold increase in discard mortality estimates than was seen in previous work (Campbell et al., 2014) through inclusion of new research and by excluding studies that only measure immediate discard mortality. A simulation study using Gulf of Mexico Red Snapper stock assessment models showed that reducing discard mortality, especially if discard mortality is larger than previously estimated, could lead to significant increases in fishing season length as well as benefits to an array of fisheries performance metrics (Bohaboy et al., 2022). Therefore, although the estimates generated here suggest that discard mortality of Red Snapper was previously underestimated in the Gulf of Mexico, continued efforts to reduce discard mortality are likely to lead to significant benefits to the fishery.

A potentially major predictor of discard mortality that was not assessed in this meta-analysis is the effect of predation through metrics of abundance or distribution of predators. Some studies in this analysis reported major effects of predation on discard mortality, including the presence of sharks or dolphins in 32% of all Red Snapper releases, 83% of discard mortality resulting from predation (Bohaboy et al., 2020), and predation was described as 'inevitable' when descended red snapper were spotted by a predator (Tompkins, 2017). However, not all studies in this analysis address predation. As shark populations continue to rebound (Froeschke et al., 2012; Peterson et al., 2017; SEDAR 54, 2017), quantifying the effect of predators on discard morality through metrics such as predator abundance, may be the next step to increasing our understanding of discard mortality.

VI. REFERENCES

Alós J. (2008). Influence of anatomical hooking depth, capture depth, and venting on mortality of painted comber (Serranus scriba) released by recreational anglers. *ICES Journal of Marine Science*, *65*, 1620–1625.

Ayala, O. E. (2020). *Testing the efficacy of recompression tools to reduce the discard mortality of reef fishes in the Gulf of Mexico*. University of South Florida.

Bartholomew, A., & Bohnsack, J. A. (2005). A review of catch-and-release angling mortality with implications for no-take reserves. In *Reviews in Fish Biology and Fisheries* (Vol. 15, Issues 1–2, pp. 129–154). https://doi.org/10.1007/s11160-005-2175-1

Bohaboy, E. C., Goethel, D. R., Cass-Calay, S. L., & Patterson, W. F. (2022). A simulation framework to assess management trade-offs associated with recreational harvest slots, discard mortality reduction, and bycatch accountability in a multi-sector fishery. *Fisheries Research*, *250*. https://doi.org/10.1016/j.fishres.2022.106268

Bohaboy, E. C., Guttridge, T. L., Hammerschlag, N., Bergmann, M. P. M. V. Z., & Patterson III, W. F. (2020). Application of three-dimensional acoustic telemetry to assess the effects of rapid recompression on reef fish discard mortality. *ICE Journal of Marine Science*, *77*(1), 83–96.

Boyd, J. W., Guy, C. S., Horton, T. B., & Leathe, S. A. (2010). Effects of catch-and-release angling on salmonids at elevated water temperatures. *North American Journal of Fisheries Management*, *30*(4), 898–907.

Brown, I., Sumpton, W., McLennan, M., Mayer, D., Campbell, M., Kirkwood, J., Butcher, A., Halliday, I., Mapleston, A., Welch, D., Begg, G. A., & Sawynok, B. (2010). An improved technique for estimating short-term survival of released line-caught fish, and an application comparing barotrauma-relief methods in red emperor (Lutjanus sebae Cuvier 1816). *Journal of Experimental Marine Biology and Ecology*, *385*(1–2), 1–7.

Burns, K. M., & Froeschke, J. T. (2012). Survival of red grouper (epinephalus morio) and red snapper (lutjanus campechanus) caught on j-hooks and circle hooks in the Florida recreational and recreational-for-hire fisheries. *Bulletin of Marine Science*, *88*(3), 633–646. https://doi.org/10.5343/bms.2011.1057

Campbell, M. D. (2008). *CHARACTERIZATION OF THE STRESS RESPONSE OF RED SNAPPER: CONNECTING INDIVIDUAL RESPONSES TO POPULATION DYNAMICS* [Doctor of Philosophy]. Texas Tech University.

Campbell, M. D., Driggers III, W. B., Sauls, B., & Walter, J. F. (2014). Release mortality in the red snapper (Lutjanus campechanus) fishery: a meta-analysis of 3 decades of research. *Fishery Bulletin*, *112*(4).

Campbell, M. D., Tolan, J., Strauss, R., & Diamond, S. L. (2010). Relating angling-dependent fish impairment to immediate release mortality of red snapper (Lutjanus campechanus). *Fisheries Research*, *106*(1), 64–70.

Cochran, W. G. (1954). The combination of estimates from different experiments. *Biometrics*, *10*(1), 101–129.

Cooke, S. J., & Schramm, H. L. (2007). Catch-and-release science and its application to conservation and management of recreational fisheries. *Fisheries Management and Ecology*, *14*, 73–79.

Curtis, J. M., Johnson, M. W., Diamond, S. L., & Stunz, G. W. (2015). Quantifying delayed mortality from barotrauma impairment in discarded Red Snapper using acoustic telemetry. *Marine and Coastal Fisheries*, *7,* 434–449.

Dallas, L. J., Shultz, A. D., Moody, A. J., Sloman, K. A., & Danylchuk, A. J. (2010). Chemical excretions of angled bonfish Albula vulpes and their potential use as predation cues by juvenile lemon sharks Negaprion brevirostris. *Journal of Fish Biology*, *77*(4), 947–962.

Davis, M. W. (2002). Key principles for understanding fish bycatch discard mortality. In *Canadian Journal of Fisheries and Aquatic Sciences* (Vol. 59, Issue 11, pp. 1834–1843). https://doi.org/10.1139/f02-139

Diamond, S., & Campbell, M. (2009). Linking “Sink or Swim” Indicators to Delayed Mortality in Red Snapper by Using a Condition Index. *Marine and Coastal Fisheries*, *1*(1), 107–120. https://doi.org/10.1577/c08-043.1

Diamond, S., Hedrick-Hopper, T., Stunz, G., Johnson, M., & Curtis, J. (2011). *Reducing Discard Mortality of Red Snapper in the Recreational Fisheries using Descender Hooks and Rapid Recompression Final Report*.

Drumhiller, K. L., Johnson, M. W., Diamond, S. L., Robillard, M. M. R., & Stunz, G. W. (2014). Venting or rapid recompression increase survival and improve recovery of Red Snapper with barotrauma. *American Fisheries Society, 6*, 190–199.

Ferter, K., Weltersbach, M. S., Humborstad, O. B., Fjelldal, P. G., Sambraus, F., Strehlow, H. V., & Volstad, J. H. (2015). Dive to survive: Effects of capture depth on barotraumas and post-release survival of Atlantic cod (Gadus morhua) in recreational fisheries. *ICES Journal of Marine Science*, *72*(8), 2467–2481. https://doi.org/10.1093/icesjms/fsv102

Froeschke, J. T., Froeschke, B. F., & Stinson, C. M. (2012). Long-term trends of bull shark (Carcharhinus leucas) in estuarine waters of Texas, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*(1), 13–21.

Hannah, R. W., Parker, S. J., & Matteson, K. M. (2008). Escaping the Surface: the effect of capture depth on submergence success of surface-released pacific rockfish. *North American Journal of Fisheries Management*, *28*(3), 694–700.

Higgins, J. P., & Thompson, S. G. (2022). Quantifying heterogeneity in a meta-analysis. *Statistics in Medicine*, *21*(11), 1539–1558.

Jenkins, S. R., Mullen, C., & Brand, A. R. (2004). Predator and scavenger aggregation to discarded by-catch from dredge fisheries: importance of damage level. *Journal of Sea Research*, *51*(1), 69–76.

Mohan, J. A., Jones, E. R., Hendon, J. M., Falterman, B., Boswell, K. M., Hoffmayer, E. R., & David Wells, R. J. (2020). Capture stress and post-release mortality of blacktip sharks in recreational charter fisheries of the Gulf of Mexico. *Conservation Physiology*, *8*(1). https://doi.org/10.1093/conphys/coaa041

Muoneke, M. I., & Childress, W. M. (1994). Hooking mortality: a review for recreational fisheries. *Reviews in Fisheries Sciences*, *2*(2), 123–156.

NMFS Fisheries Statistical Division. (2022, October 7). *MRIP Data Query*. National Marine Fisheries Service (NMFS).

Parker, R. O. (1985). *Survival of released Red Snapper progress report*.

Parsons, D. M., & Eggleston, D. B. (2005). Indirect effects of recreational fishing on behavior of the spiny lobster Panulirus argus. *Marine Ecology Progress Series*, *303*, 235–244. https://doi.org/10.3354/meps303235

Peterson, C. D., Belcher, C. N., Bethea, D. M., Driggers III, W. B., Frazier, B. S., & Latour, R. J. (2017). Preliminary recovery of coastal sharks in the south-east United States. *Fish and Fisheries*, *18*(5), 845–859.

Policansky, D. (2022). Catch-and-release recreational fishing. In T. J. Pitcher & C. E. Hollingworth (Eds.), *Recreational Fisheries: ecological, economic, and social evaluation*. Backwell Publishing Ltd.

Pulver, J. R. (2017). Sink or swim? Factors affecting immediate discard mortality for the Gulf of Mexico commercial reef fish fishery. *Fisheries Research*, *188*, 166–172.

R Core Team. (2020). *R: A language and environment for statistical computing* (4.0.3). Art. 4.0.3.

Raby, G. D., Packer, J. R., Danylchuk, A. J., & Cooke, S. J. (2014). The understudied and underappreciated role of predation in the mortality of fish released from fishing gears. *Fish and Fisheries*, *15*(3), 489–505. https://doi.org/10.1111/faf.12033

Render, J. H., & Wilson, C. A. (1994). HOOK-AND-LINE MORTALITY OF CAUGHT AND RELEASED RED SNAPPER AROUND OIL AND GAS PLATFORM STRUCTURAL HABITAT. *Bulletin of Marine Science*, *55*(2–3), 1106–1111.

Render, J. H., & Wilson, C. A. (1996). Effect of gas bladder deflation on mortality of hook-and-line caught and released Red Snappers: implications for management. In F. Arreguín-Sánchez, J. L. Munro, M. C. Balgos, & D. Pauly (Eds.), *Biology and culture of tropical* *groupers and snappers* (pp. 244–253). International Center for Living Aquatic Resources Management.

Rummer, J. L. (2007). Factors Affecting Catch and Release (CAR) Mortality in Fish: Insight into CAR Mortality in Red Snapper and the Influence of Catastrophic Decompression. *American Fisheries Society Symposium*, *60*, 113–132. https://www.researchgate.net/publication/230705644

Rummer, J. L., & Bennett, W. A. (2005). Physiological Effects of Swim Bladder Overexpansion and Catastrophic Decompression on Red Snapper. *Transactions of the American Fisheries Society*, *134*(6), 1457–1470. https://doi.org/10.1577/t04-235.1

Runde, B. J., Bacheler, N. M., Shertzer, K. W., Rudershausen, P. J., Sauls, B., & Buckel, J. A. (2021). Discard Mortality of Red Snapper Released with Descender Devices in the U.S. South Atlantic. *Marine and Coastal Fisheries*, *13*(5), 478–495. https://doi.org/10.1002/mcf2.10175

Sauls, B. (2014). Relative survival of gags Mycteroperca microlepis released within a recreational hook-and-line fishery: Application of the Cox Regression Model to control for heterogeneity in a large-scale mark-recapture study. *Fisheries Research*, *150*, 18–27. https://doi.org/10.1016/j.fishres.2013.10.008

Scyphers, S. B., Fodrie, F. J., Hernandez, F. J., Powers, S. P., & Shipp, R. L. (2013). Venting and Reef Fish Survival: Perceptions and Participation Rates among Recreational Anglers in the Northern Gulf of Mexico. *North American Journal of Fisheries Management*, *33*(6), 1071–1078. https://doi.org/10.1080/02755947.2013.824932

SEDAR 52. (2018). *Gulf of Mexico Red Snapper*.

SEDAR 54. (2017). *HMS Sandbar Sharks*.

SEDAR 74. (2022). *Gulf of Mexico Red Snapper Stock ID Process Report*.

Stunz, G. W., Curtis, J. M., & Tompkins, A. (2017). *Techniques for minimizing discard mortality of GOM of Mexico Red Snapper and validating survival with acoustic telemetry*.

Tompkins, A. K. (2017). *Utility of rapid recompression devices in the Gulf of Mexico Red Snapper fishery*. Texas A&M University.

Vecchio, J., Lazarre, D., & Sauls, B. (2020). *Utility and Usage of Descender Devices in the Red Snapper Recreational Fishery in the South Atlantic*.

Vecchio, J., Lazarre, D., Sauls, B., Head, M., & Moncrief, T. (2022). *A description of Florida's Gulf Coast recreational fishery and release mortality estimates for the central and eastern subregions (Mississippi, Alabama, and Florida) with varying levels of descender use*.

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. In *Journal of Statistical Software* (Vol. 36, Issue 3, pp. 1–48).

Wickham, H., Chang, W., Henry, L., Pedersen, T. L., Takahashi, K., Wilke, C., Woo, K., Yutani, H., Dunnington, D., & R Studio. (2022). ggplot2: Create elegant data visualisations using the grammar of graphics. *Ver 3.3.6*.

Wilde, G. R. (2009). Does Venting Promote Survival of Released Fish? *Fisheries*, *34*(1), 20–28. https://doi.org/10.1577/1548-8446-34.1.20

Williams-Grove L.J. (2015). *Red Snapper, Lutjanus campechanus, Mortality, Movements, and Habitat Use Based on Advanced Telemetry Methods*. Auburn University.

Wood, C. M., Turner, J. D., & Graham, M. S. (1983). Why do fish die after severe exercise? *Journal of Fish Biology*, *22*(2), 189–201.