

Abstract—The value of catch-and-release fishing as a conservation measure is highly dependent upon rates of discard frequency and release mortality. Therefore, it is important to understand how estimates of these variables are affected by factors such as capture depth and water temperature. The meta-analytical approach to modeling used here for red snapper (*Lutjanus campechanus*) in the Gulf of Mexico provides a robust method for dealing with study-specific differences in experimental protocols and for estimating release (discard) mortality as a function of key factors. Results of this analysis showed significant increases in mortality by depth and for the commercial sector. The most consistent result was the positive correlation between depth and estimates of release mortality, a relationship that was present regardless of study method, fishing sector, hook type used, or season of study. The effect of venting (deflating the swim bladder by puncture) was dependent on whether the study produced estimates of immediate or delayed mortality. Immediate estimates indicated that mortality rates are lowered by venting whereas delayed estimates indicated that venting increased mortality rates. This result is largely reflective of the use of submergence ability, from surface-release studies, as a proxy for mortality. The model's interaction result indicates that recompression of fish may be a viable alternative to venting and that, if a recompression device is not available, venting at least improves the likelihood that a fish can submerge and return to protective habitat. The depth-based functional relationships developed in this model were used in the most recent red snapper stock assessment in 2012, and that use was a change from previous assessments where region-specific point estimates were used.

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Release mortality in the red snapper (*Lutjanus campechanus*) fishery: a meta-analysis of 3 decades of research

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The use of catch-and-release (CAR) fishing as a conservation measure began in Great Britain during the 19th century, eventually was practiced in the United States voluntarily by the early 1900s, and was used first as a management tool in salmonid fisheries in the 1950s (Policansky, 2002). Since that time, it has been practiced successfully to promote sustainable fisheries and is widely accepted by many anglers as a wise conservation strategy. The intent behind CAR regulations is to reduce fishing mortality for important age groups of fish, often to allow young ages to grow and mature to reproductive ages or to protect spawning adults. Catch-and-release requirements in the red snapper (*Lutjanus campechanus*) fishery have expanded in recent years to encompass the release of all size classes during seasonal (or longer) closures in response to fishery management plans required by the Magnuson-Stevens Fishery Conservation and Management Act and which place strict

limits on total removals, including those in open-access recreational fisheries.

Despite the intent of CAR fishing regulations, for many species, stress from capture can lead to barotrauma injuries and reduced reflex responses that result in increased release mortality and render some CAR measures ineffective (Campbell et al., 2010a; Davis, 2010). Stressors experienced by fish during CAR fishing can include hooking trauma, physical overexertion, barotrauma, rapid thermal change, air exposure, and physical handling (Davis et al., 2001; Rummer and Bennett, 2005; Nieland et al., 2007; Jarvis and Lowe, 2008). These stressors from CAR fishing may also translate into long-term, sublethal, negative consequences, such as reduced growth and fecundity (Woodley and Peterson, 2003; Ryer et al., 2004; Davis, 2007). The effects of CAR fishing can be problematic particularly for marine species like red snapper that inhabit relatively deep water and possess a physoclis-

tous gas bladder (i.e., an air bladder not connected to the alimentary canal).

Red snapper have been fished in the Gulf of Mexico (GOM) for more than a century and compose the most economically important fishery in this region (Strelcheck and Hood, 2007). The first regulations managing the fishery were put in place in 1984 in response to the overfished status of the stock (for a comprehensive management history, see Hood et al., 2007). In general, management has focused on annual time closures and minimum-size regulations that have increased the number of regulatory discards, particularly in open-access recreational fisheries. Management of commercial fisheries has shifted recently to an annual catch share system, which removed the necessity to discard fish during seasonal closures but still does not eliminate regulatory discards if vessels do not possess catch shares or target other reef-associated species after annual catch shares are exhausted.

The focus of management efforts has also shifted to regulations intended to reduce or minimize discard mortality. Regulations adopted in 2008 in the GOM, for example, require commercial and recreational fishermen to use circle hooks and to use a venting tool when catching reef fish. Venting tools are used to puncture and deflate the swim bladder after fish are rapidly retrieved as a means to mitigate the effects of barotrauma. Recent research indicates that circle hooks are beneficial for reducing potentially fatal injuries for reef fish caught with hook-and-line gear, particularly for red snapper (Sauls and Ayala, 2012). A meta-analysis of the relationship between venting practices and release mortality indicated negligible effects of venting for red snapper (Wilde, 2009). In the Wilde (2009) meta-analysis, 1 experiment showed positive effects of venting on survival (Gitschlag and Renaud, 1994), 2 reports showed neutral results (Render and Wilson, 1994; Render and Wilson, 1996), and 1 experiment showed a negative effect (Burns et al.¹).

Regulatory discards account for an increasing portion of total catch for managed reef fish in fisheries across the United States, and, in the U.S. GOM, the ratio of discards to landings for directed reef fish fisheries was estimated at 41% (Harrington et al., 2005). The rate at which fish are discarded and quantification of their fate after release are crucial data needs for regional stock assessments in the GOM and south Atlantic. Because of the wide range in reported mortality rates (SEDAR²; Campbell et al.³) and the confounding

nature of the potential interacting factors, a comprehensive evaluation of pertinent research is needed.

Each method used to derive mortality estimates has its benefits, biases, and shortcomings that require exploration; however, in general, problems are associated with the timing of observation, exclusion of predation, insufficient tag returns, sample size, and artifacts of experimental protocols (Campbell et al., 2010b). Methods used to derive estimates in the red snapper fishery include surface-release observation, caging studies, hyperbaric-chamber simulations, acoustic tagging, and passive tagging (Table 1, Fig. 1). Mortality estimates from studies (Table 1) with the use of these methods are broadly categorized as either immediate (seconds to minutes) or delayed (hours to days) and refer to the time span over which the estimate is calculated. These different types of experiments and, therefore, different types of estimates are often treated as equivalents when used in an assessment. Although this aggregate approach is pragmatic, it may result in the use of imprecise estimates and introduce unexplored or unknown sources of bias.

We present a meta-analytical approach with the intent of identifying critical issues and deriving a model of release mortality in the red snapper fishery of the GOM as a function of important covariates, such as depth, season, and capture gear. Meta-analytical methods allow inclusion of all available point estimates, include a sample-size weighting scheme, and allow for the use of covariates in a mixed-effects modeling approach (Viechtbauer, 2010). The meta-analytical approach was developed, and is useful, because it reduces the introduction of bias that hinders nonparametric approaches often found in review papers (Sterne et al., 2000; Nakagawa and Santos, 2012).

Materials and methods

Data used in this meta-analysis were compiled from 11 studies that produced 75 distinct estimates of release mortality (Table 1). These studies represent everything the release mortality working group was aware of in 2012 in preparation for the Southeast Data, Assessment, and Review (SEDAR) of Gulf of Mexico red snapper, the SEDAR 31 stock assessment. The data workshop portion of the SEDAR process typically consists of analysis by expert panelists and assessment biologists of data sources that potentially feed into stock assessment models (for further information about SEDAR, visit: <http://www.sefsc.noaa.gov/sedar/>).

There are multiple estimates from some of the 11 studies examined for this meta-analysis because they were conducted at multiple water depths or seasons. Most of the estimates were compiled from refereed pub-

¹ Burns, K. M., C. C. Koenig, and F. C. Coleman. 2002. Evaluation of multiple factors involved in release mortality of undersized red grouper, gag, red snapper and vermilion snapper. Mote Marine Laboratory Technical Report 790, 53 p. [Available from Mote Marine Laboratory, 1600 Ken Thompson Pkwy., Sarasota, FL 34236.]

² SEDAR (Southeast Data, Assessment, and Review). 2005. Stock assessment report of SEDAR 7: Gulf of Mexico red snapper, 480 p. [Available from <http://www.sefsc.noaa.gov/sedar/>.]

³ Campbell, M. D., W. B. Driggers, and B. Sauls. 2012. Re-

lease mortality in the red snapper fishery: a synopsis of three decades of research. SEDAR31-DW22, 25 p. [Available from <http://www.sefsc.noaa.gov/sedar/>.]

Table 1

List of studies (Study) used in a meta-analysis of release mortality of red snapper (*Lutjanus campechanus*) in the Gulf of Mexico for which estimates (Mort) are categorized by 5-m-depth groups, study type (Type), timing of the estimate (Timing), fishing sector (Sector), season conducted (Season), hook type used (Hook), frequency of venting (Vent), and sample size (n). Study types: surface release (SR), caging (C), passive tagging (PT), and acoustic tagging (AT). Timing of estimates: immediate (I) and delayed (D). Sector: recreational (Rec) and commercial (Com). Season: summer (Sum), spring (Spr), winter (Win), Fall (Fall), and annual (Ann). Hook: circle hooks (C), j-hooks (J), and mixed hooks (M, both j and circles used). Venting: venting (V) and nonventing (NV).

Depth	Mort	Type	Timing	Sector	Season	Hook	Vent	n	Study
10	0.280	SR	I	Rec	Sum	J	NV	25	Dorf, 2003
10	0.700	SR	I	Com	Win	C	NV	40	Nieland et al., 2007
15	0.282	SR	I	Rec	Sum	J	NV	425	Dorf, 2003
20	0.273	SR	I	Rec	Sum	J	NV	825	Dorf, 2003
20	0.252	SR	I	Com	Win	C	NV	465	Nieland et al., 2007
21	0.090	SR	I	Rec	Ann	J	V	1064	Patterson et al., 2001
22	0.210	C	D	Rec	Ann	J	NV	14	Parker ⁵
24	0.010	SR	I	Rec	Fall	J	V	140	Gitschlag and Renaud, 1994
25	0.200	C	D	Rec	Ann	J	V	282	Render and Wilson, 1996
25	0.410	SR	I	Rec	Sum	J	NV	525	Dorf, 2003
25	0.280	PT	D	Rec	Sum	C	V	353	Sauls ⁸
25	0.260	PT	D	Rec	Sum	C	V	353	Sauls ⁸
25	0.230	PT	D	Rec	Fall	C	V	353	Sauls ⁸
25	0.160	PT	D	Rec	Fall	C	V	353	Sauls ⁸
25	0.290	PT	D	Rec	Win	C	V	353	Sauls ⁸
25	0.250	PT	D	Rec	Win	C	V	353	Sauls ⁸
25	0.170	PT	D	Rec	Spr	C	V	353	Sauls ⁸
25	0.180	PT	D	Rec	Spr	C	V	353	Sauls ⁸
27	0.140	SR	I	Rec	Ann	J	V	856	Patterson et al., 2001
30	0.110	C	D	Rec	Ann	J	NV	30	Parker ⁵
30	0.100	SR	I	Rec	Fall	J	V	31	Gitschlag and Renaud, 1994
30	0.420	C	D	Rec	Sum	M	V	47	Diamond and Campbell, 2009
30	0.130	C	D	Rec	Fall	M	V	30	Diamond and Campbell, 2009
30	0.470	SR	I	Rec	Sum	J	NV	225	Dorf, 2003
30	0.213	SR	I	Rec	Fall	C	V	137	Campbell et al., 2010a
30	0.227	SR	I	Rec	Sum	C	V	137	Campbell et al., 2010a
30	0.030	SR	I	Rec	Win	J	V	138	Patterson ⁴
30	0.060	SR	I	Rec	Spr	J	V	31	Patterson ⁴
30	0.070	SR	I	Rec	Sum	J	V	52	Patterson ⁴
30	0.120	SR	I	Rec	Fall	J	V	221	Patterson ⁴
30	0.681	SR	I	Com	Win	C	NV	789	Nieland et al., 2007
32	0.180	SR	I	Rec	Ann	J	V	1012	Patterson et al., 2001
35	0.150	SR	I	Rec	Sum	J	NV	100	Dorf, 2003
35	0.040	SR	I	Rec	Win	J	V	375	Patterson ⁴
35	0.100	SR	I	Rec	Spr	J	V	196	Patterson ⁴
35	0.130	SR	I	Rec	Sum	J	V	264	Patterson ⁴
35	0.170	SR	I	Rec	Fall	J	V	563	Patterson ⁴
35	0.370	PT	D	Rec	Sum	C	V	863	Sauls ⁸
35	0.330	PT	D	Rec	Sum	C	V	863	Sauls ⁸
35	0.280	PT	D	Rec	Fall	C	V	863	Sauls ⁸
35	0.220	PT	D	Rec	Fall	C	V	863	Sauls ⁸
35	0.220	PT	D	Rec	Win	C	V	863	Sauls ⁸
35	0.120	PT	D	Rec	Win	C	V	863	Sauls ⁸
35	0.230	PT	D	Rec	Spr	C	V	863	Sauls ⁸
35	0.210	PT	D	Rec	Spr	C	V	863	Sauls ⁸
40	0.440	SR	I	Rec	Fall	J	V	61	Gitschlag and Renaud, 1994
40	0.400	SR	I	Rec	Sum	J	NV	155	Dorf, 2003
40	0.050	SR	I	Rec	Win	J	V	65	Patterson ⁴
40	0.160	SR	I	Rec	Spr	J	V	107	Patterson ⁴

Table continued

Table 1 continued

Depth	Mort	Type	Timing	Sector	Season	Hook	Vent	<i>n</i>	Study
40	0.160	SR	I	Rec	Sum	J	V	44	Patterson ⁴
40	0.200	SR	I	Rec	Fall	J	V	60	Patterson ⁴
40	0.420	C	D	Rec	Sum	M	V	56	Diamond and Campbell, 2009
40	0.340	C	D	Rec	Fall	M	V	32	Diamond and Campbell, 2009
40	0.740	SR	I	Com	Win	C	NV	814	Nieland et al., 2007
45	0.630	SR	I	Rec	Sum	J	NV	280	Dorf, 2003
50	0.360	C	D	Rec	Fall	J	V	55	Gitschlag and Renaud, 1994
50	0.690	C	D	Rec	Sum	M	V	24	Diamond and Campbell, 2009
50	0.440	C	D	Rec	Fall	M	V	36	Diamond and Campbell, 2009
50	0.610	SR	I	Rec	Sum	J	NV	105	Dorf, 2003
50	0.790	AT	D	Rec	Sum	M	V	24	Diamond et al. ⁷
50	0.400	AT	D	Rec	Win	M	V	20	Diamond et al. ⁷
50	0.744	SR	I	Com	Win	C	NV	1638	Nieland et al., 2007
55	0.580	SR	I	Rec	Sum	J	NV	240	Dorf, 2003
60	0.380	SR	I	Rec	Sum	J	NV	125	Dorf, 2003
60	0.214	SR	I	Rec	Fall	C	V	282	Campbell et al., 2010a
60	0.258	SR	I	Rec	Sum	C	V	282	Campbell et al., 2010a
60	0.694	SR	I	Com	Win	C	NV	464	Nieland et al., 2007
65	0.370	SR	I	Rec	Sum	J	NV	50	Dorf, 2003
70	0.330	SR	I	Rec	Sum	J	NV	10	Dorf, 2003
70	0.782	SR	I	Com	Win	C	NV	404	Nieland et al., 2007
75	0.230	SR	I	Rec	Sum	J	NV	75	Dorf, 2003
80	0.470	SR	I	Rec	Sum	J	NV	100	Dorf, 2003
80	0.886	SR	I	Com	Win	C	NV	88	Nieland et al., 2007
90	0.912	SR	I	Com	Win	C	NV	68	Nieland et al., 2007
95	0.560	SR	I	Rec	Sum	J	NV	30	Dorf, 2003

lications (Gitschlag and Renaud, 1994; Render and Wilson, 1994; Patterson et al., 2001; Dorf, 2003; Nieland et al., 2007; Diamond and Campbell, 2009; Campbell et al., 2010a). One assessment was calculated from unpublished data (Patterson⁴), and 5 estimates were available only from gray literature (Parker⁵; Burns et al.⁶; Diamond et al.⁷; Sauls⁸). Data extracted from each publication included proportional mortality, wa-

⁴ Patterson, W. 2011. Unpubl. data. Univ. South Alabama, Mobile AL 36688.

⁵ Parker, R. O. 1985. Survival of released red snapper progress report. SEDAR24-RD12, 9 p. [Available from <http://www.sefsc.noaa.gov/sedar/>.]

⁶ Burns, K. M., R. R. Wilson Jr., and N. F. Parnell. 2004. Partitioning release mortality in the undersized red snapper by-catch: comparison of depth vs. hooking effects. Mote Marine Laboratory Technical Report No. 932, 43 p. [Available from Mote Marine Laboratory, 1600 Ken Thompson Pkwy., Sarasota, FL 34236.]

⁷ Diamond, S. L., T. Hedrick-Hopper, G. Stunz, M. Johnson, and J. Curtis. 2011. Reducing discard mortality of red snapper in the recreational fisheries using descender hooks and rapid recompression. Final report, grant no. NA07NMF4540078, 52 p. [Available from http://www.sefsc.noaa.gov/P_QryLDS/download/CR262_Diamond_2011.pdf?id=LDS.]

⁸ Sauls, B. 2012. Release mortality estimates for recreational hook-and-line caught red snapper derived from a large-scale tag-recapture study in the eastern Gulf of Mexico. SEDAR31-DW23, 21 p. [Available from <http://www.sefsc.noaa.gov/sedar/>.]

ter depth (in meters), study type (surface release, caging, passive tagging, acoustic tagging, or hyperbaric chamber), timing of the mortality estimate (immediate or delayed), fishing sector evaluated (commercial or recreational), season (winter, spring, summer, fall, or annual), hook type used (circle, J, or mixed), venting treatment (venting or nonventing), and sample size (*n*).

Several discrepancies about release mortality rates reported in the literature were found. The 10-, 15-, 20-, and 25-m depth groups from Dorf (2003) appeared to be aggregated and reported as a single estimate for one depth group (21–25 m) in a previous stock assessment in 2005 (SEDAR²). The 30-, 40-, and 50-m values from Diamond and Campbell (2009) also were aggregated and reported as annual estimates in the previous assessment in 2005 (SEDAR²). Because there is uncertainty about why these 2 data sets were aggregated in the previous assessment, our meta-analysis relied on published values as being representative of those works. The only data set from a commercial fishery that we found was that of the Nieland et al. (2007) study. This lone commercial-fishery study comprised data over 4 years at more than 273 separate fishing sites, the majority of which were located in coastal Louisiana. Nieland et al. (2007) originally reported site-specific estimates of release mortality, many of which had small sample sizes ($n=5-10$). Therefore, mortality

rates were recalculated for discrete depth groups from the original data by aggregating sites by depth.

Ideally, the frequency at which fish were vented would be calculated; however, some studies reported that venting occurred irregularly and at the choice of participants. If a study reported at least some amount of venting, then it was categorized as a venting treatment; otherwise, it was considered a nonventing treatment. Caging studies that reported a venting treatment were maintained as reported, but it should be noted that those experiments included recompression of fish (i.e., their air bladders) by submergence back to depth in cages regardless of whether a fish had been vented. Because few studies reported hook size, it was not included. Finally, the intent of this meta-analysis was to evaluate release mortality under normal fishing conditions; therefore, estimates from the hyperbaric-chamber study (Burns et al.⁶) were not included in our study.

The meta-analytical model used in our study is a special case of a weighted general linear model as detailed in the metafor package (Viechtbauer, 2010), a meta-analysis package for R software. The analysis was performed on effect size (*es*) rather than on raw proportions, where *es* was the logit-transformed proportion and was calculated with the following equation:

$$es = \log\left(\frac{x_i}{n_i - x_i}\right), \quad (1)$$

where x_i = the total number of individuals that experienced mortality; and
 n_i = the total sample size.

The estimate and the corresponding sampling variance were calculated by using the *escalc* function in the metafor package (Viechtbauer, 2010) in R software, vers. 2.15.1 (R Core Team, 2012).

We fitted estimates of effect size in a mixed-effects model to evaluate the effects of depth, fishing sector, timing of the mortality estimate, venting treatment, season, and hook type (Viechtbauer, 2010). For the categorical variables, the absence of group membership (i.e., setting that value to 0) by default defines the opposite group; therefore, there is no need to have all variables included. For instance, identifying estimates associated with commercial data as 1 automatically defines values set equal to 0 as being associated with recreational estimates. The full estimated model is shown below:

$$Prb(mortality) \sim depth + sector + timing + venting + season + hook\ type + rate + timing*venting,$$

where *depth* of capture in meters is modeled as a continuous variable and all other variables are modeled as categorical. *Sectors* were defined as commercial or recreational. *Timing* was defined as either immediate mortality or delayed mortality, referred to hereafter simply as immediate or delayed. *Venting* treatments

included venting and nonventing. *Season* variables included spring, summer, fall, or winter. *Hook types* were tested as circle or as J- and mixed hooks combined because we were interested in the effect of circle hook regulations. The *rate* variable represents each individual estimate and was modeled as a random effect (i.e. estimated mortality rate). Therefore, the model treated multiple estimates coming from a single study as unique estimates from the available population. Treatment of multiple estimates from the same study as unique estimates occurred when a study was conducted over different seasons or over a range of depths. Finally, because we wanted to test whether the *venting* treatment was confounded with the study type and timing of the estimate (immediate), we also included an interaction term (*timing*venting*).

Several additional model runs were performed to evaluate sensitivity of the model to various issues. The commercial data set was represented by a single study and, although it was a fairly extensive study that produced many estimates, it may not be representative of all commercial fisheries for red snapper. Therefore, we made model runs that excluded the data from Nieland et al. (2007).

Heterogeneity (τ^2) was estimated by using restricted maximum-likelihood. Coefficients for μ , β_0, \dots, β_p then were estimated with weighted least squares in which each estimate of effect size was weighted by the inverse of its variance. Wald-type tests and confidence intervals were calculated for μ , β_0, \dots, β_p , assuming normality. On the basis of the fitted model, we calculated predicted values and residuals. Cochran's *Q*-test was used to assess the amount of heterogeneity among studies (i.e., a null hypothesis of $\tau^2=0$). Model predictions were calculated with the *predict* function in the metafor package. The *predict* function allows for the input of a range of values (e.g., depths) over which to calculate model predictions and also allows for the adjustment of coefficient weights so that individual treatment effects can be isolated (e.g., venting and season). Predicted values and associated upper and lower bounds were then converted back to proportions by taking the inverse of the logit-transformed effect-size data with the following equation:

$$Proportion = \frac{exp^{es}}{(1 + exp^{es})}, \quad (2)$$

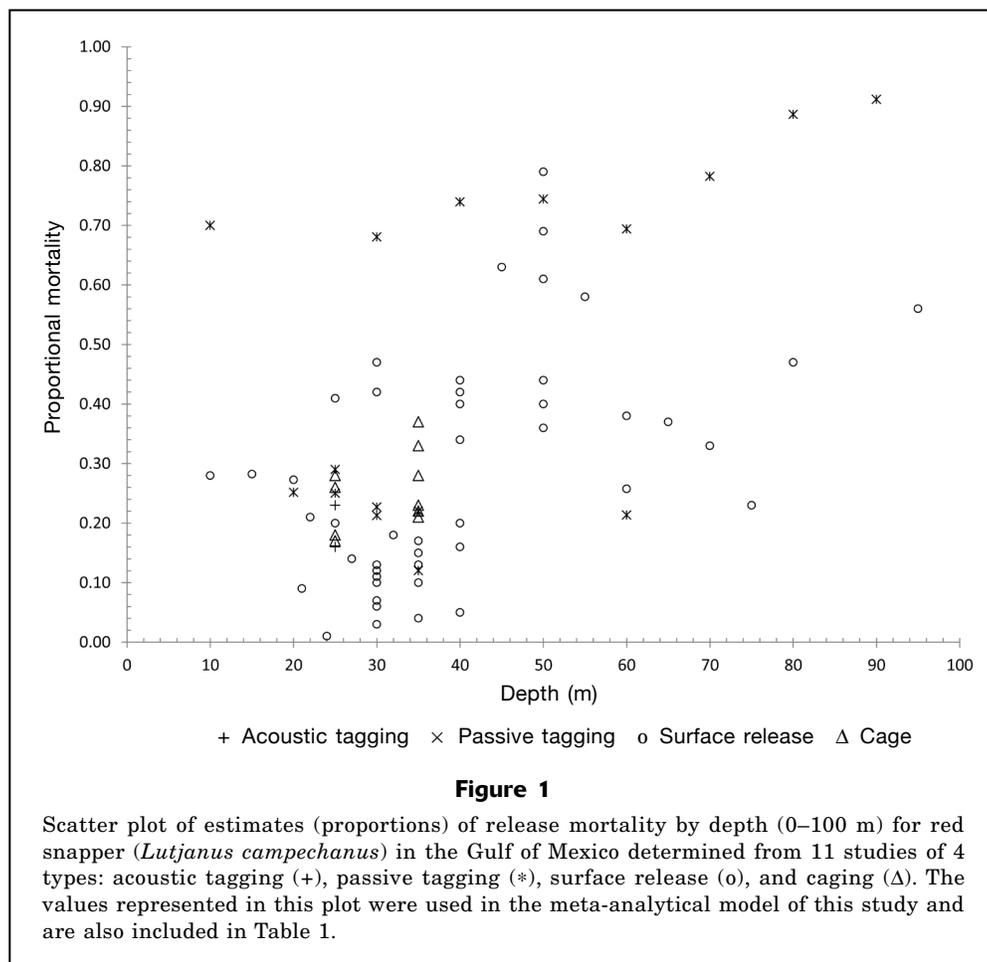
Average model predictions were evaluated by giving equal weighting to the coefficients within fishing sector, timing of mortality, venting, season, and hook type and by inputting a depth range of 10–100 m. Model predictions for the various venting and season treatments were then calculated through adjustment of the weighting scheme submitted to the *predict* function. For instance, to evaluate the effect of 100% venting, all of the weight for the venting treatments was put onto the treatment with 100% venting, and model predictions were recalculated.

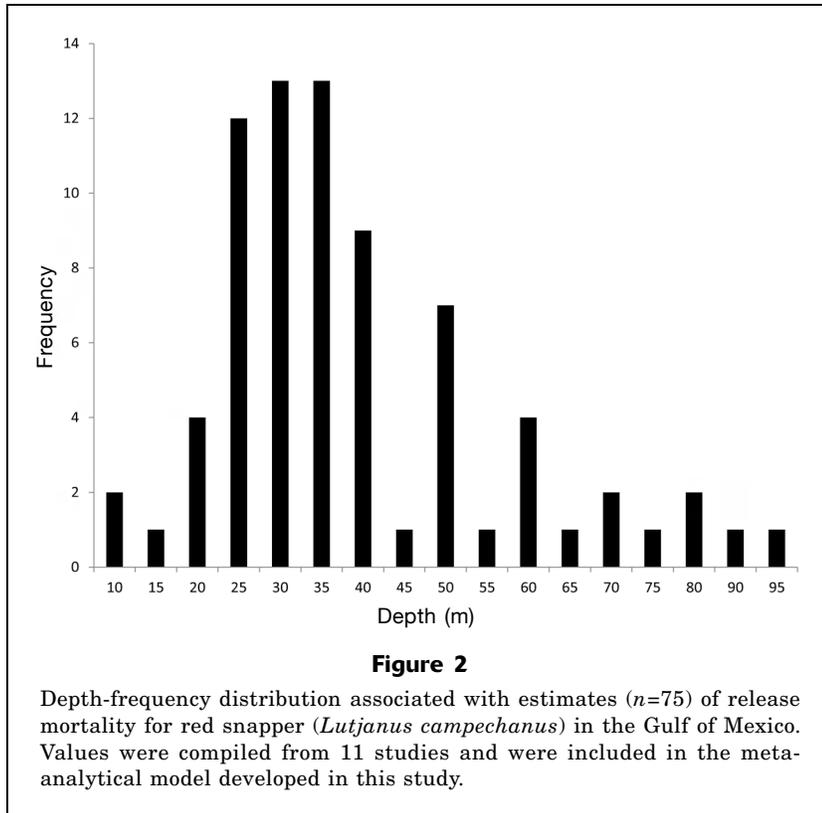
Results

Estimates of release mortality ranged from 0% to 91% over the collection of studies evaluated (Table 1, Fig. 1). The lowest estimate of 0% was associated with a hyperbaric-chamber study (Burns et al.⁶), and the highest value of 91% was associated with the only data available for the commercial fishing sector. The most common method used in these studies was surface release, followed by passive tagging, caging, hyperbaric chamber, and acoustic tagging (Table 1, Fig. 1). Release estimates were calculated most frequently from summer data, followed by winter, fall, spring, and annual (Table 1). Studies were conducted primarily at depths that ranged between 20 and 50 m; infrequent representation was found outside that range (Fig. 2). Estimates mainly were associated with the recreational fishing sector or with methods and gear commonly used in recreational fishing. Commercial fishing data were represented by a single study. Estimates of hook type were fairly balanced between the studies that used J-hooks and the ones that used circle hooks; fewer studies used a mixture of hook types. Studies that used a mixture of hook types were associated most commonly

with those studies that used direct observations in the fishery and for which gear choice was, therefore, reflective of common fishing practices. Studies in which a venting treatment was used 100% of the time always were associated with controlled scientific experiments (i.e., they did not involve direct observations of the fishery). Regardless of the fishing sector, nonventing estimates were associated most frequently with studies where fishing practices were observed from working vessels.

Results of the meta-analysis of the full complement of data showed significant effects for the following coefficients: intercept, depth, sector, timing*venting interaction, winter, and spring (Table 2). The timing, venting, fall, annual, and hook-type effects were nonsignificant. The amount of heterogeneity in effect size from the mixed-effects model was estimated to be 0.31. Cochran's Q -test for the mixed-effects model also showed significant residual heterogeneity ($Q_E=663.20$, $df=64$, $P<0.0001$), indicating that the model did not fully explain the observed variation in estimates of release mortality. Depth was the most important factor determining release mortality and consistently showed a positive relationship with mortality (Figs. 3–6). Model





coefficients indicated that the commercial fishing sector was the most influential factor that increased mortality and that the interaction and winter terms were the most influential factors that reduced mortality. That the term for the timing*venting interaction was statistically significant indicates that the effect of venting was dependent on the timing of the estimate and, therefore, indicates that immediate measurements of mortality (e.g., surface-release methods) were affected significantly decreased by venting. The venting coefficient was positive, indicating that, for delayed estimates, venting would increase mortality.

Removal of estimates of release mortality in the commercial sector had little effect on model outcomes (i.e., significant coefficients) compared with model runs that included that data. The amount of heterogeneity in effect size from the mixed-effects model without commercial-sector data was estimated to be 0.29. Cochran's Q -test for the mixed-effects model also showed significant residual heterogeneity ($Q_E=440.81$, $df=56$, $P<0.0001$), indicating that the model did not fully explain the observed variation in release mortality estimates. Model coefficients indicated that depth was the most influential factor that increased mortality and that the winter and spring seasonal conditions were important in reduction of mortality. Significant effects in this second model included the following coefficients: intercept, depth, timing*venting interaction,

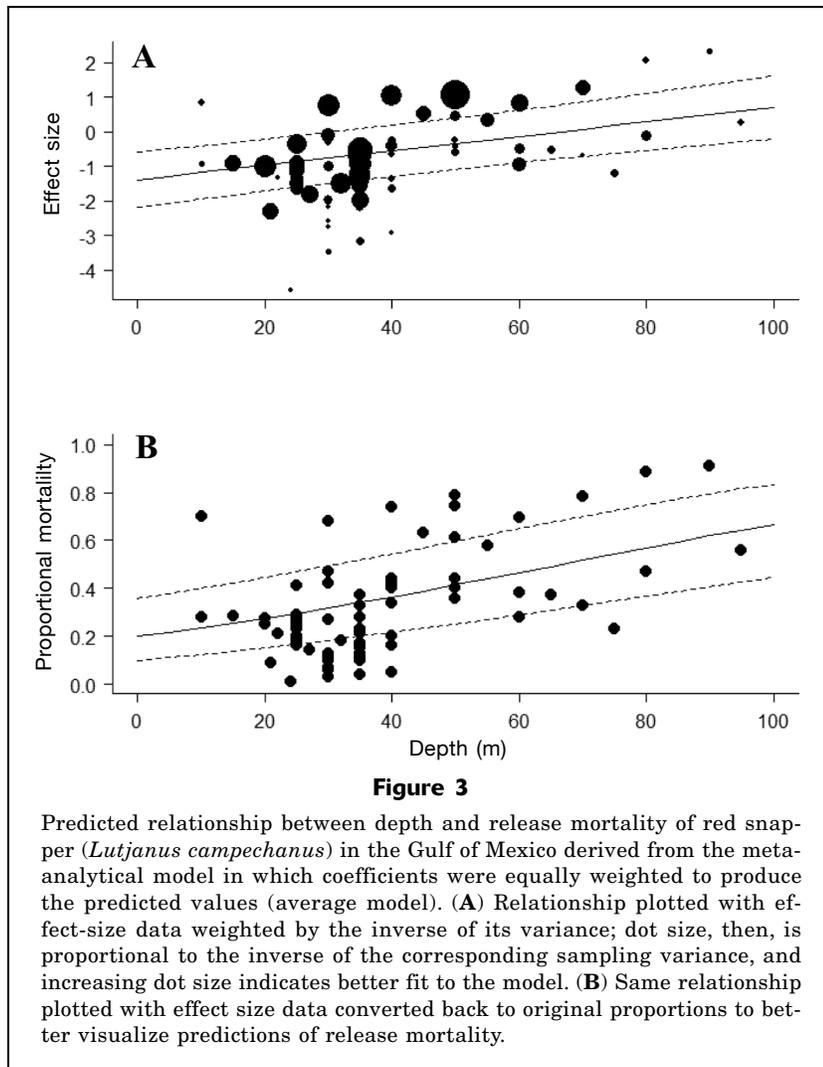
winter, and spring (Table 3). Timing, venting, fall, annual, and hook-type effects were nonsignificant. Conservation of the results despite removal of the commercial data indicated that the model was largely driven by recreational data.

Predicted rates of discard mortality by depth, mode, and season were derived by weighting model coefficients generated through the use of the full complement of data (i.e., commercial data were included). Average predictions and treatment-specific predictions were generated by weighting the coefficients accordingly. Over a depth range of 10–100 m, average model predictions (equal weighting of coefficients) of release mortalities ranged between 19% and 67% (Fig. 3; Table 4). As indicated by the statistical significance of the timing*venting interaction, the predicted rates of release mortality by venting treatments were dependent on whether a study relied on the surface-release method; this method produces immediate estimates, and other methods result in delayed estimates (Fig. 4). Immediate estimates indicated that venting decreased mortality rates, but delayed estimates indicated that venting increased mortality rates. Regardless of the model run, the winter and spring terms were significant and the predicted release mortality rates were

Table 2

Model coefficients, standard errors of the mean (SE), and P -values estimated in a meta-analysis of release mortality of red snapper (*Lutjanus campechanus*) in the Gulf of Mexico. This meta-analysis included both recreational and commercial data. Significant coefficients are highlighted with asterisks (*** $P<0.0001$, ** $P<0.001$, * $P<0.05$), and “ns” indicates nonsignificant coefficients.

Data type	Coefficient	SE	P	Significance
Intercept	-1.9136	0.7085	0.0069	**
Depth	0.0209	0.0046	<.0001	***
Sector	2.2769	0.4228	<.0001	***
Timing	0.5304	0.7009	0.4492	ns
Venting	0.6955	0.6732	0.3016	ns
Timing*Venting	-1.4858	0.7419	0.0452	*
Winter	-0.9905	0.2789	0.0004	***
Spring	-0.7701	0.2872	0.0073	**
Fall	-0.3364	0.235	0.1524	ns
Annual	-0.3668	0.3522	0.2977	ns
Hook type	0.0139	0.2107	0.9472	ns



reduced during those seasons (Fig. 5; Table 4). Inclusion of the commercial data in the model indicated that release mortality rates were significantly higher in the commercial fishing sector than in the recreational fishing sector (Fig. 6; Table 4).

Discussion

The mixed-effects modeling approach in which a random effect is estimated for each individual study, while estimating discard mortality as a function of key factors of interest, provides a robust method for dealing with specific differences due to either experimental protocols or other factors. The functional relationships developed in this model had been used in the most recent red snapper stock assessment in 2012, and that use was a change from previous assessments based on region-specific point estimates and that did not provide an estimate a depth-related function (Campbell et

al.³). The various differences in experimental protocols represented nuisance factors for the estimation of a range of discard mortality rates by depth. Nonetheless, significant residual heterogeneity was observed in the model, indicating that there likely were other unquantified variables that influence release mortality. Results from the various studies have to be evaluated within the context of the experimental methods used, but overall our meta-analytical model resulted in consistent results that isolated important factors for release mortality in the red snapper fishery.

There was a consistent, positive correlation between depth and release mortality estimates regardless of venting treatment, season, or fishing sector (Tables 1–4; Figs. 3–6). Presence of a positive correlation between depth and mortality is frequently reported in the literature, and the relationship is thought to be associated primarily with injuries sustained during decompression, such as overexpansion and rupture of the gas bladder, esophageal eversion, cloacal prolapse, exophthalmia, and gas infusion into vital organs (Davis, 2002; Rummer and Bennett, 2005; Hannah et al., 2008). The development of a predictive relationship with depth is important because previous stock assessments of red snapper, completed before this model, were based on single estimates that were fixed by region (i.e., east and west GOM) rather than on a depth relationship.

Still, although depth was a consistent factor for the explanation of release mortality, the results from the studies examined were complicated by study-specific experimental methods.

Estimated rates of release mortality were significantly higher for the commercial sector than for the recreational sector, but, unfortunately, they were derived from a single surface-release study that was conducted in a single region (Nieland et al., 2007). Further complicating the commercial data was the fact that no fish were vented before release in that study. Comparable surface-release studies of the recreational sector revealed that at least some amount of venting occurred, and all of those studies resulted in lower estimates of release mortality (Patterson et al., 2001; Dorf, 2003; Campbell et al., 2010a, Patterson⁴). Because commercial fishing operations were observed directly in the Nieland study, the estimates are at least reflective of common venting practices for that fishing sector at that time and region. Import-

tantly, our meta-analysis indicates that those estimates are highly dependent on the frequency that fish were vented before release (Fig. 4). The accuracy of surface-release estimates is tenuous because misclassification of fate after release of tagged fish can be high; therefore, significant investigation into the rate of misclassification is needed (Sauls, 2014).

Alternatively, it is possible that commercial fishing gear and practices may contribute to elevated estimates of release mortality for that sector. In the commercial sector, either electric or hydraulic bandit-gears with multiple hooks rapidly retrieve fish from depth. Rapid ascent and increased catch rates potentially result in increased sorting, handling, and air-exposure times, all of which have been shown to increase release mortality (Davis, 2002). The commercial data set in this meta-analysis may not be completely representative of that fishing sector, but the assessment process by rule is required to use the best available data to make decisions.

Finally, results of our analysis did not change after the removal of the commercial data set (Tables 2 and 3), indicating that model outcomes and predictions were driven by the recreational estimates and likely are most representative of that sector. Research clearly is needed to sort out true effects associated with commercial fishing from more general effects that are seen throughout the fishery and that are

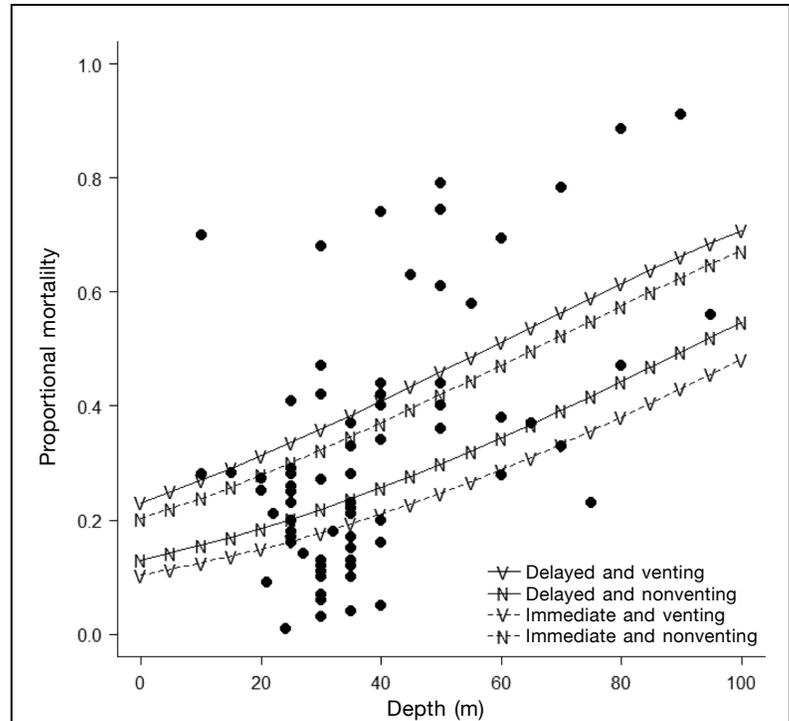


Figure 4

Predicted relationship between depth and release mortality (proportion) of red snapper (*Lutjanus campechanus*) in the Gulf of Mexico derived from the meta-analytical model for the interactions of immediate (dashed lines; seconds to minutes) and delayed (solid lines; hours to days) timing of mortality estimates with the venting (V) and nonventing (NV) treatments. Immediate estimates of release mortality indicate that venting decreases mortality, but delayed estimates indicate that venting increases mortality.

Table 3

Model coefficients, standard errors of the mean, and *P*-values estimated in a meta-analysis of release mortality of red snapper (*Lutjanus campechanus*) in the Gulf of Mexico. This meta-analysis excluded the commercial data set. Significant coefficients are highlighted with asterisks (*** $P < 0.0001$, ** $P < 0.001$, * $P < 0.05$), and “ns” indicates nonsignificant coefficients.

	Coefficient	SE	<i>P</i>	Significance
Intercept	-1.782	0.706	0.0116	*
Depth	0.0176	0.0054	0.0012	**
Timing	0.5542	0.688	0.4205	ns
Venting	0.6858	0.6611	0.2996	ns
Timing*Venting	-1.4951	0.7273	0.0398	*
Winter	-0.9974	0.2715	0.0002	***
Spring	-0.7833	0.2794	0.0051	**
Fall	-0.3397	0.2287	0.1375	ns
Annual	-0.4132	0.3446	0.2305	ns
Hook type	0.0023	0.2054	0.9912	ns

confounded by estimation methods (i.e., surface-release studies).

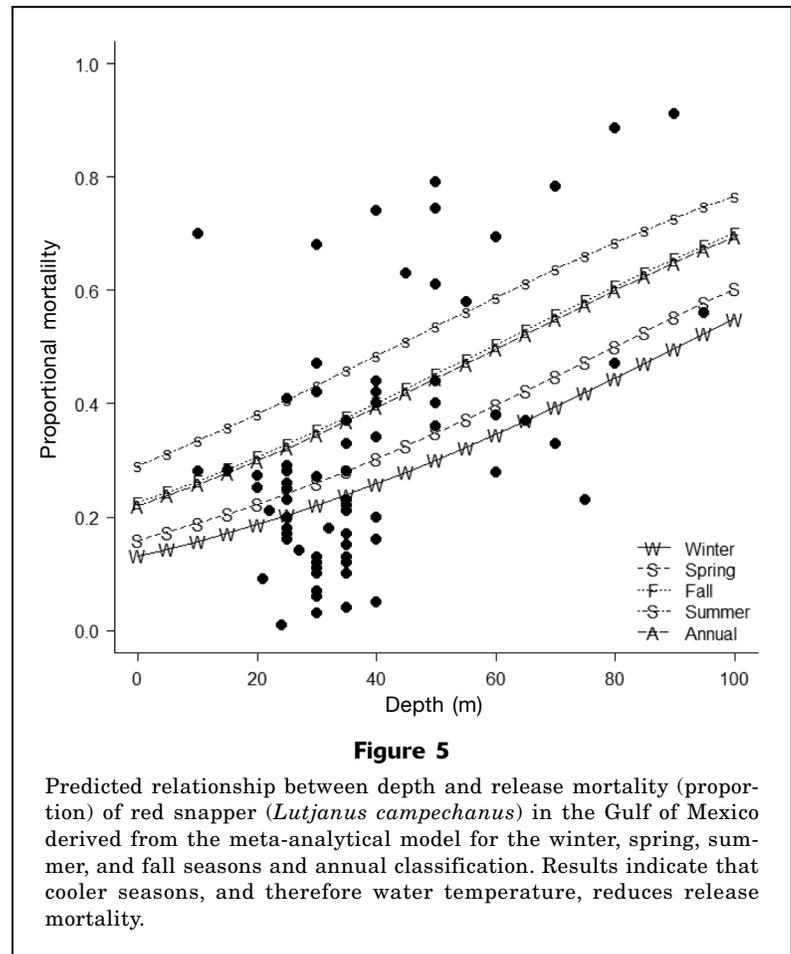
The significant interaction between the immediate timing of estimates and venting treatments indicates that the effect of venting on rates of release mortality was dependent on the timing component inherently incorporated into study-specific methods (i.e., surface-release studies produce immediate estimates). Estimates were available most commonly from surface-release studies (Table 1; Fig. 1) and those are contingent on the assumption that failure of a fish to submerge is reflective of mortality (Campbell et al., 2010a). Immediate estimates were significantly lower for the venting treatment than for the nonventing treatment (Fig. 4). For the delayed estimates (e.g., mortality estimates from caging studies), venting increased rates of release mortality—a finding that is congruent with results presented in a separate meta-analysis of venting from the same set of studies that produced delayed estimates (Wilde, 2009). Surface-release studies likely are too limited in scope to correctly evaluate the long-term effects of venting on release mortality. Furthermore, sur-

face-release studies also inject uncertainty into assessment models because of the unknown misclassification rates that result from the use of submergence as a proxy for mortality. Submergence data should be collected and used only as a last resort in the estimation of release mortality.

Both model runs, with and without the data from the commercial fishing sector, indicated that venting was not significant—a finding that agrees with the conclusions in Wilde (2009) that there was no evidence for an effect of venting. Two of the studies that produced delayed estimates specifically tested the effects of venting after fish were submerged in cages to at least 2 atm of pressure (Gitschlag and Renaud, 1994; Render and Wilson, 1994). Submergence to 2 atm halves gas volume in the air bladder and effectively recompresses the fish. Both of these caging studies reported no difference in survival by venting treatments, but neither study addressed the issue of recompression. Recompressing the gas bladder may have had the same effect as venting the fish and, perhaps, explains the lack of a difference in survival between venting treatments. Ultimately, these caging studies lend insight in regard to venting versus recompression, but they are not reflective of day-to-day fishery operations in which fish are released at the surface.

Venting is best evaluated with tag-and-recapture studies in which fish are released as they would be in regular fishery operations. The only tag-and-recapture study that directly compared venting treatments, and that was available for inclusion in either meta-analysis, simply evaluated recapture rates and did not generate a model for estimation of release mortality (Burns et al.¹). Furthermore, estimates from the Burns et al.¹ tag-and-recapture study did not account for spatial issues; nor did it incorporate fishing effort, making interpretation of the results problematic. Recently developed tag-and-recapture models from other fisheries that use fishery-dependent data and incorporate fishing effort, hook type, and venting procedures into the estimates should provide a more robust method to test venting (Hueter et al., 2006; Sauls and Ayala, 2012; Sauls, 2014). The interaction result indicates that recompression of fish may be a viable alternative to venting, but if a recompression device is not available, then venting at least improves the likelihood that a fish can submerge and return to protective habitat.

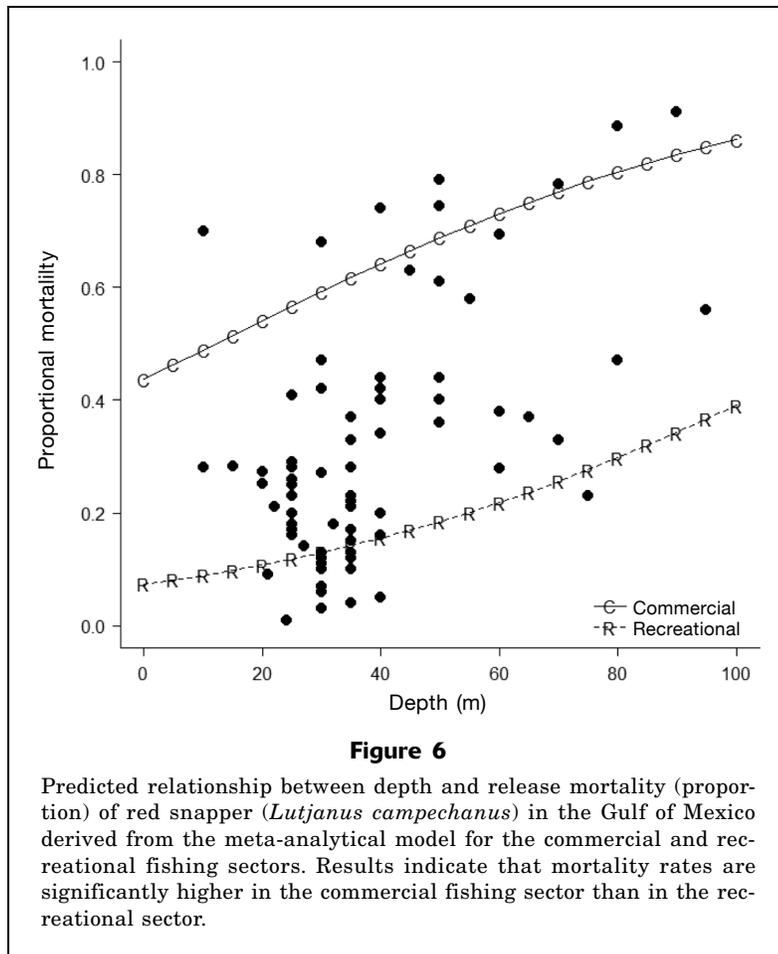
Recent research in the red snapper fishery has been focused on bottom-release devices, 2 of which have been tested experimentally. The use of a bottom-release device is similar to venting in that the goal is to reverse the effects of barotrauma, but instead of deflating the



bladder by puncture it is deflated by recompression at depth. Diamond et al.⁷ tested the Shelton Fish Descender⁹ (Shelton Products, Newark, CA) and showed that the use of that bottom-release device did not improve survival over the use of a treatment in which fish were vented and released at the surface. Another device that releases fish at a preset depth through a pressure-sensitive clamp was tested in a different study that showed that fish released through the use of that device are more likely to survive than fish vented and released at the surface (Stunz and Curtis¹⁰). At this time, it is difficult to discern if the differences between these 2 experiments were due to the gear used or some other effect, such as low sample sizes. The significant interaction term from the results of these studies indicates that release devices may be useful in reducing mortality in lieu of venting. More studies are needed

⁹ Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

¹⁰ Stunz G. W., and J. Curtis. 2012. Examining delayed mortality in barotrauma afflicted red snapper using acoustic telemetry and hyperbaric experimentation. SEDAR31-DW21, 15 p. [Available from <http://www.sefsc.noaa.gov/sedar/>]



to determine whether there is some potential for bottom-release devices to enhance postrelease survival or whether the effects of barotrauma cannot be reversed as was suggested by Wilde (2009).

Season also was a significant factor that affected release mortality and, because season is a rough proxy for water temperature, the data indicate a positive relationship between water temperature and release mortality of red snapper. Impairment-scaling metrics that evaluate sublethal effects of CAR fishing, such as reduction of reflex responses, also show similar relationships with water temperature (Diamond and Campbell, 2009; Campbell et al., 2010a, 2010b). Furthermore, impairment-scaling metrics were linked to increased immediate estimates in at least 2 of those studies. Tagging data show that the lowest returns have been for fish tagged during summer and the highest recapture rates have been for fish tagged during the winter (Diamond et al.⁷; Sauls⁸), although tag-and-recapture studies are heavily influenced by the timing of the primary effort in a fishery (i.e., winter fishing effort is low and may result in fewer recaptures during that time).

Finally, in 3 projects that required field collections before laboratory investigations could begin, red snap-

per were unable to be kept alive during collection or transport back to a laboratory during summer months (Parker⁵; Burns et al.⁶; Campbell et al., 2010a). Most investigations included in our meta-analysis had vaguely defined seasonal classifications, and other studies reported the months in which sampling took place. A single study reported water temperatures and thermocline strength. Vague seasonal classifications of sampling time frames complicate information from transitional seasons, such as fall, because September water temperatures in the GOM often are more reflective of summer conditions. Evidence of unexplained residual heterogeneity in the mixed-effects model might be associated with insufficient treatment of these thermal components; therefore, future studies should focus attention on this relationship.

Another common problem found in this meta-analysis was that the acoustic-tagging and caging studies typically had limited sample sizes. With one exception, the caging studies evaluated in this meta-analysis had depth-specific sample sizes of less than 56 fish (Parker⁵; Gitschlag and Renaud, 1994; Render and Wilson, 1994; Diamond and Campbell, 2009). The acoustic-tagging study available for inclusion split 44 fish between summer and winter sampling efforts (Diamond et al.⁷). Low sample sizes can lead to poor estimation of effects because proportions are unstable at low sample sizes. Another issue is that, because of the

ease of obtaining surface-release estimates, those studies greatly outnumbered other types of studies in this meta-analysis. Furthermore, the sample-size weighting scheme in this meta-analysis lends more weight to experiments with large samples, and that weighting potentially biases outcomes toward surface-release studies.

Acoustic or satellite tags give the ideal level of information, but until the expense of tags and required monitoring systems is reduced, those studies will be hampered by small sample sizes and poor statistical power to estimate mortality. Another complicating factor in acoustic-tagging and caging studies is that handling and abrasion can act to increase release mortality rates (Jarvis and Lowe, 2008; Hannah et al., 2012). Recent development of a novel caging system to evaluate survival was effective in reduction of mortality due to abrasion for several rockfish species (Hannah et al., 2012). Similarly, the use of an external acoustic tag to evaluate rockfish survival has shown promise in reducing handling times and may help to increase sample sizes in acoustic-tagging studies (Hyde¹¹). Methods

¹¹Hyde, J. 2013. Personal commun. NOAA Southwest Fisheries Science Center, La Jolla, CA 92037.

Table 4

Predicted estimates of release mortality from a meta-analytical model of red snapper (*Lutjanus campechanus*) in the Gulf of Mexico, by depth (0–100 m), for the average model run (Average) of equally weighted coefficients, season (winter, spring, summer, and fall), and fishing sector (Comm.=commercial and Rec.=recreational). Predicted estimates were derived with the coefficients presented in Table 2 and shown in graph format in Figures 3–6).

Depth	Average	Winter	Spring	Fall	Summer	Annual	Comm.	Rec.
0	0.199	0.131	0.159	0.225	0.289	0.220	0.437	0.074
5	0.216	0.144	0.173	0.244	0.311	0.239	0.463	0.081
10	0.235	0.157	0.189	0.264	0.334	0.258	0.489	0.089
15	0.254	0.171	0.205	0.285	0.358	0.278	0.515	0.098
20	0.274	0.187	0.223	0.306	0.382	0.300	0.541	0.108
25	0.295	0.203	0.241	0.329	0.407	0.322	0.567	0.118
30	0.318	0.221	0.261	0.352	0.432	0.345	0.592	0.130
35	0.341	0.239	0.281	0.377	0.458	0.369	0.617	0.142
40	0.364	0.258	0.303	0.401	0.484	0.394	0.642	0.155
45	0.389	0.279	0.325	0.427	0.510	0.419	0.665	0.169
50	0.414	0.300	0.349	0.452	0.536	0.445	0.688	0.185
55	0.439	0.323	0.373	0.478	0.562	0.471	0.710	0.201
60	0.465	0.346	0.397	0.504	0.588	0.497	0.731	0.218
65	0.491	0.370	0.423	0.530	0.613	0.523	0.751	0.236
70	0.517	0.395	0.448	0.556	0.637	0.549	0.770	0.256
75	0.543	0.420	0.474	0.582	0.661	0.574	0.788	0.276
80	0.569	0.445	0.500	0.607	0.684	0.600	0.805	0.297
85	0.595	0.471	0.526	0.632	0.706	0.624	0.821	0.320
90	0.619	0.497	0.552	0.656	0.727	0.649	0.836	0.343
95	0.644	0.523	0.578	0.679	0.747	0.672	0.849	0.367
100	0.667	0.549	0.603	0.701	0.766	0.695	0.862	0.391

that reduce the effects of handling and that increase sample sizes are encouraged regardless of the study type chosen.

Because of the need for estimates derived from fishery-dependent surveys that accurately reflect fishing practices, passive-tagging studies might be the best method available, but they still have problems associated with their use. Passive-tagging surveys require large numbers of fish to evaluate survival because recapture rates are typically low in the red snapper fishery (<10%). Furthermore, only 1 of the passive-tagging studies evaluated here produced estimates through the use of a tag-and-recapture model (Sauls⁸), although the other 2 studies made use of surface-release methods (Patterson et al., 2001; Patterson⁴). Recent modeling efforts in other fisheries have shown promise in the use of recapture and impairment scaling data to calculate relative survival from risk-ratio models (Sauls⁸; Sauls, 2014). Continued development of tag-and-recapture models would be useful because 1) such models potentially avoid the biases associated with other estimation methods, 2) there is an abundance of tagging data available, and 3) studies can be designed to directly observe the fishery as it is prosecuted.

Methods for calculating or scaling the level of impairment of fish caused by effects of CAR fishing have

proven to be useful for the estimation of release mortality for many species, including walleye pollock (*Gadus chalcogrammus*, Gadidae), coho salmon (*Oncorhynchus kisutch*, Salmonidae), sablefish (*Anoplopoma fimbria*, Anoplopomatidae), northern rock sole (*Lepidopsetta polyxystra*, Pleuronectidae), lingcod (*Ophiodon elongatus*, Hexagrammidae), Pacific halibut (*Hippoglossus stenolepis*, Pleuronectidae), and red snapper (Davis et al., 2001; Davis and Ottmar, 2006; Davis, 2007; Campbell et al., 2010a, 2010b). The impairment scaling metric for the barotrauma reflex showed a positive logistic relationship between impairment level and immediate estimates of release mortality in the recreational red snapper fishery for both surface-release and caging studies (Campbell et al., 2010a; Diamond and Campbell, 2009). Because impairment-scaling studies have shown significant relationships with release mortality in both the surface-release and caging studies, these techniques may prove to be useful in tag-and-recapture models.

We did not find a significant reduction in mortality by hook type, which was surprising given that the regulation requiring circle hooks was thought to be effective in reduction of discard mortality by decreasing the frequency of gut hooking. However, any effects of circle hooks on discard mortality may have been con-

founded in this study with fishing sector because the only commercial study that was available exclusively used circle hooks and many recreational studies used a mixture of hooks and a variety of venting practices. Furthermore, few studies reported hook sizes, and it is likely that the incidence of gut hooking, which can significantly increase release mortality, is related to hook size because mouth gape limits the effectiveness of large hooks. Therefore, our ability to estimate an effect of circle hooks separate from fishing sector, study type, and season may have been diminished. We do not think that circle hooks lack positive benefits; we simply may not have been able to detect them from the available studies, and we know little about the potential interactions of other variables with hook size. Nonetheless, substantial documentation indicates that there are positive benefits associated with circle hooks (Cooke and Suski, 2004).

Conclusions

There have been significant improvements in understanding release mortality in general and particularly in the red snapper fishery. Despite the significant efforts of many researchers, fundamental biases still persist in the various approaches. Estimates from surface-release studies do not address long-term effects of barotrauma, do not account for predation, and rely on submergence ability as a proxy to calculate mortality rates. Delayed estimates have been hampered by small sample sizes, cost prohibitive designs, excessive handling, and failure to duplicate normal conditions when releasing fish. Venting results were contingent upon the timing aspect specific to the various methods being used (i.e., delayed and immediate timing of estimates).

A focus on increasing sample sizes in acoustic-tagging surveys and continued improvement of tag-and-recapture models would be useful. Passive- and acoustic-tagging appear to offer good solutions because they can measure both immediate and delayed components and fish handling biases can be minimized, particularly as technology improves and costs are brought down. Experiments in which impairment scaling is estimated and that include both immediate and delayed estimates also would be valuable for the further development of those relationships within models and potential adjustment of historical estimates. Future surveys should include some, if not all, of the following properties: quarterly sampling, appropriate range of depths, water temperature and thermocline data rather than seasonal categorization, tag-and-recapture modeling, and measurement of barotrauma and reflex responses.

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