Estimating discard mortality using meta-analysis and fishery-dependent sampling

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Abstract

Estimates of discard mortality are difficult to obtain. Meta-analysis or life-history-based approaches to estimate discard mortality could provide informed estimates when direct empirical estimates are not available. We used data from published literature across a variety of fish species to determine if hooking condition (good vs. poor) and species-specific values for the Brody growth coefficient (*K*: a measure of fish physiology) were meaningful factors influencing discard mortality in hook and line fisheries. We then examined whether a two-step approach, combining condition- and physiology-specific estimates of discard mortality with data on proportion-by-hooking-condition hooking information for a fishery, could result in an estimate of discard mortality for dolphinfish *Coryphaena hippurus* comparable to an empirical estimate. A model with hooking condition, *K* and their interaction best fitted the published discard mortality data. *K* was an important negative covariate of discard mortality for good hooking condition, with higher *K* species experiencing greater rates of survival. In contrast, species in poor condition had similarly low rates of survival across a range of *K* values. Results suggests that hooking condition is the dominant source of mortality when fish are hooked in vital areas but that physiology should also be taken into account when estimating discard mortality for good condition fish. For the recreational dolphinfish fishery in the southeastern US, we estimated a median proportional discard mortality rate of 0.12 (95% credible set: 0.07, 0.17) when combining the meta-analysis and field-collected proportion-by-condition data. This estimate was lower than the empirical estimate of dolphinfish discard mortality but the credible sets overlapped (median: 0.25; 95% credible set: 0.05, 0.39). Estimates of discard mortality from our meta-analytic approach may be applicable to fisheries where empirical estimates of discard mortality are not available and hooking injuries are the dominant source of mortality.

1. Introduction

The disposition of discards is one of the most important issues facing fishery managers (Davis, 2002). Sustainable exploitation of stocks managed with size or bag limits requires estimates of the number of discarded individuals in a fishery as well as an estimate of discard mortality for released individuals (Coggins et al., 2007). However, discard mortality rates have not been estimated or remain unknown for many species and fisheries worldwide. For these fisheries, having a reasonable estimate of discard mortality would supply information useful for stock assessments for data-rich species for which there are fully integrated stock assessments as well as data-limited species that require a time series of catch (harvest and dead discards; Carruthers et al., 2014). Additionally, estimates of dead discards can help fishery managers determine whether regulations intended to reduce rates of fishing mortality in stocks managed with size or possession limits are achieving their intended effects (Coggins et al., 2007).

Estimates of discard mortality for any given species and fishery are often measured using direct, in-situ approaches (Davis, 2002). *In situ* approaches often involve conventional tagging (e.g., Heuter et al., 2006; Rudershausen et al., 2014), telemetry (Heupel and Simpfendorfer, 2002) or satellite tagging (e.g., Horodysky and Graves, 2005). However, these are typically labor-intensive or costly. Additionally, the low tag return rates for many conventionally tagged pelagic marine species (e.g. $\leq$ 2-3%, Singh-Renton and Renton, 2009; Merten et al., 2014; Rudershausen et al., 2019) decrease the precision about estimates of discard mortality when using a relative risk modeling approach (Heuter et al., 2006; Sauls, 2014). Meta-analytic approaches have been used to develop predictive models for parameter estimation in lieu of empirically-derived estimates. For example, natural mortality (M) rates used in stock assessments are often estimated using predictive relationships developed from meta-analyses using life history or size-based predictors (Pauly, 1980; Hoenig, 1984; Lorenzen, 1996). Similarly, much has been learned about fish reproductive rates from meta-analyses of stock-recruitment data (Myers et al., 1999). While there are published rates of discard mortality across a variety of fish species in hook and line fisheries, the utility of using these studies to predict discard mortality rates when an empirical estimate is unavailable is currently unknown.

To develop a useful predictive model for discard mortality, we focused on factors known to influence discard mortality rates and that are easily obtained from the literature. Prior reviews of discard mortality have found that a combination of gear, biological, and environmental effects (Muoneke and Childress, 1994; Davis, 2002; Bartholomew and Bohnsack, 2005; Benoît et al., 2013) can influence discard mortality. We focused our predictive model on providing estimates for hook-and-line gear given the increasing levels of discarding with this gear (Arlinghaus et al., 2007; Cooke and Schramm, 2007). If specific environmental effects were the most important factors influencing discard mortality, this would suggest that species-specific data are necessary for a fishery over particular regions or seasons where a fishery operates. In contrast, if discard mortality was shown to be predominantly a function of gear injury, then discard mortality in data-limited fisheries could simply be estimated using published data where similar gear-related injuries were recorded. The latter finding would support the conclusion that hooking injury is the dominant source of mortality in hook and line fisheries; that conclusion is supported in reviews (Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Brownscombe et al., 2017). Lastly, there could be differences in physiology between species that might influence discard mortality; physiology is known to correlate with readily accessible life history metrics like growth parameters (von Bertalanffy, 1938; Beverton and Holt, 1959; Snover et al., 2005).

The meta-analytic approach we present here assumes that the main sources of discard mortality can be accounted for through limited sampling and published information on discard mortality and species biology. This does not rule out that other factors, such as a suite of environmental and biological effects, can influence discard mortality (reviewed in Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Brownscombe et al., 2017). Rather, we are testing whether, after sampling for gear trauma and obtaining an estimate of species-specific physiology, we can estimate a discard mortality rate that suffices for a species-specific empirical estimate when one is not available. If gear trauma is a determinant of discard mortality, this would indicate that a predictive model could be developed from the published literature where discard mortality and gear trauma were reported. If physiology is a determinant of discard mortality, this suggests that an accurate estimate of discard mortality should incorporate species-specific physiology. Rates of discard mortality can have a direct relationship with water temperature within species-specific preferences (Gale et al., 2013) and the wide seasonal temperature ranges of many fisheries could also contribute to variability about rates of discard mortality. Water temperature data are often published as part of discard mortality studies and could be an additional source of data incorporated into discard mortality models.

This meta-analytic approach is a means to bypass costly (e.g., satellite tagging) and labor-intensive methods (e.g., conventional tagging) to estimate discard mortality. The first step of the approach involves using published studies to develop a predictive model between discard mortality and important explanatory variables such as hook location and variables related to physiology. The second step involves fishery-dependent sampling to collect data on hook location. We then examine the utility of this approach by estimating discard mortality for a recreational fishery (dolphinfish *Coryphaena hippurus*) in the southeastern US (SEUS) Finally, we compared this discard mortality estimate to an empirically-derived estimate of discard mortality for this species. Our goal was to determine whether a discard mortality estimate from a combined meta-analytic and limited field approach could be a suitable proxy when an empirical discard mortality rate is either unavailable or impractical to estimate.

2. Methods

2.1 Modeling discard mortality from published literature

Publications in multiple natural resource journals as well as gray literature (Supplement 1) were searched for observed (e.g., tank holding) or inferred (e.g., satellite tagging) data on discard mortality. We restricted our literature search to studies that had researched the effects of the same gear type (hook and line) as our empirical test fishery (see below). We recorded numbers of dead and live fish (i.e., binomially-distributed response data) in five hook injury categories (see below) and only used studies that had discard mortality information on at least five individual fish within each category to avoid extreme mortality probabilities (close to 0 or 1) observed with small sample sizes. We restricted data collection to studies that either reported the number of specimens studied and those dying, or if these numbers could be extrapolated from text, tables, figures, or calculated values. We did not use unpublished correspondence or direct communication with authors to try to clarify ambiguous or unknown gear interactions (hooking locations), release conditions, or data summaries, owing to the spirit of our study to evaluate a novel means of estimating discard mortality solely with data accessible via research library resources. Finally, we restricted data gathering from the literature to research where the angler actively uses hook-and-line gear; thus, we did not consider other hook gears such as longline. This eliminated discard mortality studies with gears where a fish’s interactions with the hook is passive, without angler participation in the hook setting process. Mean study water temperature was obtained from each publication when reported; in several instances it was estimated from geographic location and time of year that the study took place (Supplement 1).

Our first goal was to use data from our review, initially without covariates, to estimate rates of discard mortality for fish hooked in several commonly reported hooking locations: jaw, external body, gills, stomach/esophagus, and eyes/roof of mouth. These were also hooking locations observed in our dockside sampling of dolphinfish (see below). Discard mortality by hooking location was estimated through Bayesian inference by fitting beta/binomial models (Ntzoufras, 2011) (Supplement 2). For each of the five hooking locations we assigned an uninformative beta prior probability distribution (prior) (a = b = 1) for mortality probability. We then specified a binomially distributed likelihood that looped over data sets on each hooking location, with mortality probability shared among studies.

Our next goal was to account for factors related to physiology that could explain variation in discard mortality and are easily obtained from studies of discard mortality and published information on species biology. To account for species-specific physiology in mortality modeling, we used the Brody growth coefficient (*K*); this is a parameter estimated from the von Bertalanffy growth function (von Bertalanffy, 1938) and an indication of metabolic rate (von Bertalanffy, 1938; Beverton and Holt, 1959; Snover et al., 2005). Species-specific values for *K* (where available) were obtained from the freely available *fishbase* website (*www.fishbase.org*) or from published sources when not supplied by *fishbase* (see Supplement 1 for exceptions). When more than one value of *K* was available for a species, we used the study value geographically closest to where the published study of discard mortality was conducted.

Water temperature has also been shown to influence discard mortality (Gale et al., 2013). Preliminary testing showed that *K* and water temperature reported in discard mortality studies were correlated (Pearson r = 0.45, p<0.001). Thus, we elected to retain *K* in the mortality modeling and to exclude study water temperature. Plots of *K* by hooking condition (good vs. poor) revealed a potential interaction between hooking location and physiology. For this reason we fitted mortality models that included main effects ('main effects ANCOVA') and also models that included the interaction ('interaction effects ANCOVA') (Kéry and Royle, 2015) (Supplement 3). Models were also fitted that included just hooking condition and just the regression intercept. For logistic models, hooking conditions from published mortality data were classified as either 'good' (jaw/mouth and external body) or 'poor' (gill, stomach/esophagus, and eye/roof-of-the-mouth). We assumed when a study reported 'shallow hooking' that this was synonymous with good condition and 'deep hooking' was synonymous with poor condition. Our assignment of published hooking areas to two broad anatomical locations follows the conclusion that fish hooked in critical tissues or organs suffer higher mortality rates (Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005). Using two broad hooking locations also allowed for a more direct comparison to a species-specific empirical study of discard mortality for a data-limited fishery (see below).

Mortality models were fitted using Bayesian methods and the 'means parameterization' (Kéry and Royle, 2015). Each of the four fitted models specified a binomially distributed likelihood shared among studies. Separate prior probability distributions (mean and precision of 0 and 0.01, respectively) were assigned to each hooking location for each model's intercept and (when it was fitted) the regression coefficient for the covariate *K*. Model parsimony was compared using the Deviance Information Criterion (DIC) and the Akaike weight (w_i) for each model. We evaluated the importance of the effects of hooking location and *K* on discard mortality by examining 95% credible sets; if the credible set for a coefficient of hooking condition or *K* did not overlap zero then it was considered important in predicting discard mortality.

2.2 Two-step approach to estimate discard mortality for a data-limited fishery

We used the model developed from the meta-analysis in conjunction with fishery-dependent sampling to estimate a rate of discard mortality for dolphinfish in the SEUS. The fishery-dependent sampling provides information about the proportion of individuals in each hooking condition. The dolphinfish is a highly migratory pelagic marine predator (Merten et al., 2014, 2016) found in tropical and sub-tropical waters worldwide. The dolphinfish stock in the SEUS region is considered 'data-limited' (Prager, 2000; SAFMC, 2003) despite being one of the most heavily landed species in this US federal fisheries management region (NOAA Fisheries, 2018; Shertzer et al., 2019). Recreational harvests comprise roughly 96% of the annual catch (commercial harvests ~4%) (SAFMC, 2013). Despite the use of size and possession limits to manage this recreational fishery for dolphinfish (SAFMC, 2018), the rate of discard mortality following capture with hook and line in this region was, to our knowledge, not estimated until recently (Rudershausen et al., 2019).

To collect proportion-by-condition information, we conducted post-mortem dockside sampling. In theory, this sampling could be conducted for other data-limited fisheries via observations of individuals that are either caught and released, or harvested; in this study we do the latter. Specifically, we examined dolphinfish harvested by a recreational charter boat fleet operating out of Morehead City, North Carolina (USA). While there is a minimum size limit in the SEUS fishery, this size limit does not apply to dolphinfish landed in North Carolina. This fleet is part of a larger recreational fishery directed for dolphinfish in the SEUS, Gulf of Mexico, and Caribbean that, depending on the season, uses trolling and/or bailing (casting dead natural bait to schooling fish from a stationary or slowly moving boat) for targeting this species with hook and line (Rudershausen et al., 2012). In estimating a rate of discard mortality for the fishery, we assumed that hook injuries observed in landed dolphinfish also applied to dolphinfish caught and released in this fishery. We further assumed that the breadth of our seasonal sampling accounted for fish caught via both trolling and bailing, consistent with the data collection for the empirical estimate of dolphinfish discard mortality (Rudershausen et al., 2019).

Fishery landings were sampled during springs and summers of 2016 and 2017. We binned hooking data into the two general conditions for consistency with the two condition groupings (good vs. poor) in the species-specific estimate of dolphinfish discard mortality (Rudershausen et al., 2019). Clearly visible hook marks, the presence of coagulated blood, and embedded hooks/line were used to guide our assignment of hooking condition in each sampled individual. Fish hooked in two locations were assigned the hooking location most injurious based on published studies of discard mortality rates (Supplement 1). Jaw hooking (good condition) was considered in the vicinity of the mandible, maxillary, or in the hinge between the two. Fish with unknown hooking locations were assumed jaw-hooked due to the lack of visible evidence (e.g., blood) indicating injury to vital tissues or organs. Specimens hooked in the roof of the mouth were assumed to be poor condition due to evidence that roof-of-mouth hooked dolphinfish sustain injuries more closely resembling eye- than jaw hooking (Mikles et al., 2018).

For proportion by hooking location information, each study trip to sample carcasses yielded data that were assigned to the two hooking conditions. However, the true proportion of dolphinfish hooked in different conditions is not known in the fishery due to the inability to census the recreational catch at this port or in the larger management region. For this reason, in modeling proportion by condition information, we defined the probability of sampling these hooking locations over each visit to the docks as a multinomial-distributed random variable. This variable was assigned a Dirichlet prior probability distribution with each α value (probability of obtaining the random variable for each hooking location) equal to 1, which allocates individual membership to each category uniformly across groups (Royle and Dorazio, 2008). This portion of the model was fitted to numbers-by-condition data for each sampling trip; the minimum number of carcasses to be considered a trip was one. This approach using dockside samples to characterize the behavior of anglers and disposition of fish released at sea assumes that the proportion by condition of dolphinfish sampled dockside is representative of the proportions released by anglers *in situ*. Violations to this assumption would lead to a biased estimate of discard mortality if the hooking conditions dockside were not representative of live releases at sea. For this reason, we estimated an overall rate of mortality for the fishery using all sizes of dolphinfish sampled at the dock, and then conducted a second model run just with sub-legal fish (see below).

2.3 Overall model fitting to estimate discard mortality for the dolphinfish fishery

We fitted a probabilistic model using Bayesian methods to estimate a rate of discard mortality for the dolphinfish hook and line recreational fishery (Supplement 3). The model had three sub-components: 1) an estimate of discard mortality as a function of published data and covariates (above), 2) an estimate of proportion-by-condition from sampling the fishery (above), and 3) a calculation of overall discard mortality. In calculating the overall estimate of discard mortality for the fishery, we used the most parsimonious mortality model (lowest DIC value) from the fitted sub-models (above). The overall estimate of discard mortality for the fishery was defined as the addition of two products with each product found by multiplying the estimated proportional mortality by the proportion of individuals sampled in that hooking condition. We estimated discard mortality across all sizes of dolphinfish given that this species is managed through both size limits and annual catch limits (ACLs); thus, fish of legal size may need to be discarded in the event that an ACL is exceeded. The model to estimate dolphinfish discard mortality used a value of *K* averaged across previous studies of this species in the SEUS and Gulf of Mexico regions (0.74: *fishbase.org*). Estimates of discard mortality for dolphinfish in good and poor hooking conditions were obtained by setting the last two values in each of the four data input vectors to values appropriate for dolphinfish. This allows the modeler to obtain a prediction of the posterior probability distribution given those values (Lunn et al., 2012); for dolphinfish, the last two values in each vector were the two hooking conditions (1=good and 2= poor) in the hook condition vector, an arbitrary number of trials for theoretical study subjects (100 in this case) for the "N" vector, the number of mortalities (set at NA in the "C" vector), and the value of K for dolphinfish ($0.74yr^{-1}$) in the K vector. This provided a prediction of the number of dead dolphinfish for each hooking condition that was then divided by 100 to express the mortality for each hooking condition as a proportion.

All models were fitted through *OpenBUGS* software (version 3.2.1) (Spiegelhalter et al., 2010) using *R* software (R Development Core Team, 2020) and the software interface package *R2OpenBUGS* (Sturtz et al., 2020). Each model fit was conducted using three chains of initial values that were generated by the software. Each model was updated 5,000 times with the first 2,000 updates discarded as adaptive phase. Stationarity (convergence) of each model parameter was determined by examining the values for the Gelman-Rubin statistic ($\hat{R}$) that *OpenBUGS* computes for retained updates; convergence is indicated when $\hat{R}$ for a parameter is < 1.1 (Gelman, 1996). Convergence was also assessed by inspecting trace plots of retained values.

The estimate of discard mortality of dolphinfish for the fishery using the present approach was compared to an empirically-derived estimate of discard mortality from a long-term tag-recapture study; details of this empirical study can be found elsewhere (Rudershausen et al., 2019). Briefly, in that study, dolphinfish (n = 4,648) were captured by hook and line, conventionally tagged, and released by researchers and cooperating recreational fishers in the SEUS, Caribbean, and Gulf of Mexico. A relative risk model was fitted to data on numbers of fish tagged and numbers returned in each of two release conditions (good and poor); each release condition was assigned based on hooking condition and qualitative assessment of post-release swimming performance. The 100% survival of good-condition fish assumed in estimating discard mortality with a relative risk modeling approach (Heuter et al., 2006) was tested and incorporated into that study's mortality model as a scaling factor by using the results of two known-fates experiments on good-condition fish (tank holding and satellite tagging). Due to calculated values within that model, estimated rates of proportional mortality could exceed 1 or be less than 0. Finally, an overall rate of discard mortality for the SEUS recreational fishery was estimated in the empirical study by summing across two products, each one computed by multiplying the condition-specific mortality rate by the proportion of individuals caught and released boat-side in that condition. Each posterior of overall mortality that was compared between studies was plotted by using the retained values for all three chains (n = 9,000 updates total).

Goodness of fit of the best fitting meta-analytic model was assessed by computing a Pearson residuals discrepancy measure between the observed data set of binomially distributed mortality data and a replicate data set generated using the parameter estimates produced from model fitting to the real data (Kéry, 2010) (Appendix 2). A Bayesian probability (p) value (Gelman et al., 1996) was then computed as part of each model run. This p-value (distinct from the p-value in hypothesis testing) computes the proportion of instances when the discrepancy measure for the replicated data set exceeds that for the observed data set; p-values roughly equal to 0.5 suggest adequate fits while values close to 0 or 1 suggest poorer fits (Kéry, 2010).

We conducted leave-one-out cross validation (LOOCV) to determine the accuracy of the best-fitting model. LOOCV through Bayesian inference involves sequentially omitting each observation from the data set and then re-running the model with that observation removed (Lunn et al., 2012). The model results are then examined to see whether the 95% predictive credible set for the omitted observation encompasses the observed value for that omitted observation. This process is sequentially repeated for each observation in the data set.

3. Results

We found 111 suitable published data sets, across the five different anatomical hooking categories and 33 species, which contained observed or estimated rates of discard mortality (Supplement 1). After combining the data across specific hooking locations into two general hooking conditions for any single study, this resulted in 73 rows of observations.

There were differences in discard mortality among the five hooking locations. Fish hooked in locations (jaw and external body) considered 'good' had lower median rates of discard mortality than fish hooked in locations considered 'poor' (gills, stomach/esophagus, and eye/roof of mouth). Median proportional rates of discard mortality (2.5/97.5 credible intervals) were 0.060 (0.056, 0.065) for jaw, 0.170 (0.150, 0.190) for external body, 0.450 (0.410, 0.490) for gill, 0.463 (0.436, 0.489) for stomach/esophagus, and 0.238 (0.211, 0.266) for eye/roof of mouth (Fig. 1).

When collapsed into two hooking location categories (good vs. poor), discard mortality was most influenced by hooking location while the proxy for physiology (K) had a smaller negative effect on discard mortality but only for good-condition fish (Tables 1 and 2; Fig. 1). The interaction-effects model provided the most parsimonious fit to the data (lowest DIC score); this was the only logistic model that received model support (Table 1). In this model, the influence of K was meaningful (95% credible set overlapping zero) only for the good hooking condition (Table 2). From this most parsimonious model, dolphinfish in good hooking condition were predicted to have a median rate of discard mortality of 0.019 (-0.010, 0.052) while those in poor hooking condition were predicted to have a median rate of 0.348 (0.224, 0.480) (Fig. 2). The Bayesian p-value from the goodness of fit test of this model was 0.17 suggesting adequate model fit.

There were 2,141 recreationally landed dolphinfish carcasses sampled for hooking locations over 79 trips to the Morehead City, North Carolina docks in 2016 and 2017. Unknown hooking locations (assumed to be the jaw) were recorded for 258 (12.1%) of carcasses sampled. The median estimated proportion of jaw- and external body ('good') hooking condition (0.606: 0.582, 0.630) was greater than the median estimated proportion of poor hooking condition (0.394: 0.370, 0.418). There were 142 sub-legal fish (< 508 mm FL) that were sampled during 34 trips to the docks; using just these fish, the median estimated proportion of jaw- and external body ('good') hooking condition (0.667: 0.588, 0.741) was also greater than the median estimated proportion of poor hooking condition (0.333: 0.259, 0.412). Each parameter in the beta-binomial models and logistic models (above), as well as estimated sampling proportions of good and poor conditions, had acceptable values for the convergence statistic ($\hat{R} < 1.05$) and converged based on visual inspection of trace plots.

For the overall rate of discard mortality in the recreational fishery for dolphinfish, there was overlap in posterior probability distributions between the meta-analysis and the tag-recapture approach (Fig. 3). The median rate of overall discard mortality was 0.12 (0.07, 0.17) for the meta-analytic approach using all dockside samples and 0.25 (0.05, 0.39) from the published tag-recapture experiment. Thus, the 95% credible set for the posterior distribution of overall mortality using the two-step approach was mostly contained within that of the tag-recapture approach (Fig. 3). When fitting the model to just small fish from dockside sampling, the overall rate of discard mortality was 0.13 (0.08, 0.18). The results on leave-one-out cross validation (LOOCV) for the best-fitting model (Table 1) showed that the 95% credible set for predicted discard mortality of the left-out observation encompassed the observed value of discard mortality in 32 (44%) of the 73 study observations (Supplement 4).

4. Discussion

To the best of our knowledge, this is the first study to have estimated a species-specific discard mortality rate using a combination of previously published data and fishery-dependent samples. While Bartholomew and Bohnsack (2005) conducted a meta-analysis on discard mortality, it was to determine important factors affecting discard mortality rather than to develop a predictive model. Benoît et al. (2013) used time-to-mortality during air exposure from trawl-caught fish as a proxy for discard mortality and found it was influenced by multiple factors; their time-to-mortality-in-air metric was informative in determining factors important to discard mortality but the proxy does not provide information on the percentage of live discards that die. In contrast, our models can be used to predict discard mortality by hooking condition and K and can be used along with fishery-specific information on proportion by hooking condition to estimate discard mortality in the fishery. Our method is a substitute for empirical estimates of condition-specific mortalities when the latter do not exist.

Data to estimate discard mortality in the two-step approach presented here can be obtained from published literature and from representative sampling of the fishery of interest. Our meta-analysis confirmed prior review studies of hook-and-line datasets that show hook location is the dominant driver of discard mortality (Muoneke and Childress, 1994; Bartholomew and Bohnsack, 2005; Fobert et al., 2009; Brownscombe et al. 2017). We provide meta-analysis estimates of discard mortality for specific (five categories) and general (two categories) hook injury categories for flexibility in the types of fishery-dependent data that might be collected in future applications of this approach. The influence of K was not important for fish in poor hooking condition, suggesting that hooking trauma overrides physiological effects when trauma is present. Species with higher K have higher metabolic rates (Beverton and Holt, 1959; Snover et al., 2005) and might be expected to be more susceptible to mortality from capture; however, we found that higher K was associated with lower discard mortality suggesting that physiology plays a role in determining release outcome in those cases where hook trauma does not occur. This result could be an artifact of the data available for the meta-analysis or it may mean that fish with higher K have physiological traits (e.g., higher metabolic scope for activity) that allow them to better accommodate increased oxygen demand during hook-and-line capture. We recommend future research in determining the mechanism behind the inverse relationship between K and discard mortality.

The two-step model was used to estimate discard mortality for a recreational fishery for dolphinfish. We believe that this is only the second estimate of dolphinfish discard mortality despite its many fisheries around the world (e.g., Kraul, 1999; Lasso and Zapata, 1999; Thompson, 1999). The meta-analytic approach here was motivated by the expense and logistics involved in collecting conventional tag-recapture data and satellite tag data to estimate discard mortality for the dolphinfish (Rudershausen et al., 2019). These financial and logistic considerations arose due to the open ocean habitats used by dolphinfish, intermittent catches, and limited recapture data to inform models of discard mortality. The approach presented in this paper benefitted from our knowledge of the hook and line recreational fishery for dolphinfish in the SEUS and our assumption that a principal source of discard mortality in this fishery (Rudershausen et al., 2012) could be accounted for through dockside sampling. Using the two-step approach, median overall estimates of discard mortality were 0.12 for the model run using all sizes of dolphinfish and 0.13 for the model run using just undersized dolphinfish. Rudershausen et al. (2019) ran different models (based on different assumptions) on tagging data that resulted in median estimates of overall discard mortality ranging from 0.16 to 0.41; the base model run from that paper had a median of 0.25 and is the distribution provided in Fig. 3. The overlap in credible sets and the similarities between the two-step approach and some of the empirical estimates are encouraging. We recommend future comparisons, using other species and fisheries, to confirm the utility of our two-step approach.

There are additional factors, not modeled in this study, which could influence rates of discard mortality (Muoneke and Childress, 1994; Davis, 2002; Bartholomew and Bohnsack, 2005; Cooke and Suski, 2005). Indeed, there was large and unexplained variation in discard mortality rates for poor condition fish (Fig. 2B). We acknowledge that un-sampled or un-modeled effects, such as various stress indicators (Sopinka et al., 2016), air exposure (Cook et al., 2015), post-release predation (Raby et al., 2013), and fish size (Davis, 2002), may influence rates of discard mortality. Ideally these and other indicators of impairment are measured in discarded fish to obtain a more complete understanding of factors influencing mortality for species-specific fisheries. For example, using individual fish size to model rates of discard mortality would have been ideal. However, most of the literature that we used to model discard mortality did not report fish size for each of the fates that were studied. In the meta-analysis presented here, we fitted models to factors with data that could be efficiently recovered from the literature and dockside sampling. Another improvement to the meta-analytic model would be the inclusion of a family or other taxonomic grouping as a random effect; we were unable to include a random effect because most taxonomic groupings had too few studies.

One area where our study could have been biased in estimating a rate of discard mortality is how species are represented in the literature with respect to anatomical hooking location. For example, if mortality rates for eye hooking are under-studied for obligate sight feeding species such as dolphinfish, estimates of mortality using data from our review would be biased low when applying this approach to estimating discard mortality for dolphinfish or other obligate sight feeders. The eye and roof-of-mouth areas represented fairly common hooking locations in our fishery-dependent sampling (20% of dolphinfish were hooked in the eye or roof-of-mouth into the eye). However, we found only 14 studies with data on these two hooking locations (Supplement 1). Any confinement and handling of eye or roof-of-mouth hooked fish in tank holding studies with easily obtained food and no predators would also likely mask the true effects of hook trauma on obligate sight-feeding species when they are released back into the wild.

Misidentifying hooking locations in dockside sampling may have biased the estimated proportions of each condition relative to directly observing hooking locations and swimming behavior, as was done in the tag-recapture study. In this study, it is unlikely that the estimated proportion of poor condition fish was biased high via mistaking hooking in vital organs for what was actually hooking in the jaw, given the diagnostics used dockside to determine hooking in vital areas (e.g., presence of blood, hook wounds, and deeply embedded hooks left in fish). We assumed that carcasses with unknown hooking locations were hooked in the jaw, the least lethal location among a variety of species studied for discard mortality (Muoneke and Childress, 1994; Supplement 1). Mis-classification of hooking locations assumed to be in the jaw would bias overall estimates of discard mortality low relative to true rates.

The meta-analytic approach presented here should be considered as a substitute for a species-specific estimate only when the dominant sources of discard mortality can be accounted for. For our meta-analysis, those sources were hooking location and physiology. As described earlier, there are other species and fisheries (e.g., trawl or gill net) where these would not be the main sources of discard mortality; other factors that can be dominant sources of mortality include post-release predation, air exposure, or water depth (pressure trauma). Using the approach presented in this study to estimate discard mortality where other sources are known to be a major cause of death would require a separate meta-analysis. Within a single species, Campbell et al. (2014) used a meta-analytic approach to estimate the effect of depth on discard mortality in red snapper *Lutjanus campechanus*, a species for which pressure trauma can be (depending on depth of capture) a significant contributor to discard mortality.

We assume that the rate estimated for dolphinfish from recreational landings sampled in North Carolina is representative of the larger area. A potential source of error would occur in this study if the sampled post-mortem hooking conditions do not represent live at-sea releases that occur in the fishery; if the sizes of dolphin released at sea differ from what we observed at dock then this could be a potential source of bias because hooking condition differed by dolphinfish size. A plot of 40 years of freely available US federal survey data of marine anglers (MRIP, 2018) shows that dolphinfish releases in the SEUS, Caribbean and Gulf of Mexico as a proportion of the annual catch of this species have been increasing in recent years, even before the minimum size limit in the SEUS went into effect in 2012 (Fig. 1 in Rudershausen et al., 2019). This indicates that releases of dolphin are not a result of size limits; thus, a variety of dolphinfish sizes are likely released at sea. However, it is possible that elective releases are skewed towards small fish regardless of size limits; to address this possibility, we ran a second model using dockside hooking conditions from dolphinfish that were less than the 508 mm FL (minimum size limit). The credible set for this mortality estimate also widely overlapped that for the empirical estimate, suggesting that the discard mortality rate for smaller fish did not differ dramatically from the dockside samples or our past empirical estimates across all sizes. Onboard scientific observers, while not required in this fishery, could help determine the validity of the assumption that the proportion of fish in various conditions that are brought to the docks are representative of those conditions released by anglers, provide information on sizes of dolphinfish released in this fishery, and collect data on the proportion of fish released at sea relative to those landed. The (US) South Atlantic Fisheries Management Council has begun a citizen science effort called 'MyFishCount' (https://www.myfishcount.com/about) to collect harvest, release, and fish condition data. There is also a new requirement in the SEUS that charter captains maintain logbooks of their catches. These could be additional sources of information from the fishery for the type of approach we present in this study. We remind the reader that, given that the number of dead fish is required for management and stock assessments, it is necessary to have estimates of the number of live releases to estimate the number that die given a discard mortality rate.

Different types of terminal tackle and fishing styles by fishers landing their catch at ports that we did not sample could contribute to different rates of discard mortality than estimated in this study. However, large differences in proportion-by-hooking location seem unlikely based on our previous work in this fishery. Our research group held a workshop to determine common types of tackle and fishing styles used to target dolphinfish across the SEUS and Gulf of Mexico regions (Rudershausen et al., 2012). Workshop stakeholders agreed that trolling using J-hooks rigged with natural baits and bailing using cut natural baits affixed to non-offset circle hooks were the gear styles most commonly used to target dolphinfish in North Carolina and in the larger management region. Thus, it is likely that discard mortality rates estimated from sampling in this study would be similar to other areas in the region.

The majority of the world's fisheries are considered data-poor/limited (Dowling et al., 2018). Our meta-analytic approach to estimate discard mortality might be useful in situations where fishery managers wish to determine whether the discard mortality rate is sufficiently low that regulations are achieving their intended effects. We also envision it being used to estimate discard mortality for data-rich species for which a stock assessment is being conducted but no discard mortality estimate exists. We recommend further comparison between empirically-derived estimates of discard mortality and the approach presented here to determine its applicability to other species and fisheries.

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Table 1. Logistic models fitted using Bayesian methods to published discard mortality data across a variety of fish species. The covariate considered in models was the Brody growth coefficient (*K*) while the factor considered in models was general hooking condition (HL) (good vs. poor). *K* was centered around the mean (ave(*K*)). Model parsimony was evaluated with the Deviance Information Criterion (DIC) and relative Akaike weights (proportional support) for each model (w_i). ANCOVA = analysis of covariance.

Model description	Likelihood structure	DIC	w_i
Interaction-effects ANCOVA	alpha[HL[i]] + beta [HL[i]] * (*K*[i]-ave(*K*))	1287	1
Main effects ANCOVA	alpha[HL[i]] + beta * (*K*[i]-ave(*K*))	1303	0
Binomial t-test	alpha[HL[i]]	1336	0
Intercept only	alpha	2918	0

Table 2. Median along with 2.5 and 97.5 credible estimates of parameters obtained from fitting an interaction-effects analysis of covariance (ANCOVA) model to the factor hooking location and the covariate *K* (Brody growth coefficient) to binomially distributed data on discard mortality across a variety of fish species. Parameter values were considered meaningful if the 95% credible set did not overlap zero.

Parameter name	Parameter description	2.5	Median	97.5
alpha[1]	Intercept for fish in good hooking condition	-2.91	-2.80	-2.69
alpha[2]	Intercept for fish in poor hooking condition	-0.55	-0.46	-0.36
beta[1]	Regression coefficient for *K* for fish in good condition	-3.23	-2.45	-1.75
beta[2]	Regression coefficient for *K* for fish in poor condition	-1.01	-0.36	0.27

Figure 1. Posterior probability distributions (posteriors) for the estimated proportional discard mortality of fishes hooked in five anatomical locations, based on data obtained from published literature. Each histogram displays the density (y-axis) of discard mortality estimates (x-axis) for retained updates across three chains (9,000 retained updates total).

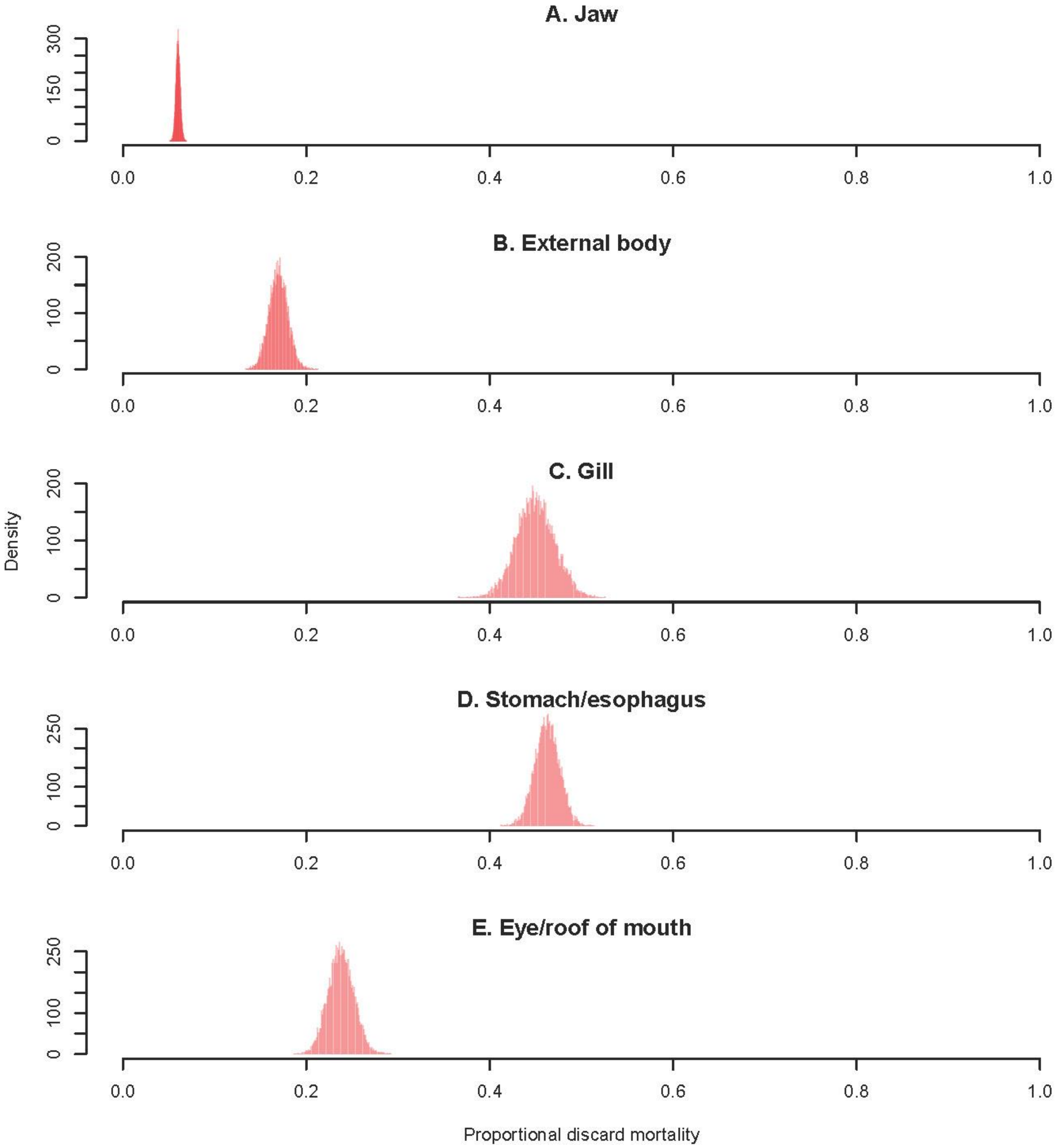

Figure 2. Observed (circles) and predicted values (lines) for relationship between the Brody growth coefficient (*K*) (x-axis) and proportional discard mortality (y-axis) for a variety of fish species from a meta-analysis of discard mortality. Predictions include the median (black line) as well as 2.5 (lower gray line) and 97.5 credible values (upper gray line). Data and predictions are broken down between good-hooking condition (panel A) and poor-hooking condition (panel B). Predictions were obtained by fitting a binomially distributed model that included the effects of hooking condition and *K* and their interaction. The scale of the y-axis is identical between panels.

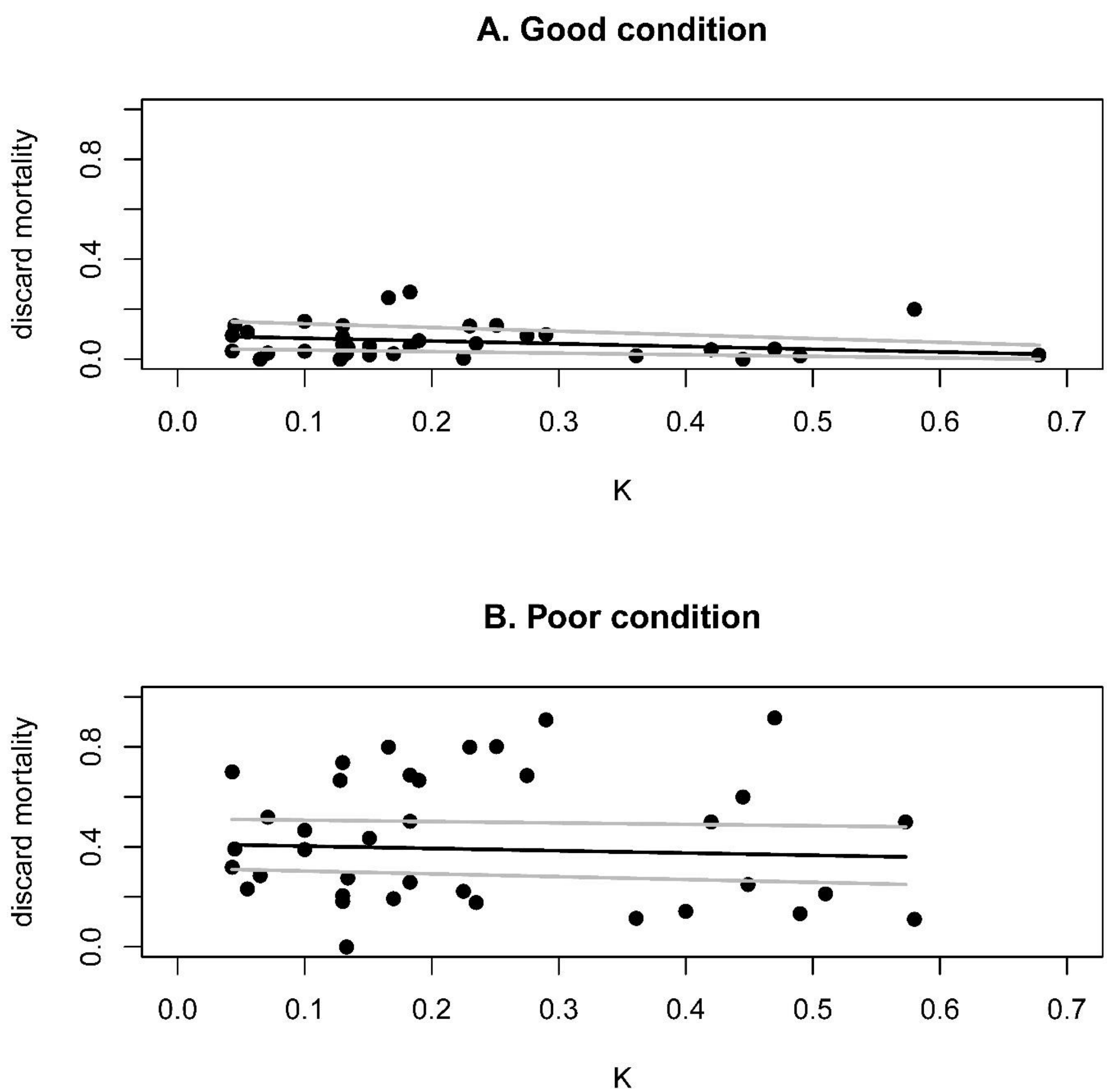

Figure 3. Posterior probability distributions (posteriors) for the estimated overall rate of discard mortality in a hook and line recreational fishery for dolphinfish *Coryphaena hippurus* sampled in the southeastern US. The blue histogram is the posterior from a published tag-recapture (‘tag-recap’) study to estimate discard mortality through fitting a relative risk model to dolphinfish released in two different conditions (see Rudershausen et al., 2019 for details). The posterior from a two-step approach (‘meta-analysis’: this study) using published data and dockside sampling to estimate discard mortality is shown in the red histogram. Blue and red vertical lines (left to right) are 2.5, median, and 97.5 credible intervals for the respective posteriors.