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Cover art: Reproduced from Scott-Denton et al. 2012

Abstract

The Shrimp Trawl Observer Program, which is administered by NOAA Fisheries Southeast Fisheries Science Center (SEFSC) Galveston Laboratory, assigns observers to shrimp otter trawl vessels in both the Gulf of Mexico (GOM) and the waters off the U.S. east coast within the jurisdiction of the South Atlantic Fishery Management Council (SATL), and vessel participation has been mandatory since 2007. We applied integrated Bayesian models to the observer data to estimate sea turtle bycatch. We also estimated mortality, defined as the total number of sea turtles that were caught in shrimp trawls and died at the time of capture. The total bycatch mortality was estimated by multiplying the probability of mortality for turtles caught in shrimp trawl nets by the total bycatch estimated from a linear model of catch per unit effort (CPUE) per strata (area, season, depth zone, time period) multiplied by the total effort in each stratum. For rare species, the bycatch rate was estimated by modeling CPUE of all species together, and multiplying this by the species composition to get species-specific CPUE. Total bycatch mortality was estimated separately for the GOM and the SATL, and for standard shrimp otter trawl nets versus "try" nets, which are small nets fishers deploy in front of the primary nets to test catch rates. About 30% of sea turtles caught in standard nets were dead, while less than 1% of sea turtles caught in try nets were dead. Thus, although many Kemp's ridley, loggerhead, and green sea turtles were caught in try nets in both regions, few of them were killed. For example, in the GOM in 2015, we estimated 95% credible intervals of 54-256 Kemp's ridley, 173-495 loggerhead and 22-114 green sea turtles caught in try nets, but only 0-7 Kemp's ridley, 0-17 loggerheads, and 0-3 green sea turtles were estimated to be killed. On the other hand, for standard nets in the GOM, we estimated 95% credible intervals of 63-369 Kemp's ridley, 18-105 loggerhead and 75-226 green sea turtles captured, corresponding to mortality of 19-130 Kemp's ridley, 5-36 loggerhead and 22-81 green sea turtles killed. In addition, we found 95% credible intervals of 24-99 turtles classified as unknown/other species killed in standard nets in the GOM. The unknown category includes sea turtles that were not identified by the observers, as well as leatherback and hawksbill sea turtles, which could not be modeled separately because there were only 3 leatherbacks and 1 hawksbill recorded. Total bycatch mortality of Kemp's ridley and loggerhead sea turtles in standard nets decreased from 2007 to 2015 in the GOM, but green sea turtle bycatch stayed constant. In the SATL, the sample sizes were lower, fewer turtles were observed, and total effort was not as well estimated. Thus, total by catch rates were estimated with wide credible intervals. There was no trend over time in the SATL from 2007 to 2016, and total mortality in standard nets in 2016 was on the order of 5-111 Kemp's ridley turtles, 9-139 loggerhead turtles, 2-86 green sea turtles, and 13-168 of unknown/other species of turtles. These estimates of total bycatch mortality include only sea turtles that are dead at the time of capture; there may be additional mortality due to stress or injuries after live release.

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Introduction

The incidental capture, or bycatch, of sea turtles in fisheries is a major source of mortality (NRC 1990) and a significant management concern. Various measures to reduce fisheries bycatch have been researched and implemented, such as the required use of turtle excluder devices (TEDs) in the southeast U.S. shrimp fisheries beginning in the early 1990s. Estimating fisheries bycatch in the southeast U.S. shrimp fisheries is essential in determining the overall effect of the fisheries on sea turtle populations, and is a legal requirement under the Endangered Species Act (ESA). This task is challenging given the broad area over which the shrimp fisheries operate, the large number of vessels participating in the fisheries, and the extensive amount of effort these vessels collectively exert annually, which is contrasted by the limited amount of fisheries effort that is observed (especially prior to 2007). Bycatch estimation is further complicated by the nature of sea turtle populations that also occur over a broad area, can be difficult to observe as they spend an extensive amount of time submerged, and the local abundance of sea turtles can fluctuate dramatically seasonally and annually. Documenting interactions in the southeast U.S. shrimp fisheries is also complicated due to the required use of TEDs, which are employed to avoid sea turtle capture in trawl nets; therefore, interactions in TED-equipped trawl nets would largely go unobserved.

Past efforts to estimate bycatch of sea turtles in the southeast U.S. shrimp fisheries (Epperly et al. 2002) were hampered by these issues along with lacking data from a comprehensive directed shrimp fishery observer program. Biological opinions issued by NOAA Fisheries attempted to use the existing, albeit dated, information and augment it with more recent population trend data. However, this approach led to unrealistic sea turtle capture and mortality estimates, as noted in the current Biological Opinion (NMFS 2014). NOAA Fisheries Southeast Fisheries Science Center (SEFSC) advised that efforts should be made to develop alternative methods to estimate sea turtle bycatch in the shrimp fisheries. Mandatory vessel participation in the Shrimp Trawl Bycatch Observer Program (administered by the SEFSC Galveston Laboratory) has been required since 2007, and these data represent a significant improvement over previously available data on sea turtle interactions with the shrimp fishery. These data are used herein, along with appropriate statistical methods, for estimating sea turtle bycatch at this time.

The Shrimp Trawl Observer Program has been assigning observers to shrimp otter trawl vessels since 1992 for both the Gulf of Mexico (GOM) and the waters off the U.S. east coast within the jurisdiction of the South Atlantic Fishery Management Council (SATL), with coverage levels around 2% of nominal days at sea (Scott-Denton et al. 2012). Observers are randomly assigned to shrimp otter trawl vessels, in a design stratified by area (states), water depth (<10 fathoms and \geq 10 fathoms), and season (January-April, May-August, and September-December). Observers record detailed information on species caught, gear and vessel characteristics, and, when sea turtles are caught, the species, size, and condition at release of the sea turtle.

To improve sea turtle bycatch estimation in the shrimp fishery, we applied integrated Bayesian models to the observer data to estimate sea turtle bycatch. We also estimated mortality, defined as the total number of sea turtles that are caught in shrimp trawls that die at the time of capture. We did not make any estimate of the number of turtles that die due to injuries or stress after

being released alive. Total bycatch mortality was estimated separately for the GOM and the SATL because the total effort data were in a different format in the two regions. Total bycatch mortality was also estimated separately for standard shrimp otter trawl nets versus "try" nets, small nets fishers deploy in front of the primary nets to test catch rates, because turtle bycatch mortality rates differ between net types and because effort is not recorded for try nets (Figure 1). Estimates of total bycatch mortality were made for each sea turtle species that was commonly caught in the GOM or SATL, including Kemp's ridley, loggerhead, green, and other/unidentified turtles. Species-specific estimates could not be made for leatherback and hawksbill sea turtles because only one hawksbill and three leatherbacks were reported in the observer data.

Methods

For sea turtle species for which sufficient individuals were observed (≥ 10 observed turtles caught in a region and net type), total bycatch was estimated in a five step process. First, a binomial generalized linear model (GLM) was used to estimate the probability of mortality for turtles caught in shrimp otter trawls based on net type (standard versus try net) and other predictor variables (Table 1). Second, sea turtle bycatch rates (catch-per-unit-effort (CPUE) in sea turtle catch per hour fishing) by strata (area, depth zone, season, era, year, definitions in Table 1) were estimated using a linear model. This analysis included all sea turtles that were caught, whether or not the turtle survived. Third, the bycatch rates in each stratum were multiplied by the total effort in each stratum to estimate the total bycatch. Fourth, the total bycatch was multiplied by the probability of mortality from step one to estimate the total bycatch mortality in each stratum. Finally, the total mortalities were summed across strata to estimate the total bycatch mortality in each year. The sub-models in each step of this integrated modeling process were fitted in a Bayesian framework using the Markov Chain Monte Carlo (MCMC) algorithm (Lunn et al. 2013). Because the model output in each step included uncertainty in the form of Bayesian posterior probability density function, the final estimates of sea turtle bycatch mortality had credible intervals that account for uncertainty in each stage of the estimate. For sea turtle species for which there were not enough observations to estimate single-species bycatch rates, we estimated the total bycatch and total bycatch mortality as above for all sea turtle species together and then multiplied these numbers by the estimated species composition to estimate the approximate total annual bycatch mortality for each species.

Step 1. Modeling the probability of mortality

In the first step, the posterior probability of sea turtle bycatch mortality, given that a turtle was caught in a shrimp trawl net, was estimated using a binomial GLM (i.e. a logistic regression model) (Coelho et al. 2012) that predicted the status at release recorded by the observer (alive or dead) as function of sea turtle species, net type, and other predictor variables . This model was fit using all observed catches of sea turtles, from July 2007 through February 2017. Observers recorded detailed information on a subset of the fishing operations in a fishing trip, recorded in the "station" dataset, but they occasionally recorded information on turtles caught during trawl sets when they were not "on station"; these turtles were included in the mortality analysis. The probability of bycatch mortality (p_i) for sea turtle *i* was modeled using a Bayesian logit-link binomial GLM, as follows:

(1)
$$\log\left(\frac{p_i}{1-p_i}\right) = b_0 + \sum_{j=1}^J b_j x_j + \sum_{k=1}^K \beta_k[x_{ki}]$$

where the logit probability of mortality (p_i) for an individual turtle *i* is predicted as a linear function of an intercept b_0 plus the slopes (b_j) associated with *J* linear predictors and the coefficients (β_k) associated with *K* categorical predictor variables.

From the observer program's database of turtle captures in the shrimp otter trawl fishery, we defined a turtle as "dead" if the disposition was listed as "DISCARDED UNMARKED DEAD/UNRESPONSIVE CARCASS" or "DISCARDED MARKED DEAD/UNRESPONSIVE CARCASS," and "alive" if the disposition was "RELEASED ALIVE." Turtles for either disposition could have been forward of the TED or have passed through the TED grid and in the cod end. Turtles were excluded from the analysis if their disposition was blank or listed as "UNKNOWN."

The explanatory variables considered were species, bottom depth (ft), net type (try net or standard net), tow time (hours), curved carapace length (cm), season (January-April, May-August, or September-December), era (2007-2011, 2012-2017), depth category (<10 fathoms or \geq 10 fathoms), and area (West Florida; Alabama and Mississippi; Louisiana; Texas; East Florida; or Georgia, South Carolina and North Carolina). All categorical variables were treated as fixed effects.

Because the sample size (number of turtles) was not large enough to include all the potential predictors in a single model, we considered only those that had a significant effect (p<0.05) when entered as the only predictor in the model, in order to focus on variables that were likely to be useful for predicting mortality. We then found the best non-Bayesian model using the Akaike Information Criterion (AIC) and the Bayesian information criterion (BIC) (Burnham and Anderson 2004). We also ran the model in a Bayesian framework with uninformative priors (normal(mean=0, standard deviation=100) for all regression parameters, except where noted), and found the best model using the Deviance Information Criterion (DIC) (Lunn et al. 2013) and the Widely Applicable Information Criterion (WAIC) (Watanabe 2013, Gelman et al. 2014, Vehtari et al. 2017). We estimated Bayesian posterior model probability using the weighting variable method of Gardner et al. (2008). This method uses the MCMC algorithm to estimate the posterior probability that each predictor variable is included in the best model. A Bernoulli random variable *w* with a prior probability of 0.5 is multiplied by each linear predictor. For example, for the model of logit(p_i) with only categorical predictor variables:

(2)
$$\log\left(\frac{p_i}{1-p_i}\right) = b_0 + \sum_{j=1}^J w_j \beta_j[x_{ji}]$$

The fraction of MCMC draws for which w_j is 1 is the probability that the associated predictor variable is included in the best model. The probability of each combination of variables can be calculated by multiplying the *w* values together. For example, the probability of a model with all four variables would be $w_1w_2w_3w_4$, and the probability of the model with only the first three predictor variables would be $w_1w_2w_3(1-w_4)$. Because this method is sensitive to uninformative priors, we used normal(mean=0, standard deviation=10) as the prior for the regression

coefficients when using weights. Multiple frequentist and Bayesian methods were used for model selection to evaluate whether different selection criteria gave consistent results. If the methods were not consistent with each other, the model posterior probabilities were used to select the best model.

Bayesian models were assumed to be converged when the Gelman Rubin diagnostic was less than 1.05 and the effective numbers of parameters was greater than 300 (Lunn et al. 2013). The best Bayesian model, according to posterior model probabilities, was used to predict the expected probability of mortality and its credible interval for all values of the predictor variables included in the model. As a diagnostic, model predictive capacity was evaluated using the area under the receiver operating curve (AUC) which is the probability that, when presented with a randomly chosen mortality and a randomly chosen survival, the model will correctly assign higher probability of mortality to the mortality event; values greater than 0.70 indicate a model with good predictive ability (Manel et al. 2001). All models were run in R version 3.4.2 (R Development Core Team 2017). The non-Bayesian GLM was run using the MASS (Modern Applied Statistics with S) library (Venables and Ripley 2002). Bayesian models were run in JAGS (Just Another Gibbs Sampler), using R2jags (Su and Yajima 2015, Plummer 2016), and the WAIC was calculated using the loo (Leave One Out) library (Ventari et al. 2017). The AUC was calculated with the pROC (proper Receiver Operating Characteristic) library (Robin et al. 2011).

Step 2: Estimating bycatch rates

The mean bycatch rate (CPUE) of a particular sea turtle species in either standard nets or try nets in either the GOM or the SATL in each stratum was estimated using a negative binomial GLM to accommodate the over-dispersed nature of the CPUE data (Maunder and Punt 2004). The sampling unit was individual fishing trips, and the models were fit to all the observer data for each net type and region. For the GOM, data were available from July 2007 through February 2017, and for the SATL data were available from June 2008 to February 2017. The mean bycatch per trip $i(\mu_i)$ was predicted as:

(3)
$$\log(\mu_i) = \beta_0 + \beta_y y_i + \sum_{j=1}^J \beta_{y,j} [x_{ji}] y_i + \sum_{j=1}^J \beta_j [x_{ji}] + \sum_{j=1}^J \sum_{k=1}^K \beta_{jk} [x_{ji,k} x_{ki}] +$$
offset(log(h_i))

where β_0 is an intercept term; x_{ji} indexes the level of one of the *J* categorical predictor variables for trip *i*; $\beta_j[x_{ji}]$ is the effect of categorical predictor variable *j* on bycatch rates during trip *i*; $\beta_{jk}[x_{ji},x_{ki}]$ is the effect of the interaction between categorical predictor variable *j* and categorical predictor variable *k* on bycatch during trip *i*; y_i is the year as a numerical variable, β_y is the slope in bycatch rates with respect to year; $\beta_{y,j}[x_{ji}]$ is the effect of categorical variable *j* on the slope of the relationship between year and bycatch rates; and h_i is the shrimp otter trawl effort during trip *i*, measured in the number of hours fished. The negative binomial distribution is parameterized with a probability θ and scaling parameter *r*. We estimated *r* as a free parameter and θ was calculated as:

(4)
$$\theta_i = \frac{r}{r+\mu_i}$$

The possible predictor variables included the stratification variables of area (states), depth zones (<10 fathoms or≥10 fathoms), and seasons (January-April, May-August, and September-December). Sample sizes (number of observed trips) were not large enough to estimate a year effect on bycatch rates, so two methods were used to test for changes over time. Either year was entered as numerical variable to test for a significant linear change over time, or a categorical variable was used (era = 2006-2011 or 2012-2017) to test for changes between the early and late part of the time series. All categorical variables were treated as fixed effects. To evaluate whether the negative binomial model adequately predicted the data, or whether a different error structure or a zero inflated model is necessary, we plotted the observed and predicted total frequencies, using a square root scale to make the smaller frequencies easier to see (Kleiber and Zeileis 2016).

To determine which predictor variables and interactions should be included in the model, we first used non-Bayesian linear models to find the best models according to the AIC. We then reran the models with the same terms in a Bayesian framework, in order to generate MCMC posterior distributions. Variable selection was done in a frequentist framework so that the process would be faster and more automated. However, a Bayesian method was used to fit the final models because posterior distributions were needed for estimating total mortality. For the Bayesian models, all the model coefficients were given uninformative priors, which were normal(mean=0, standard deviation=100) for all the regression coefficients for the main effects and normal(mean=0, standard deviation= $\sqrt{1000}$) for the interactions, and lognormal(log mean=0,log standard deviation = 1000) for the *r* parameter. All two-way interactions were considered for inclusion in the models. Year and era were not allowed to both be included in the same model, since they were considered to be alternative hypotheses about how bycatch rates had changed over time. In the case that era was included in the best model, we calculated the probability of a decrease in CPUE between eras as the fraction of MCMC draws in which the effect of being in the second era was negative. In the case that year was included in the best model, we calculated the probability of a negative trend as fraction of MCMC draws in which the slope associated with year was negative.

Trip was used as the sample unit, rather than fishing operation because the observer program assigns observers randomly at the level of trip rather than fishing operations. Season, era and year were assigned based on the date of the last day of the trip. For trips that reported fishing operations in more than one area, the area where the most fishing hours occurred was used. Across all areas, 86% of trips had more than 90% of their effort in the same area, so this seems like a reasonable approximation. Depth zone was treated the same way, and 84% of trips had more than 90% of their effort in the same depth zone.

Total effort (h_i) for each trip was calculated as the sum of the hours fished for that trip according to the "station" table in the observer dataset, without including any information about the number of nets that were deployed in each fishing operation. The station table includes only those sets for which the observer recorded detailed information although observers sometimes record information on turtles that were caught when they were not "on duty." To be consistent, we only used information on turtles that were caught on station to calculate bycatch rates, so that the bycatch rates are per fully observed fishing hour. For standard nets, CPUE was the total number

of turtles of a given species caught on station in standard nets in a trip, divided by the total on station standard net effort (in hours) for the trip. Effort data were not available for try nets, either in the observer data or in the total effort data. Therefore, we approximated try net effort by assumed that the try net effort was proportional to standard net effort. We calculated try net CPUE as the total number of sea turtles caught in try nets during a trip divided by the total number of hours of standard net fishing in the trip. This CPUE was then expanded using total standard net effort, so that the assumed ratio of standard net to try net effort canceled out in the expansion. The assumption that try net effort is proportional to standard net effort is based on the limited observations of try net effort from the observer program (Elizabeth Scott-Denton, personal communication).

The bycatch rate models were run first in R version 3.4.2 (R Development Core Team 2017) using the MASS library (Venables and Ripley 2002) and AIC to find the best combination of variables to fit the model. Bayesian models with the same variables were estimated using an MCMC algorithm in JAGS, using R2jags (Su and Yajima 2015, Plummer 2016). Bayesian models were assumed to be converged when the Gelman Rubin diagnostic was less than 1.05 and the effective numbers of parameters was greater than 300 (Lunn et al. 2013).

Step 3: Estimating total bycatch

In the third step, for each sea turtle species, the posterior distribution of the mean bycatch rates in each stratum (depth, area, season, year) were multiplied by the distribution of total shrimp otter trawl effort (in number of hours fished) in the stratum and year. For the GOM, the means and standard errors of total shrimp otter trawl effort per stratum were available from 2007 through 2015. The mean was calculated using the cell pooling method (Nance 2004, Nance et al. 2008) and the standard error for ratio estimates for each pool cell was also calculated based on Krebs (1998). Total effort was calculated in number of 24-hour days of otter trawl tow time, so that multiplying the total effort by 24 gave the number of hours fished, equivalent to the hours fished in the observer station data for standard nets. We assumed that total effort in each stratum in each year was normally distributed with the specified mean and standard deviation. For try nets, the same measure of total effort was used. Since the try net CPUE in Step 2 was calculated using standard net effort, expanding the try net CPUE to total bycatch using standard net effort should provide an unbiased estimate of total try net catch, provided that the ratio of try net effort to standard net effort does not vary between strata. If this ratio does vary between strata, then the try net estimates may be less accurate than the standard net estimates. Thus, the try net total bycatch estimates should be considered more uncertain than the standard net estimates. Since effort data were not available for 2016 in the GOM, we estimated total bycatch for 2007 to 2015 only.

For the SATL, effort data included records for each individual trip through 2016; however, the number of hours fished in each trip was often not recorded, or the recorded number was inconsistent with the duration of the trip. Thus, the hours fished information was not considered reliable. Therefore, for this region, we calculated the mean of the total effort as the number of trips in each stratum in each year, multiplied by the mean number of observed hours fishing in each trip from the observer data. As in the GOM, the total effort was assumed to follow a normal distribution, and the variance was calculated by multiplying the mean by the standard error of the mean from the observer data. This is a very approximate measure of effort compared to the

numbers in the GOM. Try net effort was assumed to be proportional to standard net effort, as in the GOM. Total bycatch was calculated for each year from 2007 to 2016.

Multiplying the posterior distribution of sea turtle bycatch rate by the distribution of total effort provided posterior distributions of the total number of sea turtles that interacted with shrimp otter trawls in each stratum in each year, for each sea turtle species in each net type (standard nets or try nets). This was accomplished by using the MCMC algorithm in JAGS. A random draw was taken from the specified normal distribution for total effort in each stratum for each MCMC iteration, and this was multiplied by the value of the mean bycatch rate for the same MCMC iteration to get an estimate of the total bycatch in the stratum. The quantiles of the estimated total bycatch in the stratum thus include the variability in both total bycatch and bycatch rates. The sum of the total bycatch of each sea turtle species in each net type in each year.

Step 4. Total bycatch mortality

To estimate the total bycatch mortality for each species in each region in each year, we multiplied the posterior distribution of the total bycatch by the posterior from step three by the probability of mortality from step one. This was done by extracting 5,000 MCMC draws for the total bycatch in each stratum and 5,000 MCMC draws for the probability of mortality and multiplying them together. Total bycatch mortality was then summed across strata for each year. The mean, median, and credible interval of the total mortality was then calculated by summarizing across the MCMC draws. This method allows for an estimation of total sea turtle bycatch mortalities with credible intervals that adequately represent uncertainty related to the estimates of total shrimp otter trawl effort and the estimates of sea turtle bycatch mortality rates.

Alternative total bycatch models for rare species

For species for which the number of observed individuals was too small to estimate the total bycatch with a single-species model (<10 individual sea turtles observed), we calculated the approximate catch of each species by multiplying the estimated bycatch of all species combined, calculated as described above, by the species composition. A multinomial model was used to estimate the posterior distribution of the species composition of turtles for each net type and region using an uninformative Dirichlet prior and no explanatory variables. To estimate the total catches per stratum of each species, we multiplied the posterior distribution of the total catch by the posterior distribution of the species composition using the MCMC method described above. This provided estimates of the total bycatch per species in each net type in each year. We then multiplied the posterior distribution of total bycatch by the posterior distribution of bycatch mortality to estimate the total mortality. This method was used to calculate the total bycatch and total bycatch mortality of all species in both regions. For species with enough observed individuals for single-species modeling, the single species estimates of total bycatch mortality from 2007 to 2016 in the GOM or 2007 to 2016 in the SATL was compared to the multispecies estimate to validate the multispecies approach. For less common species, the multispecies approach provided the only plausible estimates of total bycatch mortality.

Model checking and alternative models

The negative binomial model structure was used because the data are too over-dispersed to use a Poisson model (Maunder and Punt 2004). Delta or zero-inflated models were considered, but there was no evidence that the data included more zeros than would be expected under the negative binomial. Thus, the negative binomial error structure was appropriate. For species in which sea turtle catches were never more than one per trip, a binomial error structure would also be valid. To evaluate the robustness of the total bycatch estimates to the choice of negative binomial error structures, we also used binomial models for the species for which no more than one were ever caught in a trip.

For the binomial model, the probability of presence in a trip was modeled using a logit link binomial GLM. The log of the number of hours fished was included as a potential predictor variable, to allow for the fact that trips with more fishing hours might have a higher probability of catching a turtle.

(5)
$$\log\left(\frac{p_i}{1-p_i}\right) = \beta_0 + \beta_y y_i + \sum_{j=1}^J \beta_{y,j}[x_{ji}] + \sum_{j=1}^J \beta_j[x_{ji}] + \sum_{j=1}^J \sum_{k=1}^K \beta_{jk}[x_{ji,k}x_{ki}] + \beta_h \log(h_i)$$

where β_0 is an intercept term; x_{ji} indexes the level of one of the *J* categorical predictor variables (depth zone, area, season, era) for trip *i*; $\beta_j[x_{ji}]$ is the effect of categorical predictor variable *j* on logit probability of turtle capture during trip *i*; $\beta_{jk}[x_{ji}, x_{ki}]$ is the effect of the interaction between categorical predictor variable *j* and categorical predictor variable *k* on bycatch during trip *i*; y_i is the year as a numerical variable, β_y is the slope in logit probability of turtle capture with respect to year; $\beta_{y,j}[x_{ji}]$ is the effect of categorical variable *j* on the slope of the relationship between year and bycatch rates; β_h is the slope related to log effort; and h_i is the shrimp otter trawl effort during trip *i*, measured in the number of hours fished. Models were not allowed to include both season and year. Otherwise, the AIC was used to choose the best model.

For species for which no trip caught more than one turtle, the binomial model was used directly to estimate the total catch of turtles. The posterior probability of catching a sea turtle in each stratum was multiplied by the total number of trips, which was calculated by dividing the total number of hours by the mean number of hours per trip. These numbers were compared to the negative binomial estimates.

As a further comparison, the total bycatch from 2007 to 2015 was also estimated with a basic ratio estimator (Cochrane 1977). This was compared to the results from the Bayesian models.

Checking for potential sampling bias

It is thought that the observer program may over-sample larger vessels and under-sample smaller vessels. Part of this may be due to mandatory sampling of federally permited vessels vs non-sampled state permited vessels (Soldevilla et al. 2016). Smaller inshore vessels tow for less time than larger vessels with fewer nets and this may impact sea turtle catch rates (Epperly et al. 2002). Since the total number of nets in the water is not included in the measure of effort, it is possible that these differences in fishing methodology might influence CPUE. We did not have

data on the size distribution of the vessels in the total effort to compare to the size distribution in the observed effort, to see whether the observer data are representative. However, to see whether there was a potential for non-random sampling to bias estimates of total catch, we evaluated whether there were differences in bycatch rates depending on the type of vessel. If vessel characteristics do influence catch rates, then the representativeness of the observer data to the total effort would be an appropriate topic for future research.

There are four measures of vessel size in the observer database: vessel length, gross tonnage, engine horsepower, and crew size. Whether the vessel uses ice or a freezer is also recorded. To see if vessel size influenced catch rates, we ran a binomial GLM of presence/absence of all turtles in all regions (equation 5), running separate models for try nets versus standard nets. In case vessel length had a non-linear impact, we included a square term for length. We used AIC to find the best model. For the GOM, we also tried models where the stratification variables (area, season, era, depth zone) were included along with vessel size.

Results

Probability of Mortality

A total of 171 captured turtles were observed in shrimp otter trawl nets between July 2007 and February 2017, of which 22 were discarded dead, 141 were released alive, and 8 had unknown status at release. The species caught were: loggerhead (70), Kemp's ridley (53), green (22), leatherback (3), hawksbill (1), unidentified hardshell (20), and unknown (2). For the purposes of the mortality analysis, the hawksbill, leatherback, unidentified hardshell, and unknown species were combined into a single "unknown" category. More captures and more mortality events were recorded in the GOM than in the SATL for both net types (Figure 2, Figure 3).

There were 125 turtles for which all the potential explanatory variables had non-missing values. For this dataset, when each predictor variable was used separately to predict mortality, only species, net type, tow time, depth zone, and carapace length were significant. Area approached significance, so it was included in the subsequent analyses (Table 1). All Bayesian models converged adequately (Table 2). For both non-Bayesian and Bayesian versions of the binomial GLM, all information criteria and posterior model probabilities selected the model including only net type and depth zone as the best model (Table 2). According to the Bayesian posterior model probabilities, the model with net type only was also plausible (posterior probability=0.31). Species was not included in the best model. All the models had adequate predictive ability, with AUC ranging from 0.84 to 0.94 (Table 2).

The models with net type and depth zone, and with net type only, were re-fit using data from all 163 turtles for which disposition (alive or dead) was recorded. This was done to increase the sample size by including turtles that were missing predictor variables that were not needed in the final model. These models gave very similar results to the models for the 125 turtles with complete data but with narrower credible intervals. The predicted probability of mortality was much higher for standard nets than for try nets, and higher in the deeper depth zone than the shallower depth zone (Table 3). The mortality estimates in these models were highly uncertain,

and this uncertainty is carried forward in the estimates of total bycatch mortality (Figure 4). These models also had AUC values greater than 0.80.

Total Bycatch Mortality in the Gulf of Mexico

In the GOM, there was one sea turtle caught off station, and 130 caught on station. The majority of the sea turtles were caught in try nets (Table 4). The only commonly caught species were green, Kemp's ridley, and loggerhead. One hawksbill and three leatherbacks were also recorded, and were included in the "unknown" category for the purpose of this analysis. Loggerhead was the most commonly caught species in try nets, and Kemp's ridley was the most commonly caught on sea turtles caught on sea turtles caught on sea turtles caught on sea turtles.

For all species together, Kemp's ridley, loggerhead, and unknown/other in try nets, and Kemp's ridley, green, and unknown/other in standard nets, there were enough sea turtles observed to fit a negative binomial model to the catch rate data (Table 5). The AIC preferred different combinations of the potential explanatory variables for each species/net type. The try net based models were generally more complex and included multiple interactions. The model predicted total frequencies were very similar to the observed total frequencies (Figure 6). In particular, the models were able to predict the appropriate number of zeros, implying that a zero inflated models is not necessary to fit these data. The Bayesian models converged adequately with the same variables (Table 6, Figure 7), and estimated a total bycatch from 2007 to 2015 of about 4,000 to 8,000 sea turtles of all species together in try nets, and 5,000 to 10,000 in standard nets. The wider credible interval in the standard nets was caused by the lower number of sea turtles in try nets, and loggerhead in standard nets, the total bycatch in each year was estimated by multiplying the total bycatch from the models for all species together for each net type by the species composition for that net type.

The negative binomial models found no trend over time for green and unknown/other sea turtles in standard nets (Table 7). For all sea turtles together and for Kemp's ridley sea turtles in standard nets, there was a significant linear decrease in CPUE across years (98% probability of a decreasing trend for both species). For all species together, Kemp's ridley and loggerheads in try nets, era was included in the best model, along with an interaction between era and depth zone (Table 7). For Kemp's ridley and loggerhead sea turtles in try nets, there was a substantial decline in CPUE in the shallow depth zone, with no particular trend in the deeper depth zone. For all species together in try nets, there was a significant decrease in CPUE in shallow water and a significant increase in deep water. This pattern can be seen in the raw mean CPUE values for each year (Figure 8). When the CPUE rates were expanded with total effort, the trend in total bycatch across years appeared to decline for Kemp's ridley sea turtles in both net types, and for loggerhead sea turtles in standard nets (Figure 9, Table 8). There were no clear trends for the other species. This decrease in catches was caused by decreasing CPUE rather than a decrease in effort; effort was fairly constant across years (Figure 10).

To calculate the total bycatch mortality, we multiplied the total bycatch by the probability of mortality for the corresponding net type and depth zone in each stratum for models that included depth zone as a predictor variable. If depth zone was not a predictor in the CPUE model, we used

the probability of mortality from the mortality model with net type only. Multiplying the total number of turtles caught by the probability of bycatch mortality gave very small numbers of turtles killed in try nets, while the number of turtles killed in standard nets was relatively high (Figure 11, Table 9).

Total Bycatch South Atlantic

In the SATL, 375 trips were observed, of which 26 observed at least one captured turtle (Table 10). There were 37 turtles observed on station, and 2 not on station. Loggerhead sea turtles were the most common species observed in both try nets and standard nets, but there were also four unidentified turtles captured in standard nets (Figure 12). Due to the small sample size and low number of sea turtles observed the species proportions have wide credible intervals.

Total effort was available in the SATL region through 2016, and effort was fairly consistent from year to year (Figure 13). The observed trips were not representative of the strata that were present in the effort data. For example, there were only a few observed trips in the deeper depth zone, and they were all off the east coast of Florida (Table 11). This prevented the negative binomial models of bycatch rate from estimating the coefficients for any model that included both depth and area as factors. Thus, for each species/net combination we used the model with the lowest AIC and (for the Bayesian models) DIC that included no more than one of these two predictor variables. According to the observer data, the number of hours fished per trip was much lower in the SATL than in the GOM, although it is not known whether this reflects shorter trips, or whether observers are on station for fewer sets per trip in the SATL (Table 12). The proportional standard error of the mean hours fished per trip was 0.08 in the SATL. This information was used to generate approximate distributions of total effort in hours fished to expand the observed bycatch rates to total bycatch and total bycatch mortality.

Because of the small number of observed sea turtle captures, it was only possible to estimate a CPUE model for all turtles combined for try nets, loggerheads for try nets and all turtles combined for standard nets. The best models included only area as a predictor variable for all species in try nets, and all species in standard nets (Table 13). For loggerhead sea turtles in try nets, no predictor variables were included in the best model. The total observed frequencies and the frequencies predicted by the model were consistent, implying that the negative binomial model was adequate to fit these data (Figure 14).

All Bayesian models converged adequately and had reasonable residuals (Figure 15). The lack of significant predictor variables is probably due to the low sample sizes and small number of observed sea turtles. The negative binomial models estimated that the total number of turtles caught between 2007 and 2016 was around 7,000-13,000 in try nets and 4,000-11,000 in standard nets. Neither era (2007-2011 or 2012-2017) nor year (as a numerical variable) was significant in the negative binomial models. Thus, there was no detectable trend over time.

The pattern in total bycatch across years follows the trend in total effort, so there is no particular trend (Figure 16, Table 14). To calculate the total bycatch mortality, we multiplied the total bycatch by the probability of mortality for the model with net type as the only predictor variable, since depth zone was not a factor in any of the bycatch rate models. Multiplying the total number of turtles caught by the probability of bycatch mortality gave very small numbers of sea turtles

killed in try nets, while the number of turtles killed in standard nets was relatively high (Figure 17, Table 15). For both total bycatch and total bycatch mortality, the credible intervals were wide, reflecting the small sample sizes and small number of observed sea turtles, and (except for loggerhead sea turtles in try nets) the uncertainty introduced by multiplying the multispecies bycatch estimate by the species composition.

Model checking and alternative models

The best model for each species in each net type and region was either the single species negative binomial model, or the negative binomial model applied to all species together and multiplied by the species composition, depending on the number of sea turtles observed. For species for which trips never caught more than one sea turtle, we also used binomial models to estimate total bycatch. For comparison, we calculated total bycatch with a simple ratio estimator.

For the GOM, the ratio estimators had quite broad confidence intervals, because there were many strata with very low coverage levels (Figure 18). However, all the alternative Bayesian models gave fairly similar results, with overlapping credible intervals, and the central tendency of the ratio estimates were similar to the central tendencies of the models (Figure 18). This implies that there is value in using a model based approach rather than a ratio estimator with this data set. The models allow for estimating effects of the stratification variables and their interactions across values of the other strata, thus improving precision. The similarity between the single species negative binomial models and the models of all species multiplied by the species composition implies that the species composition method gives reasonable results.

For the SATL, a large number of strata had no observer coverage. Because we assumed that bycatch rates were zero in unobserved strata, the ratio estimators underestimated total bycatch relative to the model based estimators (Figure 19). To use a ratio estimator for this dataset, it would be necessary to impute values for the missing strata, which we did not do. For the model-based estimators, only loggerhead sea turtles in try nets had enough data to apply a single-species model. The single-species and multispecies credible intervals overlapped for this species. However, the credible intervals were wide, implying that the results are highly uncertain. Larger samples sizes and better coverage of currently unobserved strata are needed for the SATL region to provide more precise and accurate estimates of total bycatch and total bycatch mortality. It should also be noted that the assumed number of hours fished per trip was a rough approximation based on the observer data, so the estimates for the SATL region may not be as accurate as the GOM results.

Checking for potential sampling bias

There were differences between larger and smaller vessels in the dataset. In particular, larger vessels were more likely to have freezers, while smaller vessels were more likely to use ice (Figure 20), and larger vessels tended to have larger crews (Table 16).

We used AIC to find the best model to predict the probability of catching a sea turtle of any species, across all GOM and SATL areas, by net type, using the vessel size characteristics and log(effort) as predictor variables. According to the AIC, the best model included vessel length for standard nets but not try nets (Table 17). However, the fraction of deviance predicted by

vessel length was small compared to the deviance explained by the effort in the trip, even for standard nets. The predicted probability of catching a turtle in a standard net was slightly higher for larger vessels (Figure 21). We applied negative binomial GLMs for the GOM data for each species and net type with all of the stratification variables (era, depth, season, area), and their two way interactions, as well as vessel length, to see if the AIC would prefer a model that included lengh for any species and net type. Length was included in the AIC best model for many species for standard nets (Table 18). Thus, it may be possible to improve the estimates of total sea turtle CPUE by including some metric of vessel size in the predictions, if such data were available.

Discussion

The integrated Bayesian modeling approach presented here allows estimation of total bycatch and total bycatch mortality making the best use of the available observer data. We used MCMC to estimate the posterior probability distributions of the probability of mortality when captured, estimate the posterior distributions of CPUE in each stratum, generate a Monte Carlo distribution of effort in each stratum, and if necessary estimate the posterior distributions of the species compositions. Since these outputs were all MCMC random draws, they could easily be combined into a posterior distribution of the total bycatch mortality for each species in each year, with credible intervals that incorporated the uncertainty in each step of the process. Such integrated models are commonly used in Bayesian statistics, and they provide a useful way to make the best use of multiple sources of information (Staton et al. 2017). In this particular model, because the probability of mortality, CPUE, species composition (if needed) and effort model components were assumed to be independent, they could be run separately and the MCMC results combined, rather than having to run all model components simultaneously as is often necessary in integrated stock assessment models (Maunder and Punt 2013). This made computation simpler and faster. This assumes that there is no correlation between the probability of being caught and the probability of mortality. Other model structures could be considered in future research to relax this assumption. Also, it may also be possible to narrow the credible intervals of the total bycatch estimates by using the observed values of bycatch for the observed effort, and only using the model to infer bycatch for the unobserved effort. Such an approach would have the advantage that the lower bounds of the credible intervals would be at least as large as the observed bycatch, rather than including zero in some credible intervals as is the case in the current model.

The models of the probability of mortality were able to predict whether an individual turtle would survive or die, based on net type, or net type combined with depth zone, according to the AUC metrics (Table 2, Table 3). Very few sea turtles died when caught in try nets, while standard nets often caused mortality. The low mortality in try nets meant that, although try nets caught hundreds of turtles every year, they only appeared to kill a few individual turtles (compare Table 8 and Table 9 for the GOM, and Table 14 and Table 15 for the SATL). The models also indicated that sea turtles caught in deeper water had a higher probability of mortality than sea turtles caught in shallower water, for both standard and try nets. Depth zone was significant even when other variables such as species of the sea turtle and duration of the otter trawl were included in the model, so it is not clear why mortality was higher in deeper water.

The negative binomial models of CPUE were able to converge for both the GOM and the SATL when more than 10 turtles were observed. Models with only 6-8 sea turtles generally did not converge, and were not reported. The negative binomial error structure appeared to be appropriate for these data, based on the comparison of observed and predicted frequencies (Figure 6, Figure 14). We found that, for some species in the GOM, a binomial model gave very similar total bycatch results to the negative binomial model, and both were consistent with the total bycatch results from simple ratio estimators. Thus, with adequate sample sizes, the results seem to robust to the choice of modeling approach and error structure. Nevertheless, future studies should test more alternative model structures and identify the best approach. Also, the assumption that total bycatch is proportional to the observed CPUE is only valid if the observed CPUE is representative of the CPUE in the unobserved portion of the fleet. Sea turtle bycatch estimates may also be improved by using additional predictor variables in the models of sea turtle CPUE, including shrimp trawl vessel characteristics such as vessel size, environmental variables such as water temperature (Gardner et al. 2008), or the catch of target species. For environmental or fishing operational variables to improve predictions of sea turtle bycatch, the same variables must be associated with the total effort data, so that the model can expand sea turtle CPUE across the whole shrimp trawl fleet. The current estimates of total effort are not separated by vessel size, and it is not known whether the sizes of observed vessels are representative of the total fishery. This is an important topic for future research.

For try nets, the largest source of uncertainty is the lack of information about how try net effort relates to standard net effort. We recommend that observers collect data on try net effort so that it will be possible to evaluate whether try net and standard net effort are proportional, or whether the ratio varies by strata or with environmental variables or vessel characteristics. A model that predicts try net effort as a function of standard net effort and other variables could be added to the integrated modeling framework, given the data to parameterize such a model.

For the GOM, we found 95% credible intervals of current (2015) bycatch mortality in standard nets was 19-130 Kemp's ridley, 5-36 loggerhead, 22-81 green and 24-99 unknown/other species of sea turtles. The models found that CPUE varied for some species by year or era, season, area, depth zone, and in some cases interactions between era and depth or area and depth. There was a decreasing trend in CPUE of all species combined, Kemp's ridley and leatherback sea turtles in try nets in the shallow depth zone, while CPUE increased in try nets in the deep zone for all species together in try nets, and showed no change over time in the deep zone for green sea turtles and unknown/other species in try nets. These complex patterns in CPUE imply that the interactions between shrimp otter trawls and sea turtles vary widely, and there may be potential for further reducing CPUE by understanding the mechanisms behind higher bycatch rates in some areas, depth zones, or seasons.

For Kemp's ridley sea turtles, CPUE decreased over time in both try and standard nets. The decrease in CPUE for standard nets led to a substantial decrease in the estimated 95% credible intervals of the number of individuals killed, from 12-940 in 2007 to 19-130 in 2015 (Table 9). Because Kemp's ridley sea turtles were the most commonly killed species in standard nets in the GOM at the beginning of the time series, their decreasing CPUE caused a substantial decrease in the number of sea turtles killed, and also made Kemp's ridley sea turtles no more common in the bycatch mortality than green sea turtles and unknown/other species. It is not known what caused

the decrease in Kemp's ridley CPUE (Table 7). It is not likely to be caused by a decrease in abundance, since Kemp's ridley abundance is thought to be increasing in the GOM over time, except for a hypothesized decrease in 2010 caused by the Deepwater Horizon Oil Spill (Gallaway et al. 2016). The fact that Kemp's ridley CPUE decreased in both try nets and standard nets seems to imply that the cause was not sea turtle excluder devices (TED) since TEDs are not present in try nets. There may have been a change in the spatial distribution of either the fleet or sea turtles. The total bycatch mortality estimates for Kemp's ridley sea turtles were substantially smaller than estimates made by Gallaway et al. (2016). Gallaway et al. (2016) conducted an integrated assessment, in which they estimated the abundance of Kemp's ridley sea turtles and their mortality from shrimp trawls and other sources of mortality based on a range of data sources including counts on nesting beaches and mark-recapture studies. They used shrimp trawl effort data but did not use the observer data to estimate CPUE. There are several possible explanations for this difference in estimated total bycatch mortality. This study only estimated the number of sea turtles that were dead when caught in shrimp trawl vessels. We did not estimate the number that were released alive but died from stress or injuries, or those that died due to interactions with the trawl gear but escaped from the TED without being observed. It is also possible that our study underestimated the total bycatch mortality because the observer program focuses on federally licensed vessels, and may not adequately represent smaller, inshore vessels that could potentially have high CPUEs. We recommend future studies to quantify the possible sources of unseen mortality of sea turtles that interact with shrimp trawls, as well as further research on CPUE in the inshore fleet.

Loggerhead sea turtles were the most commonly caught species in try nets in the GOM, but they were rarely caught in standard nets. Estimated bycatch mortality in standard nets decreased for loggerhead sea turtles, from a 95% credible interval of 17-127 in 2007 to 5-36 in 2015. However, fewer than 10 loggerhead sea turtles were caught in standard nets in the GOM, so we estimated total bycatch for this species by multiplying the species composition by the total bycatch of all species combined. Thus, the trend over time may be driven by the trend in more common species, such as Kemp's ridley. However, we note that no loggerhead sea turtles have been caught in standard nets in the GOM since 2010, despite the fact that they remain the most commonly caught species in try nets. The estimated current bycatch mortality of loggerhead sea turtles should be considered approximate, since it is based on an assumption about the species composition of the bycatch. Higher levels of observer coverage would make it possible to estimate species specific bycatch mortalities for loggerhead sea turtles.

Green sea turtle bycatch mortality showed no trend over time, and remained relatively high (95% credible interval of 21-88 individuals in 2015). This species was sufficiently common in standard nets to allow for a species specific model, so this estimate of a lack of trend is credible. Other/unknown species sea turtles also had no trend. The current unknown/other bycatch mortality (95% credible interval of 24-99 sea turtles) was rather high, and similar to the numbers of Kemp's ridley and green sea turtles killed. The unknown/other species observed in standard nets included 3 leatherbacks, 1 hawksbill and 10 sea turtles of unknown species. The unidentified individuals are likely to be common species like Kemp's ridley, green and loggerhead sea turtles, so that the total bycatch mortality of these species is likely to be higher than estimated. There may also be a significant bycatch mortality of leatherback or hawksbill sea turtles, so it would be worthwhile to increase observer coverage so that the total bycatch mortality of these species is likely to be common species.

could also be estimated. Observers should also make every effort to identify sea turtles to species.

For the SATL, as in the GOM, the majority of the sea turtle bycatch was in try nets, and the vast majority of these sea turtles survived, at least until the time they were released. Total bycatch mortality in 2016 in the SATL region in standard nets had 95% credible intervals estimated to be around 5-111 Kemp's ridley, 9-139 loggerhead, 2-86 green and 13-168 unknown/other sea turtles. These wide 95% credible intervals were caused by the low sample size and small number of observed sea turtles, and because of this, we were unable to determine whether total bycatch mortality of sea turtles was lower in the SATL than it was in the GOM. Also, the low observer coverage meant that the CPUE models were unable to converge with more than one or two explanatory variables, because many combinations of depth zone, area and season were not sampled. Thus, while our total bycatch mortality estimates were probably the best that could be done with existing data, they should be considered preliminary. Our best models either included no explanatory variables (loggerheads in try nets), or included only area as an explanatory variable. With a larger sample size and more strata sampled, we would expect that there would be significant effects of other variables, including perhaps the trends over time, but the model was not able to find significant differences with such small samples. To improve the estimates of sea turtle bycatch in the SATL, observers should be allocated more evenly across strata, and the observer coverage levels should be increased.

Another source of uncertainty in the SATL is that the effort data did not include accurate information about the number of hours fished. Also, the data had not been summarized into strata as has been done in the GOM (Nance 2004, Nance et al. 2008). Because the total bycatch and total bycatch mortality were estimated by multiplying CPUE by total hours fished, the lack of precision in the total effort data corresponds to very wide credible intervals for the SATL region and suspect accuracy. Better estimates of total effort in each stratum would greatly improve the precision and accuracy of the total bycatch mortality estimates.

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Figures and Tables

Table 1. P values of potential predictors as first main effect in the binomial model for probability of mortality, for 125 turtles for which all variables had been recorded in the observer data between July 2007 and February 2017.

Variable	р
Water Depth (ft)	0.2145
Species	0.0004
Net Type (try vs. standard)	0
Tow Time (hours)	0
Curved Carapace Length (cm)	0.0028
Season (January-April, May-August, and September-December)	0.3302
Era (2007-2011, 2012-2017)	0.6068
Depth Zone (<10 fathoms or \geq 10 fathoms)	0.0058
Area (States)	0.0137

Table 2. Model comparison for binomial models of probability of mortality fitted to 125 captured turtles with complete data, where Δ refers to the difference in the information criteria (for non-Bayesian models AIC and BIC, for Bayesian models WAIC and DIC) between the best model and the others, and $\Delta = 0$ for the best model. All methods preferred the model with depth zone (dpz) and net type only. The model with all variables includes species, net type, tow time, carapace length, depth zone, and area. Posterior model probabilities (P_{posterior}) were calculated by the method of Gardner et al. (2008). Rhat and n.eff are model fit diagnostics for the Bayesian models, where Rhat should be close to 1, and the effective number of parameters should be more than 300. AUC indicates the fraction of correct predictions of mortality from the model, and values larger than 0.7 are adequate.

Model	$\Delta_{ m AIC}$	$\Delta_{\rm BIC}$	Δ_{WAIC}	$\Delta_{ m DIC}$	P _{posterior}	Rhat	n.eff	AUC
All variables	9.36	37.65	16.01	9.7	0	1.24	2200	0.93
Species, dpz, net	3.52	12.01	6.22	4.65	0	1.07	6300	0.91
type								
dpz, net type	0	0	0	0	0.46	1.00	5600	0.89
Net type	5.97	11.63	3.98	4.15	0.31	1.00	9500	0.84

Table 3. Predicted probability of mortality from the best Bayesian model, which includes only net type and depth zone, and from the model which includes only net type. Both models are fitted to all 163 turtles in the observer data. Rhat and n.eff are diagnostics indicating model convergence.

Depth	Net	Posterior probability					Rhat	n.eff
		mean	sd	2.50%	50%	97.50%		
Best model	(Net type +	depth zor	ne), AUC=	=0.88				
Shallow	Standard	0.165	0.067	0.058	0.157	0.316	1.00	20000
Shallow	Try	0.004	0.005	0.000	0.002	0.017	1.00	20000
Deep	Standard	0.476	0.083	0.316	0.475	0.641	1.00	20000
Deep	Try	0.017	0.017	0.001	0.012	0.063	1.00	14000
Net type on	ly model, A	UC=0.83						
NA	Standard	0.334	0.059	0.224	0.332	0.454	1.00	18000
NA	Try	0.010	0.010	0.000	0.007	0.037	1.00	6500

Table 4. Distribution of number of observed trips catching the specified number of turtles in the GOM by species and net type between July 2007 and February 2017.

Species and net type	Number of turtles					
	0	1	2	3	4	5
All Try	811	48	3	1	1	2
Kemp's Ridley Try	849	16	1	0	0	0
Loggerhead Try	837	24	1	3	1	0
Green Try	860	6	0	0	0	0
Unknown Try	858	8	0	0	0	0
All Standard	818	39	7	2	0	0
Kemp's Ridley Standard	846	17	1	2	0	0
Loggerhead Standard	860	6	0	0	0	0
Green Standard	852	14	0	0	0	0
Unknown Standard	852	14	0	0	0	0

Table 5. AIC best negative binomial models of sea turtle CPUE in the observer data using non-Bayesian GLM for each turtle category and net type in the GOM. Models were run only if 10 or more turtles were caught. Variables are era (2007-2011 or 2012-2017) or year (as a number), area (states), season (January-April, May-August, September-December), depth zone (dpz: <10 fathoms or \geq 10 fathoms).

Species	Net Type	Number of Turtles	Formula
All	Try	71	era + season + area + dpz + era:dpz + area:dpz + offset(log.effort)
Kemp's Ridley	Try	18	era + season + area + dpz + era:dpz + season:dpz + area:dpz + offset(log.effort)
Loggerhead	Try	39	era + season + area + dpz + era:dpz + area:dpz + offset(log.effort)
Green	Try	6	NA
Unknown	Try	8	NA
All	Standard	59	year + season + offset(log.effort)
Kemp's Ridley	Standard	25	year + season + area + offset(log.effort)
Loggerhead	Standard	6	NA
Green	Standard	14	area + offset(log.effort)
Unknown	Standard	14	season + area + dpz + area:dpz + offset(log.effort)

Table 6. Diagnostics and estimated total bycatch in the GOM from 2007 to 2015 for Bayesian negative binomial models with the same formulas given in Table 5.

Species	Net Type	Rhat	n.eff	Total bycatch (95% credible interval)
All	Try	1.01	640	5,958 (4,397-8,141)
Kemp's Ridley	Try	1.26	320	2,037 (1,126-3,708)
Loggerhead	Try	1.06	100	2,700 (1,722-4,212)
All	Standard	1.00	750	7,101 (5,053-10,088)
Kemp's Ridley	Standard	1.19	720	3,939 (2,165-7,685)
Green	Standard	1.04	900	1,275 (715-2,132)
Unknown	Standard	1.19	360	1,500 (836-2,492)

					Difference		Difference	
	Net	Variables	Slope with	P(decline	between eras,	P(decline,	between	P(decline,
Species	Туре	included	year	by year)	shallow	shallow)	eras, deep	deep)
		era,			-1.17		0.79	
All	Try	era:dpz	NA	NA	(-2.16,-0.24)	0.99	(-0.05,1.73)	0.03
Kemp's		era,			-1.85		0.38	
Ridley	Try	era:dpz	NA	NA	(-3.99,-0.37)	0.99	(-1.24,2.47)	0.33
		era,			-1.08		0.72	
Loggerhead	Try	era:dpz	NA	NA	(-2.66,0.38)	0.93	(-0.41,2.03)	0.10
			-0.12					
All	Standard	year	(-0.23,-0.01)	0.98	NA	NA	NA	NA
Kemp's			-0.2					
Ridley	Standard	year	(-0.41,-0.02)	0.98	NA	NA	NA	NA
Green	Standard	none	NA	NA	NA	NA	NA	NA
Green	Stundard	none	1111	1.11			1111	111
Unknown	Standard	none	NA	NA	NA	NA	NA	NA

Table 7. Changes over time in sea turtle CPUE from the GOM negative binomial models, calculated from the Bayesian models with predictor variables from the AIC best models.

Table 8. Total estimated bycatch from 2007 to 2015 in the GOM, medians with 95% credible interval, from the best models for each species and net type. "M" indicates the value was inferred from a model fitted to all species, and then multiplied by the multinomial species composition. All other values were estimated from a single species negative binomial model.

Year	Kemp's Ridley Try	Loggerhead Try	Green Try M	Unknown Try M	Kemp's Ridley Standard	Loggerhead Standard M	Green Standard	Unknown Standard
2007	337	285	67	88	1,003	149	166	200
2007	(148-711)	(139-566)	(26-150)	(38-185)	(355-2,713)	(53-358)	(93-281)	(110-337)
2008	276	294	60	78	565	102	137	162
2008	(130-553)	(145-580)	(23-137)	(35-165)	(236-1,297)	(38-231)	(76-229)	(89-274)
2000	342	352	72	93	639	111	156	192
2009	(157-719)	(176-701)	(27-160)	(41-198)	(310-1,290)	(42-235)	(87-261)	(105-321)
2010	266	297	58	75	392	75	109	130
2010	(127-541)	(149-576)	(22-128)	(33-156)	(220-701)	(30-154)	(59-189)	(71-222)
2011	251	229	52	68	354	77	135	158
2011	(114-521)	(112-445)	(20-115)	(30-141)	(212-609)	(31-155)	(76-226)	(89-262)
2012	134	279	52	67	309	71	143	158
2012	(57-268)	(166-468)	(21-108)	(30-131)	(182-542)	(29-141)	(81-241)	(87-267)
2012	123	300	53	68	231	59	136	152
2015	(54-243)	(183-496)	(21-110)	(31-133)	(124-430)	(24-123)	(77-227)	(85-255)
2014	146	307	56	72	202	57	156	172
2014	(62-298)	(182-526)	(22-115)	(33-141)	(94-405)	(22-121)	(88-262)	(96-289)
2015	127	294	55	70	158	46	134	170
2015	(54-256)	(173-495)	(22-114)	(32-140)	(63-369)	(18-105)	(75-226)	(93-305)
Total	2,037	2,700	532	687	3,939	758	1,275	1,500
Total	(1,126-3,708)	(1,722-4,212)	(217-1,079)	(322-1,306)	(2,165-7,685)	(299-1,542)	(715-2,132)	(836-2,492)

Table 9. Total estimated bycatch mortality from 2007 to 2015 in the GOM, medians with 95% credible interval, from the best models for each species and net type. "M" indicates the value was inferred from a model fitted to all species, and then multiplied by the species composition. All other values were estimated from a single species negative binomial model.

Year	Kemp's Ridley Try	Loggerhead Try	Green Try M	Unknown Try M	Kemp's Ridley Standard	Loggerhead Standard M	Green Standard	Unknown Standard
2007	2 (0-11)	2 (0-13)	0 (0-2)	0 (0-3)	332 (112-940)	49 (17-127)	55 (27-100)	58 (28-115)
2008	1 (0-8)	2 (0-10)	0 (0-2)	0 (0-2)	186 (73-457)	33 (12-82)	45 (23-82)	46 (22-88)
2009	1 (0-10)	2 (0-13)	0 (0-2)	0 (0-3)	211 (94-452)	36 (13-84)	51 (26-93)	54 (26-106)
2010	1 (0-8)	2 (0-12)	0 (0-2)	0 (0-2)	129 (65-250)	25 (9-55)	36 (18-68)	40 (19-80)
2011	1 (0-8)	2 (0-11)	0 (0-2)	0 (0-2)	117 (62-220)	25 (10-56)	44 (23-81)	50 (24-99)
2012	1 (0-7)	3 (0-15)	0 (0-3)	1 (0-4)	102 (54-196)	23 (9-51)	47 (24-87)	44 (21-85)
2013	1 (0-7)	3 (0-18)	1 (0-3)	1 (0-4)	76 (37-155)	19 (8-44)	45 (23-81)	46 (22-90)
2014	1 (0-8)	3 (0-16)	0 (0-3)	1 (0-4)	67 (28-145)	19 (7-43)	51 (26-94)	55 (26-108)
2015	1 (0-7)	3 (0-17)	1 (0-3)	1 (0-4)	52 (19-130)	15 (5-36)	44 (22-81)	50 (24-99)
Total	12 (0-69)	22 (1-118)	4 (0-22)	5 (0-29)	1,301 (646-2,687)	248 (96-556)	418 (212-764)	443 (216-861)

Table 10. Number of trips observing each number of sea turtles in the SATL from June 2008 to February 2017.

Species and net type	Number of sea turtles					
	0	1	2	3	4	5
All Try	357	13	3	0	2	0
Kemp's Ridley Try	370	3	2	0	0	0
Loggerhead Try	360	12	2	1	0	0
Green Try	374	1	0	0	0	0
Unknown Try	375	0	0	0	0	0
All Standard	367	7	0	1	0	0
Kemp's Ridley Standard	373	2	0	0	0	0
Loggerhead Standard	372	3	0	0	0	0
Green Standard	374	1	0	0	0	0
Unknown Standard	372	2	1	0	0	0

	Depth zone				
Area	1	2			
5: East Florida	10,605	28,343			
6:Georgia	24,314	13,800			
7:South Carolina	47,721	3,024			
8:North Carolina	116,363	32,418			

Table 11. Effort (hours fished) distribution in the SATL from 2007 to 2016.(a) From the effort data

(b) From the observer data

	Depth zone		
Area	1	2	
5: East Florida	81	17	
6:Georgia	86	0	
7:South Carolina	133	0	
8:North Carolina	58	0	

Table 12. Summary statistics for hours fished per trip in each region, based on observer station data from July 2007 to February 2017.

Region	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.	SE(mean)
GOM	0.4	46.5	148	174.6	249.7	902.8	5.2
SATL	1.1	4.6	7.6	23	28.1	302.8	1.9

Table 13. Model diagnostics for bycatch CPUE models, and estimated total bycatch from 2007 to 2016, for the SATL. Models marked with an asterisk were used to estimate bycatch.

Species	Net	formula	DIC	Rhat	n.eff	total bycatch (95% CI)
All*	Try	area + log.effort	154	1.03	1300	7,546(4,386-12,961)
Loggerhead*	Try	log.effort	120	1.00	2400	7,592 (4,468-12,099)
All*	Standard	area + log.effort	76	1.12	940	4,426 (1,846-11,104)
All	Standard	dpz + log.effort	78	1.00	5000	5,041 (1,941-43,785)

Table 14. Total by catch from 2007 to 2016 by species in the SATL, calculated by combining
species composition with the total by catch model for all turtles together ("M") except for
loggerhead sea turtles in try nets, which had a single species model.YearKemp's
Ridley Try MLoggerhead TryGreen Try MKemp's
Ridley
Standard MLoggerhead
Standard MGreen
Standard MUnknown
Standard M

Year	Ridley Try M	Loggerhead Try	Green Try M	Ridley Standard M	Standard M	Standard M	Standard M
2007	200 (84-428)	821 (485-1,313)	44 (6-157)	99 (20-346)	135 (35-450)	62 (9-267)	170 (50-538)
2008	205 (85-444)	786 (460-1,259)	45 (6-162)	92 (19-325)	125 (33-410)	58 (8-248)	158 (48-491)
2009	196 (82-424)	745 (436-1,181)	43 (6-154)	89 (18-316)	123 (32-397)	56 (8-241)	153 (47-477)
2010	243 (103-525)	853 (500-1,354)	53 (7-192)	96 (19-328)	131 (35-418)	60 (8-251)	165 (51-501)
2011	201 (86-426)	655 (384-1,039)	44 (6-156)	73 (15-246)	101 (27-311)	46 (7-187)	127 (40-370)
2012	227 (94-487)	868 (508-1,383)	50 (7-179)	99 (20-346)	135 (36-445)	62 (9-266)	170 (51-538)
2013	166 (70-360)	725 (426-1,159)	36 (5-131)	84 (17-311)	115 (29-391)	53 (7-234)	145 (42-471)
2014	179 (74-384)	652 (382-1,033)	39 (5-140)	73 (15-252)	101 (27-321)	47 (6-196)	127 (38-386)
2015	180 (74-397)	736 (432-1,171)	39 (5-143)	82 (16-296)	111 (29-378)	51 (7-226)	140 (42-453)
2016	154 (62-347)	750 (440-1,196)	33 (5-125)	83 (16-328)	114 (28-406)	52 (7-247)	144 (39-489)
Total	1,949 (811-4,212)	7,592 (4,468-12,099)	424 (58-1,538)	874 (177-3,085)	1,190 (315-3,897)	551 (77-2,353)	1,501 (452-4,694)

Table 15. Total bycatch mortality from 2007 to 2016 by species in the SATL.

Year	Kemp's Ridley Try M	Loggerhead Try	Green Try M	Kemp's Ridley Standard M	Loggerhead Standard M	Green Standard M	Unknown Standard M
2007	1 (0-9)	6 (0-32)	0 (0-3)	32 (6-121)	44 (11-152)	20 (3-95)	56 (16-184)
2008	1 (0-10)	5 (0-30)	0 (0-3)	30 (6-110)	41 (10-140)	19 (3-88)	52 (15-170)
2009	1 (0-9)	5 (0-29)	0 (0-3)	29 (6-108)	40 (10-134)	18 (2-85)	51 (14-165)
2010	2 (0-11)	6 (0-33)	0 (0-3)	31 (6-112)	43 (11-145)	20 (3-91)	54 (16-172)
2011	1 (0-9)	4 (0-25)	0 (0-3)	24 (5-84)	33 (8-108)	15 (2-66)	42 (12-129)
2012	2 (0-11)	6 (0-34)	0 (0-3)	32 (6-121)	44 (11-151)	20 (3-94)	56 (16-181)
2013	1 (0-8)	5 (0-28)	0 (0-2)	27 (5-107)	38 (9-132)	17 (2-83)	48 (13-163)
2014	1 (0-8)	4 (0-25)	0 (0-2)	24 (5-87)	33 (8-110)	15 (2-69)	42 (12-134)
2015	1 (0-8)	5 (0-29)	0 (0-3)	27 (5-101)	37 (9-126)	17 (2-81)	46 (13-155)
2016	1 (0-7)	5 (0-29)	0 (0-2)	27 (5-111)	37 (9-139)	17 (2-86)	47 (13-168)
Total	13 (1-91)	52 (2-292)	3 (0-27)	285 (55-1,059)	391 (99-1,330)	179 (24-841)	495 (142-1,613)

Table 16. Correlation between vessel size metrics from observer data in both regions combined.

	Length	Gross Ton	Engine HP	Crew Size
Length	1	0.923	0.751	0.710
Gross Ton	0.923	1	0.733	0.706
Engine HP	0.751	0.733	1	0.562
Crew Size	0.710	0.706	0.562	1

(a) Standard nets						
	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)	Percent deviance
NULL			1269	459.09		
log.effort	1	48.15	1268	410.94	0.000	0.063
Length	1	3.305	1267	407.63	0.069	0.004
Length ²	1	5.404	1266	402.23	0.020	0.007
(b) Try	/ nets	5				
	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)	Percent deviance
NULL			1269	558.74		
log.effort	1	45.50	1268	513.24	0.000	0.059

Table 17. AIC best binomial GLM of presence/absence of all turtles by observed trip in all areas, including vessel size metrics and effort. (a) Standard nets

Table 18. AIC best negative binomial models of turtle/presence absence in observed trips in the GOM, including vessel size and the stratification variables.

Species	Net Type	AIC Best Model
All	Try	era + season + area + dpz + era:dpz + season:dpz + area:dpz + offset(log.effort)
Kemp's Ridley	Try	era + season + area + dpz + era:dpz + season:dpz + area:dpz + offset(log.effort)
Loggerhead	Try	<pre>season + area + dpz + Length + season:area + area:dpz + offset(log.effort)</pre>
Green	Try	offset(log.effort)
Unknown	Try	era + area + dpz + era:dpz + offset(log.effort)
All	Standard	era + offset(log.effort)
Kemp's Ridley	Standard	era + season + area + Length + era:season + offset(log.effort)
Loggerhead	Standard	era + season + area + Length ² + offset(log.effort)
Green	Standard	NA
Unknown	Standard	<pre>season + area + dpz + Length + Length^2 + area:dpz + offset(log.effort)</pre>



Figure 1. Typical gear configuration for U.S. southeastern shrimp vessels equipped with four nets (figure was reproduced from (Scott-Denton et al. 2012)). In 1987, the United States began requiring trawling shrimping boats to equip their nets with turtle excluder devices (TEDs) seasonally in some locations.



Figure 2. Locations of (a) sea turtle captures and (b) dead captures by standard nets, based on mandatory observer coverage of the U.S. southeastern fishery from October 2007 through February 2017.



Figure 3. Locations of (a) sea turtle captures and (b) dead captures by try nets, based on mandatory observer coverage of the U.S. southeastern fishery from October 2007 through February 2017.



Figure 4. Posterior probability density functions of probability of mortality for the best model, fitted to all 163 turtles in the observer data from July 2007 to February 2017.



Figure 5. Species composition in the GOM for all observed catches from July 2007 to February 2017, with 95% credible intervals from a multinomial model.





Figure 6. Observed and predicted frequencies for negative binomial models from the GOM.



Figure 7. Residuals for the log(mean) of the Bayesian negative binomial models for the GOM.



Figure 8. Mean CPUE in number of turtles caught per trawling hour plus and minus one standard error, for all turtles combined, by year and depth zone.



Figure 9. Estimated total catch (alive or dead) in the GOM by year from 2007 to 2015 (the last year for which total effort was available), from the best negative binomial models (NB) or, for species with less than 10 captures, the best estimate from a negative binomial model for all species together multiplied by the multinomial species composition (NB-M).



Figure 10. Total effort in the GOM.



Figure 11. Estimated number of dead discards in the GOM by year from 2007 to 2015 (the last year for which total effort were available), from the best negative binomial models (NB) or, for species with less than 10 captures, the best estimate from a negative binomial model for all species together multiplied by the multinomial species composition (NB-M).



Figure 12. Species composition of observed sea turtle bycatch by net type, with multinomial 95% credible intervals in the SATL. Data were available from June 2008 to February 2017.



Figure 13. Total effort in the SATL by year, in number of trips.





Figure 14. Comparison of observed and expected total frequencies for negative binomial models from the SATL.



Predicted value

Figure 15. Residuals for the log of mean CPUE from the negative binomial Bayesian models for the SATL region.



Figure 16. Estimated number of sea turtles caught (alive or dead) in the SATL by year from 2007 to 2016, from the best negative binomial models (NB) or, for species with less than 10 captures, the best estimate from a negative binomial model for all species together multiplied by the multinomial species composition (NB-M).



Figure 17. Estimated number of dead discards in the SATL by year, from the best negative binomial models (NB) or, for species with less than 10 captures, the best estimate from a negative binomial model for all species together multiplied by the multinomial species composition (NB-M).



Figure 18. Total bycatch in the GOM comparing single species negative binomial models, multispecies negative binomial models (in which bycatch was estimated for all species together and multiplied by species composition), binomial models (for species and net types for which no trips caught more than one turtle), and a ratio estimator. The models used to make the annual summaries are marked with a star (multispecies for species with less than 10 observations, single species for species with 10 or more observations).



Figure 19. Total bycatch in the SATL comparing single species negative binomial models, multispecies negative binomial models (in which bycatch was estimated for all species together and multiplied by species composition), and a ratio estimator. The models used to make the annual summaries are marked with a star (multispecies for species with less than 10 observations, single species for species with 10 or more observations).



Figure 20. Vessel length (ft) by trip and vessel type, in the entire database.



Length

Figure 21. Probability of catching a turtle by vessel length (ft). The three lines show trips with a low, medium, or high effort in hours fished, corresponding to the minimum, median, and maximum number of hours observed in trip.