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Ontogenetic spatial distributions of red grouper (*Epinephelus morio)* within the northeastern Gulf of Mexico and spatio-temporal overlap with red tide events

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Abstract

Fishery-independent and fishery-dependent data were aggregated to provide sufficient data and resolution to quantify ontogenetic spatial distributions of red grouper and enable an assessment of the spatio-temporal overlap between juvenile and adult red grouper and red tide events. Using the best data available, generalized linear models predicted the probability of occurrence as a function of temporal, spatial, environmental and sampling factors. Although a few red grouper were captured west of longitude 87°W, both juvenile and adult were largely restricted to the northeastern GOM. Occurrence trends were driven primarily by longitude and gear type, with the longline responsible for the majority of red grouper catches. Spatial analyses provided quantitative evidence of increased exposure of red grouper to red tide during years of severe red tide events (e.g., 2005), however, the actual response of the red grouper population remains known. These results support the continuation of efforts incorporating red tide into SEDAR stock assessments for shallow-water grouper.

Introduction

Grouper are some of the most commercially important reef fishes in the northeastern Gulf of Mexico (GOM) (Coleman et al. 1996). Yet, uncertainty surrounding their distributions has left a critical gap in the science needed to assess how ecosystem processes such as red tide (*Karenia brevis*) events, a type of harmful algal bloom, impact population dynamics. While multiple fishery-independent surveys in the northern GOM quantify distribution and estimate abundance for many managed species throughout the northern GOM, monitoring surveys seldom capture grouper species and are often discouraged as assessment model inputs for these species (SEDAR 2006, 2009a, b). Both past (SEDAR 2006, 2009a, b) and present assessment efforts (SEDAR

2014) have emphasized uncertainty regarding grouper dynamics from stock assessment models, partly due to data limitations (e.g., lack of consistent and appropriate time series) (Suprenand et al. 2014) and unknown population impacts caused by red tide events (SEDAR 2009a, b, 2014). Alternative approaches for modeling spatial distributions are needed to enhance understanding of grouper habitats and help elucidate ecosystem impacts for both single-species stock assessments and ecosystem-based fisheries management (EBFM).

Assessing the impacts of large-scale drivers on spatial distributions is a major topic of fisheries oceanography, with the majority of research focused on the consequences of changing water temperatures for fish and fisheries (Perry et al. 2005, Nye et al. 2009). Within the GOM, regional stressors include red tide events, which can impact both local (e.g., seagrass bed) and broad-scale (e.g., West Florida Shelf) dynamics (e.g., Naar et al. 2007, Landsberg et al. 2009, Flaherty & Landsberg 2011). Suspected red tide mortality has been observed for deeper-dwelling fishes including goliath grouper (*Epinephelus itajara*) (Smith 1975), red grouper (*Epinephelus morio*), warsaw grouper (*Epinephelus nigritus*) (Walter et al. 2013), and other unidentified grouper (Smith 1975). Within grouper management, the 2009 stock assessments for red grouper and gag grouper (*Mycteroperca microlepis*) pioneered the consideration of red tide impacts on grouper dynamics in stock assessments by accounting for elevated grouper natural mortality after the severe red tide in 2005 within the assessment models (SEDAR 2009a, b). Grouper may also emigrate out of regions affected by red tide events, as observed for red grouper and scamp (*Mycteroperca phenax*) off Florida following the 2005 red tide event (Dupont et al. 2010). Projected increases in the frequency and intensity of red tide events (Moore et al. 2008), in conjunction with uncertain population responses to such events, warrant an investigation of the spatial distribution of the different life history stages of grouper populations and of their vulnerability to episodic red tide events.

Quantification of spatial distribution is a critical step in meeting federal mandates for ecosystem considerations within single-species stock assessments and in the implementation of EBFM (Mace et al. 2001, MSFCMA 2007). Habitat models can quantify a species' preferred habitat (Wintle et al. 2005, Vaz et al. 2006), facilitate investigation of ecosystem interactions (e.g., predator-prey relationships), and enable prediction of population responses to changing environmental conditions (Sagarese et al. 2014). Resulting distribution maps (e.g., spawning stock biomass maps) coupled with biophysical models (e.g., the Connectivity Modeling System, CMS; Paris et al. 2013) can produce ecosystem products such as estimates of annual recruitment deviations for incorporation into single-species stock assessment models, thereby reducing scientific uncertainty within model projections (Karnauskas et al. 2013a, Karnauskas et al. 2013c). In an ecosystem context, distribution maps are necessary as model inputs for ecosystem models, including OSMOSE (Grüss et al. 2014a) and Atlantis (Drexler & Ainsworth 2013).

In the present study, fishery-independent and fishery-dependent data were aggregated to provide sufficient data and resolution to quantify ontogenetic spatial distributions of red grouper and enable an assessment of the spatio-temporal overlap between juvenile and adult red grouper and red tide events. A generalized linear modeling (GLM) approach produced comprehensive distribution maps for juvenile and adult life-history stages throughout the northeastern GOM. Using the best data available, quantitative models predicted the probability of occurrence as a function of temporal, spatial, environmental and sampling factors. The specific objectives of the present study are to: (1) model juvenile (ages 1-3) and adult (ages 3+) spatial distributions for red grouper to highlight critical ontogenetic habitats; and (2) examine the spatio-temporal overlap between stage-specific distributions and the distribution of red tides on the West Florida Shelf

(WFS). Annual distribution maps produced within objective (1) were compared to statistically-derived spatial maps of red tide presence (Walter et al. 2013) to provide insight into how red tide events were distributed in relation to red grouper occurrence over the period 1998-2010.

Materials and Methods

Data sources

Multiple fishery-independent and fishery-dependent data sources were consulted to determine capture locations of red grouper throughout the northern Gulf of Mexico (Fig. 1). Specifics for each data source are given in Table 1 and include years and seasons sampled, sampling/fishing effort, and a summary of spatial locations (i.e., latitude, longitude).

Fishery-independent

VIDEO: The Southeast Area Monitoring and Assessment Program (SEAMAP) reef fish video survey (VIDEO) has documented reef fish occurrence in shelf waters from Brownsville, Texas to Dry Tortugas, Florida since 1993. For this survey, cameras are deployed at randomly assigned stations within stratified blocks based on geographic region and reef habitat area. Types of data collected include diversity, abundance, fish length, and habitat. Further survey details are discussed in Campbell et al. (2013). Although fish length information has been recorded since 2002, procedural inconsistencies (e.g., the use of laser versus stereo cameras), sporadic catches, and incomplete spatial and temporal coverage prevented us from using this survey for modeling red grouper ontogenetic distributions.

TRAWL: The SEAMAP groundfish trawl survey (TRAWL) has monitored annual variations in abundance of living marine resources in the northern GOM since 1987. This survey employs a semiballoon shrimp trawl with a random sampling design at depths ranging from 5 to 50 fathoms spanning Texas to Florida (Nichols 2005). General types of data collected encompass station (e.g., vessel, latitude), event (e.g., duration, speed), and biological data (catch, fish lengths). While the TRAWL survey design has remained relatively consistent since 1987, slight changes have occurred and are discussed elsewhere (Nichols 2005). This survey adequately samples new recruits for many managed species, but rarely captures adults of grouper species.

BLL: The National Marine Fisheries Service bottom longline survey (BLL) has been conducted throughout the northern GOM since 1995 to provide fisheries independent-data for stock assessment purposes. Species targeted by the BLL survey include large coastal sharks, snappers, and grouper. Types of data collected are similar to those discussed above for TRAWL. Many changes to sampling protocols (e.g., target species, hook types, spatial coverage) have complicated reliability of derived time series, details of which are provided in Henwood et al. (2004) and Ingram et al. (2005). As the time series lengthens, the utility of the BLL survey for red grouper is expected to improve since it does sample the extent of red grouper habitat (SEDAR 2006).

EASA VL, EASA LL: During 2011, an expanded annual stock assessment (EASA) survey employed both longline and vertical line gears to synoptically sample fished species throughout the northern GOM. The EASA survey sampled shelf waters (< 180 m) from Texas to the WFS. Both longline and vertical line vessels fished simultaneously at randomly selected sites. The vertical line gear was used to target hard-bottom habitat not accessible to longlines or trawls. Additional details are discussed in Campbell et al. (2011).

Fishery-dependent

SBLOP: The Panama City laboratory shark bottom longline observer program (SBLOP) has sampled commercial bottom longline vessels throughout the northern GOM since 2005. For the SBLOP survey, trained observers are randomly placed on vessels and record data on gear, targeted species, catch, fish length, bycatch, and discards. Grouper species represent both target catch and discards. Additional details are provided in SEDAR13-DW-20.

LL: The GOM reef fish bottom longline observer program (LL) has sampled commercial bottom longline vessels targeting reef fish since 2006. Quantitative biological (e.g., catch, fish length), vessel, and gear-selectivity information are provided relative to the directed reef fish fishery. Observers are randomly allocated to vessels stratified by season, gear, and region. Observer coverage is based on proportional sampling effort derived from logbook data among seasons and gears in the northern GOM. The LL gears generally target grouper (either shallow-water or deep-water), tilefish, and sharks. Further details are given in Scott-Denton et al. (2011).

VL: The GOM reef fish vertical line observer program (VL) has sampled commercial vertical line (bandit and handline) vessels targeting reef fish since 2006. Both observer allocation and the purpose of the VL survey are identical to that described above for the LL survey. The VL gears generally target shallow-water grouper and red snapper. A detailed review of the VL survey is also provided in Scott-Denton et al. (2011).

Data

Red grouper classification

For all datasets except VIDEO, length data were used to apportion red grouper into juvenile (ages 1-3), and adult (ages 3+) life-history stages based on estimated lengths at 50% maturity obtained from the literature (Table 2). All length conversions accounted for differences in lengths reported within fishery-dependent datasets (fork lengths) and fishery-independent datasets (total lengths) (Table 2).

It is important to recognize that the aforementioned life history designations (Table 2) were assumed proxies for both size and time of spawning. It is possible that some individuals may mature before or after the size used to distinguish stages and therefore may be misclassified. The influence of these individuals is assumed negligible due to relatively large sample sizes.

Data Aggregation

All data sets were manipulated so that each observation represented a single latitude, longitude, and date. Red grouper catches were summed by observation whereas all explanatory variables (see next section) were averaged to provide a single value corresponding to each observation. To provide an idea of the spatial resolution of red grouper distribution throughout the northern GOM, the percentage of red grouper catch was calculated for juveniles and adults in the northeastern GOM (longitude > 87°W). The restriction of the spatial modeling to observations of 87° W or eastward is due to minimal catches of red grouper west of this line in any dataset.

For modeling purposes, all datasets were filtered to include only relevant data. All stations outside of the U.S. domain were excluded from distribution modeling efforts. To restrict results to the GOM, all stations located in the southern Florida Keys (i.e., in the Atlantic) were also excluded from analysis. Both observer LL and VL datasets were restricted to randomly selected trips. Stations with depth estimates greater than 200 m were excluded from analysis under the assumption that red grouper is not found at depths greater than 200 m (McEachran & Fechhelm 2006).

Initial models solely used fishery-independent data since these data were generally unbiased and thought to be more reflective of actual population trends. However, the addition of fishery-dependent data was required to increase overall sample size for all life-history stages for both model building and validation. If a dataset contained less than 40 individuals of a given life-history stage, it was excluded from modeling exercises. To assess annual trends, years with fewer than 5 observations were excluded from analyses. For each life-history stage, the aggregated and filtered dataset was randomly divided into a training set (66% of observations) to be used for model fitting and a test set (remaining 33% of observations) to be used for model validation (Miller & Franklin 2002, Brotons et al. 2004). While combining multiple data sets is never desirable, this procedure provided the best data available to model ontogenetic spatial distributions for red grouper. Such an approach may impact the reliability of model results due to differences in catchability between gear types, targeting behavior, and/or spatial coverage. At this time, no attempts were made to standardize these factors within datasets nor were any comparisons made between absolute abundances.

Candidate predictors

Candidate explanatory variables reported within all datasets included year, month, hour fished or sampled, latitude, longitude, depth, and gear. Year and month were included to account for inter-annual and inter-seasonal differences, respectively, whereas hour fished helped reduce variability due to the time of day sampled or fished. Latitude was included due to documented differences in large-scale red grouper distribution (Saul et al. 2013) and red grouper ecology north and south of 28°N (Lombardi-Carlson et al. 2008), whereas longitude was included to capture differences in spatial distribution across the WFS. To enable assessment of preferred habitat characteristics, dSEABED2006 (Buczkowski et al. 2006, Jenkins 2011) sediment type data were manipulated using the natural neighbor function in ArcGIS v10.0 (Drexler & Ainsworth 2013, Grüss et al. 2014a). Habitat consisted of four categories: mud, sand, gravel, and rock. Gear type was included to account for sampling effects between all datasets with each gear type specific to each dataset (e.g., BLL = bottom longline). If the absolute value of correlation coefficients between candidate variables exceeded 0.75, then one of the variables was excluded to minimize collinearity (Booth et al. 1994, Wintle et al. 2005).

Statistical analysis

Model fitting

The distributions of juvenile and adult red grouper were modeled using generalized linear models (GLMs) (McCullagh & Nelder 1989). Generalize linear modeling is an extension of linear modeling, which allows for non-normality and non-linear relationships, and do not force data into unnatural scales (Hastie & Tibshirani 1990, Guisan et al. 2002). While two-stage GLMs, or delta-GLMs, were attempted, results presented herein are restricted to occurrence (i.e., presence/absence) due to the potential changes in catchability across gear types. The gear variable was assumed an appropriate way to account for sampling effects on the probability of occurrence between datasets.

Binomial GLMs predicted the probability of occurrence using a logit link function with the following general equation:

$$(1)\ g(\eta) = year + month + hour\ fished + lat + lon + sedtype + depth + gear$$

where latitude, longitude, and depth were treated as either continuous or binned factors. Varying bin sizes were examined and ultimately selected based on sufficient observations in each bin in conjunction with an approximated normal distribution. All other variables were solely treated as factors. All GLMs were fit in R (R, vers. 3.0.1, R Core Development Team, Vienna, Austria) using the glm() function.

Model selection

Potential models of occurrence were evaluated by testing all possible combinations of main effects. For each life-history stage, the best binomial GLM given the data and model used was selected based on both model selection criteria and performance diagnostics obtained using the test dataset. Model selection was assessed using both Akaike's information criteria (AIC; (Akaike 1974) and Bayesian Information criteria (BIC; (Schwarz 1978) along with estimated weights (Wagenmakers & Farrell 2004). Preferred performance criteria included higher values for (1) adjusted coefficient of determination (adjusted R^2) (Legendre & Legendre 1998); (2) receiver operator characteristic (*ROC*) curve, which expresses the true positive rate (sensitivity) as a function of the false positive rate (100-specificity) for each probability of occurrence (Hanley & McNeil 1982); (3) Pearson's correlation coefficient (r); and (4) Spearman's correlation coefficient (r_{sp}). For root mean square error of prediction (*RMSE*), i.e., the root of the mean of the squared differences between each prediction and each observation, lower estimates were preferred (Loots et al. 2010).

Model evaluation

Test datasets for all life-history stages evaluated each optimal model's predictive performance (Fielding & Bell 1997, Pearce & Ferrier 2000). The total deviance explained, the area under the ROC curve (AUC), the rate of false positive predictions and false negative predictions, calibrations plots and Bland-Altman plots were used to evaluate optimal models. AUC represents the model's ability to discriminate between presence and absence sites, with a value of 0.5 indicative of no improvement over a random chance (Brotons et al. 2004, Leathwick et al. 2006, Heinänen et al. 2008). AUC values greater than 0.9 are preferred as the true positive rate is high relative to the false positive rate, while values between 0.7 and 0.9 indicate reasonable discrimination (Swetz 1988, Pearce & Ferrier 2000). A contingency table specifies the rate of false positive predictions and false negative predictions for the test dataset, with low false negative rates preferable. The ability to correctly predict the proportion of sites with a red grouper life-history stage given an occupied environmental profile is determined using calibration plots, where perfect calibration is indicated by a line with a slope equal to 1 and an intercept equal to 0 (Wintle et al. 2005, Heinänen et al. 2008). Lastly, model behavior can be assessed using a Bland-Altman plot, which compares the binary responses across a gradient of bins and identifies bias by examining the relationship between the difference and mean (Bland & Altman 1986). Here, a significant relationship between the difference and mean ($BAR^2 > 0$) would reflect bias. All occurrence models were tested for discrimination and calibration using the R packages 'pROC' (Robin et al. 2011) and 'PresenceAbsence' (Freeman 2008), respectively.

Residual occurrence

Residual occurrence was estimated for each red grouper life-history stage using semivariogram models obtained using the 'geoR' package (Diggle & Ribeiro Jr 2007) in R (R, vers. 3.0.1, R Core Development Team, Vienna, Austria). Empirical variograms were fit to occurrence residuals (i.e., observed occurrence minus expected occurrence) averaged within each spatial grid cell and were created for data pairs with distances smaller than 200 km, using the classical method of moments estimator. This analysis assumed that the pattern of spatial autocorrelation remained consistent between years. Each variogram model was fit using ordinary least squares and with no fixed nugget. A regular grid of points (0.1° latitude x 0.1° longitude) was overlaid on the sampling domain, and parameters from the variogram model were used to make predictions of residual occurrence across this grid. Using the fitted semivariogram models, residual occurrence was estimated using ordinary kriging (Cressie 1988). Kriging analyses were conducted on overall means of predicted occurrence.

Distribution maps

Using the parameters estimated by the optimal binomial GLM, the expected probability of occurrence of each life-history stage was predicted across space. Predictions were made at the locations of the original data points and averaged within each grid cell. Kriged residual occurrence and associated standard errors were added to predicted occurrence and standard errors to produce a final index of occurrence throughout the northeastern GOM. An optimum probability threshold can be defined by the ROC curve where the sum of the sensitivity and the sum of specificity are at their maximum (Manel et al. 2001, Hattab et al. 2013). Using this threshold, predictions were converted to expected presence (1; above or equal to the threshold) or absence (0; below threshold). The resulting spatial distribution maps were used to investigate overlap of juvenile and adult red grouper with red tide severity.

Spatio-temporal overlap with red tide

Red tide

Predicted presence of red tide throughout the WFS was available from 1998 through 2010 from statistical models (Walter et al. 2013). Briefly, for each satellite grid cell, generalized additive models predicted the probability of a red tide bloom (Walter et al. 2013) using a suite of satellite derived remote sensing products from SeaWiFS and the Florida Fish and Wildlife Research Institute (FWRI)'s harmful algal bloom cell counts. Monthly estimates of the predicted probability of occurrence were averaged to obtain annual estimates of predicted probability of red tide throughout the WFS. To minimize uncertainty within red tide predictions, only estimates within the depth range 10 – 100 m were used in the present analysis. Further details on model development, performance, and prediction can be found in Walter et al. (2013). It is important to note that these estimates are based solely on sea surface conditions and do not account for red tide conditions at depths where larger red grouper occur.

Spatial overlap

Annual distribution maps for each red grouper life-history stage were converted into rasters to reflect mean occurrence in each grid cell using the 'raster' package (Hijmans & van Etten 2012) in R. Once the data were rasterized into a spatial resolution identical to the red tide spatial maps (0.1° latitude x 0.1° longitude), the annual percent spatial overlap (Brodeur et al. 2008) was calculated using the following equation:

$$(2)\ SO_Y\ (\%) = \frac{N_{RT,GROUPER}}{N_{GROUPER}} \times 100$$

where $N_{RT,GROUPER}$ is the number of cells with both red tide and red grouper predicted to occur and $N_{GROUPER}$ is the number of cells where a given life-history stage of red grouper is predicted to occur and where red tide prediction is feasible. For this analysis, predictions of both red tide and red grouper were converted into present (1; value above or equal to the ROC threshold) or absent (0; value below the ROC threshold) since this analysis does not depend upon the magnitude of either prediction. The "footprint" of the *SO* metric was equivalent to red grouper distribution, that is, cells with no red tide prediction available [i.e., due to cloud cover] were not included within *SO* estimation. The *SO* metric described how the predicted occurrence of red tide was distributed in relation to predicted red grouper distribution and served as a proxy of the exposure of each life-history stage of red grouper to red tide events. Low overlap indicated that red tide was infrequently predicted to occur where red grouper life-history stages were likely to occur, suggesting reduced exposure to red tide events. A higher spatial overlap was expected during 2005 based on reduced population abundance of red grouper in 2006 (SEDAR 2009a, b).

Exposure to Red Tide

The percentage of NMFS bottom longline survey catch of red grouper in areas impacted by red tide (via predictions) between 1998 and 2010 was used to infer changes in exposure of the population, in the sense that higher exposure could lead to increased mortality due to red tide events. Data from the NMFS bottom longline survey were used since this survey provides the best unbiased estimate of distribution for adult grouper in the Gulf of Mexico. Annual estimates of exposure were calculated using the following equation:

$$(3)\ Exposure_Y\ (\%) = \frac{C_{RT}}{C_{TOTAL}} \times 100$$

where C_F is the total survey catch of red grouper in grid cells where red tide is predicted to occur and C_T is the total survey catch of red grouper. This analysis assumed that survey catch was representative of trends for the red grouper stock. A high percentage indicated that a large portion of that stock was present in grid cells where red tide was predicted to occur, suggesting higher exposure, although the exact response remains unclear (mortality or movement outside of affected areas).

Results

Data

Grouper classification

For juvenile red grouper (ages 1-3), 7400 individuals were identified, with most reported from fishery-dependent datasets (Table 3). Adult red grouper were most numerous, with 157,000 individuals identified in total. Adults were predominantly captured in fishery-dependent data sources, particularly the LL, and sporadically encountered in fishery-independent datasets (Table 3).

Data aggregation

Almost all juvenile and adult red grouper catches occurred in the northeastern GOM (93 – 100%; Table 3). While juveniles were restricted to the northeastern GOM (Table 3), a few adults were collected off Alabama (Fig. 2) and from the Flower Garden Banks National Marine Sanctuary in the northwestern GOM (from fishery-dependent data).

Candidate predictors

Latitude and longitude were highly correlated (0.74) (Table 4). However, due to the expected importance of both latitude and longitude in determining distribution, both were retained in the occurrence models we fitted. No other concerning correlations were observed.

Statistical analysis

Model fitting and selection

The occurrence model for juvenile red grouper explained more deviance than the occurrence model for adult red grouper (38% versus 19%; Table 5). Relatively low deviance explained for adults suggests that additional factors are needed to enhance understanding of their distribution.

For juveniles and adults, the treatment of longitude, latitude, and depth as factors (see Tables 6 – 7 for details on bins) was consistently preferred over continuous variables, based on both model selection and performance criteria. The full model was identified as the best model given the data for both juvenile and adult red grouper, with juvenile presence driven by gear (18%), longitude (13.4%), and year (7.5%), and adult presence primarily influenced by longitude (7.3%) and gear (5.8%) (Table 5).

Model evaluation

Models generally displayed reasonable validation in terms of discrimination, calibration and/or bias (Table 5). The occurrence model for juvenile red grouper displayed high AUC, moderate correlation, relatively low FNRs and RMSEs, and low model bias (BAR^2) (Table 5). While the adult red grouper model displayed a relatively high RMSE of 0.438, all other evaluation metrics were reasonable for that model (Table 5).

Residual occurrence

Minimized weighted sum of squares from semivariogram analysis ranged from 0.082 (juveniles) to 0.137 (adults). Semivariogram models resulted in estimated ranges between 58 km (adults) and 31 km (juveniles) (Fig. 3).

Distribution maps

For juvenile red grouper, the probability of occurrence frequently exceeded the threshold throughout the WFS (Fig. 4). Relatively high probabilities of occurrence were documented on the southern WFS, particularly from Tampa Bay to Cape Sable, Florida (Fig. 4). High probabilities of occurrence were predicted throughout the WFS for adult red grouper (Fig. 4).

Spatio-temporal overlap with red tide

Spatio-temporal overlap

Spatial maps of the annual predicted probability of red tide from Walter et al. (2013) were compared to predicted maps of red grouper distributions (Fig. 5). For both juvenile and adult red grouper, spatial overlap with red tide peaked in 2005 as expected, suggesting that a greater portion of the red grouper stock was exposed to red tide during that specific year (Fig. 6). Relatively high overlap between red grouper and red tide was also identified during 2003, a year where *Karenia brevis* cells exceeded red tide levels each year (Appendix Fig. 1 of SEDAR33-DW-08), as well as during 2008.

Exposure to Red Tide

Based on NMFS BLL catches, the percentage of the red grouper stock exposed to red tide peaked in 2005 at 47% (Fig. 7), indicating that a greater portion of the population was potentially vulnerable to adverse effects of red tide, either in the form of increased mortality or movement. Other relatively large years of exposure to red tide included 2003 (32%) and 2008 (32%) (Fig.10).

Discussion

The aggregation of multiple datasets enabled spatial modeling of ontogenetic distributions of red grouper and allowed the first attempt at quantifying the potential population impact of red tide events on red grouper. Distributions of both juvenile and adult red grouper were restricted to the northeastern GOM and were driven largely by longitude and gear type, with the longline responsible for the majority of catches. Spatial analyses provided quantitative evidence of increased exposure of red grouper to red tide during years of severe red tide events (e.g., 2005), although the actual response of the red grouper population remains known.

Both juveniles and adults of red grouper displayed peak overlap with red tide in 2005. In this study, red tide predictions were based on surface conditions and did not take into account bloom conditions at depth. Because red tide events are well-recognized in coastal waters where massive fish kills wash up on local beaches, juvenile red grouper is believed to be most susceptible to these events. However, red tide blooms generally start offshore at depth (Steidinger & Vargo 1988), before being transported into near-shore areas by winds and tidal currents (Steidinger & Haddad 1981). Recording of water quality throughout the water column during red tide conditions could provide additional insight into how red tide events are distributed in relation to adult red grouper. The spatial overlap between adult red grouper and red tide may be underestimated in the present study. In addition, future research aimed at addressing the response of grouper to red tide events could help explain whether grouper experience elevated natural mortality or emigrate from affected regions (Dupont et al. 2010). Additional modeling efforts are planned to address these hypotheses directly.

Current understanding of red grouper distribution and reproductive behavior originates from field studies conducted on the WFS (Coleman et al. 1996, Koenig et al. 1996). Our results supported the importance of the WFS as critical habitat for both juvenile and adult red grouper, with ontogenetic shifts in distribution evident. Both juvenile and adult red grouper were predicted to occur in similar regions, particularly on the southern WFS. Co-occurrence of juveniles and adults has important implications regarding cannibalism and trophic dynamics for red grouper. Grouper are believed to prey upon other grouper (Grüss et al. 2013, Grüss et al. in revision). However, evidence of intraspecific predation by grouper is difficult to obtain (Grüss et al. in revision). Sampling difficulties arise because grouper brought from depth evacuate their guts.

Presence of red grouper west of the Florida-Alabama line has been suggested to relate to displacement of individuals by hurricanes (Franks 2005). Preliminary analysis of the number of red grouper caught west of longitude 87° W did not reveal any relationship with either the mean storm intensity or the maximum category of storms (Fig. 8). Data on storm intensity were obtained from hurricane track data downloaded from HURDAT (Karnauskas et al. 2013b). This analysis was performed on both lagged data (assuming individuals were displaced 1 year later) and raw data (assuming individuals were displaced and collected during the storm's year). While this hypothesis may explain individuals located off Mississippi/Louisiana, it seems unlikely that these events would reach into the westernmost portion of the GOM. Sparse fishery-independent catches of red grouper in the northwestern GOM suggest some source of recruitment, potentially from Mexican waters, assuming that species identification was correct. Additional efforts aimed at quantifying the connectivity between southern GOM grouper and northern GOM may assist in understanding red grouper distribution throughout the less-studied northwestern GOM.

The present study focused on juvenile (1-3 years old) and adult (3+ years old) red grouper. It was not possible to conduct analyses for young-of-the-year (0-1 year old) red grouper here, due to the scarcity of data for this life-history stage in available datasets (5 data points in the SBLOP survey datasets, and 4 in the TRAWL dataset). Since red grouper do not form spawning aggregations and spawn on their home sites (Heppell et al. 2006, Coleman & Koenig 2010, Coleman et al. 2010, Coleman et al. 2011), the distribution map we produced for adults in the present study was used to map red grouper egg release, and then estimate the larval dispersal and settlement patterns of the species on the WFS over the period 2003-2013 with the CMS (Grüss et al. 2014b). The mean annual spatial patterns of settlement predicted by the CMS will be explored to generate annual distribution maps for young-of-the-year red grouper.

This study represents the first attempt at estimating the potential impact of red tide on red grouper distribution in the northeastern GOM. Year 2005 exhibited the highest overlap between both juvenile and adult red grouper and red tide, and the highest percent exposure of the red grouper stock to red tide, providing supporting evidence for an adverse response by the grouper population to severe red tides which must be accounted for when assessing stock dynamics. These results support the continuation of efforts incorporating red tide into SEDAR stock assessments for shallow-water grouper, as done for the 2009 SEDAR Update for red grouper and gag grouper and SEDAR 33 for gag grouper. Future work will address different hypotheses for how shallow-water grouper respond to red tide events.

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Table 1. Data sources used to infer ontogenetic spatial distributions of red grouper in the northern Gulf of Mexico. SBLOP = Shark bottom longline observer program; LL = observer longline; VL = observer vertical line; Video = SEAMAP reef fish video survey; EASA = Expanded Annual Stock Assessment Survey (VL = vertical line, LL = longline); TRAWL = SEAMAP groundfish trawl survey; BLL = NMFS bottom longline survey. Observations are defined by a single date, latitude, and longitude and were used to produce summary statistics for effort and spatial locations.

Data Source	Year Range	Season	Effort		Latitude (°N)		Longitude (°W)	
			Total	Units	Mean	Range	Mean	Range
Fishery-independent								
VIDEO	1993-2012 (excludes 1998-2000, 2003)	Apr - Aug	5076	stations (20 minute record)	27.90	(24.50, 30.20)	-88.00	(-96.80, -81.60)
TRAWL	1988 - 2010	Jun - Nov	7058.5	hours	27.52	(25.19, 29.93)	-83.43	(-97.05, -81.65)
BLL	1995 - 2013	Jul - Sept	3035	soak hours	27.68	(18.21, 30.36)	-89.06	(-97.80, -81.50)
EASA VL	2011	Apr - Nov	9720	soak hours	28.32	(25.03, 30.37)	-88.31	(-97.30, -81.76)
EASA LL	2011	Apr - Nov	2018	soak hours	28.09	(24.99, 30.36)	-88.70	(-97.30, -81.52)
Fishery-dependent								
SBLOP	2005-2012	year-round	758569	hooks	27.01	(24.50, 30.00)	-83.90	(-88.70, -82.70)
LL	2006-2013	year-round	3629990	hooks	27.00	(24.50, 29.50)	-83.80	(-94.30, -82.70)
VL	2006-2013	year-round	41615	hooks	28.20	(24.40, 30.30)	-84.20	(-96.50, -81.90)

Table 2. Delineation of life-history stages for red grouper as determined by estimated lengths (Reference). FL = fork length (in centimeters); TL = total length (in centimeters). Note that lengths used to distinguish life stages in the present study approximate (~) values reported in the literature.

Stage	Age	FL range (TL range)	Justification	Reference
Red				
Juvenile	1 - 3	14.6 – 33.0 (14.8 – 34.1)	~ length at age 1	Size-modified growth curve, Lombardi et al. 2008 (Fig. 7)
Adult	3+	> 33.0 (> 34.1)	~ length at 50% maturity	Length at maturity curve, Fitzhugh et al. 2006 (Fig. 5)

Table 3. Catches and regional proportions of red grouper collected from multiple data sources within the northern Gulf of Mexico. Data sources include: SBLOP = Shark bottom longline observer program; LL = observer longline; VL = observer vertical line; TRAWL = SEAMAP groundfish trawl survey; BLL = NMFS bottom longline survey; EASA = Expanded Annual Stock Assessment Survey (VL = vertical line, LL = longline); and Video = SEAMAP reef fish video survey. Life-history stages include juveniles (ages 1–3), and adults (ages 3+). N = number of individuals; % East = percentage of catch east of longitude 87°W (i.e., WFS); % West = percentage of catch west of longitude 87°W. Additional details for each survey are provided in the text and in Table 1.

Dataset/ Stage	N	% East	% West	N	% East	% West
SBLOP				BLL		
All	61107	100.00	0.00	1088	100.00	0.00
Ages 1 - 3	1837	100.00	0.00	36	100.00	0.00
Ages 3+	59063	100.00	0.00	999	100.00	0.00
Obs LL				EASA VL		
All	150282	99.98	0.02	64	98.44	1.56
Ages 1 - 3	4443	99.98	0.02	3	100.00	0.00
Ages 3+	140720	99.98	0.02	60	98.33	1.67
Obs VL				EASA LL		
All	57888	99.83	0.17	994	99.90	0.10
Ages 1 - 3	957	100.00	0.00	9	100.00	0.00
Ages 3+	55778	99.83	0.17	961	99.90	0.10
TRAWL				VIDEO		
All	194	100.00	0.00	1158	93.26	6.74
Ages 1 - 3	124	100.00	0.00			
Ages 3+	68	100.00	0.00			

Table 4. Summary of data used for generalized linear modeling of red grouper distributions in the northeastern Gulf of Mexico. Gears (i.e., datasets) and life-history stages are as defined in Tables 1 and 2, respectively. Proportion positive is based on the datasets used for modeling. N = number of observations where each life-history stage was present in training (train) and testing (test) datasets; corr = correlation between predictors. Note that analyses were solely conducted on data from the eastern GOM.

	Juveniles	Adults
Years	2006 – 2013	1996 – 1997, 2000 – 2013
Excluded gears	BLL, EASA	none
Proportion positive	4.80	43.75
N_{train}	1248	11968
N_{test}	632	6233
Max + corr	0.33 (latitude, gear)	0.25 (latitude, gear)
Max – corr	-0.74 (latitude, longitude)	-0.74 (latitude, longitude)

Table 5. Summary of generalized linear model fits and validation criteria for red grouper life-history stages in the northeastern Gulf of Mexico.

	Juveniles	Adults
Model performance		
Deviance explained	38.18	19.08
Adjusted R^2	0.283	0.221
AIC	6271	30550
ΔAIC	0	0
wAIC	89.8%	96.9%
BIC	6630	31019
ΔBIC	+119	+18
wBIC	0.0%	0.0%
Variable importance		
Year	7.5	0.7
Mon	2.0	1.1
Hrbins	0.3	0.3
Lonbins	13.4	7.3
Latbins	2.2	0.8
Sedtype	0.3	0.1
Depbins	1.2	4.5
Gear	18.0	5.8
Model evaluation		
AUC	0.917	0.766
Threshold	0.040	0.410
FPR	0.165	0.445
FNR	0.140	0.175
intercept	0.000	0.001
slope	1.003	0.998
r_p	0.534	0.472
r_{sp}	0.303	0.459
RMSE	0.180	0.438
BAR^2	0.033	-0.068

Table 6. Estimated parameters from the selected generalized linear model of juvenile red grouper probability of occurrence.

Parameter	Estimate	Std. Error	z value	Pr(>|z|)	Significance
(Intercept)	-1.11	0.56	-1.99	0.046	*
year 2007	-0.19	0.29	-0.66	0.511	
year 2008	0.49	0.32	1.54	0.124	
year 2009	1.27	0.26	4.95	0.000	***
year 2010	1.10	0.24	4.52	0.000	***
year 2011	0.62	0.24	2.53	0.012	*
year 2012	-0.09	0.25	-0.36	0.716	
year 2013	-0.70	0.28	-2.50	0.012	*
month 2	-0.04	0.21	-0.20	0.838	
month 3	0.11	0.19	0.57	0.566	
month 4	0.15	0.20	0.78	0.435	
month 5	0.02	0.20	0.11	0.914	
month 6	0.37	0.22	1.71	0.088	.
month 7	0.27	0.21	1.27	0.203	
month 8	-0.78	0.27	-2.84	0.004	**
month 9	0.09	0.21	0.44	0.660	
month 10	0.39	0.21	1.86	0.062	.
month 11	-0.22	0.21	-1.07	0.284	
month 12	-0.63	0.24	-2.70	0.007	**
hrbins (12,18]	0.34	0.15	2.28	0.022	*
hrbins (18,24]	-0.30	0.23	-1.32	0.187	
hrbins (6,12]	0.31	0.15	2.15	0.032	*
lonbins (-83,-82.5]	0.04	0.35	0.13	0.899	
lonbins (-83.5,-83]	-0.99	0.37	-2.67	0.008	**
lonbins (-84,-83.5]	-1.43	0.39	-3.64	0.000	***
lonbins (-84.5,-84]	-1.65	0.43	-3.89	0.000	***
lonbins (-85,-84.5]	-2.35	0.48	-4.93	0.000	***
lonbins (-87,-85]	-3.61	0.58	-6.25	0.000	***
latbins (25,26]	0.76	0.27	2.80	0.005	**
latbins (26,27]	0.58	0.26	2.22	0.027	*
latbins (27,28]	0.31	0.27	1.12	0.261	
latbins (28,29]	0.32	0.32	1.02	0.310	
latbins (29,31]	0.41	0.39	1.07	0.285	
sedtype sand	-0.20	0.19	-1.03	0.303	
sedtype gravel	-0.69	0.24	-2.86	0.004	**
sedtype rock	-0.33	0.20	-1.64	0.101	
depbins (100,200]	-4.67	1.05	-4.43	0.000	***
depbins (20,40]	0.44	0.24	1.86	0.063	.
depbins (40,60]	0.45	0.26	1.73	0.084	.
depbins (60,80]	-0.34	0.30	-1.11	0.267	
depbins (80,100]	-0.60	0.36	-1.67	0.095	.
gear ObsVL	-2.95	0.10	-28.35	0.000	***

gear SBLOP	0.80	0.11	7.05	0.000	***
gear TRAWL	-1.64	0.24	-6.74	0.000	***

Table 7. Estimated parameters from the selected generalized linear model of adult red grouper probability of occurrence.

Parameter	Estimate	Std. Error	z value	Pr(>lzl)	Significance
(Intercept)	-2.75	0.61	-4.50	0.000	***
year 1997	-1.72	0.94	-1.83	0.067	.
year 2000	-0.91	0.85	-1.07	0.284	
year 2001	-0.03	0.68	-0.05	0.961	
year 2002	0.44	0.99	0.45	0.655	
year 2003	0.36	0.65	0.56	0.573	
year 2004	0.89	0.64	1.39	0.165	
year 2005	-0.96	0.68	-1.42	0.154	
year 2006	0.64	0.61	1.05	0.293	
year 2007	0.75	0.60	1.24	0.216	
year 2008	0.63	0.60	1.05	0.296	
year 2009	0.99	0.60	1.65	0.099	.
year 2010	0.83	0.60	1.38	0.167	
year 2011	1.30	0.60	2.16	0.031	*
year 2012	1.19	0.60	1.98	0.048	*
year 2013	1.02	0.60	1.70	0.089	.
month 2	0.33	0.08	3.94	0.000	***
month 3	0.02	0.07	0.26	0.797	
month 4	-0.29	0.07	-4.02	0.000	***
month 5	0.20	0.07	2.79	0.005	**
month 6	0.43	0.08	5.28	0.000	***
month 7	0.38	0.07	5.28	0.000	***
month 8	0.11	0.08	1.40	0.160	
month 9	0.18	0.07	2.46	0.014	*
month 10	0.21	0.09	2.45	0.014	*
month 11	0.35	0.08	4.27	0.000	***
month 12	0.06	0.08	0.75	0.455	
hrbins (12,18]	0.40	0.09	4.60	0.000	***
hrbins (18,24]	-0.10	0.10	-0.97	0.333	
hrbins (6,12]	0.33	0.09	3.82	0.000	***
lonbins (-83.5,-83]	-0.12	0.08	-1.49	0.138	
lonbins (-84,-83.5]	0.29	0.09	3.15	0.002	**
lonbins (-84.5,-84]	0.21	0.10	2.04	0.041	*
lonbins (-85,-84.5]	-0.47	0.12	-3.90	0.000	***
lonbins (-85.5,-85]	-0.93	0.14	-6.70	0.000	***
lonbins (-86,-85.5]	-1.72	0.16	-10.83	0.000	***
lonbins (-87,-86]	-2.45	0.19	-12.99	0.000	***
latbins (25,26]	1.20	0.12	9.69	0.000	***
latbins (26,27]	1.29	0.12	11.05	0.000	***

latbins (27,28]	1.02	0.12	8.54	0.000	***
latbins (28,29]	1.13	0.13	8.74	0.000	***
latbins (29,30]	1.01	0.15	6.84	0.000	***
latbins (30,31]	0.76	0.28	2.76	0.006	**
sedtype sand	0.12	0.06	1.99	0.047	*
sedtype gravel	0.06	0.12	0.52	0.605	
sedtype rock	0.20	0.06	3.16	0.002	**
depbins (100,200]	-4.15	0.22	-18.88	0.000	***
depbins (20,40]	0.20	0.08	2.52	0.012	*
depbins (40,60]	0.36	0.09	3.98	0.000	***
depbins (60,80]	0.11	0.11	1.04	0.297	
depbins (80,100]	-0.72	0.16	-4.61	0.000	***
gear EASALL	-0.17	0.21	-0.80	0.424	
gear EASAVL	-3.31	0.27	-12.36	0.000	***
gear ObsLL	1.02	0.16	6.31	0.000	***
gear ObsVL	-0.36	0.16	-2.33	0.020	*
gear SBLOP	2.00	0.19	10.66	0.000	***
gear TRAWL	-2.50	0.28	-8.97	0.000	***

Fig. 1. The northern Gulf of Mexico where grouper distribution was investigated using fishery-dependent and fishery–independent datasets. Depth contours are labeled in 20-, 40-, 60-, 80-, 100-, and 200-m contours. Important features are labeled and include the Flower Garden Banks and the West Florida Shelf. MS = Mississippi; AL = Alabama.

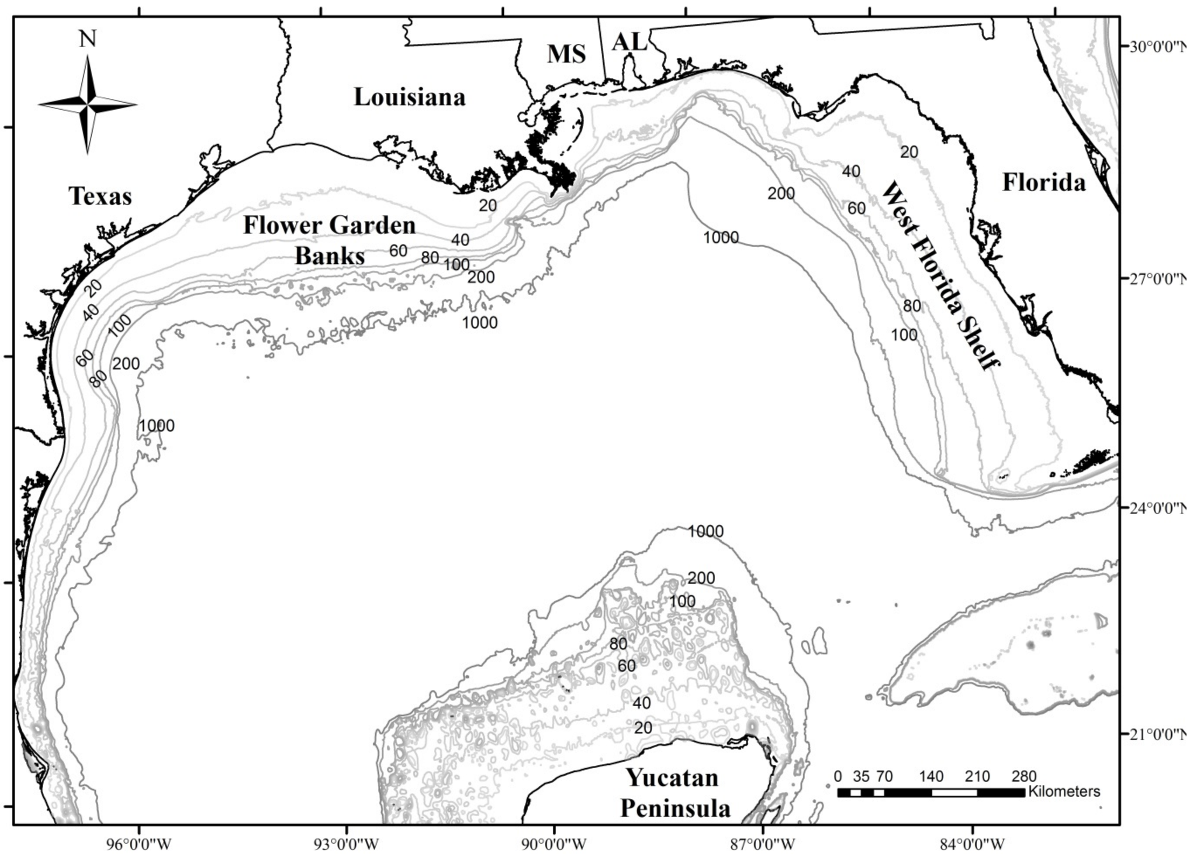

Fig. 2. Fishery-independent survey catches of red grouper throughout the northern Gulf of Mexico. Small x indicates stations where no red grouper were caught. The 200-m depth contour is shown. Note that fishery-dependent catches are not shown due to confidentiality.

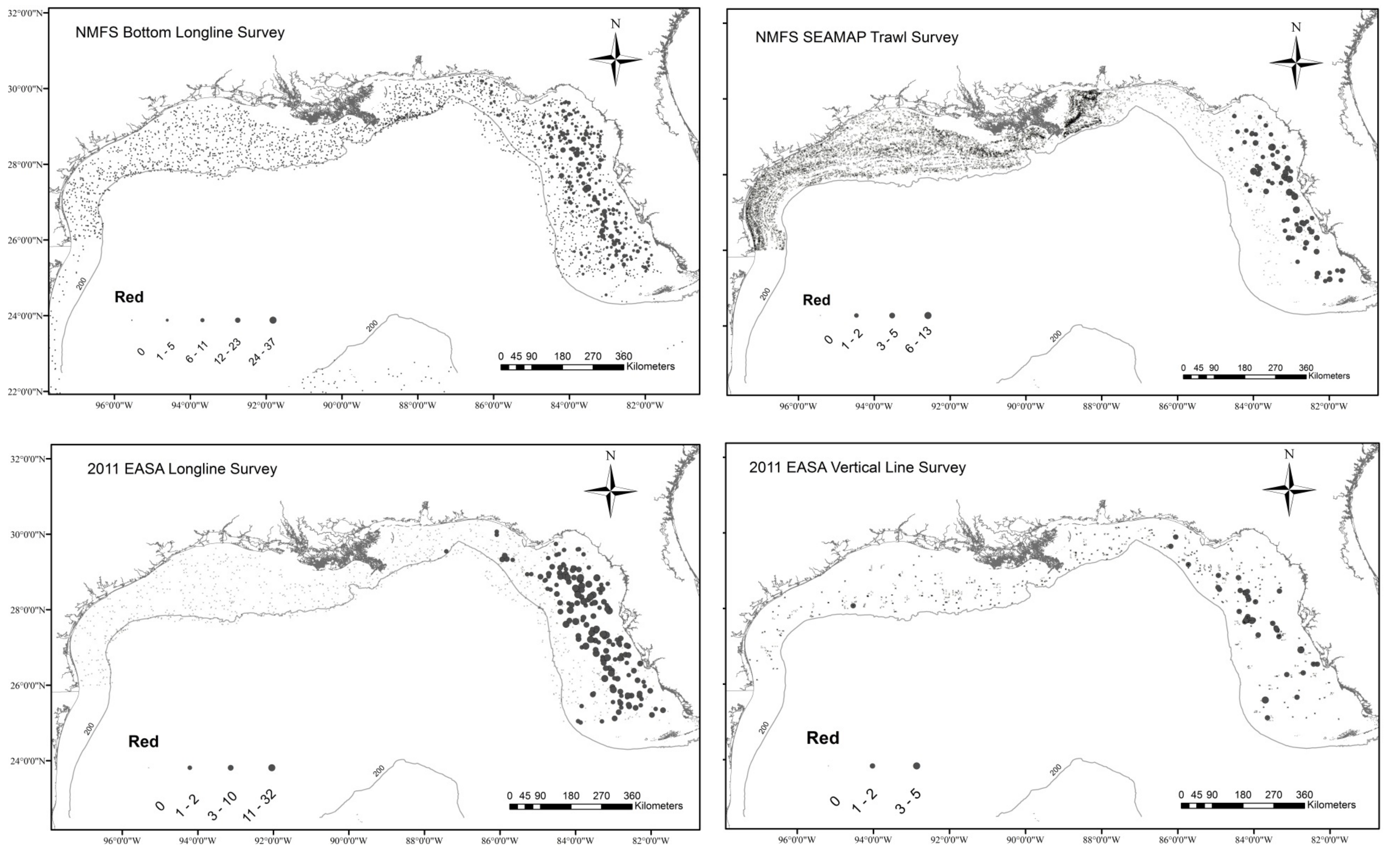

Fig. 3. Variogram model fits used for kriging residual occurrence of juvenile and adult red grouper in the northeastern Gulf of Mexico. Note that x and y axes differ between panels.

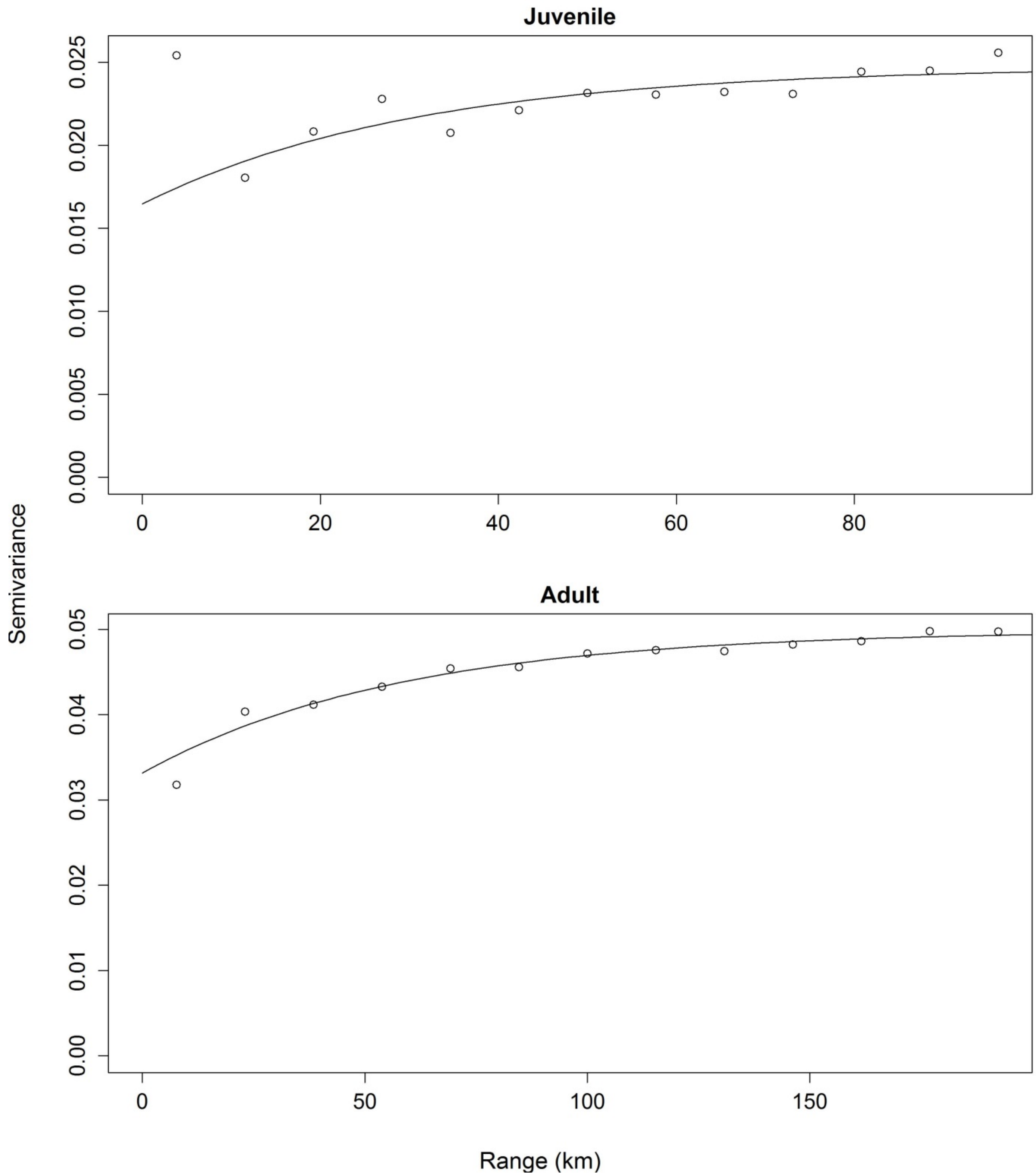

Fig. 4. Modeled distribution and associated standard error for juvenile and adult red grouper throughout the northeastern Gulf of Mexico. The index plotted combines the predicted probability of occurrence estimated by a binomial generalized linear model with residual occurrence estimated by ordinary kriging. Note that only areas where the probability of occurrence exceeded the receiver operator characteristic curve threshold are plotted.

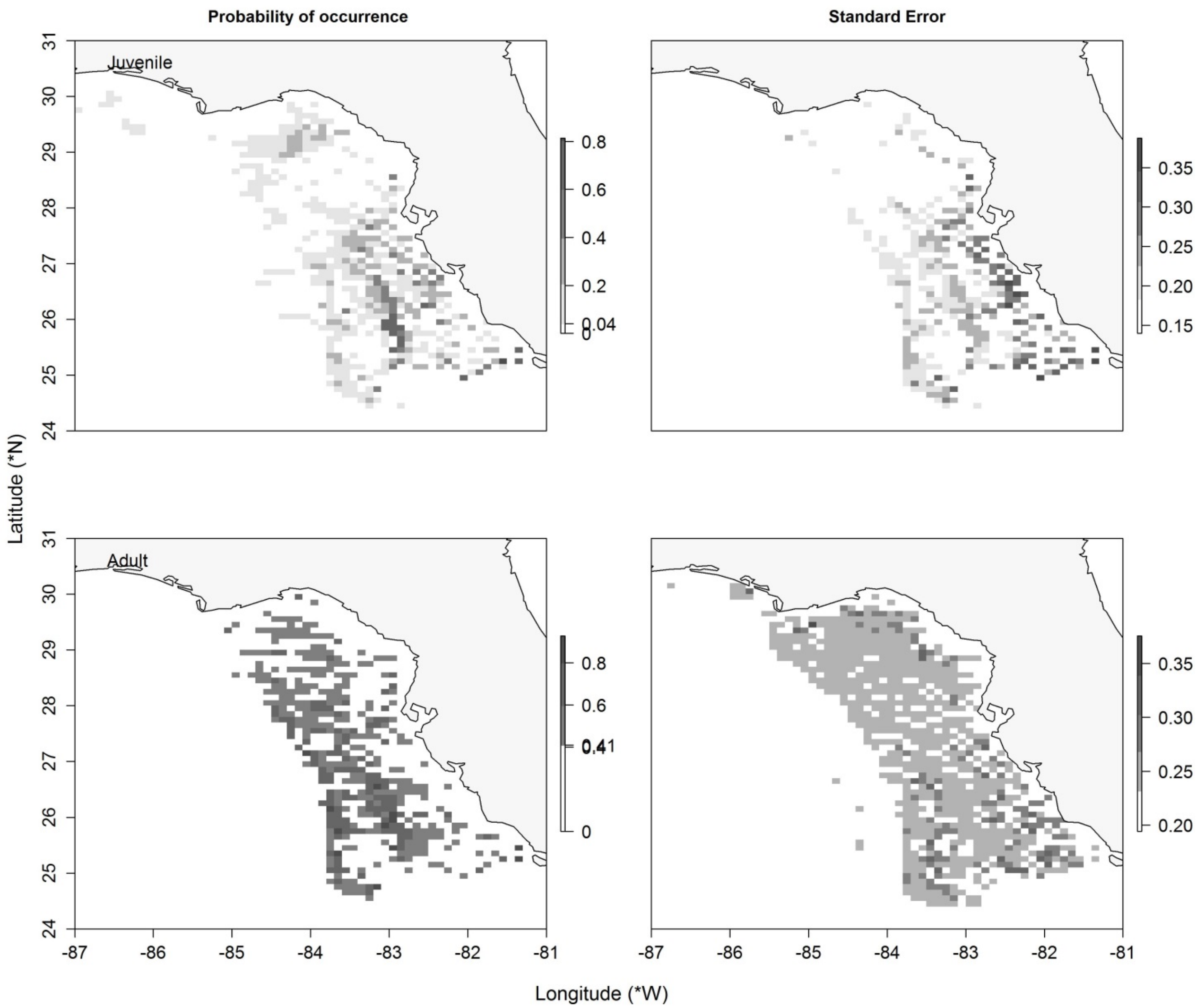

Fig. 5. Predicted presence (black) and absence (gray) of red grouper life-history stages and annual red tide events throughout the West Florida Shelf between 1999 and 2010 based on threshold values obtained through generalized linear modeling. Red grouper thresholds are given in Table 5. A threshold of 0.0541 was used for red tide (Walter et al. 2013). Red grouper distribution is assumed constant through time whereas red tide distribution changes each year. Note that red tide distribution is restricted to depths between 10 m and 100 m where the predictive model is deemed reliable.

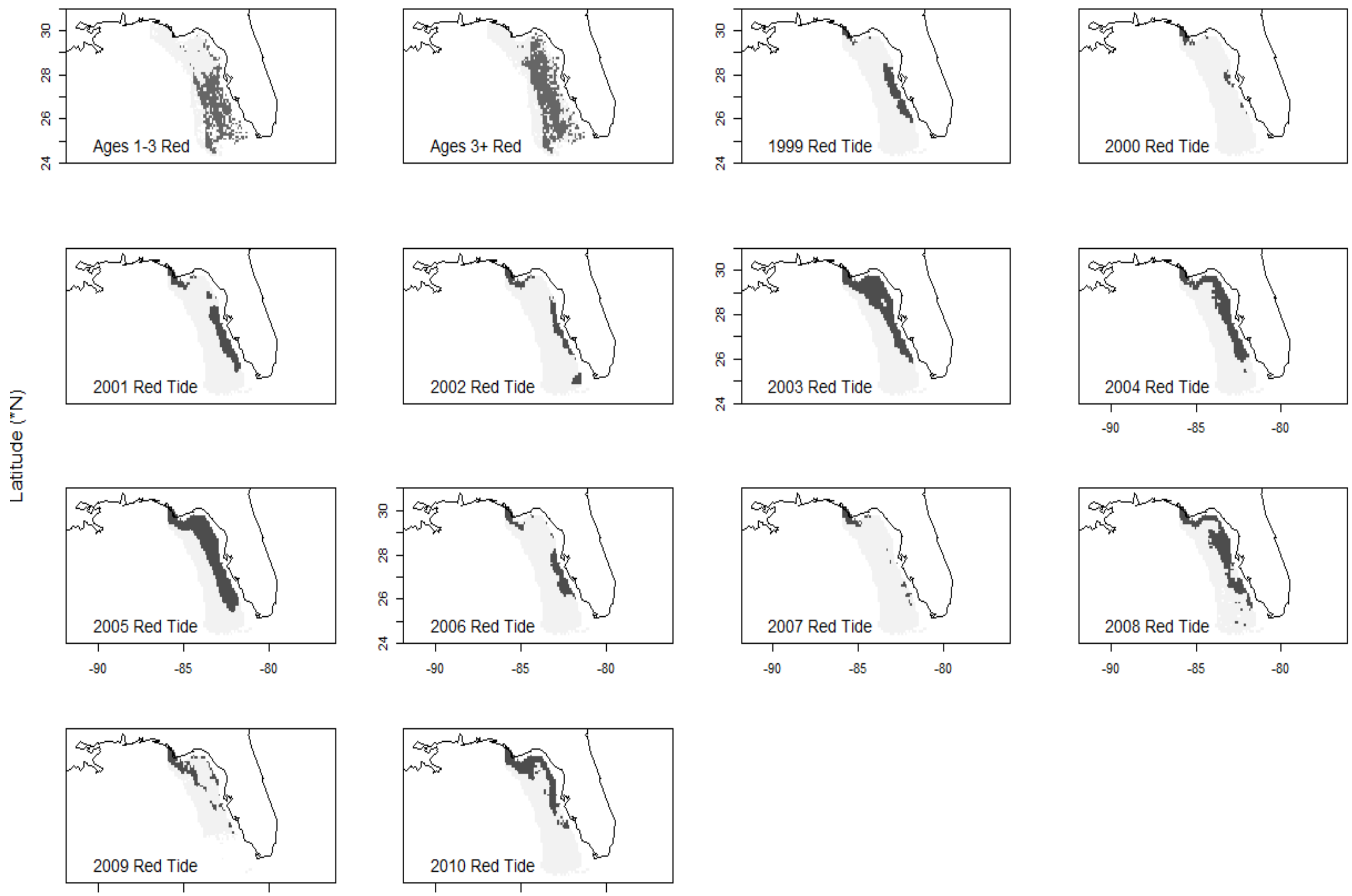

Fig. 6. Exposure of red grouper to red tide events based on percent spatial overlap (*SO*) of juvenile and adult distributions with red tide events derived from model-based predictions. *SO* was calculated as the number of cells with both red tide and red grouper predicted to occur divided by the number of cells where red grouper was predicted to occur and where red tide prediction was feasible.

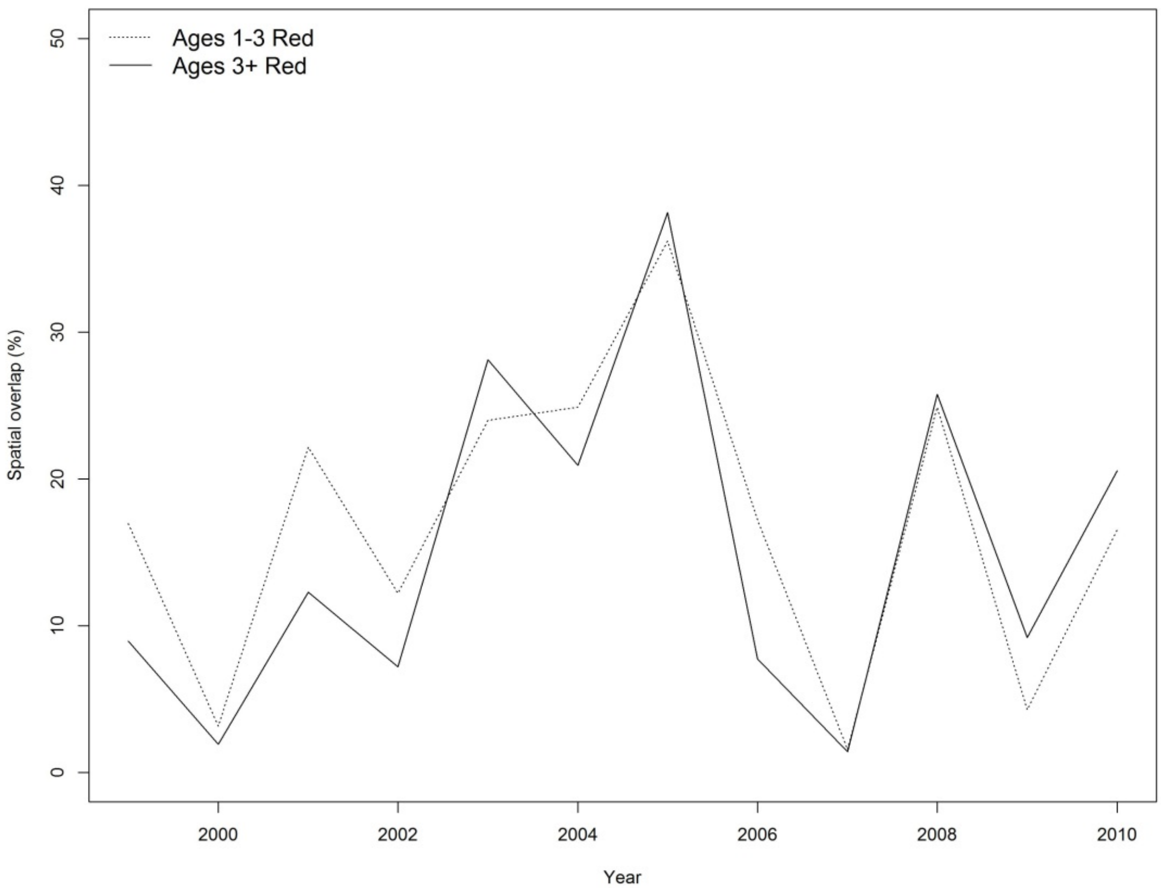

Fig. 7. Exposure of red grouper to red tide events based on NMFS bottom longline survey catches. Exposure was estimated as the percentage of total survey catch in grid cells where red tide was predicted to occur divided by the entire survey catch.

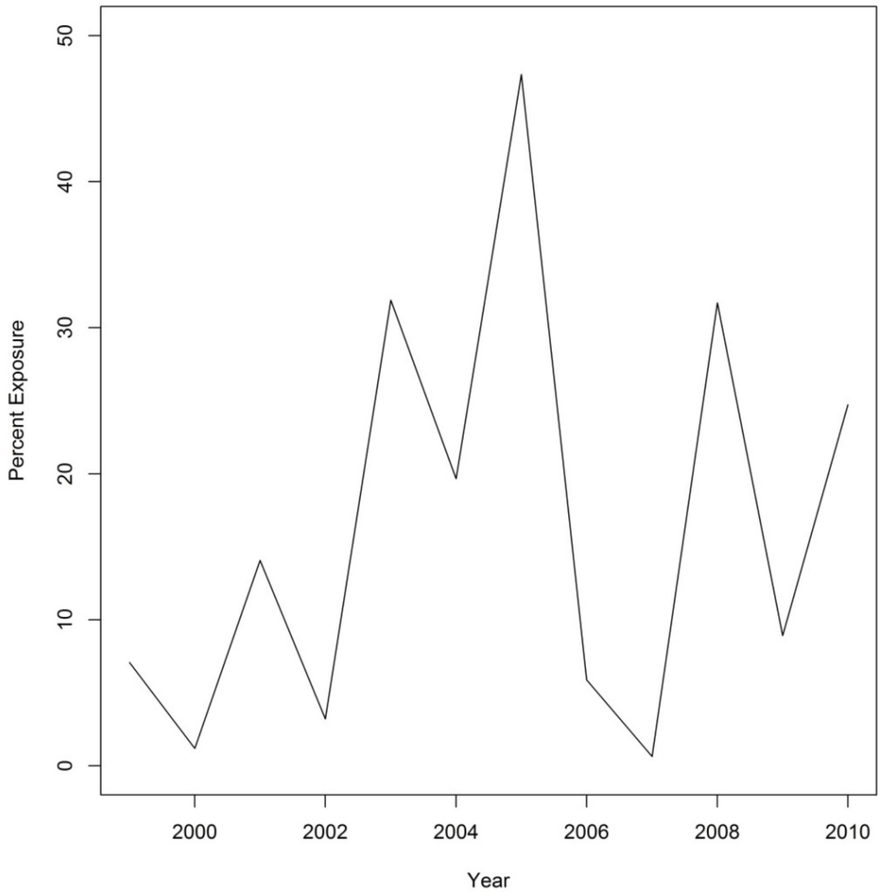

Fig. 8. Comparison between red grouper occurrence (black line) west of 87°W longitude and storm intensity. Storm intensity is measured by mean category (dashed line) and maximum category (numbers).