

Evaluating spatial management options for tiger shark (*Galeocerdo cuvier*) conservation in US Atlantic Waters

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There has been debate in the literature over the use and success of spatial management zones (i.e. marine protected areas and time/area closures) as policy tools for commercially exploited sharks. The tiger shark (*Galeocerdo cuvier*) is a highly migratory predator found worldwide in warm temperate and tropical seas, which is caught in multiple US fisheries. We used a spatially explicit modelling approach to investigate the impact of varying spatial management options in the Western North Atlantic Ocean on tiger shark biomass, catch, and distribution, and impacts to other species in the ecosystem. Results suggest that under current management scenarios, tiger shark biomass will increase over time. Model outputs indicate that protecting additional habitats will have relatively minimal impacts on tiger shark biomass, as would increasing or decreasing protections in areas not highly suitable for tiger sharks. However, increasing spatial management protections in highly suitable habitats is predicted to have a positive effect on their biomass. Results also predict possible spill-over effects from current spatial protections. Our results provide insights for evaluating differing management strategies on tiger shark abundance patterns and suggest that management zones may be an effective conservation tool for highly migratory species if highly suitable habitat is protected.

Keywords: marine protected areas, spatial modelling, tiger shark

Introduction

Populations of many migratory marine fishes, such as sharks, tunas, and billfish, are heavily exploited, and many species are exhibiting varying levels of population decline across their range (Myers and Worm, 2003; Hutchings and Reynolds, 2004; Neubauer *et al.*, 2013). A variety of management measures have been used to protect sharks from over-fishing, including catch prohibitions, catch limits, product bans, gear restrictions, and spatial zoning (reviewed in Shiffman and Hammerschlag, 2016a). There has been great debate in the literature over the use and success of marine protected areas (MPAs) and time/area closures (i.e. spatial zoning) as management tools for sharks and other highly migratory fishes (e.g. Mora *et al.*, 2006; Pelletier *et al.*,

2008; Dwyer *et al.*, 2020). This issue is exemplified in the results of a survey to members of shark and ray research societies assessing their knowledge of and attitudes toward different conservation policies for sharks (Shiffman and Hammerschlag, 2016b). Responses were mixed in terms of the most effective management tools, but respondents were generally less supportive of newer limit-based conservation tools (i.e. policies that ban exploitation without a species-specific focus such as MPAs, time/area closures, or shark sanctuaries) than of traditional target-based fisheries management tools (e.g. fishing quotas). This may be in part related to a paucity of studies evaluating the potential benefits of these newer limit-based conservation policy tools over more traditional tools (Shiffman and Hammerschlag, 2016b).

Accordingly, there is a need to further evaluate the potential use of spatial management zones for the conservation of migratory shark species.

The literature suggests that the success of spatial closures for the conservation of highly migratory fishes will depend on the size and configuration (i.e. shape) of the closure, fishing pressure outside of the closer area, if the closure is set up as a no-take vs. no-entry area, time-period of closures, the life-stages of organisms that use the closed area/s, and fish movement rates (Dinmore *et al.*, 2003; Escalle *et al.*, 2015; Speed *et al.*, 2018; Dwyer *et al.*, 2020). Several recent studies have evaluated the spatial extent to which high use areas or “hotspots” for sharks have overlapped with MPA boundaries (e.g. Espinoza *et al.*, 2015; Graham *et al.*, 2016; Acuña-Marrero *et al.*, 2017; Welch *et al.*, 2018). However, for the most part, these studies have not investigated how shark populations may respond to alternative MPA configurations, which would provide some predictive power for policy managers when assessing different management strategies.

Another key research priority is to understand whether MPA protections of large sharks, and other top predators, have food-web effects, such as conserving or restoring natural trophic interactions (Bond *et al.*, 2019, Cheng *et al.*, 2019, Hammerschlag *et al.*, 2019). For example, in coral reef atolls off Western Australia, enforcement of no-take MPAs has led to trophic changes in the shark community, with the proportion of apex species increasing and the proportion of lower trophic species decreasing (Speed *et al.*, 2018). Additional studies are thus needed to further predict how MPA-driven protections and recoveries of shark populations affect other species (hereafter both MPAs and time/area closures are referred to as spatial management zones).

Spatially explicit models (models that include spatial concepts into their formulations; DeAngelis and Yurek, 2017) can be used to investigate the potential effects of spatial management zones on fish and fisheries. The complexity of spatial models can range from simple one-dimensional models to complex models that combine movement, fishing, and population dynamics (Pelletier and Mahevas, 2005). The results of spatially explicit models can be used to help predict if and how spatial management zones benefit various species across trophic levels, can provide evidence for alternative time/area closures locations, and/or provide information on species population trends in closed vs. open areas over time.

The tiger shark (*Galeocerdo cuvier*) is a large (up to 5.5 m in length), highly migratory apex predator found worldwide in tropical and warm temperate seas (Compagno, 2005). Although primarily a wide-ranging oceanic species, tiger sharks have also been known to show site fidelity in a variety of other habitats, including coral reefs, oceanic atolls, and shallow bays or flats (e.g. Meyer *et al.*, 2009; Acuña-Marrero *et al.*, 2017; Fitzpatrick *et al.*, 2012; Hammerschlag *et al.*, 2012, 2015; Hazin *et al.*, 2013; Papastamatiou *et al.*, 2013; Werry *et al.*, 2014). This species is a generalist, opportunistic frager, exhibiting ontogenetic increases in prey diversity (Dicken *et al.*, 2017), but also known to target sea turtles at nesting beaches (e.g. Fitzpatrick *et al.*, 2012; Acuña-Marrero *et al.*, 2017). Aspects of movement, demography, diet, habitat suitability, and reproductive ecology of this species have been studied at various sites and scales within the Western North Atlantic and Gulf of Mexico (e.g. Kohler *et al.*, 1998; Driggers *et al.*, 2008; Carlson *et al.*, 2012; Hammerschlag *et al.*, 2013; Leah *et al.*, 2015; Vaudo *et al.*, 2016; Sulikowski *et al.*, 2016; Calich *et al.*, 2018; Rooker *et al.*, 2019). In addition, habitat use of this species

in relation to spatial management zones in parts of the subtropical Western North Atlantic (Graham *et al.*, 2016; Calich *et al.*, 2018) and in relation to longline fisheries within international waters of the Mid-Atlantic Ocean (Queiroz *et al.*, 2016, 2019) has been investigated. While tiger sharks remain a significant component of US recreational and commercial shark fisheries (NOAA, 2018), their populations appear to be recovering in the Western North Atlantic from historical overfishing (Peterson *et al.*, 2017). This recovery has been hypothesized to be driven in part by opportunistic protection of tiger shark highly suitable habitat within large spatial zones restricting longline fishing (Calich *et al.*, 2018). Taken together, the former studies on tiger sharks in the region provide data useful for informing and testing the results of spatially explicit models examining the effects of various spatial management strategies on the biomass of tiger sharks in the Western North Atlantic Ocean and Gulf of Mexico.

Ecopath with Ecosim (EwE) modelling has been used in previous studies to investigate various spatial management measures and to investigate rebuilding of species of interest (Zeller and Reinert, 2004; Fouzai *et al.*, 2012; Varkey *et al.*, 2012; Abdou *et al.*, 2016). Our study is a simulation study investigating the impacts of spatial management zones on a marine ecosystem. Specifically, we used an EwE spatially explicit modelling approach to investigate the potential impact of varying spatial management zones on tiger shark biomass, catches, and re-distribution, along with impacts to other species in the ecosystem, within US territorial waters of the Western North Atlantic Ocean and Gulf of Mexico. Specifically, we modelled how increasing or decreasing current spatial management zones would affect the biomass and catch rates of tiger sharks as well as other species over time. In addition, we ran several sensitivity analyses to determine the impact three parameters: (i) vulnerability, which is one of the most sensitive parameters in Ecosim (Christensen and Walters, 2004; Christensen *et al.*, 2008), (ii) fishing mortality rates, which are currently unknown for tiger sharks, and (iii) dispersal rates, which are currently unknown for tiger sharks.

Methods

The EwE software package, based on Polovina (1984), has been widely used since the 1980s to analyze exploited aquatic ecosystems through the use of food-web models (e.g. Libralato, 2006; Zhang and Chen, 2007). The Ecopath modelling system estimates biomass and food consumption of species or species groups in an ecosystem and analyzes an ecosystem’s trophic mass balance. Ecosim subsequently uses the mass-balance results from Ecopath for parameter estimation in conjunction with time series data of fishing mortality rates, abundance, catch, and/or total mortality to calibrate the model (Christensen *et al.*, 2008). Ecospace is the spatial component of the Ecopath model, which allows for the analysis of spatial management zones. Within Ecospace, the biomass of the species included in the model is dynamically allocated across a base map.

To assess the impact of spatial management zones on the biomass and catches of tiger sharks over time, we had to first develop an Ecopath model. The complete EwE model and parameters are described and explained within Christensen *et al.* (2008).

Study area

The study area that represents the modelled area is the US economic exclusive zone (EEZ) in Atlantic and Gulf of Mexico

waters (Figure 1a). The US EEZ extends 200 nautical miles offshore. The US east coast EEZ is 915 763 km² (353 578 sq mi) and the Gulf coast EEZ is 707 832 km² (273 295 sq mi) (Searounds.org). These waters include a variety of habitats including coral reefs, canyons, and seamounts and encompass essential fish habitats (EFH) for a variety of fish and

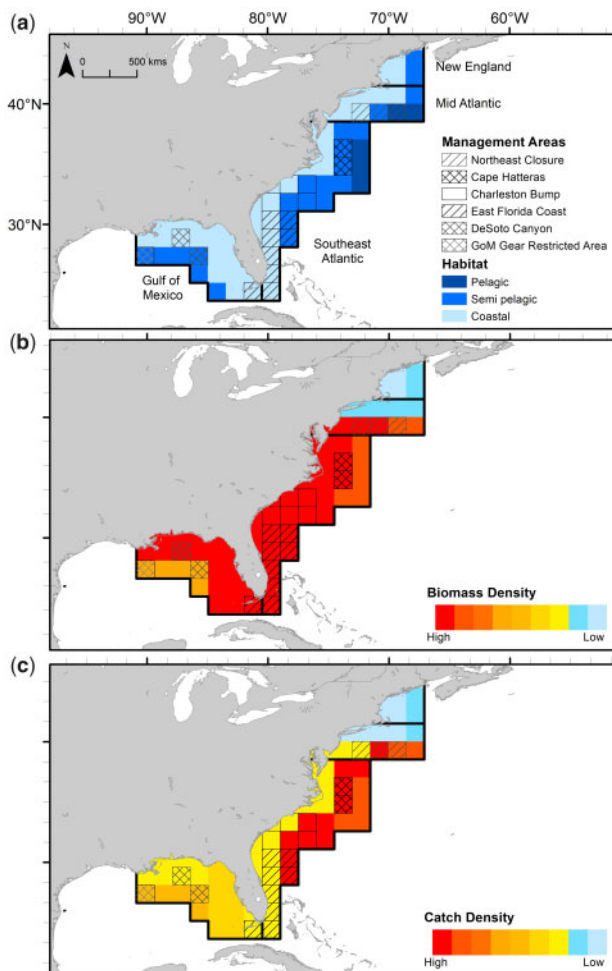


Figure 1. Pelagic longline gear spatial management zones and corresponding marine habitats (a), biomass density (b), and catch density outputs (c) used in the base case model. (a) Each of the six spatial management zones are identified with different overlay patterns (see legend for details and National Marine Fisheries Service (NMFS), 2006 for further information). Marine habitats are identified as “coastal” (light blue), “semi-pelagic” (medium blue), or “pelagic” (dark blue). Figure adapted from the raw Ecospace output to aid with visual interpretation of the results, see Supplementary Figure S1 for raw Ecospace output. (b) Ecospace baseline map output showing the relative spatial distribution of tiger shark biomass. Biomass densities range from high (red) to low (blue) and were derived from initial Ecopath values. Figure adapted from the raw Ecospace output to aid with visual interpretation of the results, see Supplementary Figure S2 for raw Ecospace biomass output. (c) Ecospace baseline map output showing the relative spatial distribution of tiger shark catches. Catch densities range from high (red) to low (blue) and were derived from initial Ecopath values. Figure adapted from the raw Ecospace output to aid with visual interpretation of the results, see Supplementary Figure S3 for raw Ecospace catch output.

invertebrate species (McGregor and Lockwood, 1985; GARFO, 2018).

Ecopath

Ecopath uses a system of linear equations to describe the flow of mass and energy between species groups (Christensen *et al.*, 2008). We have not included details of the modelling methods (i.e. equations) in this manuscript because they are well known and have already been provided in numerous other peer-reviewed publications and can be found in Christensen *et al.* (2008). The central Ecopath mass-balance equation is:

$$B_i \frac{P_i}{B_i} EE_i - \sum \left(B_j \frac{Q_j}{B_j} DC_{ji} \right) - Y_i - E_i - BA_i = 0. \quad (1)$$

B_i is the biomass of prey i ; P/B_i is the production/biomass rate or natural mortality of i ; EE_i is the ecotrophic efficiency of i and represents the fraction of the production of i transferred to higher trophic levels or exported; B_j is the biomass of predator j ; Q/B_j is the consumption/biomass of predator j ; DC_{ji} is the fraction of i in the diet of j ; Y_i is the total fishery catch rate of i ; E_i is the net migration rate (emigration-immigration); and BA_i is the biomass accumulation rate for i .

Input parameters and model balancing

Our model included 25 functional groups (defined as trophically similar species or single species) known to inhabit the modelled ecosystem, including primary producers, detritus, mid-level, and top predators (Supplementary Table S1). Input parameters biomass (B), production/biomass ratio (P/B), and consumption to biomass ratio (Q/B) were collected from published literature and stock assessment reports (Table 1). Information on the diet and fishery removals for each species/group was taken from current literature. Landings data (considered “catch” in the Ecopath model and subsequent outputs) were extracted from the National Marine Fisheries Service landings database for each species/group (except for species such as marine mammals with no landings data) (National Marine Fisheries Service (NMFS), 2018; Christensen *et al.*, 2008). Landings data from eight fisheries (gill-net, handline/troll/pole, bottom and pelagic longline, trawl, seine net, pots and traps, nets and dredge), representing fisheries for all species included in the ecosystem, were included in the model. We used the Pedigree option within Ecopath to assign confidence intervals to the data (B , P/B , Q/B , diet, and catch) based on their origin (Christensen *et al.*, 2008).

Model validation

To verify biological parameter estimates, we applied several pre-balance diagnostics identified by Link (2010). We assessed the following through these pre-balance diagnostics: (i) biomass levels across taxa and trophic levels, (ii) production to consumption (P/Q) ratio, (iii) biomass (B) ratios of predator and prey compared to the ratios of production to biomass (P/B), and (iv) consumption to biomass ratios (Q/B) compared to respiration to biomass (R/B) (i.e. vital rates) by taxa. In a biologically realistic model, the biomass levels will exhibit a generally increasing trend as the trophic levels decrease, the P/C ratios will be <1 and confined between 0.1 and 0.3, the predator to prey B ratios will be <1 (density dependent predation rates based on foraging arena

Table 1. List of species and species groups included in the model along with their Ecopath parameter outputs (trophic level, biomass in habitat area, biomass, production/biomass, consumption/biomass, ecotrophic efficiency, and production/consumption).

Group name	Trophic level	Biomass in habitat area (t/km ²)	Biomass (B) (t/km ²)	Production/biomass (P/B) (1/year)	Consumption/biomass (Q/B) (1/year)	Ecotrophic efficiency	Production/consumption	Reference
Baleen whale	3.16	0.03	0.03	0.03	6.00	0.68	0.01	Byrd <i>et al.</i> (2017)
Toothed whale	4.31	0.03	0.03	0.03	6.69	0.81	0.00	Byrd <i>et al.</i> (2017)
Tuna	3.85	0.04	0.04	1.30	5.50	0.76	0.24	SCRS (2017)
Billfish	3.84	0.03	0.03	0.80	4.70	0.18	0.17	SCRS (2017) and Froese and Pauly (2018)
Pelagic sharks	4.17	0.02	0.02	0.42	3.20	0.52	0.10	SCRS (2017) and Froese and Pauly (2018)
Tiger shark	4.07	0.01	0.01	0.35	2.00	0.87	0.16	Southeast Data and Assessment Report (SEDAR) (2006) and Froese and Pauly (2018)
Large sharks	4.03	0.03	0.03	0.32	2.50	0.44	0.13	Southeast Data and Assessment Report (SEDAR) (2006) and Froese and Pauly (2018)
Small sharks	3.72	0.03	0.03	0.70	6.00	0.67	0.12	Southeast Data and Assessment Report (SEDAR) (2007) and Froese and Pauly (2018)
Sea turtles	3.56	0.01	0.01	0.80	3.00	0.48	0.27	National Marine Fisheries Service (NMFS) (2013)
Skates and Rays	3.62	0.03	0.03	0.80	5.00	0.71	0.16	Northeast Fisheries Science Center (NEFSC) (2007) and Froese and Pauly (2018)
Reef fish	3.61	0.18	0.18	1.30	4.50	0.78	0.29	Link <i>et al.</i> (2006) and Froese and Pauly (2018)
Squid	2.91	0.10	0.10	1.60	6.90	0.91	0.23	Northeast Fisheries Science Center (NEFSC) (2011)
Cephalopods	3.51	0.20	0.20	0.70	2.50	0.93	0.28	Link <i>et al.</i> (2006)
Shrimp	2.75	0.04	0.04	2.60	113.50	0.95	0.02	Link <i>et al.</i> (2006)
Crustaceans	2.76	0.10	0.10	3.00	11.59	0.78	0.26	Link <i>et al.</i> (2006)
Invertebrates	2.66	0.14	0.14	2.00	13.50	0.47	0.15	Link <i>et al.</i> (2006)
Other fish	2.88	1.00	1.00	1.30	4.38	0.41	0.30	Link <i>et al.</i> (2006)
Bivalves	2.34	0.55	0.55	2.16	7.20	0.98	0.30	Link <i>et al.</i> (2006)
Benthic invert	2.66	0.57	0.57	2.80	24.68	0.99	0.11	Link <i>et al.</i> (2006)
Polychaetes	2.28	0.10	0.10	40.00	141.56	0.58	0.28	Link <i>et al.</i> (2006)
Gelatinous zooplankton	2.32	0.40	0.40	30.00	103.42	0.46	0.29	Link <i>et al.</i> (2006)
Macro zooplankton	2.20	0.48	0.48	50.00	227.65	0.28	0.22	Link <i>et al.</i> (2006)
Micro zooplankton	2.00	0.87	0.87	65.00	227.65	0.68	0.29	Link <i>et al.</i> (2006)
Phytoplankton	1.00	2.00	2.00	160.00	0.00	0.55		Link <i>et al.</i> (2006)
Detritus	1.00	5.00	5.00			0.46		Link <i>et al.</i> (2006)

theory; Christensen *et al.* 2008), and the vital rates will also show a general decrease with increasing trophic levels (Link, 2010).

The input parameter values, after they underwent diagnostics, were used in mass balancing the model. This final static mass-balanced model is hereafter referred to as the “base case” model.

Ecosim

Ecosim was used to run model simulations over time. Ecosim uses the balanced Ecopath parameters to produce estimates of biomass and catch rates over time and a detailed description of these equations, not included in this manuscript because they have been published numerous times, and model can be found in Christensen *et al.* (2008).

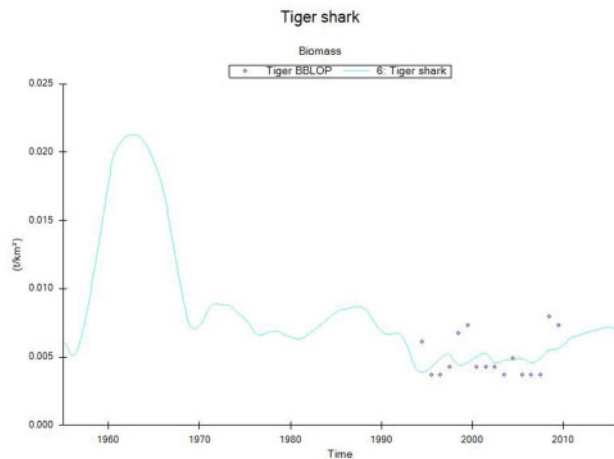


Figure 2. Ecosim estimated tiger shark biomass (straight line) (1950–2018) and catch per unit effort for the bottom longline observer programme (dotted lines).

Model fitting and performance testing

To project change over time, we first developed an Ecosim model that used time series data from a static baseline model describing conditions in 1950 (when fishing data records began). Time series of abundance, catch rates, fishing mortality, and catch were used to verify predictions of the model over 67 years (from 1950 to 2018), which allowed us to maximize the use of historical data for parameterizing Ecosim (Figure 2). Time series of abundance and fishing mortality data, when available, were collected from the most recent stock assessment reports (Table 1) (Christensen *et al.*, 2008). We calibrated the model using a step-wise non-linear optimization routine to (i) estimate vulnerability parameters (the impact of large increases in predator biomass on predation mortality of prey, a low value indicates bottom up control, and high values indicate top down control) parameters, and (ii) indicate how well the model fit the data (using Akaike’s information criteria to compare results of each model run) (Christensen *et al.*, 2008; Mackinson *et al.*, 2009). To start, the model was rescaled from the 2006 baseline, which was selected to represent when the US federal Highly Migratory Species Fishery Management Plan was adopted, to the historic 1950 baseline level. Information contained within stock assessments and other published literature was used to inform the decision to increase biomass and decrease fishing mortality and catch levels during the rescaling (Table 1). The final 1950 model estimates were compared to our original 2006 model estimates to provide confidence in the rescaled parameters. We used the following two methods to tune the model by reducing the sum of squares (Christensen *et al.*, 2008; Byron and Morgan, 2017).

- (1) Simulated the base case Ecosim model with a default vulnerability level of 2 and with all time-series.
- (2) Used the automated calibration procedure to search for sensitive vulnerabilities. Vulnerability parameters the model is most sensitive to were searched for (i) all predator–prey interactions (30 parameters) and (ii) groups with time series (nine parameters). We used the Ecosim built in Vulnerability Search for this procedure. Any gross deviations that resulted in clearly unrealistic results were manually corrected by the authors (Christensen *et al.*, 2008).

The resulting final base case model was used in all scenarios mentioned below.

Ecospace

Ecospace software was used to develop a base case model, based on the mass-balance model developed through Ecopath and Ecospace, representing the US EEZ waters within the Western North Atlantic Ocean (and Gulf of Mexico). Details of the Ecopath model can be found in Christensen *et al.* (2008). The basemap consisted of 5 km × 5 km grid cells covering 20 rows and 20 columns. The base case model represents the entire ecosystem inhabited by tiger sharks in the study area and included 12 habitats (coastal, semi-pelagic, and pelagic habitats for each of the Gulf of Mexico, Southeast Atlantic, Mid-Atlantic, and New England regions) and 6 current spatial management zones that restrict the use of pelagic longline fishing gear (Cape Hatteras Gear Restricted Area, Charleston Bump Closed Area, East Florida Coast Closed Area, Desoto Canyon Closed Area, and northeast US closure and Gulf of Mexico Gear Restricted Areas; National Marine Fisheries Service (NMFS), 2006; Figure 1a and Table 2).

Parametrizing the base case model

In the base case model, species dispersal rates (relative population dispersal rates due to random movements), relative dispersal in “non-preferred” habitats, and relative feeding rates in non-preferred habitats were set based on information provided in the literature (Ortiz and Wolff, 2002; Christensen *et al.*, 2003, 2008; Zeller and Reinert, 2004; Martell *et al.*, 2005; Chen *et al.*, 2009). Dispersal rates, which represent net residual movement rates (annual), net swimming speeds, were set to 300 km/year for species with high mobility (Christensen *et al.*, 2008), 30 km/year for species with medium mobility, and 3 km/year for species with low mobility. These rates are used in Ecospace to calculate the fraction of biomass of a species/group in a cell that would move to the adjacent cell during the next time step (Christensen *et al.*, 2008). Dispersal rates were set based on the information on movement patterns of species/groups, per Ecospace guidelines (Christensen *et al.*, 2008) and as done in other Ecospace studies (i.e. Varkey *et al.*, 2012; Abdou *et al.*, 2016). Relative dispersal rates in unsuitable habitats (dispersal rates are assumed to be different between non-preferred and preferred habitats) can range from 1.0 to 5.0 within a model, with 2.0 being the Ecospace default value (Christensen *et al.*, 2008). Values selected for our model can be found in Supplementary Table S2. Relative feeding rates in unsuitable habitats in our model ranged from 0.01 for species with trophic levels (Table 1) between 2 and 3.5, 0.3 for species with trophic levels between 3.5 and 4, and 0.6 for species with a trophic level greater than 4 (Supplementary Table S2). Relative vulnerability to predation in unsuitable habitats was set to 2, meaning that a species was twice as vulnerable to predation in unsuitable habitats compared to suitable habitats (Christensen *et al.*, 2008).

Individual species were assigned to “preferred habitats” within the base case model based on information available on the biology and ecology of the species (Supplementary Table S3). In Ecospace, preferred habitats mean the species/group will have (i) a higher feeding and growth rate, (ii) higher survival rate, and (iii) movement rate is higher outside than within good habitats

Table 2. List and description of spatial management zones.

Time/area closure	Months closed	Specific management policy	Location
Cape Hatteras Restricted Area	December–April	Reduce interactions with bluefin tuna	Coordinates for this area are as follows: clockwise from the southernmost shoreward point, starting at 34°50'N lat., 75°10'W long; 35°40'N lat., 75°10'W long; 35°40'N lat., 75°00'W long; 37°10'N lat., 75°00'W long; 37°10'N lat., 74°20'W long; 35°30'N lat., 74°20'W long; 34°50'N lat., 75°00'W long; 34°50'N lat., 75°10'W long.
Charleston Bump	February–April	Closed to vessels with pelagic longline gear	The Atlantic Ocean seaward of the inner boundary of the US EEZ from a point intersecting the inner boundary of the US EEZ at 34°00'N lat. near Wilmington Beach, North Carolina, and proceeding due east to connect by straight lines the following coordinates in the order stated: 34°00'N lat., 76°00'W long; 31°00'N lat., 76°00'W long; then proceeding due west to intersect the inner boundary of the US EEZ at 31°00'N lat. near Jekyll Island, Georgia.
East Florida Coast	Year round	Closed to vessels with pelagic longline gear	The Atlantic Ocean seaward of the inner boundary of the US EEZ from a point intersecting the inner boundary of the US EEZ at 31°00'N lat. near Jekyll Island, Georgia, and proceeding due east to connect by straight lines the following coordinates in the order stated: 31°00'N lat., 78°00'W long; 28°17'10"N lat., 79°11'24"W long; then proceeding along the outer boundary of the EEZ to the intersection of the EEZ with 24°00'N lat.; then proceeding due west to the following coordinates: 24°00'N lat., 81°47'W long; then proceeding due north to intersect the inner boundary of the US EEZ at 81°47'W long. near Key West, Florida
DeSoto Canyon	Year round	Closed to vessels with pelagic longline gear	The area is bounded by straight lines connecting the following coordinates, in the order given: 30°00'N lat., 88°00'W long; 30°00'N lat., 86°00'W long; 28°00'N lat., 86°00'W long; 28°00'N lat., 84°00'W long; 26°00'N lat., 84°00'W long; 26°00'N lat., 86°00'W long; 28°00'N lat., 86°00'W long; 28°00'N lat., 88°00'W long; 30°00'N lat., 88°00'W long.
Gulf of Mexico Gear Restricted Area (longline restricted area)	April–May	Reduce interactions with bluefin tuna during spawning season	The first area from the southernmost seaward point clockwise are: 26°30'N lat., 94°40'W long; 27°30'N lat., 94°40'W long; 27°30'N lat., 89°W long; 26°30'N lat., 89°W long; 26°30'N lat., 94°40'W long; the second area from the southernmost seaward point clockwise are: 27°40'N lat., 88°W long; 28°N lat., 88°W long; 28°N lat., 86°W long; 27°40'N lat., 86°W long; 27°40'N lat., 88°W long.
Northeast US closure	June	Reduce bluefin tuna dead discards	The area bounded by straight lines connected the following coordinates in the order given: 40°00'N lat., 74°00'W long; 40°00'N lat., 68°00'W long; 39°00'N lat., 68°00'W long; 39°00'N lat., 74°00'W long

(Christensen *et al.*, 2008). Preferred habitats of sharks and tunas were identified based on the National Marine Fisheries Service (NMFS) EFH database (NOAA, 2017). Tiger shark preferred habitats were defined based on information provided by the NMFS EFH database and Calich *et al.* (2018). Preferred habitats for other key species groups (Table 1) were taken from the current literature. Migration routes were included for several key species/groups. Monthly sequences of “preferred” cells were defined in the base case for whales, tuna, billfish, and sharks. Preferred migration cells for tiger sharks were developed using satellite tagging data (Hammerschlag *et al.*, 2015; Graham *et al.*, 2016). Whether the species was migratory and migration routes for whales, tuna, billfish, pelagic sharks, large coastal sharks, and small coastal sharks were taken from the current literature (Supplementary Table S2).

Spatial simulations

Once the base case model was developed, the spatial management zones were modified under 7 different scenarios and an additional 32 sensitivity analysis addressing the following eight questions:

- (1) What will be the relative change in overall biomass and catch of tiger sharks over 10 years (a time period which allows tiger sharks to reach sexual maturity and reproduce) under existing spatial management zones (base case model)?
- (2) For current spatial management zones that are only closed for certain parts of the year, what would be the impact on the catch and biomass of tiger sharks when closing these off to pelagic longline fishing for the entire year over a 10-year period?
- (3) How would closing off the US EEZ to pelagic longline fishing impact the catch and biomass of tiger sharks over a 10-year period?
- (4) How would opening all current spatial management zones to pelagic longline fishing impact the catch and biomass of tiger sharks over a 10-year period?
- (5) How would scenarios 1–4 impact the other key species groups in the ecosystem.

We compared the results of these scenarios to the base case model by evaluating changes in biomass and catches at the end of the simulation period (2018).

- (1) How does changing the vulnerability parameter impact the catch and biomass of tiger sharks over a 10-year period?
- (2) How does changing the fishing mortality rates of tiger sharks impact the catch and biomass of tiger sharks over a 10-year period?
- (3) How does changing the dispersal rate impact the catch and biomass of tiger sharks over a 10-year period?

Questions 2–4 were examined through the seven scenarios: (i) Charleston Bump closed year-round, (ii) Cape Hatteras closed year-round, (iii) Gulf of Mexico Gear Restricted Area (SE) closed year-round, (iv) East Florida coast open to fishing, (v) Desoto Canyon open year-round, (vi) Northeast US closures closed year-round, (vii) no MPA, and (viii) US EEZ closed to fishing. For these scenarios, the base case model was modified to simulate five scenarios in spatial management zone closures, one scenario where the US EEZ was all open to fishing (i.e. no spatial management zone closures were in place), and one scenario where the entire US EEZ was closed to pelagic longline fishing. Questions 6–8 were examined by (i) changing the vulnerability parameter in each scenario to the default value of 2, (ii) changing the vulnerability parameter in each scenario to a value of 5 to indicate top down control (a value of 1 indicating bottom up control was used in the base models), (iii) increasing catches by 20% in each scenario, and (iv) increasing the dispersal rate by 10% in each scenario.

Scenarios used EwE's built in "Ecospace fishery" and "marine protected areas" applications (Christensen *et al.*, 2008) to investigate what may happen if specific pelagic longline management areas were opened or closed to pelagic longline fishing at various times of the year. For example, as the Charleston Bump, Cape Hatteras, and Gulf of Mexico Gear Restricted Area spatial management zones are not year-round, scenarios 1–3 simulated year-round closures for these areas. In comparison, as the East Florida Coast closed area, and Desoto Canyon all currently prohibit the use of pelagic longline gear year-round, scenarios 4 and 5 investigated what would happen if these areas were opened to pelagic longline fishing year-round. Scenario 6 investigated closing the northeast US closure year-round to pelagic longline fishing. In scenario 7, all spatial management zone closures were open to pelagic longline fishing year-round. For scenario 8, we simulated a new year-round closure to pelagic longline fishing for the entire US EEZ. To ascertain the impact of changing various spatial management zones, we present results in the form of (i) ratio of the biomass (tonnes/km²) and catches (tonnes/km²) for all species/groups in the model in 2018 compared to the biomass and catches in 1960 for the base case model and (ii) changes in the biomass and catches, in terms of percentages, between the scenarios and base case model for tiger sharks (Fouzai *et al.*, 2012; Abdou *et al.*, 2016).

Results

Changes to biomass and catches over time

Base scenario

Simulating the base case model resulted in a ratio of the total biomass (tonnes/km²) in 2018 compared to the biomass the start of the simulation of 1.03 for the entire modelled ecosystem. The ratio of total catches (tonnes/km²/year) in the 2018 compared to the start of the simulation (1950) was 1.65 for the entire modelled ecosystem.

Specific to tiger sharks, the biomass ratio was 11.45 and the ratio of catches was 13.00 (Table 3). The largest biomass of tiger sharks was concentrated in coastal and semi-pelagic waters along the US east coast (South of New England) and in coastal waters in the Gulf of Mexico (Figure 1b). Pelagic waters off the US east coast had moderate levels of tiger shark biomass, while waters off New England and pelagic waters in the Gulf of Mexico had the lowest levels (Figure 1b). Tiger shark catches were highest in semi-pelagic and pelagic waters off the US East coast (South of New England; Figure 1c). Moderate catches were observed in the northern pelagic region of the Southeast Atlantic and mid-way through the Mid-Atlantic region (Figure 1c). Low levels of catches were found in the Gulf of Mexico, coastal waters along the US east coast, and off New England (Figure 1c).

Changes in biomass occurred for all 25 species/groups included in the model to varying degrees (other fish ratio is too small to present; Table 3). For example, increases in biomass were observed for 12 of the species groups. Thirteen species groups showed a decrease in biomass over the simulated time period. The largest increases in biomass ratios over time were for the tiger shark (11.45), billfish (6.78), squid (6.61), and pelagic sharks (6.20). The largest decreases in the biomass ratios were predicted for crustaceans (0.21), and skates and rays (0.25; Table 3). Nine species/groups had an increase in the ratio of catches over time, compared to 16 that showed decreases or no changes over time (Table 3). The change in catches over the time period was largest for tiger shark catches (13.00), followed by squid (7.50) and billfish (7.27). The largest decreases in catches over time were for skates and rays (0.20; Table 3).

Scenarios

Spatial management zone simulations (questions 1–4)

Several simulations were conducted to determine the impact of closing or opening current longline gear management areas to longline fishing. All scenarios that closed additional areas resulted in a slightly increased tiger shark biomass compared to the base case model (i.e. tiger shark biomass increased between 100 and 108% of the base case biomass). Closing the Gulf of Mexico Restricted Area, Cape Hatteras, the Charleston Bump, and northeast US closure to pelagic longline fishing year-round resulted in biomass estimates that were just slightly higher (100–107%) than the base value. Closing the US EEZ to pelagic longline fishing resulted in the largest increase in biomass (108%). Simulations that opened areas to fishing (east Florida coast, Desoto Canyon, and no MPA) resulted in slight decreases to biomass compared to the base case value (97–99%) (Figure 3a).

Total catches of tiger sharks decreased during all scenarios except for when the US EEZ was closed to fishing and only a slight change occurred when the east coast of Florida was open to fishing and the northeast US closure was year-round. Catches were 26–28% of the base case catches when the Charleston Bump and Cape Hatteras spatial management zones were closed year-round; De Soto Canyon was open year-round and no spatial management measures were in place (Figure 3b).

Other species groups (question 5)

Changes in biomass occurred for most species/groups for the various scenarios (Figure 3a). The largest changes to biomass in the scenarios occurred for tuna, large sharks, and pelagic sharks. Tuna biomass increased by 212–219% in all scenarios except when the northeast US closure was closed year-round, which

Table 3. Biomass (tonnes/km²) and catch (tonnes/km²/year) estimates before and after (E/S) the simulated period and their (biomass and catch) ratio to the base case model.

Species/group name	Biomass (tonnes/km ²) (start)	Biomass (tonnes/km ²) (end)	Biomass (tonnes/km ²) (E/S)	Catch (tonnes/km ² /year) (start)	Catch (tonnes/km ² /year) (end)	Catch (tonnes/km ² /year) (E/S)
Baleen whale	0.0361	0.0557	1.54	–	–	–
Toothed whale	0.0127	0.0101	0.79	–	–	–
Tuna	0.0019	0.0019	1.04	0.0000	0.0000	0.53
Billfish	0.0268	0.1817	6.78	0.0002	0.0014	7.27
Pelagic sharks	0.0267	0.1658	6.20	0.0000	0.0001	6.78
Tiger shark	0.0026	0.0295	11.45	0.0003	0.0042	13.00
Large sharks	0.0179	0.0125	0.70	0.0000	0.0000	0.65
Small sharks	0.0285	0.0887	3.11	0.0000	0.0001	2.57
Sea turtles	0.0103	0.0467	4.54	–	–	–
Skates and rays	0.0276	0.0070	0.25	0.0015	0.0003	0.20
Reef fish	0.1777	0.0951	0.54	0.0014	0.0005	0.37
Squid	0.1353	0.8936	6.61	0.0006	0.0043	7.51
Cephalopods	0.2217	0.8129	3.67	0.0000	0.0000	0.94
Shrimp	0.0800	0.1164	1.45	0.0103	0.0164	1.59
Crustaceans	0.1291	0.0277	0.21	0.0033	0.0031	0.93
Invertebrates	0.1533	0.1350	0.88	0.0024	0.0046	1.96
Other fish	0.9788	0.0000	0.00	0.0006	0.0000	0.00
Bivalves	0.5106	0.2789	0.55	0.0009	0.0016	1.72
Benthic invert	0.5332	0.5451	1.02	0.0018	0.0021	1.19
Polychaetes	0.0975	0.0839	0.86	–	–	–
Gelatinous zooplankton	0.3887	0.3623	0.93	–	–	–
Macro zooplankton	0.4652	0.4575	0.98	–	–	–
Micro zooplankton	0.8884	0.8690	0.98	–	–	–
Phytoplankton	1.9328	1.9579	1.01	–	–	–
Detritus	4.8907	4.8627	0.99	–	–	–
Total	11.7742	12.0975	1.03	0.0234	0.0388	1.66

resulted in no real change in biomass. Pelagic shark biomass was ~150% the base value in most scenarios, except when the northeast US closure was made year-round, which resulted in a similar biomass to the base case, and when the US EEZ was closed to pelagic longline fishing, which increased biomass of pelagic sharks by 342%. The biomass of large sharks increased by 168% when the Charleston Bump and Cape Hatteras areas were closed year-round and the Florida east coast was open to fishing and by 171 and 173% when the Gulf of Mexico Restricted Area and the Desoto Canyon were closed year-round, respectively. The biomass increased by almost 200% when the US EEZ was closed to pelagic longline fishing. Large shark biomass changed only slightly when the northeast US closure was closed year-round. Lower trophic level species including benthic invertebrates, gelatinous zooplankton, macro and micro zooplankton, and phytoplankton showed no significant changes in biomass between scenarios.

The impact to catches in the scenarios varied greatly by species/groups (Figure 3b). Catches remained equal or increased in all scenarios for tuna, squid, and cephalopods. In most scenarios, except for when the northeast US closure and the US EEZ were closed to fishing year-round, cephalopod catches increased by 113%. The largest increase in catches for large sharks (157%) occurred when the US EEZ was closed to fishing. The other scenarios saw an increase in catches of large sharks of between 0 and 126%, except for when the northeast US closure was year-round, where a decrease in catches was observed (70%). Large reductions in catches occurred in scenarios for other fish, bivalves, and reef

fish. Catches were reduced between 0 and 38% for bivalves and other fish and between 0 and 79% for reef fish (Figure 3b).

Sensitivity analysis (questions 6–8)

Using the Ecopath default vulnerability of 2 resulted in the biomass of tiger sharks (compared to the spatial management zone simulations) decreasing (compared to the base case model) for all scenarios, except for the scenario's where the northeast US closure was for the entire year and the US EEZ was closed (Figure 4a). Increasing the vulnerability to 5 had the opposite impact, with the biomass increasing for all scenarios, especially for the scenario where the northeast US closure was year-round and when the US EEZ was closed to fishing (Figure 4b). Increasing the fishing mortality rates by 20% on tiger sharks resulted in the biomass decreasing slightly in most scenarios (Figure 4c). The largest decrease in biomass occurred when the Charleston Bump was closed year-round. A slight increase in biomass occurred in the scenario's where Cape Hatteras was closed year-round. Increasing the dispersal rate showed similar results, but the decrease in biomass when the Charleston Bump was closed year-round was not as large as when fishing mortality rates were increased (Figure 4d).

The reduction in catches seen in the scenarios (compared to the spatial management zone simulations) was slightly less when the vulnerability parameter was increased to 2, except for the scenario where the east Florida coast was open to fishing (Figure 5a). There was no change to the catch in the scenario where the northeast US closure was closed year-round (Figure 5a). When the vulnerability was increased to 5, catches were higher than in the base case model for all scenarios (Figure 5b). Similar trends in results

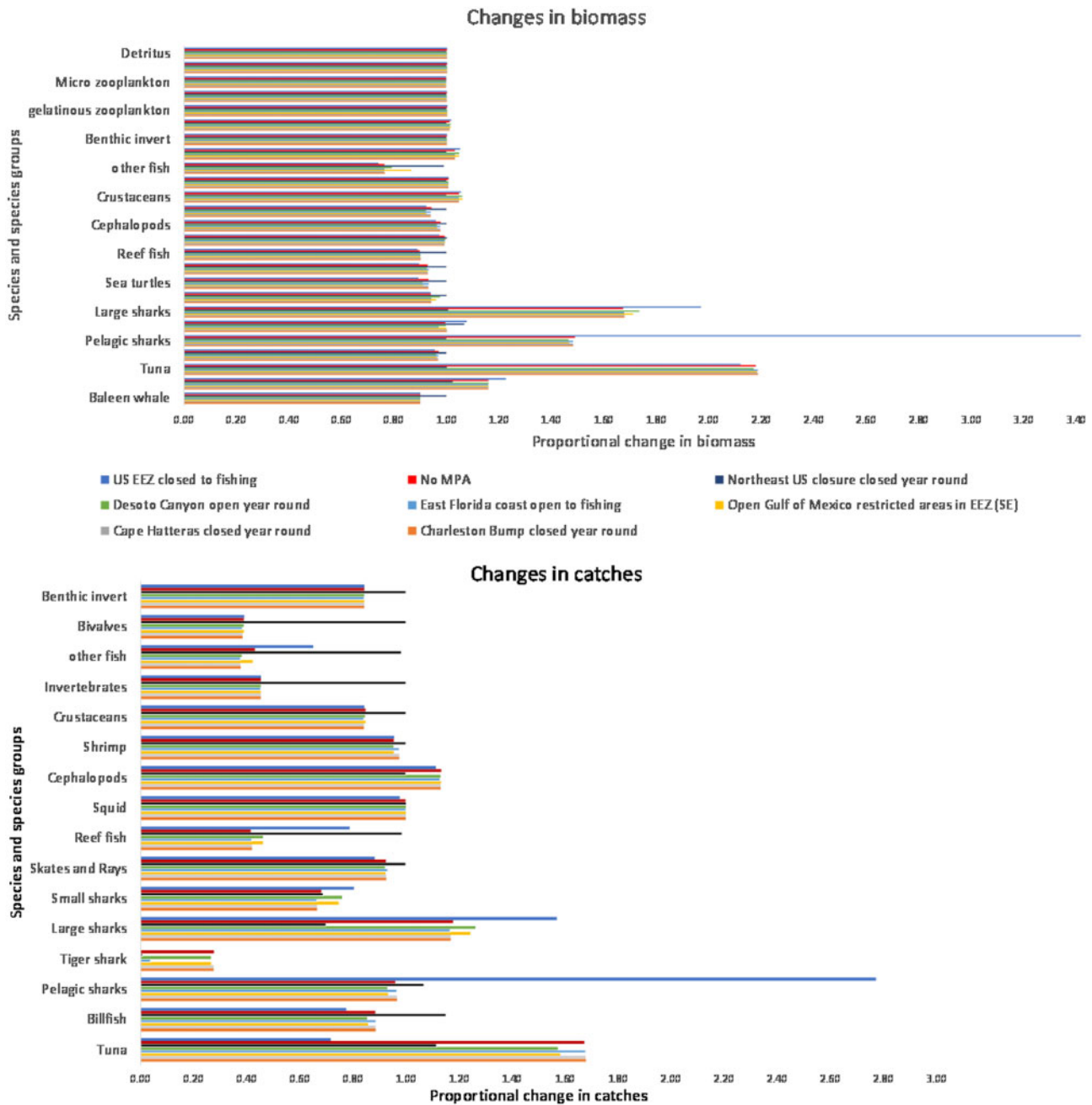


Figure 3. Proportional changes in (a) biomass and (b) catches for each species/group seen in each scenario compared to the base case model [the following species/groups were not included in (b) because no catches have been reported: baleen whale, toothed whale, sea turtles, polychaetes, gelatinous zooplankton, macro zooplankton, micro zooplankton, phytoplankton, and detritus].

were seen when the fishing mortality rate was increased (Figure 5c). Increasing the dispersal rate resulted in very similar results to those seen when the vulnerability was changed 2, with very little change in catches compared to the spatial management zone simulations (Figure 5d).

Discussion

Within the Western North Atlantic Ocean, several spatial management zone closures have been established to restrict pelagic longline fishing in US waters (Federal Register (FR), 2018). This study investigated the potential impacts of these closures on the

relative abundance of tiger sharks in the US EEZ of the Western North Atlantic Ocean. The results of the base case model predicted that the biomass of tiger sharks will increase over time with the current spatial management zone closures. This increase in tiger shark abundance over time has also been shown in other studies conducted in the region (Peterson et al., 2017). This result is likely due to large amounts of highly suitable tiger shark habitat already being protected from longline fishing under current spatial management as identified in Calich et al. (2018). Model results further suggest that additional spatial management zone closures would likely have some

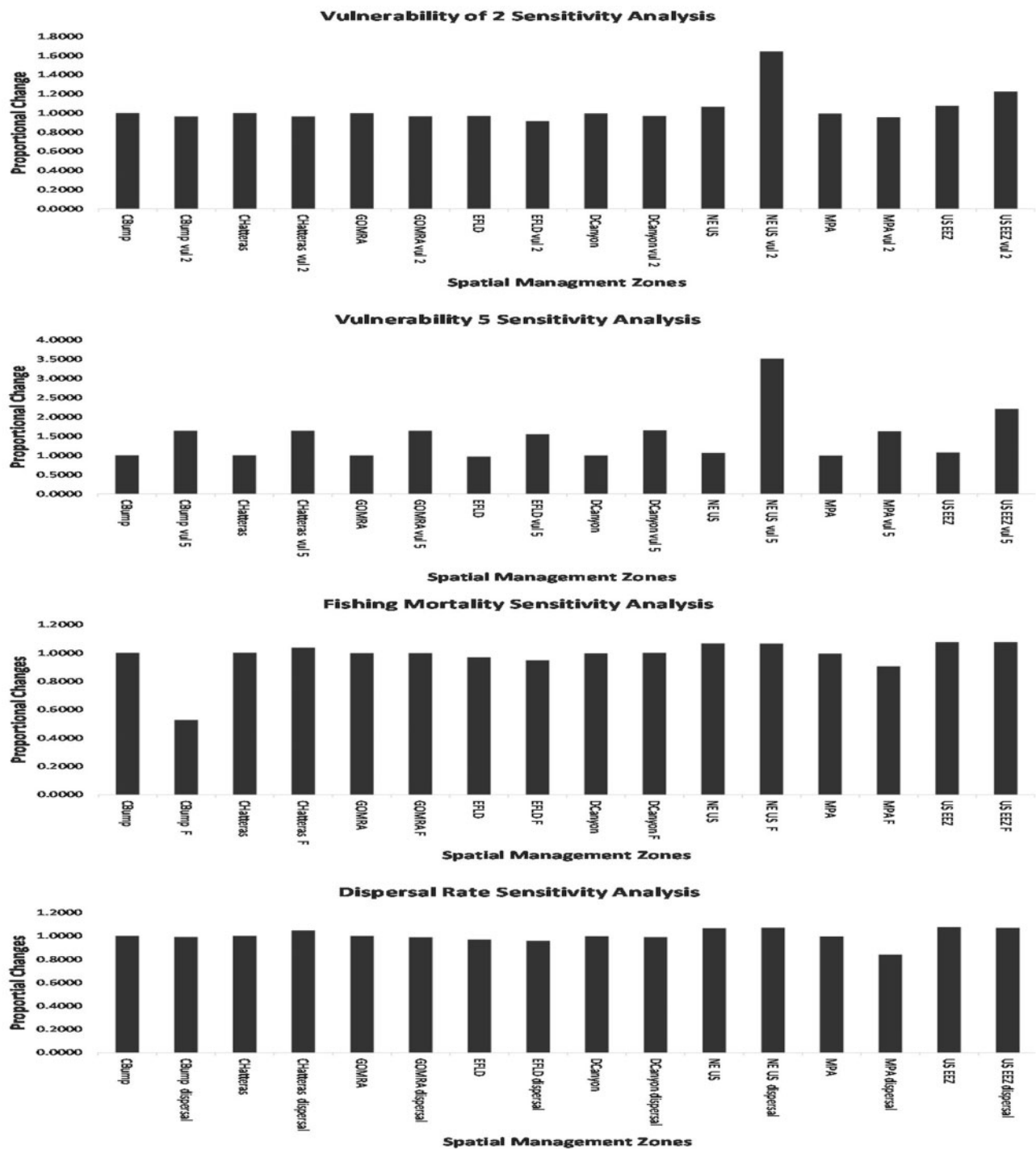


Figure 4. Proportional changes in tiger shark biomass seen in each scenario and sensitivity analysis [(a) vulnerability 2, (b) vulnerability 5, (c) fishing mortality, and (d) dispersal rate] compared to the base case model. Legend: CBump, Charleston Bump closed year round; CHatteras, Cape Hatteras closed year round; GOMRA, Open Gulf of Mexico restricted areas in EEZ (SE); EFLD, East Florida coast open to fishing; DCanyon, Desoto Canyon open year round; NE US, Northeast US closure closed year round; MPA, No MPA; US EEZ, US EEZ closed to fishing; vul 2, vulnerability of 2; vul 5, vulnerability of 5; F, fishing mortality; dispersal, dispersal rate.

positive impacts to tiger shark biomass in the US EEZ. Scenarios that increased the closure in highly suitable habitats resulted in the largest increases in tiger shark biomass over time. However, scenarios under which current spatial management zones on Florida's east coast were opened to longline fishing (i.e. opening

the East Florida Coast Closed Area to longline fishing) and when there were no spatial management zones in place resulted in no increase to tiger shark biomass. Taken together, these modelling results suggest that protecting tiger shark highly suitable habitat will have positive effects on their biomass over time

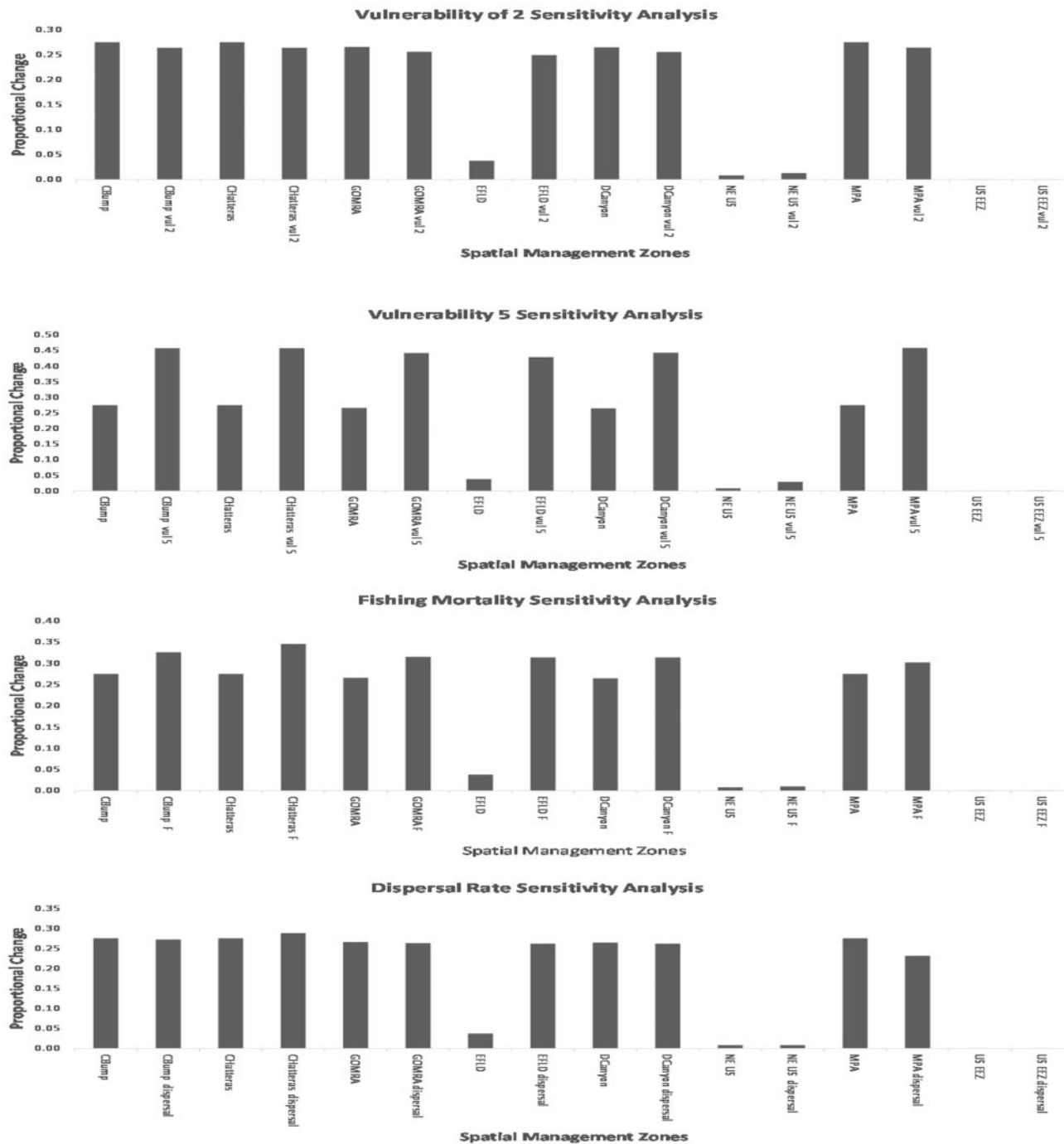


Figure 5. Proportional changes in tiger shark catches seen in each scenario and sensitivity analysis [(a) vulnerability 2, (b) vulnerability 5, (c) fishing mortality, and (d) dispersal rate] compared to the base case model. Legend: CBump, Charleston Bump closed year round; CHatteras, Cape Hatteras closed year round; GOMRA, Open Gulf of Mexico restricted areas in EEZ (SE); EFLD, East Florida coast open to fishing; DCanyon, Desoto Canyon open year round; NE US, Northeast US closure closed year round; MPA, No MPA; US EEZ, US EEZ closed to fishing; vul 2, vulnerability of 2; vul 5, vulnerability of 5; F, fishing mortality; dispersal, dispersal rate.

(base case), whereas decreasing protection of highly suitable habitat will lessen this impact, and extending protections beyond high suitable habitat will have a negligible effect on tiger shark biomass. Accordingly, spatial management zones may be an effective conservation tool for highly migratory species if highly suitable habitat is protected.

Modelled tiger shark catches were highest surrounding spatial management zones, and sensitivity analysis from this study suggests that increasing tiger shark's dispersal rate resulted in decreased biomass and catch amounts more similar to the base case model. This could suggest the possibility of a spill-over effect, which can be defined as the movement (net) of fish from marine

reserves to the fishing grounds that remain open (Buxton *et al.*, 2014). The amount of spillover in other fisheries has been related to the growth and movement of the protected species and typically positive benefits from spill-over effects are seen after the fishery has been heavily fished (Buxton *et al.*, 2014). Therefore, net positive spill-over effects, where spillover amounts are enough to offset fishing, are more typically seen in fisheries that are not well managed (Buxton *et al.*, 2014). Spill-over effects can be enhanced when the habitats in and outside of a spatial zone are similar and when smaller in size (Roberts, 2000; Ashworth and Ormond, 2005). However, the amount of time for spill-over impacts to be detected can vary substantially and increased fishing along a spatial management border can make it difficult to detect actual spill-over effects (Kellner *et al.*, 2007). Net spillover effects have been shown in several studies (Halpern *et al.*, 2009; Goñi *et al.*, 2010; Harrison *et al.*, 2012; Da Silva *et al.*, 2015; Chan and Pan, 2016). To date, spill-over effects from spatial management zones have not yet been demonstrated for sharks.

Of particular interest was that the biomass of tiger sharks prey items, including smaller sharks, reef fish, squid, cephalopods, and other fish, showed reductions in biomass under simulations where tiger shark biomass increased over time. Given tiger sharks are generalist predators known to consume these species (Ferreira *et al.*, 2017; Dicken *et al.*, 2017), this result could be the outcome of increased predation pressure from an increasing tiger shark population. These modelled results demonstrate the potential for unintended consequences (i.e. impacts to prey species) arising from single-species management. Consequently, increasing the vulnerability value to simulate a top down environment, where prey is rapidly replaced after being depleted, resulted in a larger increase in tiger shark biomass.

No species-specific stock assessment has been conducted on tiger sharks in the Western North Atlantic Ocean, but tiger sharks have been assessed as part of a multi-species group (Southeast Data and Assessment Report (SEDAR), 2006) and through catch rate analysis (Carlson *et al.*, 2012). Neither analysis suggested any significant decline in tiger shark biomass over the past decade (2011–2020). Our results suggest that tiger sharks in this region will likely continue to increase over time under current management scenarios, with possible small changes in biomass from additional spatial management zoning. However, to better understand this relationship, future research could investigate how differences in size and configuration of spatial zones would affect different age groups or life stages of tiger sharks. Tiger sharks are ectothermic species, and previous research has found that temperature is a key driver of their habitat use (Ferreira *et al.*, 2017; Lea *et al.*, 2018), swimming activity levels, and coastal abundance patterns (Payne *et al.*, 2018). Therefore, another important consideration is that distributions of their highly suitable habitat could shift in response to climate driven oceanographic changes, such as warming seas. This could subsequently increase or decrease the current spatial overlap between their highly suitable habitat and the management zones that restrict longline fishing.

As with any modelling study, there are limitations that should be considered when interpreting results. As outlined by Heithaus *et al.* (2008), mass-balance models, like Ecopath and Ecosim, assume that all energy is cycled within a system and that each species' diet is inflexible, which is not the case, especially given tiger sharks are generalist predators. Moreover, these models cannot integrate variation in behaviour among species, which may lead

to inaccurate predictions. Despite these limitations, mass-balance models are useful for providing null models for testing. Moreover, these models provide relative information, providing a means for getting insights on varying relative changes from varying modelled scenarios, serving as basis for decision-making and empirical testing (Christensen *et al.*, 2008).

In summary, this study used a EwE spatially explicit modelling approach to investigate the potential impact of varying spatial management zones in the Western North Atlantic Ocean on tiger shark biomass, catches, and distribution, along with impacts to other species in the ecosystem. Model predictions suggest that under current spatial management scenarios, tiger shark biomass will continue to increase over time and that implementing additional closures, particularly in highly suitable habitats, will have additional positive impacts on tiger shark biomass. However, our data also suggest that reducing spatial protections in highly suitable habitats for tiger sharks, such as the Florida east coast, would have less of a positive impact on tiger shark biomass. Taken together, spatial management zones may be an effective conservation tool for highly migratory species if highly suitable habitat is protected. Moreover, model predictions indicate the evidence of possible spill-over effects and prey species impacts from spatial protections of tiger sharks. It is important to note that model results should not be interpreted as absolutes, but rather be considered as relative changes to tiger shark biomass and catch rates under varying management scenarios, providing insights for evaluating differing management strategies and as a basis for testing against empirical data collections.

Data availability

Data are archived in the Animal Telemetry Network Portal here: <https://portal.atn.ioos.us/#metadata/a449cbcb-0082-43dd-b0f3-1cacab07dcb4/project>.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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