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Potential distribution of critically endangered hammerhead sharks and overlap with the small-scale fishing fleet in the southern Gulf of Mexico

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ABSTRACT

Understanding the degree to which fishing operations overlap with the distribution of exploited populations is essential for population assessments and in the formulation of management measures. Here we used ecological niche models to estimate hammerhead sharks' potential distribution that allowed the first assessment of their overlap with small-scale fishing operations in the southern Gulf of Mexico (GOM). The models were better than random models, with bathymetry as the most important predictor variable for bonnethead shark and average Chl-*a* for scalloped and great hammerheads. Shallow and intermediate waters of the GOM are of high environmental suitability for bonnethead shark and great hammerhead, and intermediate and deep waters within the continental shelf are more suitable for scalloped hammerhead. The spatial distribution of the small-scale fleet that operates on the western Yucatán Peninsula, southern GOM, had a high overlap with the estimated high environmental suitability of both bonnethead and great hammerhead sharks. We highlight the bonnethead shark, since its coastal habitat preference spans all ontogenetic stages, thus making it highly vulnerable to coastal anthropogenic impacts, including several small-scale fisheries.

1. Introduction

Small-scale shark fishing in the Mexican waters of the Gulf of Mexico (GOM) is a traditional activity (Bonfil, 1997) and is recognized as part of multi-specific fisheries that operate based on the seasonal abundance of sharks and teleost species (Castillo-Geníz et al., 1998). In the western Yucatan Peninsula (off Campeche), a small-scale coastal fishery based in San Francisco de Campeche, targets three small shark species (Atlantic sharpnose, *Rhizoprionodon terraenovae*, bonnethead *Sphyrna tiburo*, and blacknose *Carcharhinus acronotus*), and mackerels (*Scomberomorus* spp) due to their high acceptance in the local market, by using a specific gear (nylon gillnets), and selecting specific fishing areas for catching them. Scalloped hammerhead *Sphyrna lewini* and great hammerhead *Sphyrna mokarran* are incidentally caught in this and other fisheries in this region (Pérez-Jiménez and Méndez-Loeza, 2015) and are retained as a byproduct. The studied fishery is among the primary sources of fishing mortality for hammerheads in the southern GOM (Pérez-Jiménez and Méndez-Loeza, 2015), and a decrease in their catch frequencies in the last three decades has been perceived (Pérez-Jiménez et al., 2012). However, there are no population assessments for these species in the southern GOM.

Population assessments of scalloped and great hammerheads in the northern GOM and northwestern Atlantic also indicate a population decrease (Baum et al., 2003; Hayes et al., 2009). Both species are classified as Critically Endangered by the International Union for the Conservation of Nature (IUCN) (Rigby et al., 2019a,b) and are included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Pavitt et al., 2021). On the other hand, the bonnethead shark has recently been upgraded to be an Endangered species by the IUCN, with a current decreasing global population trend (Pollom et al., 2020). Although this species has a high reproductive potential and relatively stable population status and has not been considered an overexploited species in the GOM and U.S. South Atlantic (Cortés and Brooks, 2018), the same trend is not observed in other regions. For example, Pérez-Jiménez (2014) suggested that bonnethead shark is possibly extirpated from the Gulf of California (Mexican Pacific). Furthermore, the bonnethead shark has been considered infrequently landed and probably collapsed in Brazil (Reis-Filho et al., 2014), indicating that this species is highly vulnerable to the effects of fishing.

Despite the commercial importance and concerns on their population status, little is known about their distribution and

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overlap with coastal fishery operations in the southern GOM (Pérez-Jiménez and Méndez-Loeza, 2015). Understanding the spatial distribution and identifying environmental variables that drive endangered fish species abundance (Rufener et al., 2017) and the degree to which fishing operations overlap with the distribution of exploited populations is essential for population assessments when there are limited data (e.g., rapid assessment methods, such as ERAEF, Hobday et al., 2011), and in the formulation of management measures (Daw, 2008; Reeves et al., 2008).

Species' distribution can be approximated through Ecological Niche Modeling (ENM). The ENM associates environmental variables with species' presence data to estimate the environmental space (the approach to the ecological niche) occupied by the species (Peterson et al., 2011). These models do not include biotic and historical dispersion factors, and their projection in the geographical space is considered a potential distribution, only based on an index of environmental suitability (Soberón and Peterson, 2005; Peterson et al., 2011, 2015).

Construction of potential distribution maps for hammerhead sharks will allow a first assessment of the overlap with small-scale fishing operations in the southern GOM, where there are limited fishery data. Thus, the objectives of this study were (1) to predict the potential distribution of three hammerhead shark species in the GOM, (2) to estimate the horizontal spatial operations of a small-scale coastal fleet in the southern GOM, and (3) to estimate the proportion of horizontal overlap between the potential distribution of hammerheads and spatial operations of a small-scale fleet in the southern GOM.

2. Material and methods

2.1. Hammerhead shark's presence-only records

Presence-only records were obtained from two sources: (1) online available information accessible through the Global Biodiversity Information Facility (GBIF, http://www.gbif.org), Ocean Biogeographic Information System (OBIS, www.obis.org), Smithsonian Tropical Research Institute (SFTEP, http://biogeodb.stri.si.edu/caribbean/es/pages), Computer Unit for Biodiversity of the Institute of Biology of the National Autonomous University of Mexico (UNIBIO, by its acronym in Spanish; http://unibio.unam.mx/), National Information System on Biodiversity (SNIB, by its acronym in Spanish) of the National Commission for the Knowledge and Use of Biodiversity (CONABIO, by its acronym in Spanish), and (2) scientific literature (Bessudo et al., 2011; Hendon et al., 2013; Graham et al., 2016; Guttridge et al., 2017). Records lacking georeferenced data were not considered. Each species' presence-only records were adjusted to the modeling area using the NicheToolBox package (Osorio-Olvera et al., 2020) for RStudio (version 3.4.3).

A spatial thinning of the presence-only records was carried out to address the associated problems with sampling bias and spatial autocorrelation (Aiello-Lammens et al., 2015), which could lead to an over-representation of the environmental conditions associated with regions to large amounts of presence data (Kadmon et al., 2004). This algorithm randomly removes presence records that violate the nearest neighbor distance constraint (Aiello-Lammens et al., 2015). These analyses were performed using the spThin package (Aiello-Lammens et al., 2015) for RStudio (version 3.4.3). Presence-only data by species were divided into two sets: calibration and evaluation (Peterson et al., 2011), in a proportion of 70 and 30%, respectively (Guisan and Zimmermann, 2000; Phillips et al., 2006). The ideal way to evaluate the performance of a static model is with an independent data set. However, when not enough data are available, two alternatives have been proposed: (1) separate a fraction of the data set for calibration (with the proportion indicated above), or (2) use another data source such as previous maps (Guisan and Zimmermann, 2000; Phillips et al., 2006). The first alternative, adopted in the present study, is the most used to evaluate Maxent models.

Table 1
The oceanographic variables used in the construction of ecological niche models of hammerhead sharks. Data for all variables were obtained on a monthly basis, in the period of January 2000 to December 2016, except bathymetry. Bathymetry data was obtained in 2014.

Variables	Source	Spatial resolution
Diffuse attenuation coefficient at 490 nm	OCW	9 km
Concentration of chlorophyll *a* (mg/m^3)	OCW	9 km
Bathymetry (m)	GEBCO	3″
Salinity (ppt)	COPERNICUS	9 km
Sea surface temperature (°C)	OCW	27 km
Concentration of dissolved oxygen ($mmol/m^3$)	COPERNICUS	27 km
Absolute current speed (m/s)	COPERNICUS	27 km

2.2. Environmental variables

Environmental variables (Table 1) were selected based on a literature review of environmental factors that correlate or that are known to influence the presence of each studied hammerhead shark (Heithaus et al., 2007; Ubeda et al., 2009; Froeschke et al., 2010; Belcher and Jennings, 2010; Ketchum et al., 2014a; Ward-Paige et al., 2015; Yates et al., 2015; Calich et al., 2018). Seasonal variation was not considered due to presence records limitations; thus, resulting maps are integrated static images that show no temporal variations (Guisan and Zimmermann, 2000; Ramírez-León et al., 2021). Environmental data were downloaded from the Ocean Color Web, OCW (http://oceancolor.gsfc.nasa.gov/cms/), the Global Bathymetric Chart of the Oceans, GEBCO (http://www.gebco.net/) and COPERNICUS (http://marine.copernicus.eu/services-portfolio/access-to-products/) websites. Biotic factors should also be considered. However, they are challenging to obtain (e.g., prey availability), though Chl-*a* concentration is commonly used as a productivity proxy.

Subsequently, a Principal Components Analysis (PCA) was carried out to select only those non-correlated predictive variables (see supplementary material). Variables with coefficients larger than 0.8 were considered highly correlated. PCA allowed selecting only those uncorrelated predictive variables that retain a high proportion of the original information (Tabachnick and Fidell, 2007). This procedure was performed with RStudio version 3.4.3. From each variable, minimum, maximum, and average annual values were obtained and standardized to geographic coordinates (Datum WGS-84) at a spatial resolution of 27 km using MATLAB version R2015a. Then, we delimited the environmental variables using the modeling area of each species.

2.3. Modeling area

In order to develop the Ecological Niche Models (see below), we established a modeling area that included the six marine ecoregions in the western Central Atlantic (Fig. 1) (Spalding et al., 2007). By this, we considered the whole area, which is assumed to be accessible to the GOM hammerhead populations according to the literature (Bethea and Grace, 2013; Chapman et al., 2009; Tyminski et al., 2007; Driggers et al., 2014; Guttridge et al., 2017). Also, this area was used for calibration as the space that a species accesses is the appropriate area in which the models should be calibrated (Soberón and Peterson, 2005; Barve et al., 2011). The area of interest for modeling the potential distribution of hammerheads was the GOM and for the assessment of overlap between fishing fleet and potential distribution of each species was the western Yucatan Peninsula.

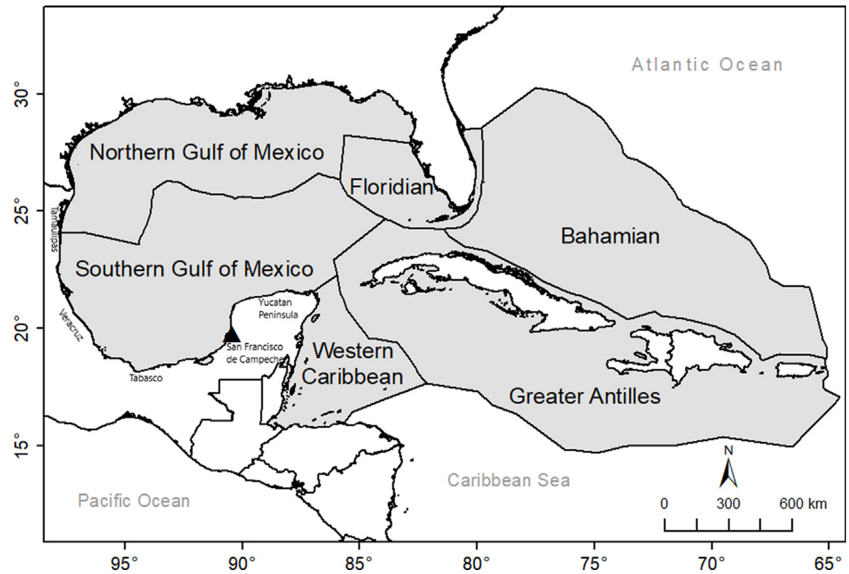

Fig. 1. Marine ecoregions in the western Central Atlantic. San Francisco de Campeche's port is marked with a triangle in the western Yucatan Peninsula.

2.4. Ecological niche models

The ecological niche models (ENM) of hammerhead sharks were generated using the Maximum Entropy approach (Maxent version 3.4.1, Phillips et al., 2006). Maxent is an algorithm that makes a rough estimate of the species' ecological niche using presence-only records (Phillips et al., 2006; Elith et al., 2011). Maxent's logistic output was used. This output assigns an approximated presence probability value to each pixel, under the assumption of knowing the real presence or absence probability of a species in a pixel (Soberón, 2012). Presence probability is interpreted as a relative environmental suitability index (ESI). The highest values represent a prediction of the best conditions for the species' presence (Phillips et al., 2006). In this study, the Grinnellian niche classification was considered. This niche classification considers non-interactive environmental variables that influence organism occurrences and is suitable to estimate species distribution at low spatial resolution (Soberón, 2007; Larson et al., 2010; Soberón and Arroyo-Peña, 2017).

Maxent was adjusted to 1000 iterations as a limit for each run of the model, 30 replicates with random resampling, and the autofeature functions were chosen to create the variables' response curves (Phillips and Dudík, 2008). The jackknife method was used to determine how each environmental variable (%) contributes to the models (Elith et al., 2011). Maxent offers the following functions (feature class): linear (L), quadratic (Q), product (P), threshold (T), hinge (H), category (C), and the autofeature. In this study, the autofeature function was selected to calibrate the models. The autofeature function applies the appropriate functions according to the occurrence records' sample size (Phillips and Dudík, 2008). In this study, Maxent's combination of functions was LQH to calibrate the models due to the range of presence records of hammerhead sharks. The use of several functions allowed to develop models that predict presences well. However, complex response curves are challenging to interpret and indicate possible overfitting (Merow et al., 2013), so caution is needed to interpret the results.

2.5. Model evaluation

Models' predictive capacity was evaluated using two methods, the omission error test and the partial receiver operating characteristics (partial ROC) analysis. The omission error test is the fraction of the observed presences predicted by the model as absences and takes values from 0 to 1. Values close to 0 are models with a low omission rate and are considered an optimal model (Peterson et al., 2011). In this test, the logistic output map was converted to a binary map using the expected error rate of 5% as a threshold. Pixels with values above and below the threshold were considered present and absent, respectively. Presence records used for evaluation were overlapped on the binary map, and the omission rate was estimated.

A partial ROC analysis was applied because the omission error test is considered exploratory (Peterson et al., 2008). This analysis generates AUC ratio values of 1 to 2, where a value of 1 represents a model equal to a random model (Peterson et al., 2008). A z-test tested whether the AUC ratio values of the niche models were statistically better than a random model (Peterson et al., 2008). Analysis was performed with the RStudio version 3.5.0 and NicheToolBox package (Osorio-Olvera et al., 2020) adjusted to 1000 bootstrap replicates and an omission error of no more than 5% (Saupe et al., 2011).

2.6. Fishing operations and their overlap with the potential distribution of hammerhead sharks

Fishing information was obtained from a fishery-dependent sampling of the small-scale fleet (n = 40–50 boats) based in San Francisco de Campeche port (Fig. 1) that used small outboard fiberglass motorboats with 7.5–9 m in length. Fishers used nylon gillnets (mesh size ranged from 7.5 to 12.7 cm) to catch small shark species (*R. terraenovae*, *S. tiburo*, and *C. acronotus*), mackerels (*Scomberomorus* spp.), and other teleost species. The gillnets operate mainly at the surface, but sometimes at the bottom, in areas with a variable depth of 5–109 m. Although there are seasonal variations, fishers change gears and fishing areas from trip to trip, sometimes carrying two different fishing gears (two gillnets with different mesh sizes) and moving from one fishing area to another during the same trip that lasts 5 to 6 days. Between 2011 and 2016, the number of sharks landed from 813 fishing trips was recorded by species for each boat. Fishers were asked about the fishing location in each fishing trip (i.e., distance and heading from the fishing port and depth to identify fishing points) and the number of days of the fishing trip.

Catch per unit of effort (CPUE) by species was estimated as the number of hammerheads per fishing day. Fishing trips

Table 2
Total presence records of hammerhead species, records for calibration, records for evaluation, omission error rate and AUC ratios.

	Total records	Records filtered	Records for calibration	Records for evaluation	Omission error rate	AUC ratio
Bonnethead shark	467	56	39	17	0.11	1.20
Scalloped hammerhead	463	35	24	11	0	1.67
Great hammerhead	174	22	15	7	0.28	1.50
Total	1104	113	78	35		

with and without hammerhead catches were included. Data from fishing points were interpolated within a polygon assumed to be the "potential fishing area available" (PFAA) for the studied fishing fleet. Interpolation was performed using the kriging method (Fortin and Dale, 2005) to predict the spatial distribution of fishing operations. Kriging is a set of linear regressions that determine the best combination of weights to interpolate the data and uses spatial parameters estimated by an experimental variogram (Fortin and Dale, 2005). Variograms are provided as supplementary material. CPUE data were transformed using Log for values >1 and Log (x + 1) for zero values because data were not normally distributed; nevertheless, after transformation, the normality assumption was not met (Shapiro–Wilks test, $p < 0.001$). However, normality of the CPUE data was assumed because kurtosis (0.56–0.51) and skew coefficient (-1.05–1.2) values were close to zero, and the mean and median values were similar. From the available data it was not possible to standardize CPUE.

To assess the overlap between the spatial distribution of the small-scale fleet's operations and the potential distribution of the species, the PFAA was delimited in the environmental suitability map (logistical output). The new extent of the environmental suitability map was classified in high environmental suitability index (ESI) and low ESI, using the Jenks Natural Breaks method, which grouped the data, maximizing the variation between groups and minimizing the standard deviation within them (Jenks, 1967).

The spatial distribution of the CPUE was classified into high CPUE and low CPUE. Pixels with values above the average CPUE were considered "high CPUE" areas. Lastly, the percentage of overlap between CPUE and environmental suitability areas within PFAA was made. Four areas were generated: low CPUE in high ESI, low CPUE in low ESI, high CPUE in high ESI, and high CPUE in low ESI. These procedures were performed with the Spatial Analyst toolbox in ArcGIS version 10.7.1.

3. Results

A total of 1104 presence-only records of hammerhead sharks were obtained (see supplementary material), which were reduced, after the spatial thinning, to 113 records for calibration (N = 78) and evaluation (N = 35) of the models. Each species' model had high and significant AUC ratio values (Z-test, $p < 0.001$), meaning that the models are better than random models. The highest omission error rate was for the great hammerhead model; therefore, this model may be less predictive than bonnethead shark and scalloped hammerhead models (Table 2). The increase of the number of records, when available, could increase the precision of the predictive models in future studies, particularly for scalloped and great hammerhead.

3.1. Environmental suitability index (ESI) of hammerheads sharks

Bonnethead shark's environmental suitability index was predicted in areas on the continental shelf (isobath 200 m). Highest ESI occurred mainly in shallow (<10 m depth) and intermediate-deep (10–30 m depth) waters (Fig. 2a). Bathymetry was the most important variable contributing to the model calibration (Table 3), with the presence probabilities increasing at depths less

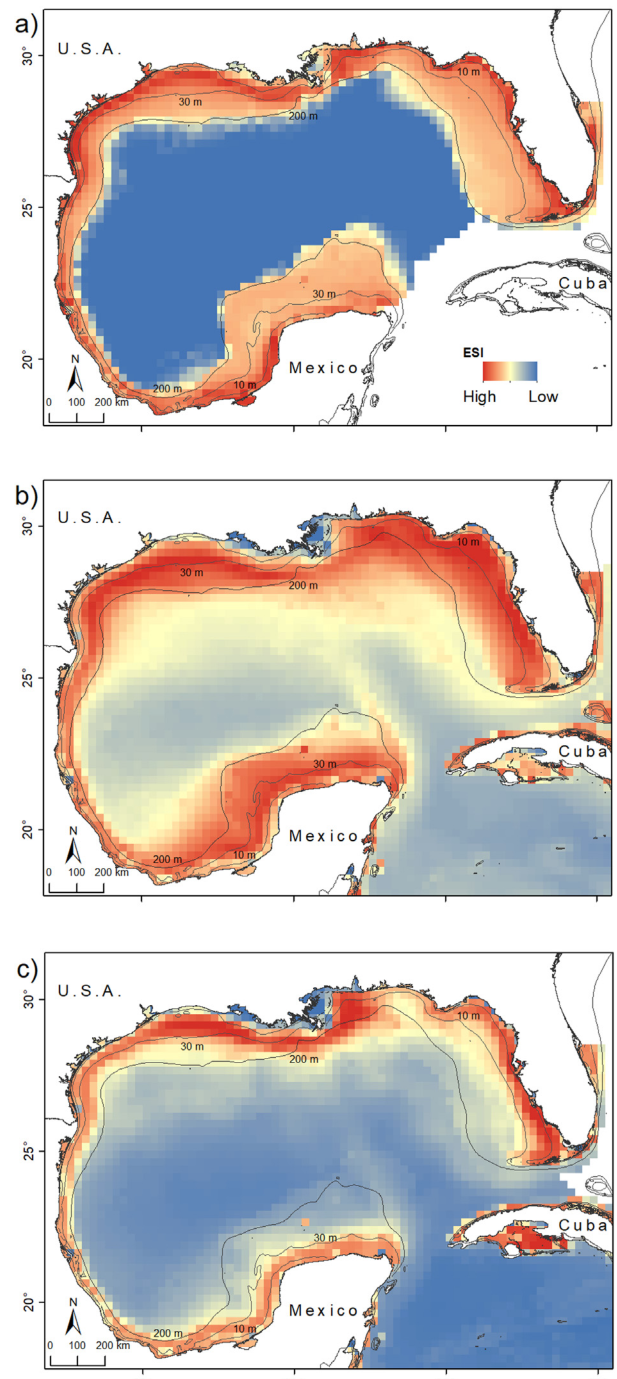

Fig. 2. Models of potential distribution based on Environmental Suitability Index (ESI) of (a) bonnethead shark *Sphyrna tiburo*, (b) scalloped hammerhead shark *S. lewini*, and (c) great hammerhead shark *S. mokarran* in the Gulf of Mexico.

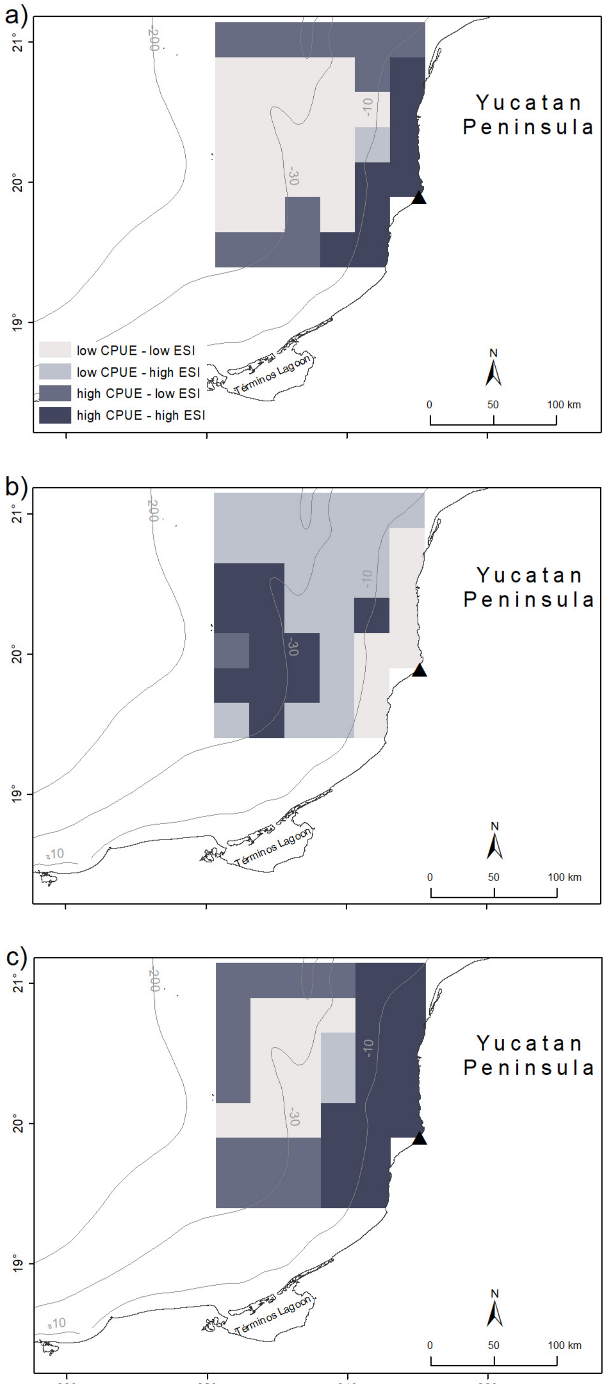

Fig. 3. Binary models of potential distribution based on the Environmental Suitability Index (ESI) of (a) bonnethead shark *Sphyrna tiburo*, (b) scalloped hammerhead shark *S. lewini*, and (c) great hammerhead shark *S. mokarran* in the potential fishing area available (gray square) in the southern Gulf of Mexico. Combinations of low and high CPUE with low and high ESI are shown in grayscale.

than 50 m and between ∼2 to ∼5 mg/m^3 chlorophyll a (Chl-*a*) concentrations (see supplementary material).

ESI for scalloped hammerhead was predicted in areas inside and outside of the continental shelf. High ESI was predicted in intermediate and deep waters (>30 m deep) (Fig. 2b). Average Chl-*a* concentration was the most important variable contributing to the model calibration (Table 3), with ∼0–1.2 mg/m^3 increasing the scalloped hammerhead presence. Current speed was the second most important variable, with presence probability increasing from ∼0.1 to ∼0.2 m/s and from ∼0.4 to 0.7 m/s (see supplementary material).

Table 3
Oceanographic variables and percentage contribution (%) in the ecological niche models of hammerhead sharks.

Species	Variables	Contribution (%)
Bonnethead shark	Bathymetry	71.5
	Chl-*a*	25.5
	SST	3
Scalloped hammerhead	Chl-*a*	81
	CS	12.3
	O	6.7
Great hammerhead	Chl-*a*	83.4
	SST	8.4
	CS	5.7
	Bathymetry	2.5

ESI for great hammerhead was predicted in areas on the continental shelf (isobath 200 m). Highest ESI occurred mainly in shallow and intermediate-deep waters (Fig. 2c). Average Chl-*a* concentration was the most important variable contributing to the model calibration (Table 3), with ∼1 to ∼3 mg/m^3 increasing this hammerhead's presence. Other important variables in the model were temperature, current speed, and bathymetry. Great hammerhead's presence increased between ∼31 to ∼32°C, at ∼0.1 m/s of current speed, and coastal waters (<200 m) (see supplementary material).

3.2. Fishing operations of the small-scale fleet and their overlap with the potential distribution of hammerheads

The highest CPUE was estimated for bonnethead shark (1.94 ± 2.36 SD), followed by scalloped hammerhead (1.81 ± 2.72) and great hammerhead (0.13 ± 0.20). The percentage of PFAA having high ESI was 22.5% for bonnethead shark, 80% for scalloped hammerhead, and 42.5% for great hammerhead shark (Table 4). These percentages represented a 100% of high ESI by species in the PFAA. The percentage of PFAA having high CPUE in high ESI was >38 for the three studied species (Table 4, Fig. 3a, b, c). Therefore, high catch rates occur in the 89% of high ESI for bonnethead shark, 35% of high ESI for scalloped hammerhead, and 88% of high ESI for great hammerhead.

4. Discussion

The spatial distribution of the small-scale fleet that operates on the western Yucatan Peninsula had a high overlap with the high environmental suitability of species with coastal preferences, such as bonnethead shark and great hammerhead. The predicted environmental suitability for both bonnethead and great hammerhead sharks comprised areas within the continental shelf, while for the scalloped hammerhead areas inside and outside the continental shelf had higher suitability. Predictive models for each species were better than random models, with bathymetry as the most important variable for bonnethead shark and average Chl-*a* for scalloped and great hammerheads.

4.1. Potential distribution of hammerhead sharks

Areas with a relatively high environmental suitability for the bonnethead shark were located in coastal areas (<30 m depth) because this small hammerhead is distributed in estuaries and shallow bays, mainly between 10 to 25 m deep (Compagno et al., 2006). In the present study, results showed that bathymetry is the variable that contributed most to the bonnethead shark model, followed by Chl-*a* concentration. The presence probability

Table 4
Percentage of spatial distribution of CPUE and high environmental suitability index (ESI) in the Potential Fishing Area Available (PFAA) of the small-scale fleet.

Species	Low CPUE in high ESI	Low CPUE in low ESI	High CPUE in high ESI	High CPUE in low ESI	High ESI in PFAA
Bonnethead shark	50	2.5	20	27.5	22.5
Scalloped hammerhead	17.5	52.5	27.5	2.5	80
Great hammerhead	25	5	37.5	32.5	42.5

of this species increased at <50 m depth and Chl-*a* concentrations between ∼2 to ∼5 mg/m^3.

The present study shows that, although Western GOM has coastal areas with high environmental suitability, index values are not as high as in the northern and southern GOM (Campeche and Florida banks), where there is a wider continental shelf. For example, low catch records have been obtained in Veracruz and Tamaulipas (western GOM) (Castillo-Geníz et al., 1998), and the species is more common in Tabasco, close to the Campeche bank (Pérez-Jiménez et al., 2020), and Campeche bank itself (Pérez-Jiménez and Méndez-Loeza, 2015).

Mexican waters have experienced high shark exploitation rates since the 1970s, and probably coastal species like bonnethead shark have been one of the more affected due to high interaction with small-scale fishing operations. Martínez-Candelas et al. (2020) suggested that reductions in this species' distribution occur in the southern GOM. This species is increasingly restricted to the coast of Campeche, western Yucatan Peninsula. This trend, together with the genetic differences found between the southern Gulf of Mexico, western Florida coast, and southeastern U.S. Atlantic coast, due to the site fidelity of bonnethead shark to estuaries, makes the species require special attention in terms of fishery management (Díaz-Jaimes et al., 2021).

Instead, regarding the scalloped hammerhead, areas with a relatively high environmental suitability were located in intermediate-deep waters (>10 m) up to the 200 m isobath. Wells et al. (2018) found that high habitat suitability occurs in intermediate areas and beyond the 200 m isobath. They suggested that scalloped hammerhead's presence increased in areas with depths below 1500 m, low Chl-*a* concentrations (∼0–4 mg/m^3), and short distances to artificial habitats (0–20 km). In the present study, we found that Chl-*a* was the main factor in the model prediction, increasing scalloped hammerhead's presence at low concentrations (∼0–1.2 mg/m^3). Other variables contributing to the model were maximum dissolved oxygen (230–305 mmol/m^3, equivalent to 5.15–6.82 ml/l) and two intervals of the current speed (∼0.1 to ∼0.2 m/s and ∼0.4 to 0.7 m/s).

Chl-*a* concentration in areas influenced by the Mississippi River, coastal lagoons, and cyclonic gyres can be greater than 5 mg/m^3 (Müller-Karger et al., 1991). Therefore, this species' association with low Chl-*a* concentrations could explain why certain coastal areas have a low number of records. For example, Wells et al. (2018) found that scalloped hammerhead sharks avoid the Mississippi River's mouth's surface waters. In the southwestern region of the GOM, areas with high Chl-*a* concentrations (>3 mg/m^3) have been found in areas of rivers' discharges and at upwelling areas on the Yucatan coast (Aguirre-Gómez, 2002; Zavala-Hidalgo et al., 2006). In these areas, low environmental suitability for scalloped hammerhead was estimated in the present study. However, Cuevas-Gómez et al. (2020) found a nursery ground for this species in the area of river discharges, where there is high turbidity, corroborating how multiple factors and requirements of the different life-history stages play essential roles in the distribution of each species.

Maximum dissolved oxygen was the second most important variable in the scalloped hammerhead model. Dissolved oxygen content in the GOM is uniform in the surface mix layer with 4.5 ml/l within the shelf of Campeche (southern GOM), Veracruz (western GOM), and the Caribbean Sea (De Lanza-Espino and Gómez-Rojas, 2004). However, concentrations of dissolved oxygen in Campeche coastal areas can reach up to 2.6 ml/l on the surface during the rainy season due to the rise of deep waters produced by cyclonic gyres (De Lanza-Espino and Gómez-Rojas, 2004). Therefore, the above could explain the high environmental suitability indices within the continental shelf and limited to some coastal areas. Concentrations indicating the presence of the species (5.15–6.82 ml/l) is within the range of dissolved oxygen that is associated with catches of scalloped hammerhead (2.5–7.4 mg/l) (Grace and Henwood, 1997), suggesting that this species avoids highly hypoxic areas (<3 mg/l) (Carlson and Parsons, 2001). However, in the Gulf of California, scalloped hammerhead has been detected in deep hypoxic zones (0.5 ml/l), possibly to access prey such as squid and avoid competition with other predators (Jorgensen et al., 2009). Thus, this species' possible tolerance to hypoxic conditions could be compensated with higher prey consumption (Wells et al., 2018). Finally, two intervals of the absolute current's speed increased the presence probability of scalloped hammerhead. Previously, a correlation between the movements of scalloped hammerhead and the speed of the current has been documented, showing a preference for areas of high speeds (>0.8 m/s), where there is probably a high accumulation of potential prey (Ketchum et al., 2014b).

On the other hand, great hammerhead's potential distribution within the GOM was generally observed within the continental shelf (200 m isobath). The highest environmental suitability was predicted in coastal and intermediate areas (<30 m depth), similar to bonnethead shark. Compagno (1984) mentions that this species is distributed in the continental shelf or outside it, mainly at 1–80 m deep. The variable that had the most significant contribution to the model was Chl-*a*, where the concentration that increased the species' presence was from ∼1 to ∼3 mg/m^3, followed by temperature and current speed.

Distribution of great hammerhead is associated with low Chl-*a* concentration (<∼3 mg/m^3), similar to *S. lewini*. This result differs from Queiroz et al. (2016) findings, where hammerhead sharks (*Sphyrna* spp.) preferred high productivity areas on the continental shelf. For example, in Florida, great hammerheads use mangroves, which are highly productive, temporarily for feeding (Guttridge et al., 2017), highlighting the importance of the scale considered in calculating the potential distribution of this species.

It was observed that the presence of the great hammerhead sharks increased between ∼31 to ∼32 °C. Several studies have found that temperature influenced sharks' distribution patterns (Froeschke et al., 2010; Yates et al., 2015). Moreover, it is one of the most studied abiotic factors in these species' spatial ecology (Schlaff et al., 2014). However, in the present study, the temperature was not significantly important for the three hammerhead species' models, probably as result of the spatial scale here considered. Finally, the absolute speed of the current related to the probability of great hammerhead's presence showed a peak at ∼0.1 m/s and from ∼0.4 m/s to ∼1.4 m/s in the present study. Calich et al. (2018) also found that great hammerhead's distribution increased between 0.06–1.4 m/s current speed. The use of areas with high current speeds by great hammerhead could be associated with high prey accumulation, as found for scalloped hammerhead. Roemer et al. (2016) also observed that great hammerhead uses areas with high current speeds, possibly to help maximize oxygen consumption and recover from energy expenditure and physiological stress due to low levels of dissolved oxygen in shallow areas which they use to forage.

4.2. Overlap between the potential distribution of hammerhead sharks and the small-scale fleet

Potential fishing area available (PFAA) for the small-scale fleet studied in the western Yucatan Peninsula has areas of high CPUE in shallow (<10 m depth), intermediate (10–30 m depth), and deep (>30 m depth) waters, although the highest proportion was located in areas between <10 m and 30 m depth. The studied fleet has two main fishing seasons, from November to March to target mackerels (*Scomberomorus* spp.) and from April to June to target small sharks, mainly the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*), with fishers operating between 20 and 50 km from the coast (Pérez-Jiménez and Méndez-Loeza, 2015). There is a high overlap of the small-scale fleet operations and the three hammerhead shark species' distribution in both fishing seasons. From August to November, the fleet has a third fishing season to catch the four-eyed octopus (*Octopus maya*), so the fishing effort towards other resources, including sharks, decreases (Pérez-Jiménez and Méndez-Loeza, 2015). However, the bonnethead shark is also caught in other coastal gillnet fisheries targeting teleost fishes during this last period. Furthermore, a yearly fishery closure was established in 2014 to protect sharks during their reproductive process, spanning from 15 May to 15 June and 1 to 29 August, which interferes with the second and third fishing periods. Changes in fleet operations modify the overlap degree with hammerhead shark populations, but these variations were not modeled, and the maps are a static representation of the spatial distribution of each species. Also, future studies may include additional standardized CPUE data to improve the modeling.

Although the fishing pressure on sharks in the southern GOM has declined since the 2000s due to shark catch reduction in the traditional fishing areas, there are still seasonal target fisheries for small shark species, including bonnethead shark in this region (Martínez-Candelas et al., 2020). The scalloped hammerhead is one of the most frequently caught sharks in the small-scale fleet studied. Juveniles of this species are the most common stage in catches landed in the southern GOM, where adults' catches are sporadic (Pérez-Jiménez and Méndez-Loeza, 2015). Neonates and juveniles of hammerhead species are also common in catches of another small-scale fleet operating off Tabasco, near the Campeche bank (Pérez-Jiménez et al., 2020). Thus, in addition to the small-scale fishery off Campeche, both fisheries represent the primary sources of fishing mortality for scalloped hammerhead and great hammerhead (at a lesser degree) in the southern GOM.

Regarding bonnethead shark, despite its high reproductive potential (Cortés and Brooks, 2018), this species is more susceptible to coastal fisheries and other anthropogenic impacts resulting from its site fidelity to estuaries, like in South Carolina, USA (Driggers et al., 2014). Knip et al. (2010) suggested that species that use nearshore areas for most of their lifespan (e.g., bonnethead shark) are highly vulnerable to varying coastal processes, such as habitat degradation and fishing pressure. Additionally, Brook et al. (2008) and Field et al. (2009) added that species with small range size and limited dispersal capacity (like bonnethead shark) are vulnerable to population declines, increasing their extinction risk and reducing their population recovery capacity after exploitation. This condition could be happening with bonnethead shark in the southern GOM, where Martínez-Candelas et al. (2020) have already documented a reduction of this shark distribution. A situation that can become extreme is in the Gulf of California and the Central Mexican Pacific, where Pérez-Jiménez (2014) reported the bonnethead shark's extirpation.

4.3. Conclusions

Results of the present study were highly predictive as a first approximation of the potential distribution of hammerhead sharks in the Mexican waters of the GOM. Shallow and intermediate waters of the GOM are of high environmental suitability for bonnethead shark and great hammerhead, and the intermediate and deep waters within the continental shelf are more suitable for scalloped hammerhead. The highest catch rates of hammerhead sharks by the small-scale fleet off the western Yucatan Peninsula occur in shallow-intermediate waters. The highest overlap of high environmental suitability with high catch rates occurred in hammerhead sharks of coastal preferences such as bonnethead shark and great hammerhead. It is recommended to carry out more studies related to the spatio-temporal dynamics of small-scale fleets' fishing effort and continuing with the biological and fishing monitoring of hammerhead sharks. It is also essential to identify and understand each species' habitat utilization and migratory patterns to estimate the degree of overlap between fishing fleet operations and the species' spatial distribution. This understanding will quantify the effect of fishing on the hammerhead shark populations in the Mexican waters of the southern GOM.

CRediT authorship contribution statement

Mercedes Yamily Chi Chan: Conceptualization, Data curation, Formal Analysis, Writing - original draft. **Oscar Sosa-Nishizaki:** Conceptualization, Funding acquisition, Supervision, Validation, Writing - review & editing. **Juan Carlos Pérez-Jiménez:** Conceptualization, Supervision, Visualization, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.rsma.2021.101900.

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