

Identifying priority areas and spatial fisheries impact for addressing shark conservation in a data-limited context

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Abstract

Shark distribution and fishing grounds used by local communities are usually overlapped, although this coincidence is not straightforwardly distinguished in a data-limited context. We aim to delimit critical areas for shark conservation using a comprehensive spatial model for determining the co-occurrence area of the most fished shark species considering the distribution of the fishing effort and protection effectiveness of the marine protected areas in the Colombian Caribbean. Predicted distribution areas for nine frequent landed species were obtained using a maximum entropy (MaxEnt) species distribution model fed with species presence and environmental open-access data, while the fishing effort was derived from interview-based maps already available. The co-occurrence areas (COAs) were derived from the nine shark species habitat suitability models by using a 70% and 85% threshold cut, for defining a general and highest probability areas of distribution, respectively. Three independent co-occurrence areas were delimited along the Colombian Caribbean Sea: Morrosquillo Gulf, Santa Marta-Guajira and San Andres and Providence Archipelago, without finding an environmental link between them. By considering the highest probability of co-occurrence, 16 areas were well differentiated. Fishing grounds and COAs were unequally overlapped (total: 45%, mean: 26,76%) while marine protected areas did not offer effective protection against fishing pressure in areas identified as critical for conservation of the shark species included in the analysis. This suggests a noticeable spatial relationship between co-occurrence shark areas and fishing grounds used by local fishing communities. The use of this methodology enables identification of co-occurrence areas in a data-limited context, which can be used as starting point for defining the priority areas for shark conservation in the Colombian Caribbean. This allows stakeholders to implement future management guidelines in well-defined areas with the highest probability of involving the iconic and most fished shark species.

Keywords: Habitat-suitability model, co-occurrence areas, shark conservation, data-limited spatial modeling, small-scale fisheries.

1. Introduction

The Colombian Caribbean Sea contains 15.3% of the elasmobranch species of the world, (Mejía-Falla et al., 2007), which includes 88 shark species grouped in 34 genus and 19 families

(Ramírez & Davenport, 2013). However, only 49 species (55.68%) have been confirmed (Mejía-Falla et al., 2007; INVEMAR, 2010). Almost 50% of confirmed species have been categorized under “Data Deficient” and 24% as “Nearly Threatened” by the IUCN -International Union for the Conservation of Nature (IUCN, 2017). In Colombia, the lack of knowledge about shark ecology and fishery landings has led to vague reports and monitoring. Thus, most of the available information on the elasmobranch group consists of species listed as present in specific locations (Puentes et al., 2009; Puentes et al., 2012; De la Hoz & Manjarrés–Martínez, 2016).

The Colombian National Action Plan for Sharks, Rays and Skates- PAN became official in 2010 (ICA, 2010). This document prioritizes elasmobranch species for conservation and research following the Domingo et al., (2008) grading matrix that takes into account distribution areas, species interaction with fisheries, market demand and conservation status. From the 96 shark species reported for the country (Caribbean Sea and Pacific Ocean), 24 species were prioritized, establishing general guidelines to develop research and conservation aims.

In the Colombian Caribbean Sea, small-scale fisheries represent 61% of the total fishing activities, involving more than 12,000 fishers (Beltrán Turriago, 2001; INVEMAR, 2010). Despite, the economic importance for local economy, fishery landings are not systematically documented through time and space in the area. Available documents include governmental statistics gathered discontinuously and in many cases, species-specific information is incomplete due to common names and identification limitations when species were landed (Puentes et al., 2009; Ramírez & Davenport, 2013; De la Hoz & Manjarrés–Martínez, 2016). Although fisheries in the Colombian Caribbean do not target shark species, bycatch is common in small-scale fisheries (Beltrán Turriago, 2001; Puentes et al., 2009).

In 2009, shark by-catch was estimated 2.971 tons, but landings composition and species-specific information was not recorded and thus not available (Acevedo et al., 2007; INVEMAR, 2010). Usually, sharks by-catch is recorded as “other” and reported together with pelagic and demersal fish, and estimated to representing 81% of the total landings from small-scale fisheries in the continental part Colombian Caribbean region (INVEMAR, 2010). The available information about the most frequent and abundant shark species caught points out to *Rhizoprionodon porosus*, *Rhizoprionodon lalandei*, *Ginglymostoma cirratum* *Carcharhinus perezii* and *Carcharhinus falciformis* (Manjarrés, 1993; Manjarrés y González, 1993; Puentes et al., 2009; De la Hoz & Manjarrés–Martínez, 2016). Nevertheless, quantities, sizes and year-specific information are not usually recorded.

According to the above-mentioned data-limited context, identification of the impact of fisheries on shark species offers a great challenge. In order to establish science based management guidelines, several worldwide evaluation methods have been extensively used, ranging from stock assessments (Cortés, 1998; Baum et al., 2003), habitat use studies through telemetry (Chapman et al., 2005; Simpfendorfer & Heupel, 2012; Graham et al., 2016) and identification of critical habitats such as nursery areas (Kinney & Simpfendorfer, 2009; Ward-Paige et al., 2015). Nevertheless, all of these approaches require significant amount of information, time series and financial resources.

Recently, species distribution models have become an important tool in shark conservation because of its potential to determine species distributions and delimit critical areas by correlating environmental parameters and presence records to define its ecological niche. Thus, these models are capable to predict the occurrence probability over an extended area. These studies are particularly valuable when species are distributed along large regions, when few presence records are available and when there is lack of information on basic biology and ecology of species (Salas et al., 2007). Specifically, shark distribution models have been developed using species specific

data obtained from fisheries, including target or by-catch (Sequeira et al., 2012; 2014), observer programs (Lucifora et al., 2015; Lezema-Ochoa et al., 2016), systematic surveys (Hacohen-Domené et al., 2015; Lauria et al., 2015; Siders et al., 2013) and satellite telemetry data (Sleeman et al., 2010; Vandeperre et al., 2016). However, this type of data is not always accessible.

Designing areas for species conservation requires specific information on species distributions throughout the region of interest, while in data-poor areas that is far from being achievable (Ferrier et al., 200a; Ferrier, 2002). Nevertheless, determining the more probable location for data-limited resources strongly impacted for fisheries and other factors (e.g. climate change) is crucial. In this sense, the use of presence-only public data to delimit species distribution models, co-occurrence areas and its relation to fishing effort and prior established Marine Protected Areas-MPA's has not been attempted before.

In order to elucidate the spatial impact of small-scale fisheries on the highest-probability distribution areas (co-occurrence areas) for the most caught shark species in the Colombian Caribbean Sea, as well as to identify the spatial protection that the Marine Protected Areas (MPAs) may offer to the prioritized sharks species, we used open-access data of species presence and environmental variables, as well as interview-based fishing spatial effort data. For this purpose, 1) we determined single-species habitat suitability model for nine shark species including (*Carcharhinus falciformis*, *Carcharhinus limbatus*, *Carcharhinus perezii*, *Ginglymostoma cirratum*, *Galeocerdo cuvier*, *Mustelus canis*, *Rhizoprionodon spp.*, *Sphyrna lewini* and *Sphyrna mokarran*) over the Gran Caribbean Sea by conducting maximum entropy models (MaxEnt), 2) we then re-scaled to the Colombian Caribbean region and overlapped the species suitability habitats for determining the nine-shark species co-occurrence areas and 3) estimated the spatial overlapping among the co-occurrence, marine protected areas and fishing grounds. Finally, the shark co-occurrence model limitations, outlooks and the shark conservation measures under a small-scale fishery impoverished framework are discussed.

2. Methods

2.1 Study area

The Colombian Caribbean Sea covers over 75,101.88 sq. miles from latitudes 16°N to 7°N (see Figure 1). Oceanographic conditions in the mainland are modulated principally by the Panama-Colombia countercurrent, the Caribbean Current and upwelling cores in the northeast continental shelf (Chollet et al., 2012; Rueda-Roda & Muller-Karger, 2013). The continental shelf extends unevenly from north to south along the Colombian Caribbean, showing both short (e.g. Santa Marta) and large (e.g. Middle Guajira) dimensions. The bathymetry in the insular area conformed by the Archipelago of San Andres and Providence and numerous keys follows a circular pattern around the emerged continental platform and declines abruptly as distance increases from keys and islands.

2.2 Presence data

Habitat suitability was modeled for the most landed sharks in small-scale fisheries in the Colombian Caribbean following information from Puentes et al., (2009). Nine shark species were selected for the study, *Carcharhinus falciformis*, *Carharhinus limbatus*, *Carcharhinus perezii*, *Ginglymostoma cirratum*, *Galeocerdo cuvier*, *Mustelus canis*, *Rhizoprionodon spp.*, *Sphyrna lewini* and *Sphyrna mokarran*. Selection was based on the most fished shark species reported by Puentes et

al. (2009). *Rhizoprionodon spp.* consisted of pooled occurrences from *R. porosus* and *R. lalandii*, as visual separation between both species is not conspicuous and may lead to errors in the presence data (Mendoça et al., 2009; 2011). Distributions models for each species were constructed taking into account the entire Gran Caribbean in order to incorporate the natural distribution without incorporating geopolitical boundaries and then re-scaled to the Colombian Caribbean for further analysis (Bentlage et al., 2013). Georeferenced records of shark presence by species were obtained from the Global Biodiversity Inventory Facility -GBIF (<http://www.gbif.org/>) and the Ocean Biogeographic Information System -OBIS (<http://iobis.org/>). These databases included observations collected by research institutions, monitoring programs from academia, governmental institutions and scuba diving citizen science observations. A total of 1,171 occurrence locations were obtained. Duplicates and occurrences registered as preserved specimens, fossils, records without geographic coordinates or institution name, records before 1985 and records falling out of the study area delimitation were not considered.

Due to the nature of the presence data used, some areas within the study region may have been more extensively sampled than others. A bias file was constructed using presence data for all nine-shark species in order to correct sample spatial bias in each species habitat suitability model. Presence data density values were estimated for each cell using the Kernell density tool in ArcGIS 10.3.1 (ESRI, 2011) and negative values were reclassified as No Data. Bias File was incorporated into each model and evaluated using a sensibility analysis for each species. This type of spatial correction method generates background points to evaluate model performance following sampling effort (as density values) correcting spatial bias present in each species presence data (Phillips et al., 2009).

2.3 Environmental data

Sea surface temperature (SST), chlorophyll-*a* concentration (Chl), bathymetry (Depth) and salinity (Sal) (Table 1) were used as predictors for suitable habitats for the nine shark species. These environmental variables were selected according to previous findings that correlate them with shark presence (Sequeira et al., 2012; Siders et al., 2013; Curtis et al., 2010). SST, chl-*a* and salinity layers were downloaded from the public databases Bio-Oracle (<http://www.bio-oracle.org>) and depth from the General Bathymetric Charts of the Oceans -GEBCO (<http://www.gebco.net/>). Each environmental layer was prepared using ArcGIS 10.3.1 (ESRI, 2011) by adjusting extent and resolution to the highest data available (1 arcmin - 4.97 mi). All environmental data was clipped to match latitude -90°N, -7°S and longitude -55°E, 25°W (Figure S1) excluding areas corresponding to the Pacific Ocean. Cell size in all layers was standardized at 0.00559 sq. miles. All layers were projected into WGS 1984 World Mercator.

2.4 Habitat suitability model by specie

A habitat suitability model (i.e. predicted probability of occurrence) was developed for each shark specie using a maximum entropy approach under R environment (R Core Team, 2013), with the aid of ENMeval package (Muscarella et al., 2014). Inputs into the model consisted of presence data and the environmental variables above mentioned. The final model setup by species was reached after performing sensitivity analysis, including sample bias correction with a Bias File (Dudik et al., 2005) or a spatial thinning method of presence data (Aiello-Lammens et al., 2015). Spatial correction of presence data through spatial thinning or use of a Bias File granted spatial independence of calibration and evaluation data reducing spatial correlation among points (Radosavljeć & Anderson, 2014).

Several ‘feature’ types (lineal, quadratic, product feature and their possible combinations) for representing a function of the environmental variables relation given the number of presence points in each model were also explored (Phillips et al., 2009). In order to limit model overfitting, a regularization multiplier was included in sensitivity analysis giving a penalty value to each variable used (Radosavljevic and Anderson, 2014, see Table 1). Finally, models were validated selecting one of three approaches tested: 1- Random k-fold cross-validation, 2-Checker geographically structured approach or 3-Block geographically structured approach, as described by Radosavljevic and Anderson (2014).

Best model fit for each specie was determined using Area Under the Receiver Operating Characteristic Curve (AUC) and delta of the Akaike Information Criteria corrected for small samples (AICc). AUC values reflect the discriminative power of the model ranging from 0 to 1; with values above 0.5 discriminating areas of habitat suitability better than random (Phillips et al., 2006; Phillips et al., 2009). Areas of habitat suitability for each species were selected for further analysis using a threshold value of AUC >0.50. Delta of AICc selects the best model according to the settings established by model assigning 0 value to the optimal model between models with different settings. Only AUC values are reflected in Table 1 as all delta AICc values were equal to 0. Additionally, predictions of highly suitable areas (i.e highly predicted probability of occurrence areas) in each distribution model were qualitatively visually inspected according to species ecology knowledge and environmental variable contribution (Table 1).

2.5 Co-occurrence areas

Areas of co-occurrence (COA) were calculated by the Raster Calculator function in ArcGIS 10.3.1 (ESRI, 2011), employing each species habitat suitability model as a layer. The predicted probability of occurrence for each nine species (i.e. habitat suitability) was added in each cell giving equal weights to each specie. A final layer with predicted probability of co-occurrence of all nine-shark species was obtained and used for further analysis.

The highest co-occurrence values for nine species were obtained in Yucatan (Mexico) and Florida (USA) peninsulas (0.47), while in Colombia the maximum co-occurrence was estimated as 0.43. Considering the Colombian to the whole Caribbean ratio, two threshold cuts were applied to COA in the study region; 0.307 (70%) and 0.375 (85%). 70% threshold was chosen to avoid overestimating the combined distribution of the nine shark species given that the co-occurrence values may be considered low (below 0.50). Additionally, an 85% threshold cut allowed to be focused on the areas where the predicted probability of co-occurrence of nine species was higher, promoting better conditions for implementing accurate management measures.

Species contribution to each COA derived from 85% threshold was determined by extracting species predicted probability and environmental variables values in each cell and a multivariate analysis was performed using PRIMER 6 PERMANOVA+ software (Clarke et al., 2006). A subset of 30% cells for each COA was analyzed. For those areas composed of more than 10,000 cells, a subset of 10% of the cells (Guajira North and Quitasueño) was analyzed. Areas with less than 300 cells were entirely analyzed (Santa Marta, Manaure and Morrosquillo North). Values were transformed using a square root and Bray-Curtis Similarity index was calculated for a total of 9 variables (species) and 6010 observations (cells). Visual relation among variables was inspected applying a cluster analysis and a Principal Coordinate Analysis (PCoA). Graphic observations were supported by PERMANOVA and PERMIDISP statistical analyses in order to test the existing significant differences in each species contribution between COA. Factors considered included:

geographic position (oceanic, east, center and west) and depth (<50m, 100-200m, 200-300m, 300-500, >500m). PERMANOVA was conducted using one factor at a time assuming homogeneity for the other factor as well as both factors at the same time. Finally, a SIMPER analysis was conducted to identify the species causing differences among COAs (Table S1).

2.6 Fishery grounds and Marine Protected Areas

Co-occurrence areas (COA) were spatially contrasted with local small-scale fishing grounds (FG) downloaded and digitized from interview-derived maps (http://gis.invemar.org.co/anh_caladerospesca/). Fishing grounds polygons were drawn in ArcGIS 10.3.1 software (ESRI, 2011) and discriminated by gear type (gillnets, seine nets, trawl nets, handlines, loglines, fishing traps and speargun). Fishing grounds were overlapped with COA (70% and 85%) and total overlapping areas were calculated based on two criteria: 1) Direct and indirect impact of small-scale fisheries on shark species (all gears) and 2) only direct impact by fishing sharks (handlines and longlines). Fishing grounds were parceled around COA within 20 km from the border of each 85% COA following a perpendicular line to the coast. Overlapping areas for each COA were estimated only with the parceled fishing grounds in order to capture only those fishing grounds with direct impact over each co-occurrence area. Additionally, the co-occurrence areas estimated to 85% and fishing grounds were overlapped with Marine Protected Areas (MPA's) in the Colombian Caribbean. The MPA's areas were downloaded from the Colombian GIS public database (<http://sigotn.igac.gov.co/sigotn/>) and projected into WGS 1984 World Mercator. Terrestrial areas of MPA's were eliminated of all further analysis.

3. Results

3.1 Habitat suitability models

Sensitivity analysis provided similar model fit for all nine species, and the models performance discriminated areas of habitat suitability better than random (AUC>0.50). Final model setup ranged from AUC values from 0.77 to 0.949 for *G. cuvier* and *G. cirratum*, respectively (Table 1). Correction of sample bias for the nine models was properly addressed by spatial thinning, excepting the *S. mokarran* model that fitted better by the Bias Files method, probably due to the low number (n=9) of occurrence points in this model, in which spatial thinning does not correct sample bias, whereas the use of a Bias File permits evaluating all suitable areas equally taking into account areas less sampled. Both regularization multipliers and feature types selected varied among species models as shown in Table 1, according to species ecological affinity. Validation method had no significant influence on model performance; thus, the same method (Checker) was used for all species according to Radosavljevic & Anderson (2014).

The definition of the habitat suitability model mainly depended on the bathymetry, contributing from 60.11% to 97.48% for all species. When bathymetry contribution decreased (< 88%), chl-*a* gained importance for *C. perezii* (16.20%), *M. canis* (11.57%) and *S. mokarran* (31.26%). Conversely, the models of *S. lewini* and *Rhizoprionodon spp.* were more benefited by contribution of SST (36.66%) and salinity (28.89%), respectively. *G. cuvier* and *C. falciformis* required moderate contribution from all environmental variables for defining their suitable habitat (Table 1).

Suitable habitats in the Colombian Caribbean Sea were mainly predicted along coastal areas. *C. limbatus*, *C. perezii*, *M. canis* and *Rhizoprionodon spp.* were predicted above 600 m of

depth, while *G.cirratum* was estimated inhabiting shallower waters above 200 m. Particularly, *C. perezii* suitable habitat was predicted occupying continental shelf and slope. Contrastingly, *S.lewini* and *S. mokarran* were estimated inhabiting between 50m and 1000m in depth, but *S. lewini* was only predicted in the Guajira peninsula. The predicted suitable habitat for *G. cuvier* and *C. falciformis* ranged from 600m to 1000m, focusing in the pelagic habitat away from the continental shelf.

3.2 Co-occurrence areas

The co-occurrence areas defined by a 70% threshold provide insights on the wide distribution of the nine shark species in the Colombian Caribbean, but 85% threshold indicate areas exhibiting higher predicted probability of co-occurrence (Figure 2). The lower threshold value evidenced three well-separated large co-occurrence areas identified in the southwestern (Morrosquillo Gulf), northeastern (Santa Marta-La Guajira) and insular (San Andrés and Providence Archipelago) regions. The southwest and northeast continental shelf co-occurrence areas were mainly separated by the effect of the mouth of the Magdalena River on coastal waters (Rueda-Roa & Muller-Karger, 2013; Beier et al., 2017), implying that the nine shark species were modeled as little prone to inhabit low salinity waters. The insular COA was separated from the two continental shelf co-occurrence areas, mainly by being far away from the Colombian mainland (480 mi). This distance implied a different influence of water bodies between continental and insular COAs (Chollet et al., 2012), meaning that the spatial link between COAs from the modeled suitability habitats for the nine species was not evident from the environmental variables used.

Sixteen co-occurrence areas were identified when the higher threshold was considered (Figure 3). The Morrosquillo Gulf COA was reduced to 18.49% and remaining area was separated in two differently sized areas but holding similar distance from the coastline and exhibiting an average deep of 600m (Figure 3). The Santa Marta-La Guajira COA was differentiated in six co-occurrence areas, comprising 36.68% of the large co-occurrence area (70% threshold cut). These six COAs exhibited different distance from the coastline, as well as comprised distinct depth ranges. Finally, the large co-occurrence insular area was scattered in six small co-occurrence areas accordingly to the same number of keys and islands, covering the 17.26% of the San Andrés and Providence Archipelago 70% threshold cut COA (Figure 3). The size of each COA importantly depended on the continental shelf size associated with each insular land.

Cluster analysis and PCoA revealed more than 90% similarity from the sixteen COAs, suggesting a similar influence of the used environmental variables for defining the habitat suitability by species (Figure 4). Nevertheless, PERMANOVA analysis revealed significant differences in depth and position among COAs, with 71.8% of the total variation among cells explained by the location and only 19.7% explained by depth. However, PERMADISP indicated significant dispersion of data, preventing to assign differences in COA to an unequal shark contribution among co-occurrence areas. SIMPER analysis only identified differences of 8.19% between the contribution of each shark species at depths <50m and >500 m (Table S1-S16) attributed to the low contribution of *G. cirratum* at greater depths (>300m) and the increasing contribution of *C. falciformis* in area deeper than 300m.

3.3 Interaction among COA, fishery grounds and Marine Protected Areas

Small-scale fisheries are mainly carried out on coastal waters shallower than 100 m in the Colombian Caribbean (Figure 3). Despite that most COA are not entirely located in depths below 100 m, 45.43% of the fishing grounds are located inside COA identified in the 70% threshold (Table 2). When overlapping co-occurrence areas obtained from the 85% threshold with the entire area of the fishing grounds (no parceling), the total amount of overlapping area decreased to 3.25%.

Superposition of the parceled fishing grounds with total COA (85%) was higher in Morrosquillo South COA (59.68%), Dibulla (55.59%) and Providence (35.37%). Contrastingly, no overlapping areas (0%) were identified for Morrosquillo North, Bajo Alicia, Bajo Nuevo, Serranilla and North Guajira COA (Figure 3, Table 3). When assessing only the spatial impact of shark small-scale fishing gears (i.e. direct impact on sharks), overlapping areas between fishing grounds and COA increased to 10.58% (Table 2). Co-occurrence areas Dibulla (25.84%), Santa Marta (13.30%), Providence (10.12%), San Andres (7.85%) and Morrosquillo South (7.52%) were again identified with the highest percentage of overlap (Table 3).

Regarding protection of MPA over identified co-occurrence areas, percentages vary according to COA geographic location. Two of the eight continental co-occurrence areas, Morrosquillo South and Santa Marta, overlapped with MPA's in 56.58% (Corales de Profundidad National Natural Park) and 42.05% (Tayrona National Natural Park) respectively (Table 3). Co-occurrence areas in the insular region such as San Andres, Serranilla, Serrana, Providence, Roncador and Quitasueño are entirely protected (100%) by the Seaflower MPA. Still, this area is divided into subareas with different fishing regulations where extraction is permitted. Contrastingly, other insular areas such as Bajo Nuevo, Bajo Alicia and Serranilla fall out of the MPA (Figure 3). Nevertheless, COAs still exhibit significant spatial relation with fishery grounds although marine extraction practices are banned in all MPA's in National Natural Parks of the country. All marine protected areas in the Colombian Caribbean have some degree of overlap with fishing grounds, evidencing poor enforcement MPA fishing regulations (Figure 3).

4. Discussion

In this study, we constructed species habitat suitability models for the most fished nine shark species in the Colombian Caribbean from open-access data. The habitat suitability models were used for defining the highest predicted probability of co-occurrence areas and were overlapped with small-scale fishery grounds and marine protected areas. Our results show an unequal but important fishing effort on the 16 shark co-occurrence areas identified, while marine protected areas offer only a partial but not enforced protection to fishing pressure.

Achieving habitat suitability for shark species

We obtained reasonably accurate model performance values for all modeled species (AUC>0.77) in the Caribbean Sea according to that identified by Phillips et al., (2009). By tuning each species settings independently and comparing different model settings with quantitative evaluations such as delta of AICc, we assured the best model fit from the available data. Appropriate setting of the feature type and regularization multiplier contributed to final model setup as already noted by Elith et al. (2011). In all cases, validation method and number of occurrence points had no significant influence on the model and AUC was independent of these two parameters. In this sense, habitat suitability models used with the methodology in this study can be used with limited number of presence data and species with different ecologies, as here involved. The use of

data from the entire Caribbean Sea allowed us to capture the broad favorable environmental conditions for the habitat suitability of each species instead of only modeling the Colombian Caribbean (Bentlage et al., 2013). By setting up and modeling each of nine species, we obtained models that predict potential distribution in the study area according to species-specific ecological characteristics. Accordingly, highly suitable areas predicted by our study for *G. cuvier* and *S. mokarran* for the Gran Caribbean Sea are consistent with findings from other studies using satellite tracking to develop core habitat use areas off the Florida peninsula (Hammerschlag et al., 2012; Calich, 2016; Graham et al., 2016). This may reflect, in this case, the ability of the model to predict areas of high suitability in the Caribbean. However, this type of information is not available for all nine species comprehended in this study.

Although bathymetry had the highest environmental variable contribution to every habitat suitability models, contribution from the other variables varied among species. In most of the cases, contribution from bathymetry was followed by either chl-*a* or salinity. Nevertheless, each model does display habitat preference according to that described by other authors. For example, preference to coastal habitat has been documented for *C. limbatus* (Wiley & Simpfendorfer, 2007), *C. perezii* (Brooks et al., 2013), *G. cirratum* (Castro, 2000), *Rhizoprionodon lalandii* (Tagliafico et al., 2015), *Rhizoprionodon porosus* (Mendoça et al., 2011) and *M. canis* (Giresi et al., 2015); while *C. falciformis* (Clarke et al., 2015), *S. lewini* (Yates et al., 2015), *S. mokarran* (Hammerschlag et al., 2011) and even *G. cuvier* (Heithaus, 2001) have been identified as inhabiting more pelagic areas. This explains our habitat prediction following a bathymetric gradient mainly along the continental platform for all species included in the study, excepting *G. cuvier* and *C. falciformis*.

Moreover, temperature in the Colombian Caribbean remains mostly stable throughout the year with no significant decreasing temperature in winter and slight variations in chlorophyll peaking from December to March- 0.05 mgm^{-3} (Andrade & Barton, 2005; Chollet et al., 2012). Consequently, although temperature is an important factor influencing metabolic rates and physiological functions for ectotherms such as most shark species (Schlaff et al., 2014), this environmental variable was only significantly important in the contribution of *S. lewini* habitat suitability model. Abundance of *S. lewini* has been formerly related with SST, explaining identified contribution of this variable (Yates et al., 2015).

Despite that the environmental variables selected had previously been correlated with shark presence, other species-specific factors not included in our study may influence the predicted distribution. Species with high mobility and seasonal migrations are an example. Migrations may not follow only physiological constraints (included in the models) but also follow prey abundance availability. This may explain *G. cuvier* lowest model performance (0.77) among the nine species in the study, previously documented on migrating to higher latitudes in warmer periods following prey abundance such as turtles and marine mammals (Heithaus, 2001).

Additionally, complex ontogenic and reproductive interactions were not taken into account in this study, thus, imposing limitations to the models associated to species specific ecology. Consequently, the habitat suitability models are not size discriminative and ontogenic niche shifts are not considered, including changes associated to diet (Brooks et al., 2013; Alfonso & Hazin, 2015; Yates et al., 2015). For example, *C. limbatus* has been identified as using the Everglades in Florida, USA for wintering grounds (Wiley & Simpfendorfer, 2007) and shallow bay areas in the Yucatan coast as nursery areas (Keeney et al., 2005). Likewise, *C. falciformis* uses inshore habitats at smaller lengths than 1.10 cm LT moving into deeper waters at greater lengths (Clarke et al., 2015). Similarly, seasonal residency found in *S. mokarran* (Hammerschlag et al., 2011) and *S. lewini* (Duncan et al., 2006), cannot be predicted by this methodology because presence data was

not discriminated into different temporal scales. Habitat preference modeled for each species may change seasonally and may be associated to changes in the prey availability (Calich, 2016). Therefore, suitable habitats identified in each model display only spatial and not temporal habitat preference. Moreover, these models may not respond to aggregations such as the ones displayed for mating purposes or niche sexual segregations, as these aggregations may not be reflected by occurrence data especially when happening in small time scales (Robinson et al., 2011; Gallagher et al., 2014).

Potential limitations of the methodology used (maximum entropy models) include those imposed by intrinsic limitations of the model type and the ones added by the use of open-access occurrence data. Although Maxent models have proven to be very competitive against the highest performing methods, using presence-only data increases the possible interference of sample spatial bias of occurrence records (Elith et al., 2011). Therefore, we have addressed this issue by carefully correcting possible bias in our data with the use of the Bias File or spatially thinning presence data before model development (See methods). Additionally, by fin-tuning specie-specific model settings with the aid of a sensibility test, the best possible trade-off between model-fit and model complexity was assured. Additionally, each model was fitted on feature type, known to influence the performance of Maxent, allowing the potential complex relation of the species to its environment to be modeled (Phillips & Dudik, 2008; Elith et al., 2011). Therefore, we assured that the model selected was the best possible model for each species according to the corresponding input data. Moreover, by modeling all the Gran Caribbean Sea, we included a wide sampling of background and modeled a broad landscape where each species had previously been reported. This included a full environmental range of the species and therefore models did not have to be transferred into space eliminating this potential methodological limitation (Elith et al., 2011).

Regarding the opportunistic nature of the presence records used for constructing each model, we assured minimum quality eliminating all doubtful records of the compiled dataset including those without an institution affiliation. Guaranteed that each data point can be verified, we included records since 1985 in order to avoid losing any valuable information in a data-poor region, but additionally, permitted use to use open-access information that may reflect a broader view of the distribution of each species, versus specific private data with better quality but limited in space (Hacohen-Domené et al., 2015; Lucifora et al., 2015). We recognize year-to-year variation in environmental variables, which could affect shark distribution on a small scale. However, our objective was to generate the first habitat suitability model for each of the nine species for the Caribbean Sea, and thus, have pooled all available information since 1985 (at least 30 years of occurrence data) although environmental layers have been constructed from data after 2002. The use of this environmental layer suite and variation between model input data has been considered and proven useful when addressing this type of objective (Tyberghein et al., 2012; Siders et al., 2013).

Identifying co-occurrence areas

Highest co-occurrence values (0.47 and 0.43) obtained for the Gran Caribbean and Colombian Caribbean respectively, account for the probability of encountering all nine species evaluated. Maximum probability obtained in the Colombian Caribbean represents 92% of the maximum probability in the whole area studied. Although probability values below 0.50 may be considered low for species-specific habitat suitability models (Phillips et al., 2009), values of co-occurrence as found for the nine study species in Colombian Caribbean may be considered high. Moreover, with the use of two threshold cuts (70% and 85%) we assured only highest probability values were included in the model (i.e. co-occurrence values greater than 0.307) and then selected a

85% (0.375) to further demarcate co-occurrence areas and evaluate overlapping areas with fishery grounds and MPA's. For management purposes, co-occurrence areas identified for the nine shark species can be used as starting point for defining the priority areas for shark conservation in the Colombian Caribbean. This allows stakeholders to implement future management guidelines in well-defined areas with the highest probability of involving the iconic and most fished shark species. Nevertheless, the use of these thresholds does not necessarily mean areas out of the COA threshold may also have presence of several shark species and may be of interest.

Through the construction of habitat suitability models, we then identified three co-occurrence areas in the Colombian Caribbean Sea using a 70% threshold cut, distributed in the mainland (2 COA) and insular (1 COA) regions. Segregation of the two COA along the continental coast may be explained by freshwaters inputs from the Magdalena River mouth (Beier et al., 2017). Near-shore shark species such as *C. limbatus*, *G. cirratum* and *C. falciformis*, can be greatly influenced by freshwater inputs and reduction of metabolic demands of osmoregulation may have a strong impact on species energetic costs (Froeschke et al., 2010; Wiley & Simpfendorfer, 2007; Lezema-Ochoa et al., 2016). The Colombian Basin is characterized by strong salinity gradients between coastal and offshore waters due to freshwater discharges from rivers, freshwater runoff in Central America, considerable precipitation and notorious upwelling system in the Guajira Peninsula (Beier et al., 2017). Therefore, avoidance of areas with salinity fluctuations close to the coastline could explain the interruption of co-occurrence areas in this part of the coast.

Although bathymetry explains most species habitat preferences, salinity also plays an important role. This is especially noticeable when comparing COA in the continental and insular areas of the study area. Insular COA only follows a bathymetric pattern around the continental shelf because of none existing freshwater inputs. Additionally to depth and salinity gradients, the location of COA along the mainland coast (COA Morrosquillo Gulf and Santa Marta-Guajira) can also be related to upwelling foci (Andrade & Barton, 2005; Chollet et al., 2012). These two areas are characterized for holding large percentage of small pelagic biomass where the presence of clupeids, anchovies, carangids, scombrides and barracudas may enhance food availability promoting predators such as sharks (Rueda-Roa & Müller-Karger, 2013). Upwelling plumes may extend as far as 250 km of the coast but additionally as far south as Cartagena (75.5°W) (Beier et al., 2017). This, promotes COA to extend beyond upwelling foci and may help to support the presence of the COA in the Morrosquillo Gulf.

Additionally, coral reef and seagrass distribution in the Colombian Caribbean partially overlaps with COA identified in this study such as Morrosquillo Gulf (North and South), SAP Archipelago and Santa Marta COA. This type of marine substrates house a high biodiversity and primary production, hence food resources for sharks species such as *C. perezii* (Castro, 2000), *G. cirratum* (Brooks et al., 2013), *S. mokarran* (Heithaus 2001) and *G. cuvier* (Acuña et al., 2017) that have been known to inhabit. In the Colombian Caribbean Sea coral reefs and seagrass habitats are distributed mainly in the Rosario and San Bernardo National Natural Park, Morrosquillo Gulf, Santa Marta and Tayrona National Natural Park and SAP Archipelago (Garzón-Ferreira et al., 2001). This also support the COA identified in these areas and implies a relation between areas of high productivity and diversity such as coral reefs and sea grass flatlands and shark co-occurrences.

Co-occurrence areas may also have similar limitations to those mentioned earlier for habitat suitability models. As a result of the presence data used in the construction of habitat suitability models, COA may only display adult habitat preferences and may be sexed and/or size-biased due to the fact that presence data has no additional information on this type of characteristics. Although

potential nursery areas for several species could have been identified when using sexed-biased presence data (e.g. only female data), it is impossible to differentiate inasmuch as only high suitability areas were described indicating possible high abundance of sharks in the area. In the same way, co-occurrence areas may delimit high abundance areas but probability and habitat suitability are not direct measures of abundance. Nevertheless, the co-occurrence areas meets the first criteria for establishing nursery areas but further information is needed (Heupel et al., 2007). As an example, Morrosquillo Gulf area identified in this study as a co-occurrence area, has been recognized with frequent and abundant *R. lalandi* and *R. porosus* juveniles (Dallos et al., 2012). Nevertheless data is still raw and needs further complement in order to define this type of critical habitat. If COA were to be used as a starting point for defining priority areas for shark conservation as mentioned earlier, further studies on specie-specific information such as size, gender and abundance are needed. Moreover, fishermen in the Cordoba Department (Morrosquillo Gulf) registered *Carcharhinus* sp., *Sphyrna* sp., and *Rhizoprionodon* sp. as 32% of their main daily catch. Although quantities and species-specific information is not available, it does help validate how good the model is at predicting areas of high suitability for sharks (Rueda et al., 2010).

Additionally, as mentioned earlier in species model limitations, consideration of seasonal differences was not made and data was pooled together regardless of the temporal framework. The Caribbean Sea has less drastic seasonal changes than temperate regions and remains mostly stable throughout the year with no significant decreasing temperature in winter and slight variations in chlorophyll (Andrade & Barton, 2005; Chollet et al., 2012). Therefore, the habitat suitability models and co-occurrence areas were constructed with the objective of defining year-round consistent areas useful in management and conservation of the shark species in the study. Nevertheless, changes in habitat preference may result of climate changes, probably shifting co-occurrence areas (Jones & Cheung, 2015; Calich, 2016). Although this is impossible to predict using the methodology implemented in this study, several modeling climatic scenarios can be implemented with the use of open-access data and are a valuable impact on future species conservation guidelines.

Fisheries spatial interaction and conservation

Almost 50% of small-scale fishing grounds are located inside COA (70% threshold) and 10% when accounting only for grounds where gears that may potentially catch sharks are used. Considering that studies have demonstrated that 31 species from 6 extant orders exhibit at least one kind of residency, philopatry or fidelity (Chapman et al., 2015), overlapping areas between COA and fishing grounds may have impacts on shark populations. From the nine species in this study, all, excepting *S. mokarran*, *M. canis* and *Rhizoprionodon spp.*, exhibit one or a combination of philopatry, fidelity and/or residency. Regional philopatry, that is, the return to birth region for parturition or mating, was evidenced in *C. limbatus* (Keeney et al., 2005) and *S. lewini* (Chapman et al., 2009; Daly-Engel et al., 2011). Additionally residency and/or seasonal residency has been corroborated for *C. limbatus* (DeAngelis et al., 2008; Heupel & Simpfendorfer, 2002), *C. perezii* (Garla et al., 2006; Bond et al., 2012; Brooks et al., 2013), *G. cuvier* (Papastamatiou et al., 2013) and *G. cirratum* (Ferreira et al., 2012). In all cases, this type of behavior generates population structure (subpopulations treated as different stocks). Populations with any form of philopatry or residency may display higher risks of being overfished and will not recover through immigration (Chapman et al., 2015). Moreover, juvenile and adult habitats may be located in the same site or very close to the areas identified, closing migration and gene flow, enhancing the need of effective MPA's at heavily fished areas (Bond et al., 2012). This, when examined at the light of this study,

emphasizes the effect of overlapping COA with fishery grounds and the possible effect that it may have on resident shark populations.

The use of fishing grounds information derived from interviews used in this study may influence the degree of overlapping areas identified as it may be subjective. Data may be biased towards coastal and more frequented areas and does not reflect temporal use changes of fishing grounds. For this reason, although we identified high degree of overlapping between fishing grounds and COA, percentages may change seasonally within COAs and other areas farther from the coastline may also have great impact from this activity. When evaluating protection by MPA over COA identified by this study, Morrosquillo South and Santa Marta COA (56.58% and 42.05% respectively) were identified as having the highest overlapping areas in the continental part of the Colombian Caribbean. Nevertheless, both areas exhibit high degree of overlapping with fishing grounds and those with higher probability of promoting shark by-catches. Contrastingly, the Guajira Peninsula region, was identified with having lower overlapping areas, but this is probably due to the fact that fishing grounds in the northern part are not displayed in the original database from which fishing grounds were obtained. This, suggest that the impact of small-scale fisheries in the northern part of Colombia may be underestimated.

Likewise, the SAP Archipelago COA encompasses an area of 65,018 sq. km of MPA (Seaflower MPA) declared in 2005, in which five of the 8 keys and island are protected 100%. Nevertheless, overlapping areas with fishing grounds are still present. Although our database does compile information from this subarea, it may also be miscalculated in some parts of the MPA as a result of low fishery management and monitoring activities. For this reason, although this MPA is zoned according to the type of use (No-entry zone, No-take, Artisanal fisheries, Special use and General use) we determined total overlapping areas without taking into account zoning regulations (Sanchez-Jabba, 2012). Fishery grounds mentioned by this author are only present in San Andres, Providence, Roncador, Serrana and Quitasueño. Therefore, there is no regulation, management or monitoring of shark fisheries (direct or bycatch) in other areas located in the SAP Archipelago that may also display overlapping. COA identified in our study partially overlap with MPA in the Colombian Caribbean, while fishing grounds have been also reported inside MPAs. This implies a doubtful enforcement in regulations. Especially when taking into account that in Colombia, all type of fishing activities are banned in National Natural Parks area (Artículo 13, Ley 2, 1959) and that fishing activities inside MPA area likely to be higher than registered by our data as fishing grounds may be underestimated especially in MPA's.

In this study, we constructed a highly precise and straightforward methodology to obtain co-occurrence areas for several shark species in a data-limited context, without the use of extensive systematic surveys, large budgets and in a limited time frame. Our findings support the definition of the habitat suitability models of iconic and threatened species by borrowing data by other geographic but linked areas. We, then, identified overlapping of shark co-occurrence areas in the Colombian Caribbean with small-scale fishery grounds and MPA's. Although data used in the construction of this study is limited, the general scenario of the spatial impact of small-scale fisheries and protection degree of MPA's in the Colombian Caribbean reflects high degree of spatial impact on shark co-occurrence areas by fishing grounds used by local communities and poor enforcement of MPA. For management purposes, co-occurrence areas identified for the nine shark species can be used as a starting point for defining priority areas for shark conservation where future management guidelines are to be implemented in order to alleviate identified fishing pressure over resident shark populations. Future works need to contemplate validation of each species model

and co-occurrence areas identified. For this purpose, reliable catch data by species should be recorded as well as tagging or systematic survey data by species should be prioritized.

5. Supplementary material

Habitat suitability models in the Caribbean Sea for *Carcharhinus falciformis* (Figure S1), *Carcharhinus limbatus* (Figure S2), *Carcharhinus perezii* (Figure S3), *Ginglymostoma cirratum* (Figure S4), *Galeocerdo cuvier* (Figure S5), *Mustelus canis* (Figure S6), *Rhizoprionodon spp.* (Figure S7), *Sphyrna lewini* (Figure S8) and *Sphyrna mokarran* (Figure S9), are included in the supplementary material. Additionally, the PERMANOVA, PERMADISP and SIMPER analysis performed for 16 COAs are presented.

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7. Tables

Table 1. Habitat Suitability Model settings selected in each species model by performing the sensibility tests, Area Under the Curve (AUC) values and environmental variable contribution.

Species	Model settings				AUC	Variable contribution (%)			
	Spatial bias correction	Validation method	Reg. multiplier	Feature		Bathymetry	Chl-a	Salinity	SST
<i>C. falciformis</i>	Checker	SpThin	1	LQ	0.8405	67.3467	12.8295	16.8351	2.9888
<i>C. limbatus</i>	Checker	SpThin	1	L	0.9126	94.1945	5.8055	0	0
<i>C. perezii</i>	Checker	SpThin	7	L	0.947	83.7998	16.2002	0	0
<i>G. cirratum</i>	Checker	SpThin	15	LQP	0.949	97.4884	2.1479	0.0012	0.3625
<i>G. cuvier</i>	Checker	SpThin	3	LQ	0.7767	63.6284	15.8256	11.8286	8.7174
<i>M. canis</i>	Checker	SpThin	10	LQ	0.886	88.4223	11.5777	0	0
<i>Rhizop. spp.</i>	Checker	SpThin	12	LQP	0.8691	64.996	2.1042	28.8986	4.0011
<i>S. lewini</i>	Checker	SpThin	1	L	0.8647	60.1173	3.2166	0	36.6662
<i>S. mokarran</i>	Checker	Bias File	2	L	0.9072	65.1183	31.2621	0.5389	3.0808

Table 2. Total overlapping areas between Co-occurrence (COA) areas using 70% and 85% threshold cut for iconic sharks, small-scale fishing grounds (FG) and fishing grounds exhibiting higher probability of producing shark catches from gear type use (SSSF) in Colombian Caribbean Sea.

Area Name	Area (sq. mi)
Total co-occurrence areas-70% (COA)	51023.98
Total Fishing grounds area (FG)	2800.9
Overlapping area between FG and COA	1286.37
Overlapping Area (%)	45.93
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Total co-occurrence areas-85% (COA)	11231.89
Total Fishing grounds area (FG)	2800.9
Overlapping area between FG and COA	91.09
Overlapping Area (%)	3.25
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Small-scale shark fishery grounds (SSSF)	2012.94
Overlapping area between SSSF and 85% COA	213.00
Overlapping Area (%)	10.58

