Ecological niche modeling reveals manta ray distribution and conservation priority areas in the Western Central Atlantic

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Abstract

The Western Central Atlantic (WCA) hosts a population of manta rays whose distribution and habitat preference is poorly understood. Addressing this lack of knowledge will be essential to aid the effective implementation of targeted conservation measures. Here, we use ensemble ecological niche modeling to predict the monthly distribution of manta rays in the WCA using multiple sources of species occurrence data, and consequently identify core areas, which represent suitable habitat in all months of the year. Models suggest a seasonal cycle of expansion and contraction of suitable habitat from coastal areas in spring-summer, to open ocean in autumn-winter. Core areas are concentrated along the coast of the USA, Mexico, and Venezuela. Only 24% of predicted suitable habitat is encompassed by the present regional network of MPAs, and is intersected by numerous, heavily trafficked shipping lanes. Manta rays are slow-growing animals that only produce a limited number of offspring; as such, this species is sensitive to even moderate increases in mortality rates. For this reason, the existing regional network of MPAs may offer them limited protection. As manta rays in the WCA are challenged by a complex landscape of threats and protective measures, future marine conservation planning in the region should explicitly address the conservation of manta rays, focusing on areas identified as key habitats for the species.

INTRODUCTION

Understanding the habitat requirements and distribution patterns of a species is important to the design of effective conservation measures. For many marine species this information is missing or incomplete, due to financial, logistical or geographic challenges to collecting relevant data in the marine environment. Biologging (the practice of collecting information from animals at liberty via electronic tags; Hussey *et al.*, 2015; Kays *et al.*, 2015), along with remotely sensed environmental information, can help to close such information gaps. In this regard, ecological niche modeling (ENM), sometimes also referred to as species distribution modeling (SDM), has become a widely implemented tool to study the spatial ecology and distribution of a variety of species both on land (Robinson *et al.*, 2011) and increasingly, at sea (Melo-Merino, Reyes-Bonilla, & Lira-Noriega, 2020). One of the most interesting features of ENM is the ability to predict species distribution over spatial and temporal scales larger than those in which data collection occurred (Franklin & Miller, 2009) or in regions different to the primary data

collection location (known as transferability; Werkowska *et al.*, 2016; Hazen *et al.*, 2017). As such, with relatively little data, scientists can make judicious estimates of presence and absence of a species over large areas that would otherwise be prohibitively costly to survey (Ferrier, 2002). Applications of ENM to elasmobranch species to date have highlighted the potential for this technique to resolve uncertainty in the spatial ecology of this group (e.g. McKinney *et al.*, 2012; Sequeira *et al.*, 2012; Hacohen-Domené *et al.*, 2017; Austin *et al.*, 2019; Báez *et al.*, 2020). For planktivorous species, the reliance on zooplankton means that their movements are strongly linked to changes in the biophysical environment that determine the distribution and abundance of their prey (Boucher, Ibanez, & Prieur, 1987; Richardson, 2008; Rohner *et al.*, 2013). For this reason, ENM (which builds on the correlation between environmental variables and the probability of presence of a species to forecast its distribution) is likely to be optimally suited to fulfill the existing gap in knowledge for planktivores.

Manta rays are a group of three large vertebrate planktivorous species in the genus *Mobula* (White *et al.*, 2018).

Although manta rays are globally distributed, uncertainty remains around their fine scale habitat selection and distribution patterns. Insights into the spatial ecology of manta rays across their geographic ranges have been obtained through the use of satellite telemetry (e.g. Graham *et al.*, 2012; Braun *et al.*, 2014, 2015; Jaine *et al.*, 2014). Manta rays have been found to favor topographically complex areas (Dewar *et al.*, 2008) and are often found in association with seamounts and oceanic islands (Marshall, Bennett, *et al.*, 2018), where upwelling of cold water currents often result in high relative plankton concentration. The reliable presence of manta rays at these sites has incentivized the growth of ecotourism businesses (Anderson *et al.*, 2011; O'Malley, Lee-Brooks, & Medd, 2013). However, the predictability of manta ray aggregations has also been exploited by artisanal and small-scale fisheries (Couturier *et al.*, 2012). A recent surge in demand for manta ray gills from the Asian traditional medicine market has further incentivized fishing for Mobulid species (Couturier *et al.*, 2012; Croll *et al.*, 2016; O'Malley *et al.*, 2017). The global manta ray population is believed to have suffered a 30% decline over the last three generations (although for some regions the estimates suggest declines of up to 80%; Rohner *et al.*, 2013; Rhoner *et al.*, 2017; Marshall, Bennett, *et al.*, 2018; Marshall, Kashiwagi, *et al.*, 2018). Both the oceanic manta ray *M. birostris* and the reef manta ray *Mobula alfredi* are considered 'vulnerable' to extinction by the IUCN (Marshall, Bennett, *et al.*, 2018; Marshall, Kashiwagi, *et al.*, 2018). No assessment exists for the Yucatan manta ray *Mobula cf. birostris*; however, given the restricted area of occurrence and likely smaller population size, its conservation status would likely be similar to, or worse than that of other manta ray species. In the Western Central Atlantic (WCA, including the Gulf of Mexico and Caribbean Sea), there are no known directed fisheries for manta rays (Ward-Paige, Davis, & Worm, 2013); however, other indirect threats, including unintentional fisheries catch, likely exist. The Gulf of Mexico (GOM) and the Caribbean basin have been identified as areas of medium to high cumulative human impact (Halpern *et al.*, 2008, 2015), and deterioration of the marine environment has been documented (Linton & Warner, 2003), particularly in coastal areas where mantas are thought to aggregate. Schools of manta rays in the WCA have been reported to be historically small (one to five individuals) and the yearly number of sightings of this species has been declining since 1993 (Ward-Paige *et al.*, 2013). Despite the existing threats and observed declines, a region-specific assessment of the conservation status of oceanic manta rays within the WCA does not exist, and spatially explicit conservation measures directed at protecting manta rays are lacking (Ward-Paige *et al.*, 2013).

Additional information on the distribution and environmental preferences of manta rays in the WCA would not only facilitate regional conservation, but also contribute to the global understanding of manta rays' spatial ecology (Lawson *et al.*, 2017). The description of the environmental drivers of manta ray distribution has recently been recognized as a research priority for mobulid conservation (Stewart *et al.*, 2018), to better target conservation efforts and predict future conservation needs in response to climate change. Consequently, this study presents the first ensemble ecological niche model (EENM) for manta rays covering the WCA, and provides insights into the spatial ecology and distribution of the species that can create a basis for conservation planning in the region.

Materials and methods

Two species of manta ray occur in the study area within the WCA (i.e. Caribbean Sea and GOM), including all Atlantic-facing countries between the latitudes of 7 and 32°N, and the limit of their Exclusive Economic Zones (EEZs; Fig. 1): the oceanic manta ray *M. birostris* and the Yucatan manta ray *M. sp cf. birostris*. The two species are morphologically similar (Hinojosa-Alvarez *et al.*, 2016) and apparently share environmental preferences (Hinojosa-Alvarez *et al.*, 2016), consequently sightings of both species were used for ensemble ecological niche modeling.

Distribution data

Data describing the occurrence of manta rays were obtained from a variety of sources: (1) Satellite tracking. Six manta rays (four females, one male and one unsexed juvenile) tracked in the southern Gulf of Mexico, offshore from the Yucatan peninsula, between July and September 2010 (Graham *et al.*, 2012). A total of 376 location points were available to be used as presence data for the model. (2) Direct observations. Sightings made from offshore oil and gas platforms in the northern Gulf of Mexico were sourced on a voluntary basis. A total of 29 sightings were recorded between August 2006 and September 2010 (Data S1). (3) Online repositories, including sightings from the Ocean Biogeographic Information System Spatial Ecological Analysis of Megavertebrate Populations (OBIS-SEAMAP http://seamap.env.duke.edu) and Global Biodiversity Information Facility (GBIF, https://www.gbif.org). The datasets were filtered to exclude duplicates, entries of sightings before 2006, or incomplete information. In total, 4580 sightings were obtained from GBIF and 98 from OBIS databases. (4) Social media. An exhaustive search of photos and videos of manta ray encounters between 2006 and 2018 in the WCA was conducted from YouTube and Facebook. For each photo or video of a manta ray encountered, the date and location of the sighting were obtained from information listed in the post. Only records for which the position could be estimated to within 2 km (i.e. the lowest accuracy available from satellite tracking data Argos Location class 1; Witt *et al.*, 2010) were retained. A total of 54 reliable sightings were obtained from this search (Data S1). In total, 5,137 sightings records were available from this exhaustive search.

All sightings records (from hereon referred to as "presence locations"; Fig. 1) were collated and grouped by the month in which sightings occurred. For each month, spatially coincident presence locations were eliminated, and k-means clustering was applied to group locations in close proximity to
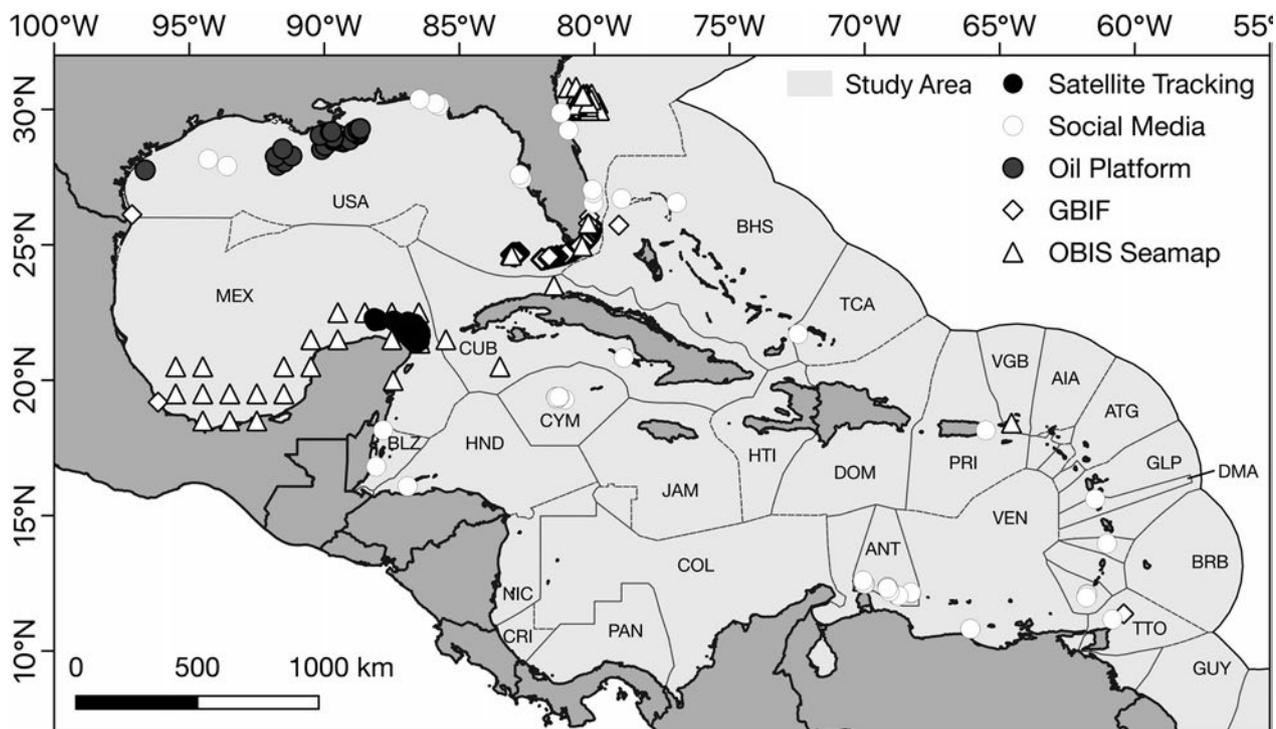
Figure 1 Manta ray sightings in the Western Central Atlantic (showing Caribbean Sea and Gulf of Mexico) derived from species occurrence datasets (shapes). Three letter codes denote Exclusive Economic Zones (EEZs) according to ISO 3166 country codes.

each other, to reduce bias from oversampling. K-means clustering used a radius of 4 km, which matched the spatial resolution of satellite environmental data used within the ecological niche modeling. Following filtering, 655 presence locations (13% of original locations) were retained.

Since no true absence data was available for the study species in the WCA, artificial absence data (i.e. 'pseudo-absences') were generated and placed randomly within the study area (grey area in Fig. 1). One pseudo-absence was created to complement each presence location, and was temporally coupled to the corresponding presence location (Wells et al., 2018). The temporal match between presence and absence locations is intended to result in higher accuracy in determining unfavorable environmental conditions in successive modeling steps. To minimize the effect of stochasticity on the final predictions, five sets of pseudoabsences were created and ecological niche models were created using each pseudo-absence dataset repeatedly with the same presence dataset.

Environmental data

Four environmental variables, bathymetric depth, bathymetric slope, Night-time Sea Surface Temperature (NSST) and chlorophyll-α concentration (Chl-α), were used to describe habitat preference within the ecological niche models. These are important factors that influence the distribution of manta rays and other large marine vertebrates (Panigada et al., 2008; Embling et al., 2010; Freedman & Sen Roy, 2012;

Jaine et al., 2012; McKinney et al., 2012; Sequeira et al., 2012; Hacohen-Domené et al., 2017). Monthly Chl-α concentration and NSST were downloaded in spatially referenced gridded layers (2006–2018; from now on referred to as rasters) from NASA's Ocean Color Web (https://www.oceancolor.gsfc.nasa.gov), depth was obtained from the General Bathymetric Chart of The Ocean (GEBCO http://www.gebco.net), and bathymetric slope was derived from depth data. All environmental variables were used at the finest spatial resolution available for NSST and Chl-α (4×4 km^2). Long-term averaged rasters (mean) of NSST and Chl-α (2006–2018) were created for each month (January to December). Spatially concurrent environmental conditions were extracted from the respective monthly average rasters for all presence points, and then for paired pseudo-absence locations; these data were subsequently used to train the ENMs. Using long-term means of environmental conditions has been found to improve predictions of spatial distribution while retaining good levels of accuracy in the estimation of ecological preferences (Pennino, Vilela, & Bellido, 2019). Chl-α concentration and bathymetric slope values were highly left skewed, and as such were log-transformed prior to modeling. Correlation between environmental variables was tested using the values of each environmental variable extracted at the location of presence and pseudo-absence data. Bathymetric depth was found to be significantly and strongly correlated with both bathymetric slope (Spearman rank correlation, $\rho = 0.5$, $P < 0.001$) and Chl-α concentration (Spearman rank correlation, $\rho = -0.7$, $P < 0.001$). As

such, bathymetric depth was not used in further ecological niche modeling. All other variables were either non-correlated or showed low correlation coefficients (Table S1) and were retained as explanatory variables in the ecological niche models.

Habitat modeling

In order to construct ecological niche models of habitat relative suitability (RS), an ensemble ecological niche modeling approach was adopted (EENM; Araújo & New, 2007). Several statistical algorithms were used, including: Generalized Linear Model (GLM), General Additive Model (GAM), Generalized Boosted Model (GBM), and Maximum Entropy (MaxEnt) model. GLM is a regression-based modeling approach and can perform well with geographically widely spread data (Aguirre-Gutiérrez et al., 2013). GAM has been observed to perform well when predicting suitability in poorly surveyed areas (Drexler & Ainsworth, 2013). MaxEnt is a machine-learning based algorithm and is the only one of the four selected which was built to handle presence-only data directly (Phillips, Anderson, & Schapire, 2006), and GBM combines two algorithms, decision trees and boosting, producing a much smoother gradient in models that can handle sharp discontinuities in data (Elith, Leathwick, & Hastie, 2008). Modeling was conducted within the biomod2 package (Thuiller et al., 2020; R package version 3.4.6) for the statistical software R (R Core Team, 2020; R version 4.0.1), using the environmental data extracted for paired presence and pseudoabsence points in the previous step. All individual ecological niche models (ENMs) were run using 10-fold cross validation with a 75–25% random split of the presence/pseudo-pseudoabsence data for calibration and model testing, respectively, (Guisan & Zimmermann, 2000). Two scores were computed to evaluate the performance of the models: the true skill statistic (TSS; Allouche, Tsoar, & Kadmon, 2006) and the area under the curve of the receiver-operating characteristic (AUC or ROC; Hanley & McNeil, 1982). Both scores were used to evaluate goodness of fit of the models, but only the ENMs with TSS of 0.7 or above were combined to form ensemble models using a weighted average (mean) across models. Only TSS was used in selecting models for the ensemble as this metric is more closely related to the accuracy of predictions (Allouche et al., 2006) and had higher variability amongst models, leading to stronger selection for accuracy in the final predictions. Variable importance scores for all individual models and for the ensemble were calculated through the 'variable_importance' function available in the biomod2 package. The function uses a random-forest based algorithm to calculate variable importance by sequentially re-shuffling one variable and comparing the accuracy of predictions of a model built with this data compared to the original dataset, and returns a score (i.e. the correlation between reference dataset predictions and shuffled dataset predictions) that is used as indicator variable importance. The higher the score, the higher the importance of the variable. Because variable importance scores calculated in this manner do not necessarily sum to

one, the relative importance of each variable was calculated as a fraction of the sum of all absolute variable importance scores for each model; this allowed for the comparison of variable importance between algorithms and multiple runs of the same algorithm type. Spatial projections of the predictions from ensemble models were subsequently created for all months (Jan. to Dec.; see Fig. S1). These projected EENMs described the RS of each cell in the grid, scaled between 0 and 1, where 0.5 represents areas of typical habitat suitability, 0 represents lowest suitability and 1 indicates greatest suitability. Moran's Index was calculated to investigate residual spatial correlation in the final EENMs; no evidence was subsequently found for non-random distribution of residuals (z-scores 1.467–1.480, $P > 0.05$).

Suitable habitat for manta rays was defined as cells having a RS $\geq$ 0.5. Differences in extent and distribution of suitable habitat between months were visually assessed. In order to describe areas of year-round importance to manta rays (from hereon 'core habitat'), all monthly EENMs were coerced to binary rasters, where the value of 1 was assigned to cells having a RS $\geq$ 0.5. All monthly binary rasters were then summed, and the resulting cells with a value of 12 (i.e. RS $\geq$ 0.5 in all months) were extracted and converted to polygons, which described core habitat.

MPA and threat data

A geodatabase of Marine Protected Areas was sourced from the MPAtlas website (http://www.mpatlas.org); The surface area of suitable habitat (RS $\geq$ 0.5) and of core habitat occurring within each MPA in the Caribbean was calculated for each monthly EENM produced (i.e. January to December). To estimate overlap with potential threats, the density of ship traffic and marine pollution information were obtained from Halpern et al. (2015), and the location of major ports in the region was sourced from Natural Earth (https://www.naturalearthdata.com). To quantify manta ray exposure to marine traffic, the mean ship movement density (number of ship tracks/km^2, including both commercial cargo ships and recreational vessels) within and outside core habitat areas was calculated. Similarly, average ship density within core areas was estimated for each country. In order to identify critical overlap areas of particularly high traffic, areas of core habitat where ship movement density was equal to or higher than the 50% of quantile ship density were extracted and investigated separately.

Results

Model evaluation

All 200 ecological niche models built (4 algorithms for each of 5 sets of pseudoabsences, repeated for 10 cross validation runs) were run successfully. In both individual and ensemble models, Chl-α concentration was the most important variable in explaining the distribution of manta rays, followed by bathymetric slope (Table 1). NSST was assigned the least importance overall. All models had moderate to high AUC

Table 1 Summary statistics of ecological niche models of manta ray distribution in the western central Atlantic, including evaluation scores (which indicate goodness of fit metrics), variable importance estimations (all values given as average and standard deviation, in parentheses), and number of models that were selected to be included in the ensemble model for all algorithm types and the ensemble model (EENM)

Algorithm	Evaluation Scores		Variable importance			Models in EENM
	TSS	AUC	Slope	Chl-α	NSST	
GLM	0.641 (0.038)	0.867 (0.018)	0.063 (0.033)	0.933 (0.039)	0.004 (0.012)	5
GAM	0.666 (0.037)	0.888 (0.015)	0.100 (0.0337)	0.829 (0.053)	0.070 (0.030)	9
GBM	0.711 (0.033)	0.920 (0.015)	0.248 (0.039)	0.721 (0.037)	0.032 (0.010)	40
MaxEnt	0.646 (0.088)	0.875 (0.049)	0.105 (0.038)	0.661 (0.121)	0.234 (0.119)	5
Ensemble	0.730	0.931	0.200	0.781	0.019	59

Abbreviations: AUC, area under the curve; Chl- α, chlorophyll-alpha concentration; GAM, general additive model; GBM, generalized boosted model; GLM, general linear model; TSS, true skill statistic; NSST, nighttime sea surface temperature.

values (range 0.54–0.95) and highly variable TSS scores (range 0.09–0.78). A total of 59 models (40 GBM, 9 GAM, 5 GLM, and 5 MaxEnt) had a TSS score ≥ 0.7 and were therefore used to compute the ensemble model as their weighted (mean) average (according to TSS scores).

The majority of manta ray sightings were from coastal waters, which may either be because they are more abundant there, or because they are more likely to be sighted by human observers closer to land (e.g. on day trips). To account for this, we ran a second iteration of the EENM with coastally constrained pseudo-absences. This model predicted a much more concentrated distribution of manta rays with high areas of relative suitability close to the coast year-round, with little predicted suitable habitat offshore. We
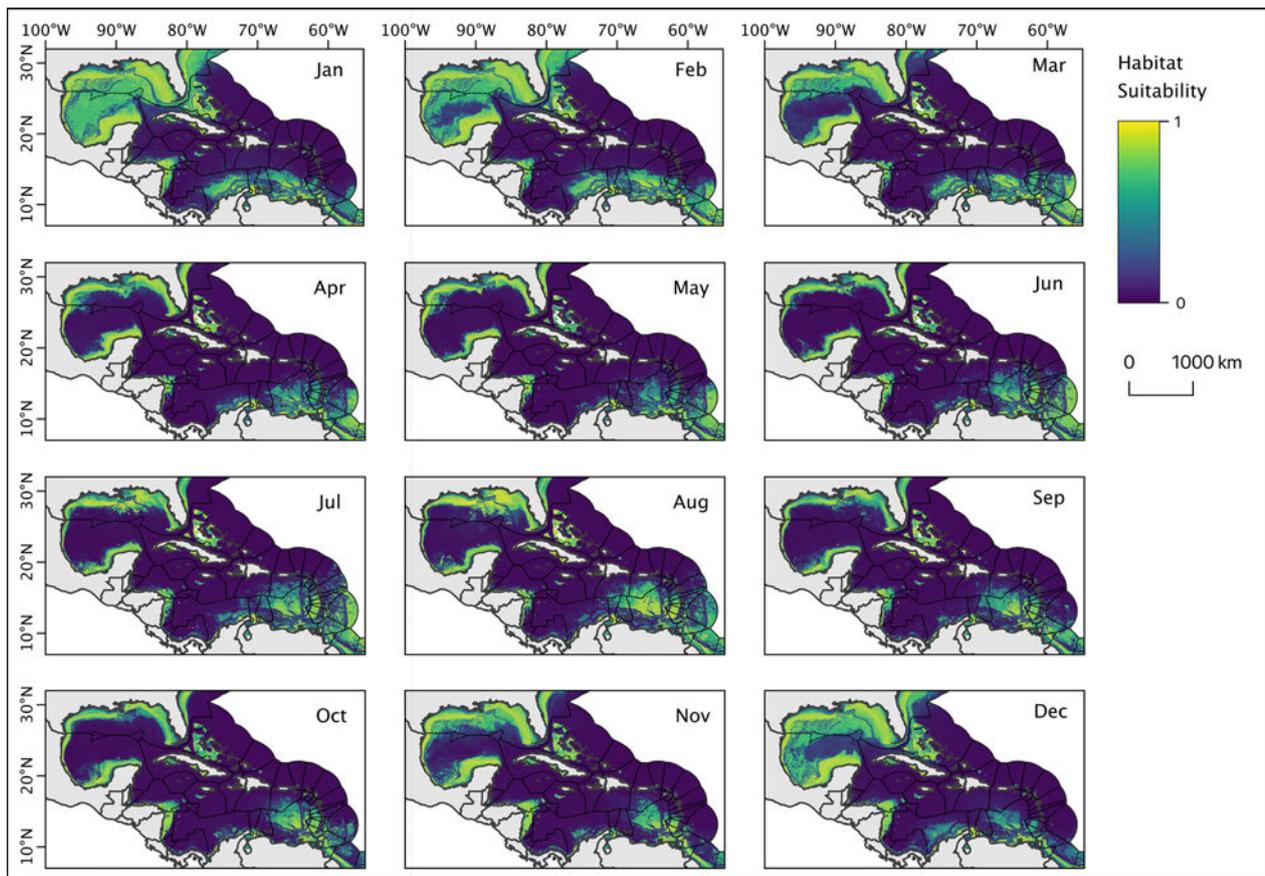

Figure 2 Monthly prediction of relative habitat suitability for manta rays in the western central Atlantic derived from ensemble ecological niche modelling (shading indicates habitat suitability from unsuitable (dark) to extremely suitable (light)). See also Suppl. animation.

considered this alternative model was likely to be less reflective of manta ray ecology, and was not considered further in analyses.

Predicted suitable habitat

The distribution and extent of area predicted as suitable habitat (RS ≥ 0.5) by the EENMs varied considerably between months (Fig. 2, Table 2), revealing an expansion and contraction of the predicted suitable habitat throughout the year. The extent of suitable habitat was predicted to be higher during the colder dry season (December to March), with the maximum extent observed in January (2,332,313 km^2; Table 2). Wide areas of offshore waters became suitable to manta rays during this period, while a contraction of suitable habitat towards coastal areas was observed during the warmer months, beginning with the onset of the tropical rainy season in May when the smallest extent of suitable habitat was observed (1,098,963 km^2). Despite monthly spatial variations, several areas could be identified that were consistently suitable throughout the year ('core habitat', areas with RS ≥ 0.5 in all months, Fig. 3), covering 546,959 km^2. All core habitat was located relatively close to the coast (minimum distance from coastline to core habitat centroids; mean 47 km, range 0.7–306 km). The countries whose EEZ contained the largest predicted areas of core habitat for manta rays in the WCA were the USA (200,213 km^2), Mexico (92,797 km^2), Venezuela (62,278 km^2) and The Bahamas (54,504 km^2, Table 3), with the USA encompassing 37% of manta ray core habitat. These four countries alone encompassed 75% of the total predicted core habitat for manta rays. Two other noteworthy regions of core habitat were identified on the shallow shelf extending from Nicaragua and Honduras (39,050 km^2, 7% of total), and in southern Cuba (30,694 km^2, 6%; Table 3).

MPA coverage

Predicted suitable habitat for manta rays was identified within 240 of the 939 MPAs present in the Western Central Atlantic (Fig. 4). Only 14.6% (79,616 km^2) of core habitat occurred within MPAs and little variation was observed in the extent of suitable habitat covered by the MPA network between months (Table 2). The country with the highest proportion of manta ray core habitat that lays in protected areas was Nicaragua (65%, Table 3); while the USA had the absolute greatest extent of core areas within protected habitat (39,840 km^2, Table 3), accounting for half of the total protected core habitat in the study area.

Maritime traffic

Average ship movement density inside manta ray core habitat (2.5 ± 1.6 ship tracks per year per km^2, mean ± SD) was found to be somewhat lower than the rest of the study area (3.1 ± 1.1 ship tracks per year per km^2), though spatial variability in this estimate was high both inside and outside core habitat. The highest mean ship density within manta ray

habitat was recorded in Saint-Martin (5.1 ± 0.3, mean ± SD) and in the Netherlands Antilles (4.3 ± 0.4), though very little manta ray core habitat was identified in these EEZs. Among the countries with the highest concentration of suitable habitat, The Bahamas was the highest scoring country in terms of ship traffic (3.2 ± 0.8), followed by the United States (3.0 ± 1.6), and Venezuela (2.8 ± 1.1). Mexico had the lowest mean ship density of all four top-countries (1.8 ± 1.2; Table 3). The largest area of overlap between core habitat and high maritime traffic (i.e. core habitat regions where ship movement density was higher than or equal to 50% quantile) was recorded in the USA (102,762 km^2), followed by Venezuela (17,140 km^2) and The Bahamas (13,707 km^2; Table 3 and Fig. 4).

Discussion

This study describes, for the first time, the likely distribution pattern of manta rays in the WCA, providing information that is key to informing future conservation efforts in the region. Given the inherent difficulty of collecting information on mobile marine species, we suggest that the method described here (i.e. the combination of satellite tracking, online repositories, and social media posts and subsequent analysis through ecological niche modeling) could constitute a valuable tool in the creation of the information required

Table 2 Monthly description of presence locations, extent of suitable habitat identified by relevant month-specific ensemble ecological models, and extent of protected suitable habitat for manta rays in the western central Atlantic, as forecasted by ensemble ecological niche modelling. Values are also given for core habitat (areas that retained suitable habitat throughout the year, identified as those areas having a predicted relative suitability>=0.5 in all months). All areas are given as km^2. Monthly suitable habitat is also expressed as percentage of the whole study area, while protected suitable habitat is also given as the percentage of the total identified suitable habitat for the month (or the total core habitat area)

| Month	Presence locations	Suitable habitat		Protected suitable habitat	
		Area	% Study area	Area	% Suitable habitat
January	11	2,332,313	33.9	307,798	13.2
February	12	2,139,588	31.1	264,614	12.4
March	17	1,663,766	24.2	219,663	13.2
April	13	1,226,710	17.8	199,558	16.3
May	45	1,098,963	16.0	197,476	18.0
June	100	1,201,952	17.5	217,305	18.1
July	94	1,383,311	20.1	243,420	17.6
August	95	1,527,869	22.2	262,732	17.2
September	96	1,234,364	17.9	241,589	19.6
October	92	1,227,599	17.9	244,974	20.0
November	73	1,438,671	20.9	257,352	17.9
December	7	1,713,038	24.9	284,056	16.6
Core Habitat		546,959	8.0	131,329	24.0
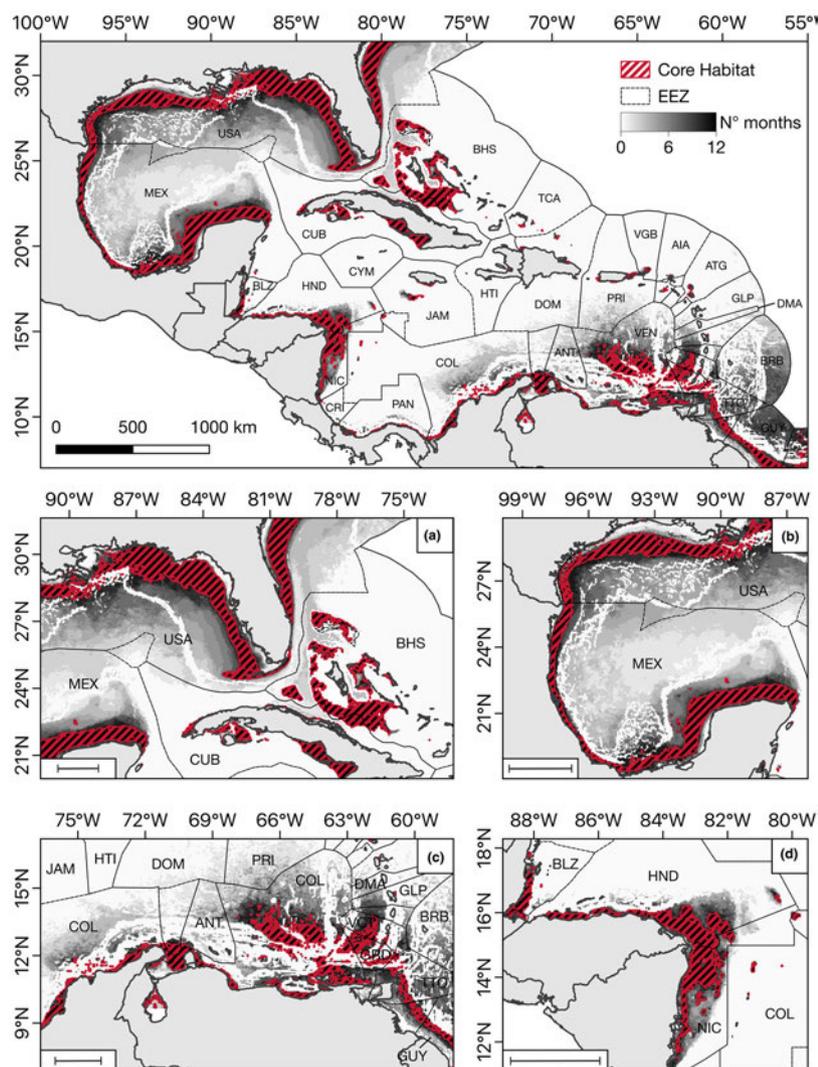
Figure 3 Predicted core habitat areas for manta rays in the western central Atlantic derived from ensemble ecological niche models (areas where suitability is higher than 0.5 in all months; striped polygons); grey shading indicates the number of months in which an area was predicted to have suitability higher than 0.5. Three letter codes denote national Exclusive Economic Zones according to ISO 3166 country codes. Areas of core habitats: Southern USA and The Bahamas (a), Gulf of Mexico (b), Venezuela (c), and Honduras-Nicaragua (d). Scale bars in zoom-in maps are 300 km.

for the conservation of other data deficient populations across wide regions.

Patterns of seasonally suitable habitat in the Gulf of Mexico and the South-Eastern Caribbean Sea are likely linked to patterns of primary production, which also increases in coastal areas of the WCA during the rainy season (May-October; Condal, Vega-Moro, & Ardisson, 2013) due to seasonal upwellings and increased river output (Morey, Zavala-Hidalgo, & O'Brien, 2013). Key seasonal sites of manta ray presence and abundance have been identified in the Yucatan Peninsula (Graham *et al.*, 2012; Hacohen-Domené *et al.*, 2017), and outside the WCA in Australia (Wilson, Taylor, & Pearce, 2001), French Guiana (Girondot *et al.*, 2015), and other sites in the Indian Ocean (Dewar *et al.*, 2008; Anderson, Adam, & Goes, 2011; Kashiwagi *et al.*, 2011). The

contraction of suitable habitat towards coastal zones would explain the observed seasonally increased abundance of manta rays in these areas. At the same time, expansion of habitat during winter months suggests that manta rays use a bigger area than expected from information based solely on sightings at coastal aggregation sites. The seasonal movement between coastal and demersal zones likely leads manta rays to experience a complex landscape, characterized by highly variable nature and intensity of threats and protective measures.

Manta ray sightings in the WCA have declined since 1993 (Ward-Paige *et al.*, 2013), likely due to a combination of stressors such as bycatch mortality, habitat destruction and pollution and boat strikes (Marshall, Bennett, *et al.*, 2018). Although manta rays are often incidentally caught as

Table 3 Extent of predicted manta ray core habitat in the Esclusive Economic Zones (EEZ) of countries bordering the western central Atlantic derived from ensemble ecological niche models (only countries that contain at least 0.1% of the total core habitat are shown), and the extent that is covered by national protected areas. Core habitat extent is expressed as area and as percentage of the total (for protected core habitat, percentages are given relative to the national core habitat area and to the total protected core habitat in the region). Information on shipping intensity is also given as mean (average) shipping intensity inside core areas, and area of core habitat with shipping instensity $\geqq$211 ship tracks $\times$ km^{-2} $\times$ year^{-1} (75% quantile of shipping intensity within core areas)

EEZ	Core habitat		Protected Core Habitat			Shipping	
	Area	% Total	Area	% Country core habitat	% Regional Protected Habitat	Mean shipping intensity Ship tracks/	Area of high shipping intensity
	km^2		km^2			(km^2 × year)	km^2
United States	200,213	36.6	39,840	19.9	50.0	3.03	102,762
Mexico	92,797	17.0	5,714	6.2	7.2	1.76	8,566
Venezuela	62,278	11.4	949	1.5	1.2	2.78	17,140
The Bahamas	54,504	10.0	3,971	7.3	5.0	3.17	13,707
Cuba	30,694	5.6	3,332	10.9	4.2	1.11	2,756
Honduras	21,320	3.9	7,991	37.5	10.0	2.68	5,347
Colombia	18,038	3.3	1,557	8.6	2.0	2.07	4,724
Nicaragua	17,732	3.2	11,544	65.1	14.4	1.89	1,945
Guyana	13,614	2.5	0	0.0	0.0	0.64	0
Grenada	6,718	1.2	55	0.8	0.1	3.56	3,081
Saint Vincent and the Grenadines	4,637	0.8	80	1.7	0.1	3.38	1,608
Trinidad and Tobago	4,391	0.9	0	0.0	0.0	3.67	1,976
Belize	4,349	0.8	1,361	31.3	1.7	0.58	0
Panama	2,688	0.5	313	11.7	0.4	0.89	159
Jamaica	2,357	0.4	455	19.3	0.6	2.33	263
Puerto Rico and Virgin Islands	2,306	0.4	348	15.1	0.4	2.36	382
Suriname	2,305	0.4	0	0.0	0.0	1.74	0
Antigua and Barbuda	943	0.2	120	12.8	0.2	3.65	409
Dominican Republic	724	0.1	471	65.1	0.6	2.58	299
Netherlands Antilles	625	0.1	0	0.0	0.0	4.32	604
Haiti	600	0.1	236	39.4	0.3	0.21	0
Guatemala	589	0.1	449	76.2	0.6	0.81	0
Turks and Caicos Islands	588	0.1	251	42.7	0.3	3.04	144
British Virgin Islands	547	0.1	59	10.9	0.1	3.87	453
Study Region	546,602	100	79,616	14.6	100	3.08	166,876

by-catch in industrial fisheries (Trent, Parshley, & Carlson, 1997; White *et al*., 2006; Zeeberg, Corten, & de Graaf, 2006; Amandè *et al*., 2010; Croll *et al*., 2016), the magnitude of bycatch incidents remains unknown for the WCA, where fishing pressure is likely lower than in other parts of the species' range (Ward-Paige *et al*., 2013). Nonetheless, occasional reports of manta ray landings have been documented in the region (Trent *et al*., 1997; Graham *et al*., 2012), yet these have not been identified as *M. birostris* or *M. sp. cf. birostris*. Just 15% of manta ray habitat occurs within MPAs, suggesting that very little protection exists for manta rays, regardless of the species or season. Of the 31 countries within the region with suitable manta ray habitat, only the state of Florida and Mexico have legislated national protection for manta rays, in the form of a fishing ban (Stevens *et al*., 2018). As a shark and ray sanctuary, commercial fishing for all ray species is also prohibited within the EEZ of the British Virgin Islands. If all other shark sanctuaries in the WCA (The Bahamas, Honduras, Bonaire, Cayman Islands, Dominican Republic, St. Marten, and Saba) expanded their ban on commercial fishing to include ray species, this would increase the area of protected core habitat by 60% and obtain an overall coverage of 25% of manta ray core habitat. Owing to the life history characteristics of manta rays (i.e. slow growth rate, late maturity and low fecundity rates), even very low levels of by-catch could have significant detrimental effects on the population (Dulvy *et al*., 2014). As only 0.2% of WCA seas are completely closed to fishing activities, it might be the case that the network of MPAs across the WCA, in its present shape, does not offer manta rays a sufficient level of protection.

Excluding Nicaragua and Honduras, all countries bordering core manta ray habitat have high levels of tourism along their coasts (Jayawardena, 2002), and all have medium to high coastal population densities (Cincotta, Wisnewski, & Engelman, 2000; Goldewijk, 2005), both of which have been shown to negatively impact biodiversity and ecosystem integrity (Tratalos & Austin, 2001; Davenport & Davenport,
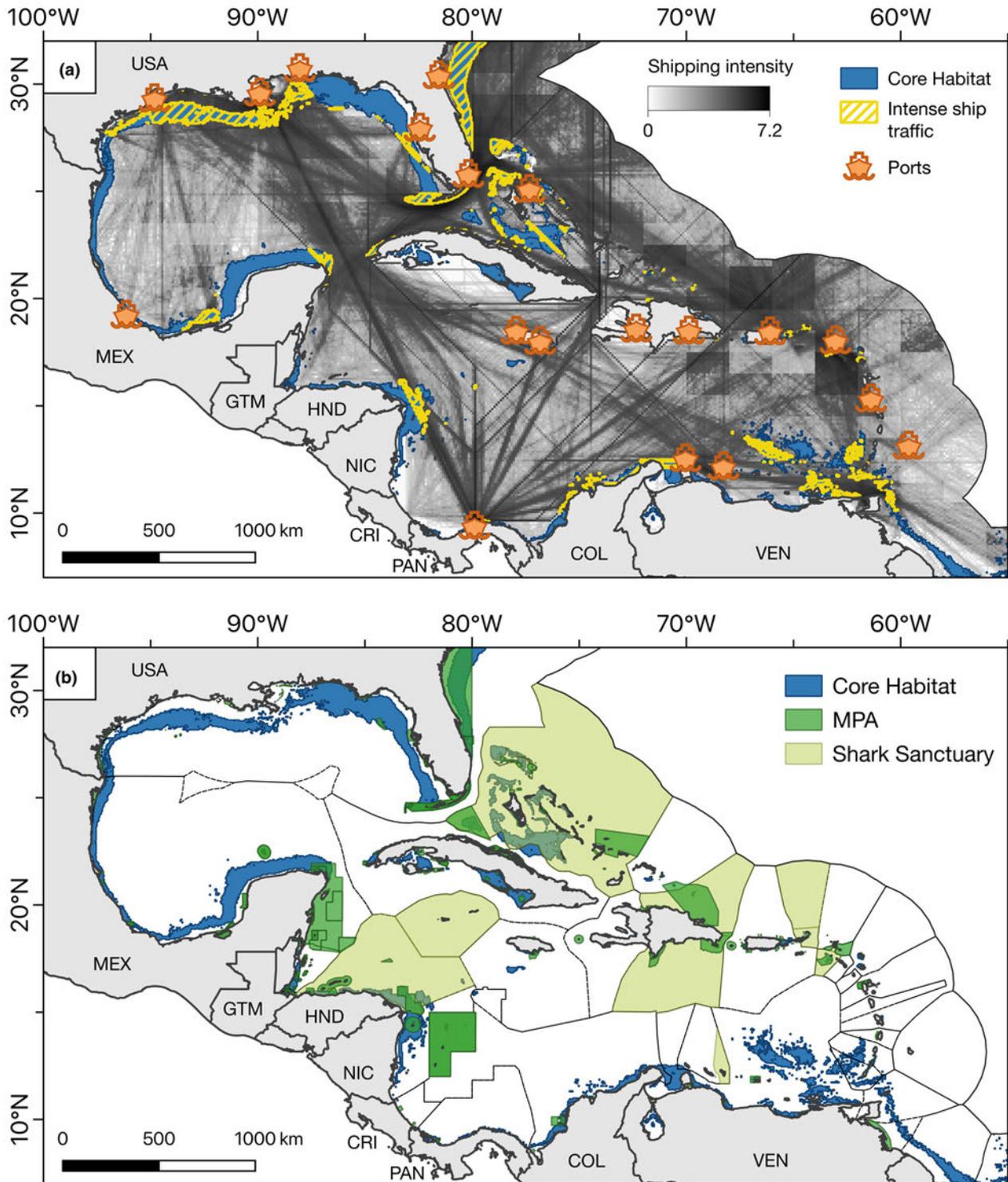
Figure 4 Manta rays, shipping and MPAs (Marine Protected Areas). Core manta ray habitat predicted through ensemble ecological niche models (blue polygons) with (a) shipping routes and major ports across the western central Atlantic, and (b) Marine Protected Areas and Shark Sanctuaries. Shipping data includes both recreational and commercial shipping routes and was sourced from Halpern *et al.* (2015). Black lines indicate country boundaries on land or between Exclusive Economic Zones, denoted by three letter codes according to ISO 3166 country codes.

2006; Mora, 2006; CIinner et al., 2013). Some suitable habitat for manta rays along the coast of western Florida, USA and the Yucatan peninsula, Mexico, is located in regions that have been reported to have low to medium human impact (Halpern et al., 2015), while most of the predicted core habitat is located in areas of medium to very high impact (Halpern et al., 2015). Highly trafficked marine areas furthermore intersect core manta ray habitat, and manta rays' seasonal proximity to the coast puts them in close vicinity to some of the busiest ports in the region. The shipping traffic data used here describes the movement of both commercial shipping and boat traffic related to recreational activities. The latter can be locally extremely high and thus represent an important threat; However, the temporal and spatial variability of recreational ship traffic may lead to potentially crucial high-traffic areas to be underestimated by the algorithm that generated the dataset, since occasional peaks in ship traffic density can be counter-balanced by low ship density at other times of the year. The number of potential key threat areas of overlap between manta ray habitat and high shipping traffic was therefore likely underestimated. Boat strikes have been suggested as a likely important cause of mortality for manta rays (Germanov & Marshall, 2014; Marshall, Bennett, et al., 2018). In the WCA, where directed and incidental fishing pressure is thought to be lower (Ward-Paige et al., 2013), intense marine traffic could be one of the biggest threats to the species. Furthermore, intense boat traffic is an indicator of high organic and inorganic pollution, also a potentially serious threat to manta rays (Fossi et al., 2017; Germanov et al., 2018, 2019).

Despite the good level of confidence in the model predictions given by AUC and TSS scores, ground truthing of these newly identified core areas is suggested to validate the predicted suitable habitats. Obtaining additional data on manta ray behavior and their temperature and depth preferences to explicitly include in future modeling efforts would allow for the description of critical foraging and nursery habitats that could not be distinguished in this study, and would focus MPA expansion or creation for specific life history events (Druon et al., 2016) and under changing climate regimes. Furthermore, knowledge of depth use by manta rays would allow for modeling to be carried out in three dimensions (i.e. the present EENM does not account for movement through the water column; Braun et al., 2014). It has been shown that when three-dimensionality is accounted for, more accurate predictions can be made (Duffy & Chown, 2017). Modeling suitable habitat at multiple depths could also lead to the description of corridors linking the core areas described here, which would be important features to be considered in spatial conservation planning.

In conclusion, we have presented the first ensemble ecological niche model of manta ray distribution across the WCA, and highlight that four key countries host core manta ray habitat (USA, Mexico, Venezuela and The Bahamas). We also showed that a small proportion of manta ray habitat lies in protected waters, and in some areas they may be exposed to high levels of threat from shipping traffic, suggesting that protection measures are likely insufficient across

much of their range. Overall, the results of the present study highlight two regions as potentially important for future conservation of manta rays in the WCA: (1) in the USA the extensive network of protected areas that already covers manta ray habitat could be expanded and improved by including manta ray conservation explicitly in management planning, and introducing regulations directed at their protection, such as speed limits to minimize likelihood of fatal collisions; (2) in Mexico and Nicaragua expansion of existing protected areas, and creation of new sites, could be focused on regions where habitat suitability is high and human impact is low, thus maximizing their efficacy.

Acknowledgements

Data Availability Statement

All data used for analysis in this study is available either in online repositories (mentioned in-text), or in the online supplementary material of this article.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. List of sightings obtained from social media searches and individual submissions.