Hawksbill presence and habitat suitability of a marine reserve in Honduras

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ABSTRACT

Marine protected areas (MPAs) have been established to decrease the negative impacts of human activities on important marine habitats. Several sea turtle species reside within MPAs; however, analyses of habitat suitability for sea turtles within many MPAs is typically lacking. Habitat modeling and species mapping have become essential tools in determining areas suitable for species inhabitance. MaxEnt is a popular machine-learning program that uses presence-only occurrence data and is considered the best modeling method in discriminating between suitable and unsuitable habitats. Using MaxEnt, we created species distribution models (SDMs) from presence-only occurrence points for juvenile hawksbills and three environmental variables: boat traffic intensities, prey item distributions, and benthic characterizations, within the Sandy Bay West End Marine Reserve (SBWEMR) in Roatán, Honduras. Area under the receiving operator curve (AUC) values were greater than 0.75, indicating high model accuracy. Jackknife evaluations indicated algal prey item *Dictyota* spp., boat traffic intensity, and *Geodia neptuni* sponge abundance had the greatest influence on species distribution. Areas of suitability shifted based on time of day and ranged from a low probability of hawksbill presence (0.0) to a high probability of hawksbill presence (0.8). Regardless of time of day, the SBWEMR is classified as at least moderately suitable (>0.2–0.4), with least suitable habitat (0–0.2) prevalent in the most northeastern region of the reserve. The greatest suitability (>0.6–1) was evident within the mid-region and southern most regions of the reserve. Probability of hawksbill presence increased in accordance with increasing boat traffic, although there was no clear causative relationship between the two. Although the reserve overall is mostly moderately suitable, the SBWEMR remains an important local recruitment and foraging ground for juvenile hawksbills. Hawksbills have been considered resilient, continually functioning beneath their operational limits. However, with continued global depletion of essential habitats over time and lack of effective MPA management, areas of habitat suitable for hawksbill inhabitance may decrease below levels sufficient for hawksbill presence in protected areas of the Western Caribbean.

1. Introduction

Sea turtles are marine reptiles that can be found in tropical and subtropical regions of the world. They utilize wide areas of the ocean, spanning over 110 countries and territories (Bjorndal and Jackson, 2003). According to the International Union for Conservation of Nature (IUCN), all seven species are currently classified as either data deficient, vulnerable, endangered, or critically endangered. Declines in sea turtle

populations can be attributed to anthropogenic activities, such as exploitation of eggs, accidental by-catch, exposure to pathogens or pollutants, and the destruction or alteration of nesting beaches and foraging areas (Jackson et al., 2001; Gaos et al., 2012; Marcovaldi et al., 2007; Finkbeiner et al., 2011; Guimarães et al., 2017). Currently, the hawksbill sea turtle (*Eretmochelys imbricata*) is classified as critically endangered (IUCN, 2020). Over the past several decades, hawksbill populations have decreased approximately 80% due to threats specific

to hawksbills (Bowen et al., 2007; Mortimer and Donnelly, 2008), which are victims of turtle harvesting, specifically targeted for the tortoiseshell trade (Canin, 1989, Nahill et al., 2020). Due to the unsustainable harvest of hawksbills, estimates suggest that more than 4 million turtles have been killed globally within the past 150 years (Miller et al., 2019). To replenish population numbers, conservation strategies require the adequate protection of this critically endangered species, and the habitats in which individuals reside.

Terrestrial and aquatic protected areas have been implemented to reduce the negative impacts of human activities on species' survival, to preserve remaining individuals, and to ultimately replenish and restore populations (Wang, 2019). Specifically, marine protected areas (MPAs) have been implemented to decrease the negative impacts of human-driven activities on marine life (Lubchenco et al., 2003). Effective management of MPAs requires consistent observation and monitoring of human pressure (Geldmann et al., 2014) and species presence (Sánchez-Carnero et al., 2016). Sea turtle presence has been recorded within the bounds of several protected areas (Selby et al., 2019; Herren et al., 2018; Gorham et al., 2014; Rouphael et al., 2013); however, current management practices of few protected areas have been assessed or reformed to ensure policies benefit sea turtles and their vital habitats (Hayes et al., 2017; Fernandes et al., 2017). Typically, assessments of sea turtle habitat use in protected areas are limited to nesting regions (Christianen et al., 2014; Witt et al., 2008) or corridors used during internesting periods (Witt et al., 2008). Few studies assess both sea turtle distribution and suitability of foraging areas located within protected zones (Cuevas et al., 2007; Schofield et al., 2010; Rincon-Diaz et al., 2011a, 2011b). Several studies suggest the establishment of new MPAs or the extension of existing MPAs due to sea turtle presence (Fuentes et al., 2018; Dawson et al., 2017; Hays et al., 2014; Lea et al., 2016), yet do not further assess essential habitat characteristics and the suitability of existing areas, nor do they suggest a reformation of management strategies to ensure these habitat qualities are maintained.

Habitat modeling and species mapping have become essential tools in predicting species distributions and identifying suitable regions for species inhabitance (Hooker et al., 2011). Species distribution models (SDMs) utilize species occurrence data and corresponding environmental variables to make applications in ecology and conservation. Environmental variables can be divided into three categories: disturbances, which are any disruptions that affect the environmental system; resources, which are compounds that provide energy; and regulators, which control species ecophysiology (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000). SDMs have been used to estimate global distributions of species (Yesson et al., 2012), to map the geographical range shifts of species (Gotelli and Stanton-Geddes, 2015), and to predict the impact of climate change on species distributions (Briscoe et al., 2016). Within marine environments, SDMs have been used to identify critical habitats of migratory species, such as fin whales (*Balaenoptera physalus*), striped dolphins (*Stenella coeruleoalba*) (Panigada et al., 2008), harbor porpoises (*Phocoena phocoena*) (Embling et al., 2010), bottlenose dolphins (*Tursiops truncatus*), grey seals (*Halichoerus grypus*), and harbor seals (*Phoca vitulina*) (Bailey and Thompson, 2009). Generally, SDMs utilize climate data, such as temperature and precipitation, as environmental variables (Soria-Auza et al., 2010; Gardner et al., 2019), and analyze species distribution at a global scale (Fournier et al., 2017). Overall, SDMs can be used to estimate suitability of various regions for species inhabitance, and to predict and map the extent of a species across wide-ranging terrestrial or aquatic landscapes (Alatawi et al., 2020; Rickbeil et al., 2014; Biber et al., 2020). However, few studies have utilized SDMs to determine habitat suitability and species distributions on smaller local scales (Gogol-Prokurat, 2011), while still fewer have been used to assess the distribution of foraging sea turtles (Hart et al., 2018; Duncan, 2012). However, most SDM's relating to sea turtles have focused on nesting studies utilizing these types of environmental data (Santos et al., 2006; Lichstein et al., 2002; Pike, 2013). Ultimately, none have yet assessed the suitability of foraging areas for sea turtles in existing marine protected areas.

MaxEnt is a popular machine-learning program used to create SDMs and map habitat suitability of regions varying in scale from worldwide to entire continents, countries, and smaller regions (Coxen et al., 2017; De La Estrella et al., 2012; Dos Santos et al., 2017; Santos et al., 2013). MaxEnt facilitates the use of presence-only occurrence data, continuous and categorical environmental variables, and is considered to be the best modeling method in discriminating between suitable and unsuitable habitats (Merow et al., 2013).

Many SDMs utilize only climate data as the environmental variables (Austin and Van Niel, 2011), but additional environmental variables, such as disturbance, resource, and regulator variables, have been introduced. Disturbance variables are described as natural or human-induced factors that lead to animal anxiety or uneasiness (Guisan and Thuiller, 2005). Boat traffic has been shown to alter activity patterns, increase stress, and lead to physical injury in various marine animals and is therefore categorized as a disturbance variable (Bracciali et al., 2012; Niemi et al., 2014; Shimada et al., 2017). Prey item distribution has been categorized as a resource variable since prey items can be assimilated by organisms (Guisan and Thuiller, 2005). In addition, prey item abundance and distribution have been shown to influence species presence and distribution (Pyke, 1984). Lastly, since sea turtle presence can be associated with various benthic habitat types (Wood et al., 2013; Walcott et al., 2014), benthic characterization has been described as a regulator variable, a limiting factor controlling species presence (Guisan and Thuiller, 2005).

The Sandy Bay West End Marine Reserve (SBWEMR) is a small marine protected area off the northwestern coast of Roatán, Honduras. The reserve was initially created to protect the reef and its inhabitants from destructive human practices (RMP, 2015, Doiron and Weissenberger, 2014). However, although human population density, tourism, and aquatic-based activities in the region have increased (900 visitors in 1969 to > 1 million visitors in 2014; Ministry of Tourism, unpubl. data), reflective restructuring of management practices with respect to sea turtle survivability has not been undertaken in any area of the Bay Islands (Forest, 1998). Using species distribution modeling, we aimed to assess the suitability of the SBWEMR by combining hawksbill occurrence data with environmental variables likely influencing hawksbill distribution throughout the reserve. We also aimed to evaluate which environmental variables have the greatest effect on hawksbill distribution, assess which regions of the SBWEMR are most suitable for hawksbill use, and subsequently provide recommendations for MPA management to maintain or increase suitability.

2. Methods

2.1. Study site

Roatán is one of the Bay Islands of Honduras located approximately 55 km from the north coast of mainland Honduras. The SBWEMR is an MPA located off the northwestern coast of the island (16°21′ 44″ N, 86°25′ 06″ W) (Fig. 1). The reserve lies within the Mesoamerican Barrier Reef and is made up of barrier, fringing, patch, and sloping reefs ranging in depths of approximately 5–40 m (Gonzalez, 2013). The reserve encompasses 13 km of Roatán's coastline, stretching from the westernmost tip of the island in West Bay through West End to Sandy Bay, extending approximately 1 km offshore (RMP, 2015, Gonzalez, 2013). More detailed descriptions of the benthic environment in the SBWEMR is provided in Hayes et al. (2017) and Baumbach et al. (2019).

2.2. Species occurrence data

2.2.1. Sea turtle surveys

Hawksbill occurrence data were collected through a series of in-water surveys while SCUBA diving. Surveys took place throughout the SBWEMR from June to September 2016–2018. In-water surveys lasted
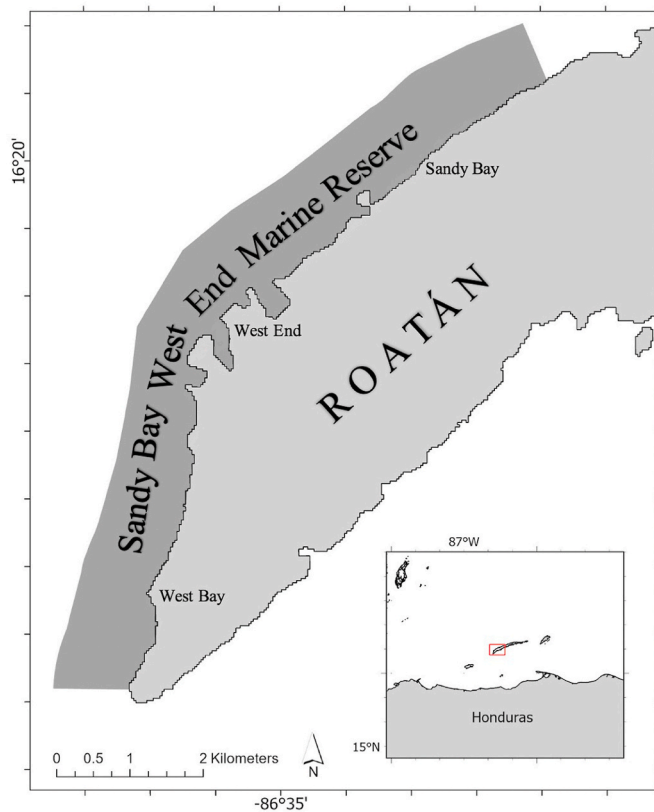
Fig. 1. The Sandy Bay West End Marine Reserve (SBWEMR). The protected area is located off the Northwestern coast of Roatán, Honduras and spans 13 km of coastline, extending 1 km from the shore.

approximately 1 h and were undertaken randomly in approximately 0.9 km² area blocks of the 13 km² reserve. We completed surveys in each block in the morning (8:30–10:30) and afternoon (14:30–16:30) time periods, where 2–5 divers traversed the area in a transect pattern, similar to the strip transect method described by Baumbach et al. (2019). Upon sighting hawksbill turtles, locations were recorded based on the dive site latitude and longitude using a handheld GPS (Garmin – GPSMAP 64s).

2.3. Environmental data

2.3.1. Boat traffic assessment

Boat traffic throughout the SBWEMR was quantified through a series of boat count surveys. Surveys were completed throughout the entire SBWEMR, along approximately 13 km of coastline, and were conducted 2–3 times per week from July to September 2016–2018. We conducted counts for 20 min during the morning (8:30–10:30) and afternoon (14:30–16:30) time periods, indicating the number of boats that remained stationary or traveled through an ∼ 1 km² area. We termed the number of boats traveling through a region in 1 h 'boat intensity' and calculated boat intensity by the equation:

$$(B_M - B_A) \times 3 = boats \times hour^{-1} \tag{1}$$

where B_M equals the number of boats that moved through an ∼ 1 km² area in the 20-min period and B_A equals the number of boats that remained stationary in the same 20-min period. Since the difference of moving and stationary boats was calculated during a 20-min observation period, the difference was multiplied by three to estimate the number of boats moving through an ∼ 1 km² area per hour. For further details on this method, refer to Wright et al. (2020).

2.3.2. Prey item distribution

To characterize prey item distributions, we utilized area and line transect surveys. Area transects were used to estimate percent cover of potential algal prey items *Dictyota* spp., *Halimeda opuntia*, *Lobophora variegata*, and *Kallymenia limminghii*, and line surveys were used specifically to quantify presence of the sponge, *Geodia neptuni*. These prey items were selected because they are known to be common prey for hawksbills in the area of Roatán (Berube et al., 2012; Baumbach et al., 2022). For area transects, a 30 m transect line was placed randomly along the reef and six, 1 m² quadrats were placed consecutively along the transect line every 5 m, with the quadrat centered on the transect line. Transects were located near dive site buoys, as dive sites are relatively evenly spaced throughout the marine reserve (see Wright et al., 2020 for details of dive sites within the reserve). Photographs of each quadrat were taken, edited, and transferred to Coral Point Count with Excel extensions (CPCe, Ver. 4.1, National Coral Reef Institute, Fort Lauderdale, FL) (Kohler and Gill, 2006). To calculate the percent cover of potential algal prey items, a simple area analysis was completed using CPCe's tracing function to outline all occurrences of each algal species in the quadrat photograph. In order to quantify *G. neptuni* abundance throughout the SBWEMR, in-water *G. neptuni* sponge counts were conducted by line transects, as described by Baumbach et al. (2019).

2.4. Remote sensing benthic data

2.4.1. Image capture

A 4-band (Blue, Green, Red, Near Infrared) multispectral scene of QuickBird satellite data with 2.44 m spatial resolution was obtained from Satellite Imaging Corporation (formerly known as Digital Globe Inc., Colorado, USA). The image was captured by the QuickBird satellite on 15 March 2004. Although some short-term, small-scale changes are inevitable, a visual comparison with Allen Coral Atlas (Atlas (2020) does not show any significant large-scale changes since 2004. Satellite data were radiometrically and geometrically corrected by the vendor to remove radiometric noise and geometric distortions. The georectification was performed with a nearest-neighbor interpolation which resulted in a root mean square error (RMSE) of ±1 pixel.

2.4.2. Image processing - atmospheric correction

We converted raw digital numbers (DNs) or pixel values to top-of-atmosphere (TOA) radiance using QuickBird provided calibration coefficients. Land areas were masked using a near-infrared (NIR) band-based binary mask. Cloud cover and cloud shadows were also removed using a NIR-Red combined binary mask (Mishra et al., 2005). The image was processed through a first-order single scattering albedo atmospheric correction to remove Rayleigh and aerosol scattering. The aerosol scattering component was derived from an optically deep-water area covering a 50 × 50 pixel window. Band-specific Rayleigh and aerosol scattering components were subtracted from the TOA radiance which subsequently converted to remote sensing reflectance (R_{rs}). Details of the atmospheric correction procedure can be found in Mishra et al. (2005).

2.4.3. Benthic habitat mapping

In this study, we recalibrated the Lyzenga (1978) bathymetric model using *in situ* and principal component (PC) transformed QuickBird R_{rs} data (PC1) representing a uniform reflectance bottom type (i.e., seagrass substrate type). The bathymetric map was used in the radiative transfer model by Lee et al. (1994), which decomposes total R_{rs} to R_{rs} by water column, and R_{rs} by benthic substrate. Water column inherent optical properties (i.e. band-wise absorption and backscattering coefficients) were derived from the optically deep-water window using empirical models proposed by Lee et al. (1998). Finally, we used water depth, absorption, and backscattering parameters to derive the bottom albedo or benthic reflectance image. We clustered the benthic reflectance image to classify the benthic habitat types using the Iterative Self Organizing

Data (ISODATA) algorithm to derive 100 clusters. We then grouped these 100 clusters into five bottom types (seagrass with sand, dense seagrass, coral, coral with sand, and sand) for accuracy assessments (supplemental Figure1). Details of the water column correction and benthic habitat mapping procedure can be found in Mishra et al. (2006).

2.5. Model and map compilation

2.5.1. Environmental layer creation

We used ArcGIS Pro (ESRI, Redlands, CA) to create 12 spatial data layers for insertion into MaxEnt; 11 environmental spatial data layers and a single background layer, depicting the area of the study site. We used a spatial resolution of 2.8 m for these environmental data layers. More detailed aspects of layer descriptions are as indicated in Supplemental Table 1. Benthic environmental data acquired from remote sensing (dense seagrass, seagrass with sand, sand, coral with sand, coral) were imported into ArcGIS Pro in raster format and converted to American Standard Code for Information Interchange (ASCII). Environmental data collected from field surveys (boat traffic intensity, *Dictyota* spp., *L. variegata*, *K. limminghii*, *H. opuntia*, *G. neptuni*) were imported into ArcGIS in table format and joined to a vector layer of the SBWEMR. We transformed all environmental variable vector layers to raster layers with identical coordinate projections, extent, and spatial resolutions. Multicollinearity tests were performed in ArcGIS Pro using band collection statistics spatial analyst tool. We excluded *H. opuntia* and *L. variegata* prey item layers from the model due to multicollinearity.

2.5.2. MaxEnt conditions and model creation

To create SDMs and map habitat suitability within the SBWEMR, we used the MaxEnt interface version 3.4.1. In-water turtle surveys provided 94 occurrence points in the morning and 81 in the afternoon, 75% of which were used for model training and 25% as test data. To avoid overfitting the model, the regularization value was kept as 0.5 for both morning and afternoon models. To reduce the effects of spatial autocorrelation, bootstrapping replication run type was used for 10 replicate runs, and iterations were fixed at 1,000. Remotely sensed environmental variable layers were classified as categorical, while the remaining environmental variables were classified as continuous. We kept all other programable values at their defaults. Linear, quadratic, product, threshold, and hinge features were used to generate both the morning and afternoon models. The threshold value was chosen using the minimum training presence (Pearson, 2007). Area under the receiving operator curve (AUC) values were used to assess model accuracy and predictability, and the jackknifing method was used to indicate the importance of each environmental variable on species distribution *via* gain. We indicated probability of hawksbill presence (PHP) in relation to each predictor variable with response curves for continuous variables and response bar graphs for categorical variables. We classified PHP as low (0.0–0.2), slightly moderate (>0.2–0.4), moderate (>0.4–0.6), and high (>0.6–1.0).

We imported final outputs of both the morning and afternoon models into ArcGIS Pro and clipped each output to display the suitability of the geographic region of the SBWEMR. Suitability of habitat within the SBWEMR was classified as unsuitable (0.0–0.2), moderately suitable (>0.2–0.4), suitable (>0.4–0.6), and highly suitable (>0.6–1.0). Additionally, using ArcGIS Pro, we inserted hawksbill occurrence points and estimated kernel density using the kernel density spatial analyst tool. Occurrence points and kernel density estimates were used to indicate actual hawksbill presence and density in relation to suitable and unsuitable habitats. On our resulting maps, we used a range of colors from light purple to indicate estimates of very low hawksbill kernel density, to dark purple to indicate very high hawksbill kernel density.

Additionally, to provide confirmation of our results we input our habitat characteristics and presence/absence data into an automated kuenm (R package, Cobos et al. (2019)) protocol and compared the results of both the kuenm models and the MaxEnt models for all features

and the probability of hawksbill sightings throughout the SBWEMR.

3. Results

3.1. Sea turtle surveys

We completed 243 in-water surveys for sea turtles from June–September 2016–2018. Of these, 115 surveys were completed in the morning, and another 128 surveys were completed during the afternoon. A total of 180 juvenile hawksbill sightings were recorded.

3.2. Boat traffic assessment

Boat traffic assessment within the SBWEMR took place for ten weeks from June to September for three years (2016–2018). During the observation periods, we counted 6,999 boats. The overall mean of boat traffic intensity was significantly higher in southern regions of the reserve when compared to the northern region of the reserve (F = 33.26, df = 2, P < 0.0001. There was no significant difference in boat traffic intensity between the morning and afternoon time periods (F = 2.091, df = 1, p < 0.01).

3.3. Prey item distribution

To characterize prey item distribution in the SBWEMR, we conducted 143 transect line surveys, and photographed and assessed 839 habitat quadrats. We also completed sponge counts throughout the reserve. Transect surveys and quadrat assessments indicated that macroalgae accounted for 26.87% of the area assessed in the southernmost region of the reserve, 33.46% in the mid-region, and 48.98% of the area assessed in the northernmost region of the reserve. However, *Kallymenia* specifically, was not evident in transect surveys. Sponge counts indicated that 43% of *Geodia* sponge counted within the reserve was found in the southernmost region of the reserve, while 51% was found in the mid-region, and 7% was found in the northernmost region.

3.4. Model performance and variable input

Models created to predict species distribution in both the morning and afternoon exhibited high accuracy. Area under the receiving operator curve (AUC) values were 0.96 in the morning and 0.95 in the

Table 1
Environmental Variable Layers. Eleven environmental variables were assessed for use in our study. Nine (bolded) variables selected through a correlation test, were used to create a model corresponding to the morning and afternoon time periods. Relative percent (%) contribution of each variable to the MaxEnt model creation is provided.

Environmental Variable	Unit	% Contribution Morning	% Contribution Afternoon
Dense Seagrass	0 (absent); 1 (present)	3.4	0.8
Seagrass with Sand	0 (absent); 1 (present)	1.4	2.2
Sand	0 (absent); 1 (present)	5.4	1.2
Coral with Sand	0 (absent); 1 (present)	1.4	2
Coral	0 (absent); 1 (present)	2.1	4.7
Boat Traffic Intensity	boats/hr.	64.1	50.7
Dictyota spp.	%/m^2	3.3	11.6
Lobophora variegate	%/m^2	–	–
Kallymenia limminghei	%/m^2	2.7	0.5
Halimeda opuntia	%/m^2	–	–
Geodia neptuni	#/km^2	16.3	26.5

afternoon. Overall percent contribution of each environmental variable to the model's creation varied between the morning and afternoon (Table 1). In the morning model, jackknife evaluation of regularized training gain indicated *Dictyota* spp. percent cover had the greatest influence on species distribution, followed by *G. neptuni* sponge count, boat traffic intensity, sand, *K. limminghii* percent cover, and lastly the remaining benthic characterizations (Fig. 2A). Jackknife estimates of testing gain in the morning model implied that boat traffic intensity had the greatest influence on species distribution, followed closely by *Dictyota* spp. percent cover and *G. neptuni* sponge count. The remaining benthic variables had the least influence on species distribution in the morning (Fig. 2B).

Jackknife estimates of regularized training gain in the afternoon suggested that boat traffic had the greatest influence on species distribution, followed by *G. neptuni* sponge abundances, *Dictyota* spp. percent cover, coral, seagrass with sand, followed by *K. limminghii* percent cover, and the remaining benthic characterization (Fig. 3A). In the afternoon model, jackknifing estimates of test gain revealed that boat traffic intensity had the greatest influence on species distribution, followed by *Dictyota* spp. percent cover, *G. neptuni* sponge count, coral, seagrass with sand, followed by *K. limminghii* percent cover, and the remaining benthic makeup (Fig. 3B). Response curves for the probability of hawksbill presence (PHP) based on boat traffic intensity indicated an increase in the PHP as boat traffic intensity increased in both the morning and afternoon (Fig. 4A & B). However, in the morning, PHP plateaued and decreased after reaching an intensity of 50 boats/hour (Fig. 4A). Response curves for PHP based on *Dictyota* spp. (Fig. 5A and B) and *K. limminghii* (Fig. 5C and D) percent cover indicated a decrease in the PHP as percent cover increased in both the morning and afternoon. In contrast, response curves for PHP based on sponge counts indicated an increase in the PHP as *G. neptuni* sponge counts increased in both the morning (Fig. 6A) and afternoon (Fig. 6B). Unlike response curves for continuous variables, general trends of categorical variables were indicated using bar graphs. In the morning model, an increase in PHP was evident in the presence of all environmental variables, the greatest being dense seagrass (Fig. 7A). In the afternoon model, an increase in PHP was also evident in the presence of all variables, however, the greatest being
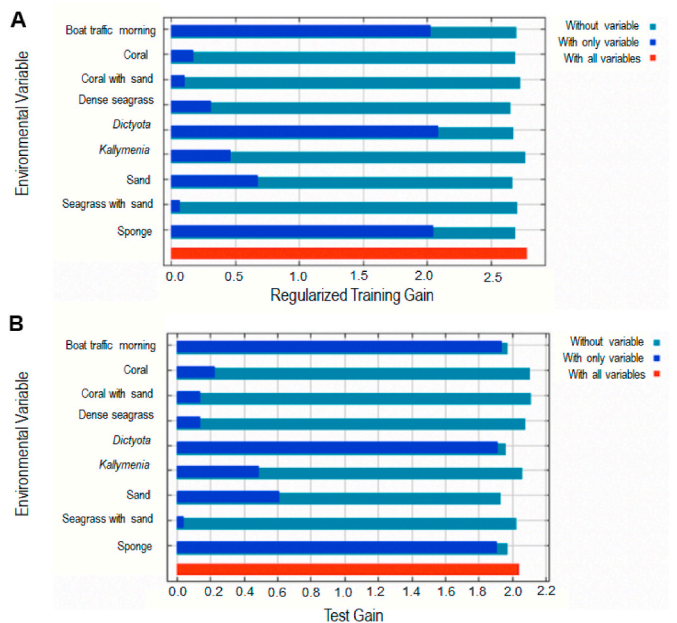

Fig. 2. Jackknifing estimates depicting variable importance on hawksbill distribution in the morning. Jackknife of regularized training gain (A), Jackknife of test gain (B). Teal bars represent testing gain when variable is omitted, dark blue bars represent testing gain of variable when used in isolation, and red bars represent testing gain with all variables present.
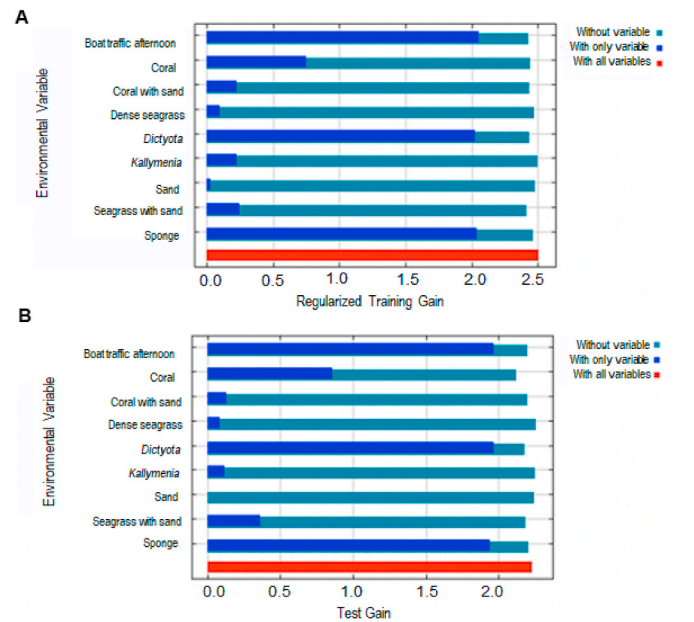

Fig. 3. Jackknifing estimates depicting variable importance on hawksbill distribution in the afternoon. Jackknife of regularized training gain (A), Jackknife of test gain (B). Teal bars represent testing gain when variable is omitted, dark blue bars represent testing gain of variable when used in isolation, and red bars represent testing gain with all variables present.

coral in the afternoon (Fig. 7B). Still, regardless of the presence or absence of benthic variables, the morning and afternoon models suggested moderate to high PHP when associated with all categorical environmental variables.

3.5. Hawksbill distribution model

Using the environmental parameters associated with hawksbill occurrence data, MaxEnt logistic output indicated regions of varying suitability within the SBWEMR in both the morning and afternoon. Areas of suitability shifted based on time of day, and ranged from unsuitable (0.0) to highly suitable (0.8). Regardless of time of day, the majority of the SBWEMR can be classified as at least moderately suitable (>0.2–0.4), with least suitable habitat (0.0–0.2) most evident in the northeastern most region of the reserve. High suitability (>0.6–1.0) was evident within the mid-region and southern most regions of the reserve in both the morning (Fig. 8A) and afternoon simulations (Fig. 8B). Kernel density estimates also indicated greater hawksbill density in the southwestern region of the SBWEMR in both the morning (Fig. 8C) and afternoon (Fig. 8D), corresponding to more suitable habitat. However, higher hawksbill density is more concentrated in the afternoon when compared to the morning time period (Fig. 8C and D).

3.6. Confirmation model

Results from the kuenm automated protocol produced essentially identical results as those provided by MaxEnt, using the parameters we placed in the protocol. Therefore, we do not report the details of the kuenm models, and instead have reported only those results from our main modeling program, MaxEnt.

4. Discussion

SDMs have previously been used in sea turtle conservation efforts (Duncan, 2012; Guo, 2014; Varo-Cruz et al., 2016; Pike, 2013). However, aside from Hart et al. (2013) and Selby et al. (2019), few models assess hawksbill distributions in association with several environmental
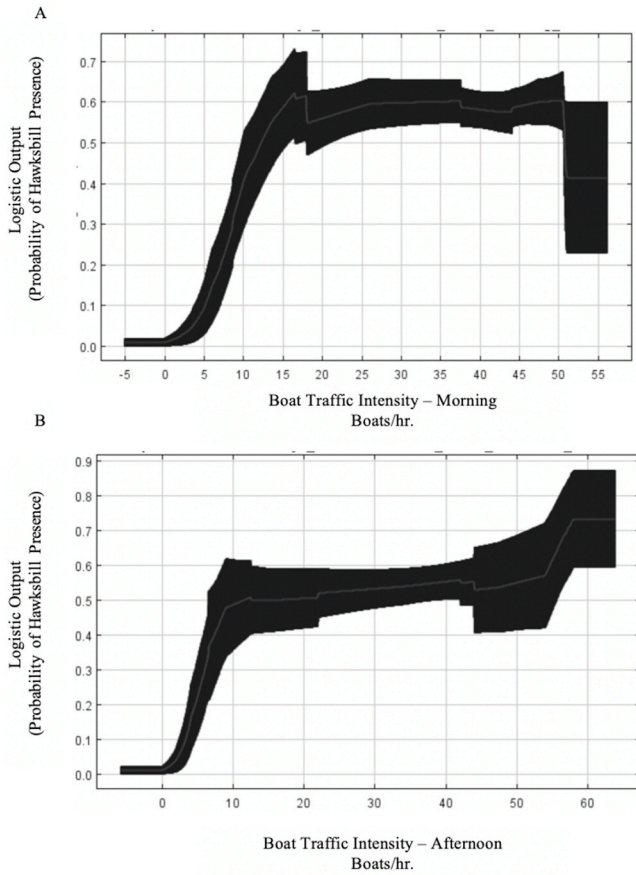
Fig. 4. Response curves of probability of hawksbill presence in relation to boat traffic intensity in the morning (A) and afternoon (B). Response curves indicate the dependence of predicted suitability on boat traffic intensity. In both figures, boat traffic intensity (boats/hour) is depicted on the x-axis and logistic output (probability of presence) is depicted on the y-axis. Black outline indicates one standard deviation.
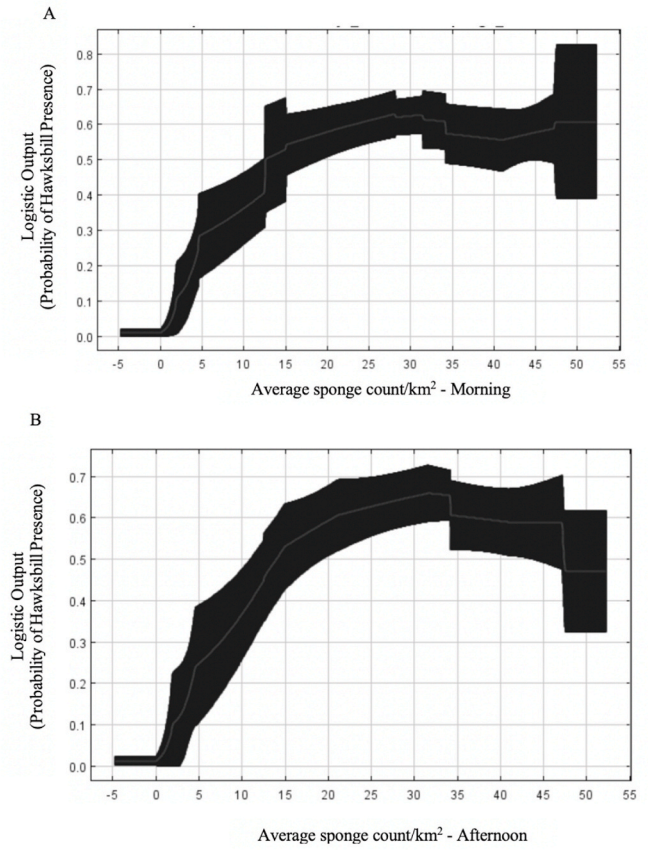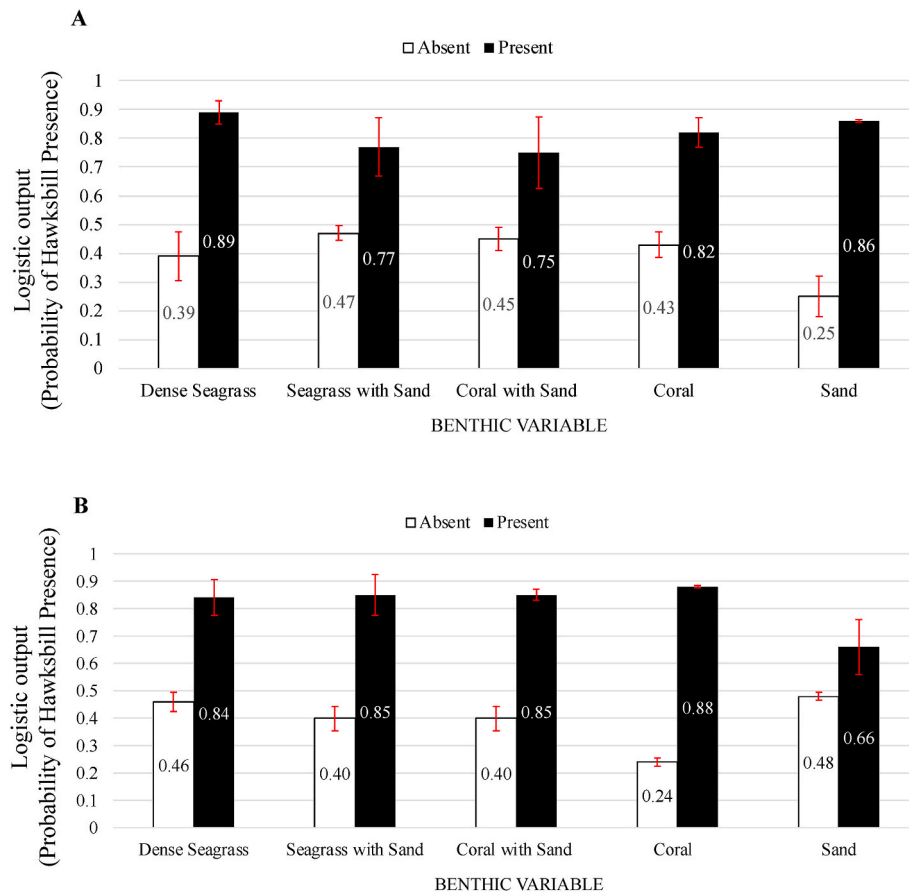

Fig. 6. Response curves of hawksbill probability of presence in relation to potential prey item, *G. neptuni* in the morning (A) and afternoon (B). Response curves indicate the dependence of predicted suitability on *G. neptuni* count per squared kilometer. In both figures G. neptuni count per squared kilometer is depicted on the x-axis and logistic output (probability of presence) is depicted on the y-axis. Black outline indicates one standard deviation.
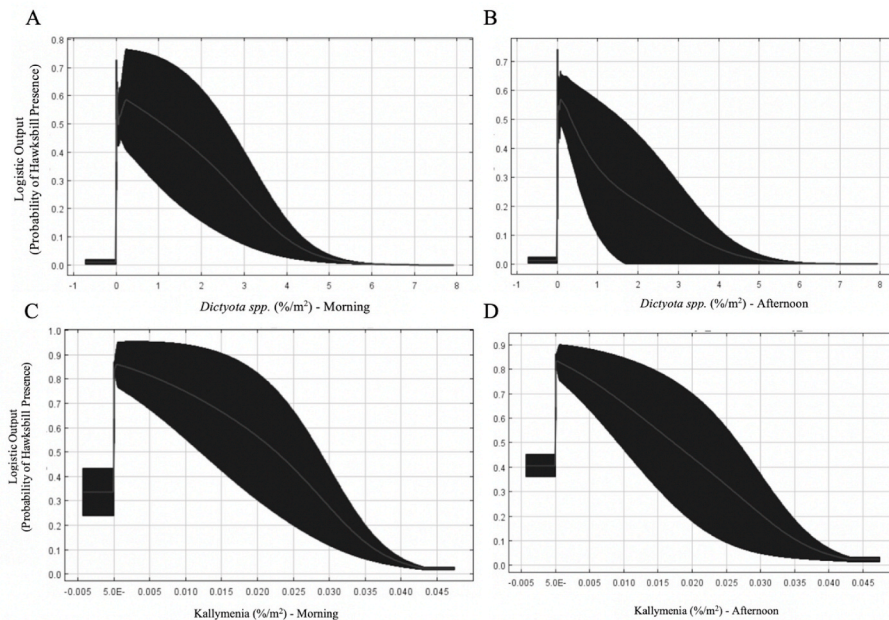
Fig. 5. Response curves for probability of hawksbill presence (PHP) in relation to potential prey items, *Dictyota* spp. in the morning (A) and afternoon (B), and *K. limminghii* in the morning (C) and afternoon (D). Response curves indicate the dependence of predicted suitability on *Dictyota* spp. and *K. limminghii* percent cover. In both figures, percent cover is depicted on the x-axis and logistic output (probability of presence) is depicted on the y-axis. Black outline indicates one standard deviation.

A

B

Fig. 7. Response bar graphs of hawksbill probability of presence in relation to benthic makeup in the Morning (A) and Afternoon (B). Benthic type is depicted on the X-axis, while probability of hawksbill presence in relation to the benthic type is depicted on the Y-axis. Error bars are depicted in red.

factors in MPAs. Furthermore, the suitability of protected areas for hawksbill presence is often overlooked and management strategies may remain unadjusted to account for population growth at regional scales (Santos et al., 2021). Several models have focused on evaluating the suitability of nesting sites (Santos et al., 2006; Lichstein et al., 2002; Pike, 2013), meanwhile foraging regions remain overlooked. Our study is one of the few to evaluate the suitability of an MPA for the continued presence of foraging hawksbills, and the first to use MaxEnt to assess the distribution of foraging juvenile hawksbills in the Western Caribbean.

Using MaxEnt, we deviated from the typical environmental predictors, such as climate data, and sought to create our model from presence-only hawksbill occurrence points and three environmental categories: disturbance (boat traffic), resource (prey items), and regulator variables (benthic makeup). In our model, resource predictors, *G. neptuni* and *Dictyota* spp., had the greatest influence on suitability. However, with respect to algal prey item percent cover (*K. limminghii* and *Dictyota* spp.*)*, we noted a negative correlation with PHP decreasing as percent cover of *K. limminghii* and *Dictyota* spp. increased. Although algal prey items are a potential source of nutrients and are found in the diets of hawksbills foraging off the coast of other regions, such as Australia (Bell, 2013) and Costa Rica (Santoro et al., 2015), our results suggest that PHP is not reliant on the presence of these algal species, and that hawksbills foraging within the reserve may not be heavily reliant on these algae to obtain nutritional requirements.

Initial individual observations (i.e. focal follows) of foraging hawksbills in the SBWEMR by Baumbach et al. (2015), suggested hawksbill diet was composed of the algal species *Dictyota* spp., *H. opuntia*, *L. variegata*, and *K. limminghii*. However, recent work by Baumbach et al. (2022) suggested that ingestion of other algal species was incidental during attempts to ingest *K. limminghii*, and that

K. limminghii, although present in hawksbill diets, makes up only a small proportion of their diet, although this proportion may be nutritionally important. The small proportion consumed by SBWEMR hawksbills may, in part, be due to the cryptic nature of *K. limminghii*, which grows on the undersides of coral and rocky outcrops, and is therefore difficult to detect during habitat surveys, as well as by foraging hawksbills. Algae has been found in the diet of some hawksbills foraging off the coasts of the Dominican Republic (León and Bjorndal, 2002), Puerto Rico (Van Dam and Diez, 1997), and other regions of Roatán (Berube et al., 2012), yet our model suggests that algae may not be a large component of hawksbill diets in the SBWEMR. This conclusion aligns well with the established, mainly spongivorous foraging ecology of hawksbills in the Caribbean (León and Bjorndal, 2002; Blumenthal et al., 2009). Nevertheless, studies in the Pacific and Indian oceans have shown that hawksbill diets can be comprised mainly of algae (Bell, 2013; Limpus and Fien, 2009) and hard corals (Obura et al., 2010). However, shifts to primarily algal diets were likely due to the decimation of sponge prey items within the foraging ranges of hawksbills in those studies. According to optimal foraging theory, prey item selectivity and foraging patterns may vary based on prey item availability (Pyke, 1984). Still, according to Rincon-Diaz et al. (2011b), hawksbill prey item selection is not always associated with abundance. In some cases, selectivity may be strong for rare items. In the current study, we found *Kallymenia* may appear rare in benthic surveys because of its tendency to grow on the undersides of rock and coral overhangs. Therefore, hawksbills may spend increased time (and therefore demonstrate increased PHP) during foraging efforts for this particular algal species. The fact that sponge prey is highly abundant may also influence PHP.

In our models, sponge abundance of *G. neptuni* had the second greatest positive influence on suitability. Unlike algal prey item percent
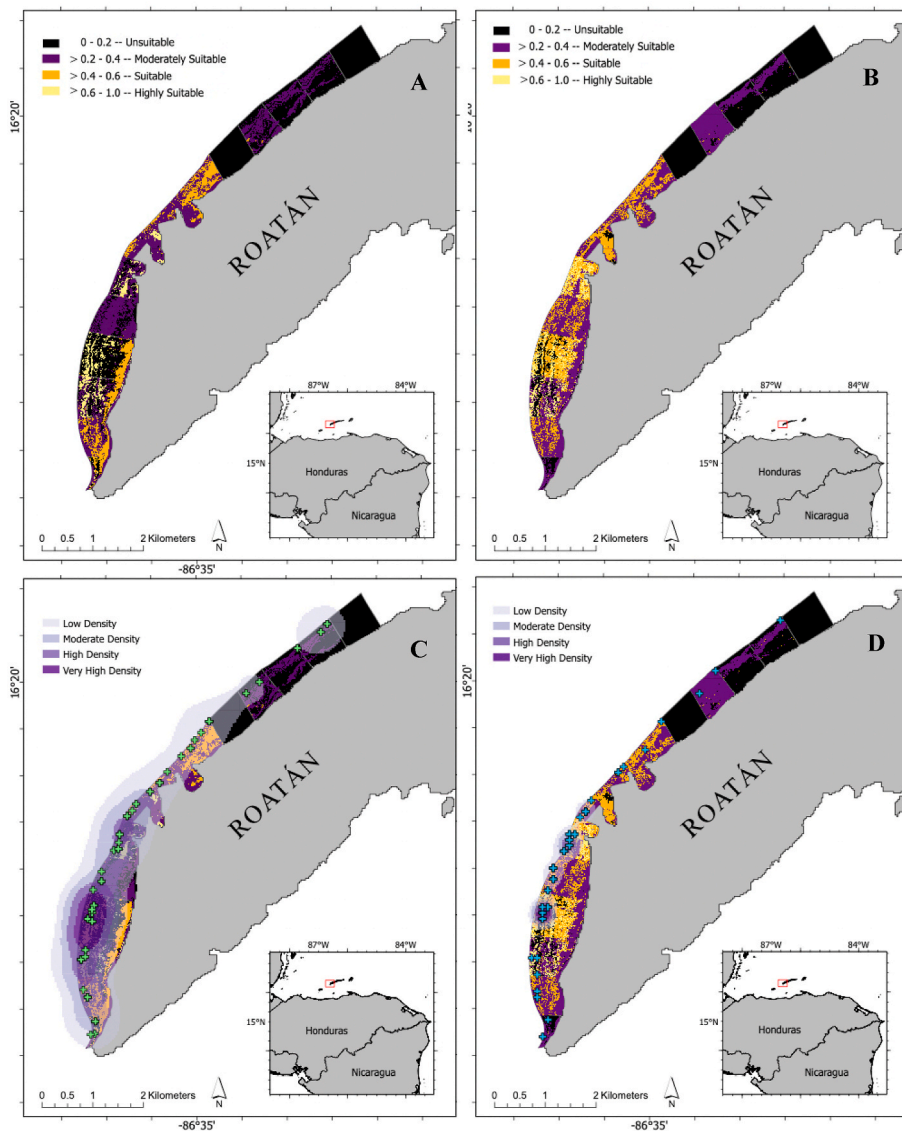
Fig. 8. Predicted habitat suitability of the SBWEMR in the morning (A) and afternoon (B). MaxEnt logistic output depicted varying suitability throughout the SBWEMR. Suitability was classified as either unsuitable (0–0.2), moderately suitable (>0.2–0.4), suitable (>0.4–0.6), or highly suitable (>0.6–1). Hawksbill occurrence and kernel density in the morning (C) and afternoon (D). Instances of hawksbill sightings are signified by lime green crosses, while hawksbill density is indicated by the varying shades of purple.

cover, PHP positively correlated with *G. neptuni* distribution. Since increasing presence of *G. neptuni* in the reserve indicated increasing PHP, our findings continue to support the positive influence of sponge availability on hawksbill presence and distribution. With respect to resource environmental variables, the model output suggests that regions of high *G. neptuni* abundance and low *K. limminghii* (again, most likely due to their cryptic distribution, and therefore rarely detected through the type of transect surveys we undertook) and *Dictyota* spp. abundance are considered regions of moderate to high suitability for hawksbill presence within the SBWEMR. We suggest that PHP was higher in regions of high *G. neptuni* count and low *K. limminghii* and *Dictyota* spp, since home range and core use areas are influenced by prey item availability and preference. In-water observations, esophageal lavages, and stable isotope analyses performed by Baumbach (2020) indicated that hawksbill diets within the SBWEMR are predominantly comprised of *G. neptuni* (68.8%) when compared to the alga *K. limminghii* (18.8%), supporting the results of our model.

In addition to prey item availability, the presence of predators and other disturbances may influence home range extent and species distributions, limiting habitat use, species ranges, and abundance (Wood et al., 2017; Heithaus et al., 2002). Our model indicated that increasing boat traffic intensity positively correlated with an increase in PHP.

Furthermore, our model outputs suggested regions with higher boat traffic intensities were "suitable" habitats within the reserve. These results contradict the general theory of predator avoidance. However, rather than a positive effect on sea turtle presence, we suggest that boating has no effect on sea turtle distribution, and rather that the influence of prey item distribution dictates hawksbill presence independent of boat traffic intensity. Recent underwater auditory studies performed by Tyson et al. (2017), indicated that in-water hawksbill behavior did not appear to be affected by sounds emitted from boat traffic. Other studies suggest that when nonintrusive, turtles become accustomed to disturbances, unaware of their potential threats (Von Brandis et al., 2010, Nanninga et al., 2017). These results are supported by recent studies in Roatán by Wright et al. (2020), where hawksbills remained undisturbed and showed no obvious stress response to boats passing overhead during feeding events. While Hayes et al. (2017) found that small groups of non-threatening SCUBA divers approaching juvenile hawksbills in the SBWEMR reduced times turtles spent feeding, searching, and breathing at the surface, those authors found no evidence that diver presence was impacting hawksbill abundance in the reserve.

Overall, greater hawksbill distribution and density corresponded to the southwestern regions of the SBWEMR more than in the northern areas of the reserve. In these southwestern regions, *G. neptuni* was more

abundant, algal cover was less wide-spread, and there were higher boat traffic intensities. While our model was able to predict habitat suitability, there were nevertheless, several limitations and assumptions to the model. SDMs are limited, since they are unable to analyze compounding effects and ecological processes that define the relationship between a species and the environmental variables (Elith and Leathwick, 2009). In addition, the small spatial extent of our study site also limited the number and type of environmental variables that could be applied to the model. The range of spatial resolution and extent of coverage for many available layers are broad, with a single resolution unit equivalent to approximately 1° (Yesson et al., 2012), 25 km (Ferrier et al., 2002), or other similar resolutions that are greater than the spatial scale of the SBWEMR in its entirety. Although spatial resolution could be resampled to fit the scope of our study site, the small degree in change of these environmental variables would render the layer insignificant in our small study area. Studies by Lowen et al. (2016) also indicated that model performance does not increase by resampling spatial resolution. We found the MaxEnt model was confirmed by running our parameters in the kuenm protocol, and that model results were essentially indistinguishable between the two systems. Therefore, we remain confident that our model outputs may be used to identify regions of ecological importance within the SBWEMR. In addition, AUC values obtained in our study were greater than 0.75, indicating each model contained useful information (Elith et al., 2006), and was able to predict habitat suitability greater than chance (AUC = 0.5).

Although testing gain data suggested our model had a poor ability to estimate suitability if extrapolated and used to test other regions, training data were able to assess suitability within the SBWEMR. If fine-tuned further by the addition of subsequent environmental variables and occurrence points which are more precise, a model with sufficient extrapolation capability may potentially map hawksbill distribution and habitat suitability along the entire coast of Roatán. Hawksbills have been considered a resilient species, with some studies suggesting they continually function beneath their operational limits with respect to routine foraging activities (Von Brandis et al., 2010). Although hawksbills have also been known to supplement their diets with additional prey items (Berube et al., 2012; Bell, 2013; Carrion-Cortez et al., 2013), continued depletion of suitable habitats over time may reduce resource items below sustainable levels for hawksbill inhabitance. Once suitable habitats are depleted, juvenile hawksbills may need to expand their range, shifting their spatial distribution (Matley et al., 2019).

Management of changing protected areas is important for continued hawksbill inhabitance. Based on the relationship of resource variables with hawksbill presence in the SBWEMR, we recommend that strategies to improve suitability should focus on resource replenishment. To ensure adequate supplies of potential resource items (specifically sponges), we further recommend that hawksbill foraging areas in the SBWEMR should be monitored for anthropogenic runoff and other pollutants that may potentially inhibit the growth of important resource items. Additionally, although hawksbills were able to coexist with boat traffic (the disturbance variable in this study), boat traffic and other potential disturbance activities may pose a threat to hawksbill survival and should be managed accordingly.

Although MPAs are designed to exclude deleterious human activities, global tourism and human presence within and near to MPAs are increasing (Milazzo et al., 2002; Mccarthy, 2004; Halpern et al., 2008). In the current study, however, we found that although human activity in the reserve is increasing over time, these activities are not, yet, resulting in the loss of juvenile hawksbill abundance. However, continuing degradation of the reserve may negatively impact the abundance and distribution of key prey items, resulting in the possibility of reduced turtle presence in the future.

Declaration of competing interest

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocecoaman.2022.106204.

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