Inter-Research Science Publisher
Marine Ecology Progress Series
Volume 766:91–106
Published August 7, 2025
https://doi.org/10.3354/meps14906

Characterizing seasonal whale shark habitat in the western North Atlantic

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ABSTRACT: There are significant knowledge gaps in the ecology of whale sharks *Rhincodon typus* beyond well-studied coastal aggregation sites. We synthesize several disparate data types, including scientific aerial and shipboard surveys, environmental impact assessments, and opportunistic citizen science records, in a species distribution model framework to characterize whale shark distribution across the northwest Atlantic Ocean (NWA), Gulf of Mexico, and the Caribbean Sea. Based on 2010 occurrence records spanning 1993–2023 from the Bay of Fundy to the North Brazil Current off the northern coast of South America, we developed a species distribution model to characterize seasonal habitat suitability for whale sharks. The model indicated that bathymetry (44.9%), sea surface temperature (20.5%), and sea surface height (16.1%) explained the most variability in habitat suitability. The model predicted high suitability in known coastal aggregation areas and continental shelf edges along the US east coast from southern Florida to Cape Hatteras year-round, expanding north to the USA–Canada border in summer and autumn. Suitability was also high in the north-central Gulf of Mexico during summer and autumn and in the Yucatan and Caribbean region throughout the year. These findings underscore a broad whale shark distribution across the NWA beyond known aggregation sites, emphasizing seasonal suitability along the US east coast and in the Gulf of Mexico. Given rapid climate-induced changes in the NWA, our findings are a critical step toward understanding climatic impacts on this charismatic species and can support marine spatial planning and conservation efforts.

KEY WORDS: *Rhincodon typus* · Continental shelf edge · Pelagic habitat · Whale shark distribution · Species distribution modeling · Movement ecology

1. INTRODUCTION

Whale sharks *Rhincodon typus* Smith, 1828 are the world's largest extant fish, and despite their size, they are filter feeders (Rowat & Brooks 2012). Whale sharks boast a broad distribution across all major temperate and tropical seas (Rowat & Brooks 2012), likely driven by periodic pulses in prey availability (Heyman et al. 2001, Graham & Roberts 2007, de la Parra-Venegas et al. 2011, McKinney et al. 2012, Hoffmayer

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et al. 2021). However, basic whale shark ecology remains poorly understood, including their spatial and temporal distribution outside of well-studied aggregation sites (Rowat & Brooks 2012). As a highly migratory species capable of crossing international maritime boundaries (Castro et al. 2007, Graham 2007, Hueter et al. 2013, Sequeira et al. 2014) and diving into deep oceanic habitats (Graham et al. 2006, Tyminski et al. 2015, Andrzejaczek et al. 2022), characterizing whale shark movement ecology remains challenging. Extensive research has focused on several known seasonal aggregation sites where whale sharks can be reliably encountered, including the Yucatan Peninsula, Mexico (de la Parra-Venegas et al. 2011), Ewing Bank, USA (Hoffmayer et al. 2021), Gladden Split, Belize (Heyman et al. 2001), Utila, Honduras (Fox et al. 2013), Nosy Be, Madagascar (Diamant et al. 2021), Gulf of Aden, Djibouti (Rowat et al. 2011, Boldrocchi et al. 2020), the Red Sea (Berumen et al. 2014, Cochran et al. 2019), the Arabian Gulf (Robinson et al. 2013), and Ningaloo Reef, Western Australia (Norman & Stevens 2007). These well studied sites are primarily dominated by juveniles and subadults (Graham et al. 2006, Rowat & Brooks 2012, Norman et al. 2017), leaving the distribution and ecology of adult whale sharks poorly understood.

Historically, information on the ecology of large pelagic animals, including whale sharks, has been constrained to sparse observations that are limited geographically. For example, the majority of our knowledge on whale shark ecology comes from surface observations in coastal waters. Yet, recent evidence from electronic archival tags suggests that the majority of their lives are spent offshore in epipelagic environments and include dives to depths well below the euphotic zone to as deep as 2500 m (Hoffmayer et al. 2021). Electronic tagging of whale sharks in the Gulf of Mexico have reported movements across the basin (Hueter et al. 2013, Hoffmayer et al. 2021) and throughout the northwest Caribbean Sea and into the North (Daye et al. 2024) and South Atlantic Ocean (Graham et al. 2006, Gifford et al. 2007, Hueter et al. 2013).

Nevertheless, electronic tags have not fully resolved gaps in our knowledge of whale shark spatial ecology in the northwest Atlantic Ocean (NWA). The US east coast is recognized as part of the worldwide distribution of whale sharks by the International Union for Conservation of Nature (IUCN) (Pierce & Norman 2016), and there have been extensive survey efforts in the Gulf of Mexico (Hueter et al. 2013, Hoffmayer et al. 2021, Daye et al. 2024). Yet, observations of whale sharks in the NWA are limited, which has precluded the ability for population level characterizations of whale shark distributions in the NWA beyond aggregation sites.

Species distribution models (SDMs) can harness disparate data sources, such as opportunistic citizen science and scientific surveys, to help fill gaps in our understanding of whale shark ecology in the region. Here, we synthesize whale shark occurrence data from multiple sources to more fully describe whale shark distribution in the NWA. We align these observations with a suite of dynamic oceanographic variables in an SDM framework to identify seasonal characteristics of whale shark habitat use in the region. These results represent a significant advance in characterizing whale shark distribution, harnessing opportunistic data with a broader spatiotemporal extent to complement existing telemetry and survey data. Our findings provide a foundational understanding of the species' spatial and temporal distribution in the NWA. These results also serve as a baseline to assess potential distributional shifts under climate change and have broad implications for the international management of this IUCN Red List Endangered species (Pierce & Norman 2016).

2. MATERIALS AND METHODS

2.1. Species occurrence data: aggregated sightings

We collated data from 8 databases and >14 distinct data collection efforts (Fig. 1, Table 1; Table S1 in the Supplement at www.int-res.com/articles/suppl/m766p091_supp.pdf) that consisted of aerial and shipboard surveys, environmental impact surveys, and opportunistic sightings (e.g. Wildbook for Whale Sharks, https://www.sharkbook.ai). Aerial, shipboard, and environmental impact observations included cetacean abundance surveys completed by the National Oceanic and Atmospheric Administration (NOAA) Southeast Fisheries Science Center (Rapucci et al. 2017), the North Atlantic Right Whale Consortium (2023), offshore wind planning surveys such as those contracted by the New York State Energy Research and Development Authority (Normandeau Associates & APEM Inc. 2016), and underwater weapon testing by the United States Department of the Navy (McAlarney et al. 2016, Cotter 2019, Foley et al. 2019), among others (see Table 1 and Table S1 for details on data origins and data collection methods).

In addition to these multiple survey efforts, we compiled opportunistic sightings from 3 databases:

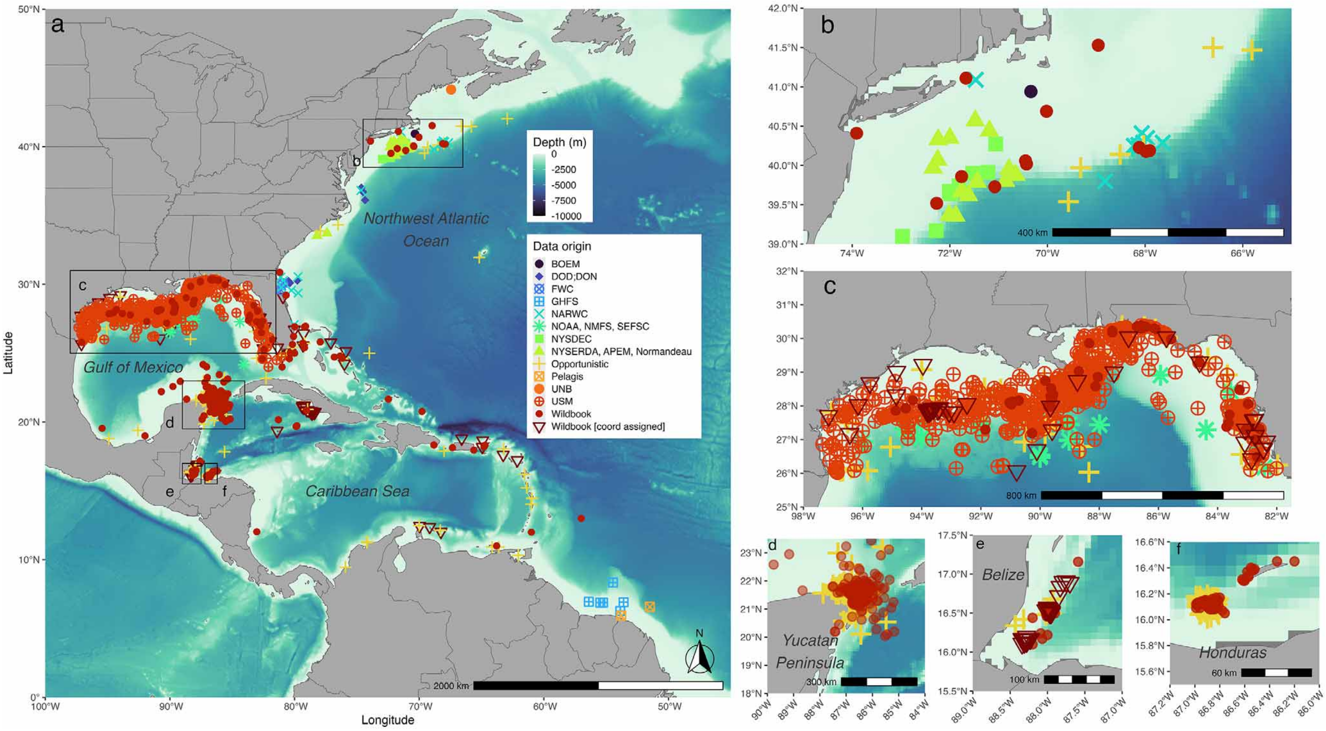

Fig. 1. Aggregated whale shark *Rhincodon typus* sightings from 1933 to 2023 (n = 2453 total occurrences) by sighting origin. (a) Entire study area (100—40° W, 5—50° N), (b) northeast USA, (c) northern Gulf of Mexico, and aggregations from (d) the Yucatan Peninsula, (e) Belize, and (f) Honduras. See Table 1 and Table S1 for additional information on occurrence origins

the Global Biodiversity Information Facility (GBIF 2023), the Ocean Biodiversity Information System (OBIS 2023), and Wildbook for Whale Sharks (Holmberg et al. 2008, Norman et al. 2017). The Global Biodiversity Information Facility and Ocean Biodiversity Information System are international open-access databases hosting a mix of survey and citizen science records. For these databases, sightings were obtained by querying '*Rhincodon typus*,' and then downloading associated occurrences for additional quality control. Wildbook for Whale Sharks is a citizen science database that uses photo identification to document individual whale shark sightings (Holmberg et al. 2008, Norman et al. 2017). Most observations contained geographic coordinates and a timestamp; however, for those that did not have spatial coordinates, we completed manual filtering of these occurrences by reviewing notes associated with the sightings and photo/video footage, if applicable, and used these to assign a location (see Text S1 for full details). The resulting spatial extent of aggregated observations spanned the northernmost sighting in the Bay of Fundy (Turnbull & Randell 2006), south along the eastern USA to the North Brazil Current off the northern coast of South America, including the Caribbean Sea and the Gulf of Mexico. Data cleaning, such as the removal of locations on land, duplicate records, and non-whale shark occurrences, was performed in R (version 4.3.1, R Core Team 2023) using the packages 'tidyverse' (Wickham et al. 2019), 'raster' (Hijmans 2023), 'terra' (Hijmans 2024), and 'sf' (Pebesma 2018).

2.2. Species occurrence data: model preparation

Aggregated sightings data were used to construct an SDM. We considered all occurrence data as presence-only. Although some true absence data were reported from systematic surveys, very few data sources, including opportunistic or citizen science surveys, reported absences and/or effort (Table 1; Table S1). To address this, we generated pseudoabsences as a consistent method to proxy absence across the varying data sets in the study region (sensu Barbet-Massin et al. 2012, Hazen et al. 2021, Braun et al. 2023; Section 2.3). To account for the spatial autocorrelation and bias inherent in the presence data set, we thinned presence observations to ensure a maximum of 1 event per 0.01° grid cell for each month in a given year. Together, sampling pseudoabsences from the study region and systematically thinning pres-

Table 1. Cleaned presence data background information. N: number of sightings. See Table S1 for data sources with n < 10

Group	Source	Data collection	Years	N	Latitude (° N)	Longitude (° W)	Area	Description
University of Southern Mississippi (USM)	Northern Gulf of Mexico Whale Sharks Sightings Survey	Opportunistic	1989–2020	808	24.0–30.4	81.4–97.4	Gulf of Mexico	Sightings database developed by researchers at the USM
Wildbook	Wildbook for Whale Sharks	Opportunistic	1992–2023	620	11.0–41.5	57.0–97.1	Caribbean Sea; Gulf of Mexico, eastern USA	Photo-identification library of whale shark encounters
Ocean Biodiversity Information System (OBIS)	OBIS	Opportunistic	1933–2009	464	9.5–42.0	61.4–97.0	Caribbean Sea; Gulf of Mexico, eastern USA	Compilation of opportunistic sightings; research grade observations
Wildbook (coordinates assigned)	Wildbook for Whale Sharks	Opportunistic	1995–2021	282	12.0–30.0	62.1–97.2	Caribbean Sea; Gulf of Mexico, eastern USA	Photo-identification library of whale shark encounters. Coordinates manually assigned
Global Biodiversity Information Facility (GBIF)	GBIF; personal communications	Opportunistic	1995–2022	194 (excluding additional GBIF source counts below and in Table S1)	10.9–41.5	61.0–96.8	Caribbean Sea; Gulf of Mexico, eastern USA	Compilation of opportunistic sightings; research grade observations
North Atlantic Right Whale Consortium (NARWC)	NARWC	Survey	1980–2022	17	27.1–41.1	67.6–81.1	Eastern USA	North Atlantic Right Whale Consortium surveys
New York State Energy Research and Development Authority (NYSERDA), APEM, Normandeau	NYSERDA	Survey	2016–2018	14	39.4–40.6	70.7–72.3	Northeastern USA	APEM Inc. and Normandeau Associates aerial digital baseline survey of marine wildlife in support of offshore wind energy for NYSERDA
NOAA, NMFS, SEFSC	GBIF-SEAMAP, GULFCET (SEFSC GOMEX OCEANIC)	Survey	1992–2001	14	24.2–28.9	84.1–96.0	Gulf of Mexico	Southeast Area Monitoring and Assessment Program and Gulfcet I and II shipboard survey programs

ence observations have been demonstrated to consistently yield robust machine-learning based models when working with geographically biased data and/or data sets with unknown or variable effort and representation of species' absences (Fourcade et al. 2014, Braun et al. 2023a). Finally, given that whale sharks are presumed to primarily transit, rather than forage, in the open ocean (Arrowsmith et al. 2021), presences were further spatially limited to on-shelf and near-shelf regions that included exclusive economic zones (EEZs) across the study region, inclusive of the entire Gulf of Mexico basin. Data for which coordinates were manually assigned, such as the above-described Wildbook for Whale Sharks occurrences, were withheld from SDM training and were strictly used to describe the distribution of whale sharks in the NWA.

2.3. Pseudoabsence generation

Pseudoabsences were used to represent locations that were available to whale sharks. Using pseudoabsences has been found to improve model predictions compared to presence-only SDMs (Barbet-Massin et al. 2012). Here, pseudoabsences were generated via background sampling, without replacement, and assigned a random date from the corresponding species-presence data set, as recommended for previous and similar modeling efforts (Hazen et al. 2021, Braun et al. 2023a). Previous studies of presence-only model performance identified that using pseudoabsences developed with background sampling yielded model predictions that most closely aligned with presence–absence models (Barbet-Massin et al. 2012, Hazen et al. 2021, Braun et al. 2023a). Quality control of pseudoabsences followed the same routines as used for presences, spatially limiting to regions within EEZs and spatially filtering to ensure only 1 pseudoabsence for each 0.1°grid cell (~10 km) for a given month of a year. Pseudoabsences were then randomly subsampled to a 1:1 ratio of presences to pseudoabsences, in line with previous recommendations for SDMs (Barbet-Massin et al. 2012, Brodie et al. 2022).

2.4. Oceanographic data

The resulting model training data (presence and pseudoabsences) were filtered to match the timeframe of the Global Ocean Physics Reanalysis (GLORYS, Copernicus Marine Environmental Monitoring Service; Lellouche et al. 2018), a data-assimilating ocean model with 50 vertical levels at 1/12° horizontal resolution. Environmental variables were extracted from the oceanographic model for the associated year–month of each sighting and pseudoabsence observation. Environmental data consisted of 7 dynamic surface variables: sea surface temperature (SST) in °C, sea surface salinity (SSS) in PSU, sea surface height (SSH) in m, their corresponding standard deviations (SST_sd; SSS_sd; SSH_sd) calculated over a 0.25° square, eddy kinetic energy (EKE) in m s^{-2}, 1 subsurface dynamic variable, mixed layer depth (MLD) in m, and 2 static variables, bathymetry (ETOPO1 obtained from www.ngdc.noaa.gov/mgg/global/global.html, coarsened to 1/12°) in m, and rugosity (calculated as the spatial standard deviation of bathymetry over a 0.25° square) in m.

2.5. Model design

We used boosted regression trees (BRTs) to construct the SDMs. BRTs were selected as the occurrence data exhibited some sampling effort (Phillips et al. 2009) and previous investigations have revealed that correcting for sampling bias in presence-only frameworks, e.g. MaxEnt, can be unreliable (Syfert et al. 2013, Fourcade et al. 2014). BRTs, in contrast, are widely used to model distributions of highly migratory species (Hazen et al. 2018, Abrahms et al. 2019, Brodie et al. 2022, Braun et al. 2023a,b, Lezama-Ochoa et al. 2024), and are robust to non-linear relationships and collinearity among variables interactions (Elith et al. 2008, Farchadi et al. 2024).

Model training data were sourced from the complete 1:1 presence to pseudoabsence data set drawn from the entire study area (100–40° W, 5–50° N). BRTs generated in this study adopted the same properties as those in Braun et al. (2023a), which used a Bernoulli family, 2000 fixed trees with a learning rate of 0.05, bag fraction of 0.75, tree complexity of 5, and *k*-fold partition of $k = 10$ (where data are randomly subsampled into 10 subsamples, and the model trains on 9 of the subsamples and uses the last subsample for testing). To assess spatial uncertainty, BRTs were bootstrapped 100 times by sampling (with replacement) 2010 presences and 2010 pseudoabsences from the training data set to maintain the 1:1 presence to pseudoabsence ratio. Fitted models were predicted to monthly environmental data during the study period (1993–2023), then averaged by season. Seasons were defined as winter (December–February), spring (March–May), summer (June–August), and autumn (September–November). Model predictions assess habitat suitability for whale sharks on a continuous scale from 0 to 1, where 1 is associated with higher suitability. Presence data included in model training were collected between January 1993 and August 2023, and complete environmental data were available from GLORYS. Presence data were excluded if they preceded the temporal span of the oceanographic model GLORYS (before January 1993), lacked complete environmental data from GLORYS, or had manually assigned coordinates.

2.6. Model performance

We evaluated model performance using 3 metrics: explanatory power, predictive skill, and ecological realism (see Braun et al. 2023a). Explanatory power, represented by R^2, quantified the ability of the explanatory variables in the model to capture variability observed in the training data set. Predictive skill was assessed via the area under the receiving operating characteristic curve (AUC) and true skill statistic (TSS), which assess the ability of the model to discriminate between presence and absence (Norberg et al. 2019) and the accuracy of model predictions compared to random chance, respectively. TSS, independent of species prevalence, has been found to yield more conservative and ecologically realistic values compared to other predictive skill metrics (Shabani et al. 2018). Further, spatial uncertainty in model predictions was assessed by determining the standard error of bootstrapped models. Resulting SDMs were predicted monthly to the spatial extent of the data. We determined the models' median predicted habitat suitability for presences and pseudoabsences against respective training data to discern ecological realism. All ecological realism analyses determined a presence to occur when suitability exceeded the 75% quantile and an absence when suitability was less than the 25% quantile (Braun et al. 2023a).

3. RESULTS

3.1. Aggregated sightings

In total, 2453 whale shark sightings were collected from 1933 to 2023 (Fig. 1a, Table 1; Table S1) and after quality control and thinning, a total of 2010 observations made between 1993 and 2023 were retained as training data for the SDM. Quality control filtering involved removing 43 observations that occurred before the availability of the oceanographic model (pre-January 1993), 86 observations that were missing temporal information, and 282 that were manually assigned an approximate location from supplemental comments in the Wildbook for Whale Sharks database (https://www.sharkbook.ai). Among all available sightings (n = 2453), a total of 69 sightings occurred north of 30° N in the US EEZ, including in the Mid-Atlantic Bight and near George's Bank offshore from Cape Cod, Massachusetts (n = 50; Fig. 1b). Extensive sightings of whale sharks occurred within the northern Gulf of Mexico (n = 983; Fig. 1c). Nearly half of the total sightings (n = 1211; 49.7%) originated from known aggregation sites offshore of the Yucatan Peninsula, Mexico (n = 652; Fig. 1c), Belize (n = 223; Fig. 1d), and Honduras (n = 359; Fig. 1e). Temporal information was available for 2395 of the 2453 total sightings. Of these sightings, 182 occurred during winter (Fig. 2a), 564 in spring (Fig. 2b), 1239 in summer (Fig. 2c), and 367 in autumn (Fig. 2d), representing a gradual northward shift from lower latitudes in winter to higher latitudes in summer (Fig. 2e).

3.2. Model performance

Model performance was robust across explanatory power (mean $R^2 = 0.76$; range = 0.73–0.78) and predictive skill: mean AUC = 0.99 (0.98–0.99), mean TSS = 0.89 (0.86–0.91). The ability of the model to yield ecologically realistic predictions, represented by the mean of median model-predicted habitat suitabilities at known presences and pseudoabsences (where a value closer to 1 is desirable for presences and a value closer to 0 is desirable for pseudoabsences), was 0.94 (0.93–0.95) and 0.03 (0.03–0.04), respectively. Among environmental drivers included in the model (Fig. S1), bathymetry explained the most deviance (mean = 44.9%, range = 40.2–47.8%; Table 2, Fig. 3; Fig. S2), followed by SST (20.5%, 17.1–23.2%), SSH (16.1%, 13.3–19.7%), and rugosity (7.0%, 4.7–10.0%). Habitat suitability increased with bottom depth <1500 m, SST >25°C, and negative SSH values, indicating use of habitats shoreward of the Loop Current and Gulf Stream, which are the primary gradients in SSH in the region (Fig. 3). The remaining environmental variables exhibited relatively minimal influence (<3% each) on habitat suitability (Fig. S2).

3.3. Habitat suitability: monthly and seasonal patterns

Generally, the summer season yielded increased amounts of suitable habitat compared to the winter

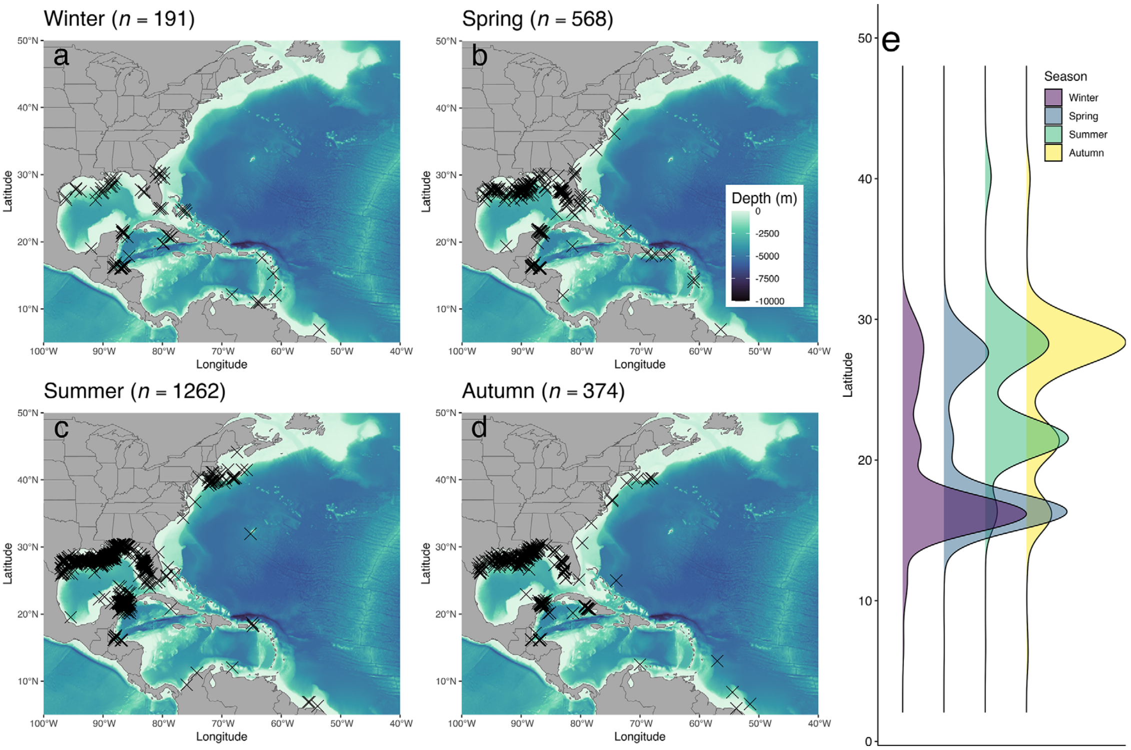

Fig. 2. Whale shark *Rhincodon typus* occurrences with available date (n = 2395 from 1933 to 2023) by (a) winter, (b) spring, (c) summer, and (d) autumn. (e) Seasonal latitudinal distributions

Table 2. Mean relative influence of each environmental variable in bootstrapped sightings species distribution model. Ranges are given in parentheses

Environmental variable	Relative influence (%)
Bathymetry (m)	44.9 (40.2–47.8)
Sea surface temperature (°C)	20.5 (17.1–23.2)
Sea surface height (m)	16.1 (13.3–19.7)
Rugosity (m)	7.0 (4.7–10.0)
Sea surface height SD (m)	2.9 (1.9–4.7)
Eddy kinetic energy (m s^{-2})	2.7 (1.7–4.2)
Mixed layer depth (m)	1.8 (0.9–3.4)
Sea surface salinity (PSU)	2.0 (1.0–3.0)
Sea surface salinity SD (PSU)	1.3 (0.7–2.4)
Sea surface temperature SD (°C)	0.8 (0.2–1.4)

(Figs. 4 & 5a; Figs. S3 & S4). The models predicted high habitat suitability along the US east coast from southern Florida to Cape Hatteras, North Carolina, throughout the year (Fig. 4a; Fig. S4). Starting in June, increased habitat suitability extended northward of Cape Hatteras (Figs. 2b & 4b; Fig. S4), reaching the Northeast Canyons offshore from Cape Cod, Massachusetts, by July (Figs. 2c, 4c, & 5a,b). Enhanced habitat suitability in the region remained for the summer and began to decrease in September (Fig. 4d; Fig. S3). By November, the northern boundary of suitable habitat retreated southward again toward Cape Hatteras. Regardless of season, the models predicted suitable habitat year-round in the southeastern USA along the continental shelf edge (Fig. 4).

Overall, the models predicted high suitability during all seasons in the southern Gulf of Mexico and at known aggregation sites further south, such as the Yucatan Peninsula and regions offshore Belize and Honduras (Fig. 4; Fig. S3). The northern Gulf of Mexico exhibited moderately suitable habitat during the winter months (Figs. 4a & 5a,d), and predicted suitability increased starting in March (Figs 4b & 5a,e) through early summer. By May, the northern Gulf of Mexico exhibited highly suitable habitat, lasting through the summer months (Fig. 4c) before declining again in October (Fig. 4d). Nevertheless, suitable habitat was available year-round in the northern Gulf of Mexico. Generally, the model predicted increased suitability in nearshore relative to offshore habitats. Similarly, known aggregations around the Yucatan Peninsula (Fig. 5a,f,g), off Belize (Fig. 5a,h,i), and off Honduras (Fig. 5a,j,k) were characterized by increased suitability during summer compared to the

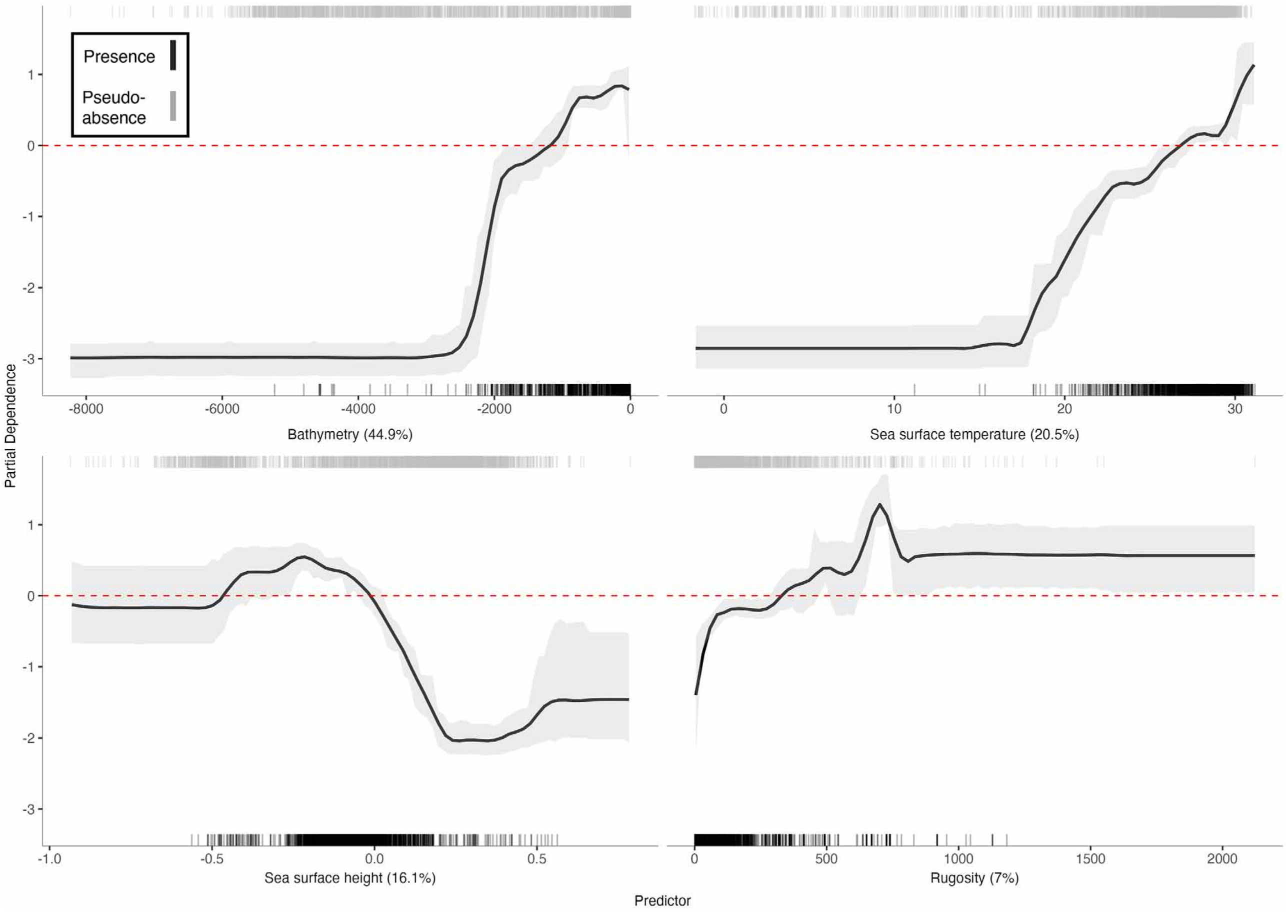

Fig. 3. Response curves and relative influence of the 4 most influential environmental drivers of suitable whale shark habitat derived from bootstrapped boosted regression tree model. Ribbons represent 95% confidence intervals. Rug marks on the plot represent presence (black, bottom) and pseudoabsence (grey, top) points

winter; however, conditions were suitable year-round (Fig. 4).

Regions of greatest uncertainty varied depending on the time of year. In winter, uncertainty was moderate throughout the study region, decreasing along the US east coast north of Cape Hatteras (Fig. 6a; Fig. S5). Uncertainty increased in the northern Gulf of Mexico and the southern US east coast in spring but remained moderate off Belize and Honduras (Fig. 6b; Fig. S5) and low in the Northeast Canyons region offshore Cape Cod. During summer, the regional patterns of uncertainty were reversed, with relatively low uncertainty in the northern Gulf of Mexico and offshore aggregation sites but moderate uncertainty along the US east coast, peaking in the Northeast Canyons region (Fig. 6c; Fig. S5). In autumn, trends observed in summer continued with higher uncertainty in the northern Gulf of Mexico, Yucatan Peninsula, Belize, and Honduras regions (Fig. 6d; Fig. S5).

4. DISCUSSION

4.1. Whale shark habitat use

Our results indicate that whale sharks are seasonally distributed throughout much of the NWA (Fig. 1a), not only within known coastal aggregations but also in oceanic regions along the US east coast as far north as Atlantic Canada. Many of the sightings located in oceanic regions revealed several whale shark observations beyond aggregation sites in the NWA, particularly along the US east coast that have not been previously reported in the primary literature. Further, occurrence data and SDM revealed a northward shift in the distribution of sightings and extensive suitable habitat in the summer and autumn months to as far north as 44° N, a region where there has been only a single published occurrence (i.e. Bay of Fundy) (Turnbull & Randell 2006). The records presented herein indicate a substantially greater use of

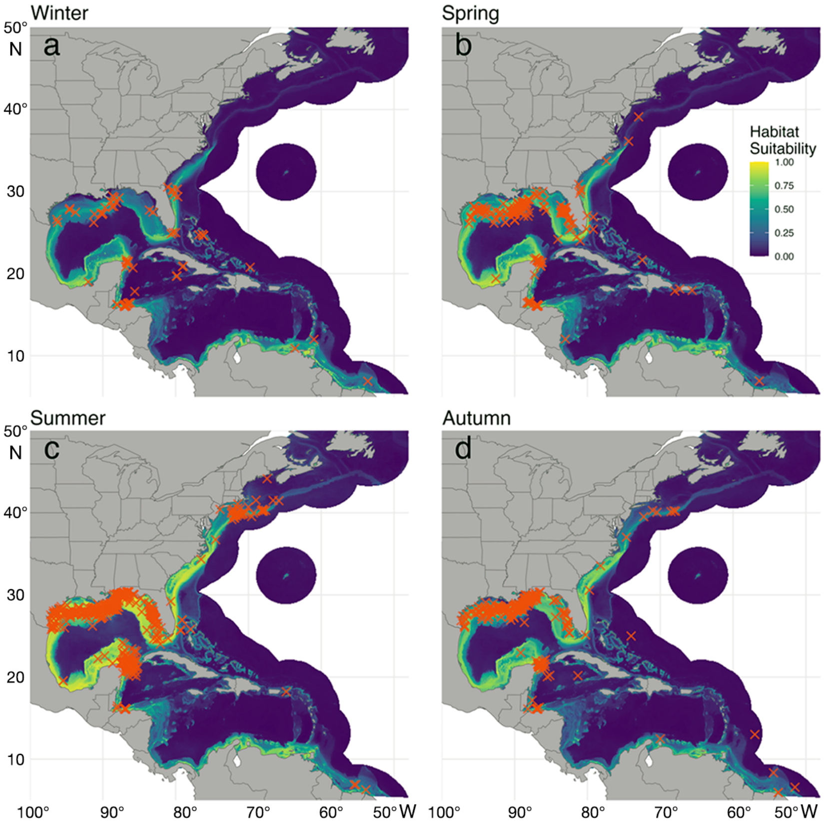

Fig. 4. Mean of bootstrapped model-predicted seasonal (averaged monthly; e.g. winter: December, January, February) habitat suitability from 1993 to 2023. Presence data used to train the model are overlaid in red (n = 2010). A monthly version of this figure is shown in Fig. S4

high latitudes than previously identified, with 69 total records north of 30° N between 1974 and 2023 (Fig. 1b). These presences likely represent migratory movements to the northern edge of whale shark distribution in the region. Indeed, 52 of these presences were located north of Cape Hatteras (35.2° N). Of the 69 presences above 30° N, 67 had available temporal information: 7 observations occurred between 1974 and 1998, and 60 observations occurred between 1999 and 2023. Of these sightings, presences largely occurred in the summer and autumn seasons, with 4 occurrences during winter, 6 in spring, 46 in summer, and 11 in autumn.

Presence data revealed that whale shark occurrence across the region throughout the year was characterized by seasonal peaks in habitat suitability at aggregation sites and within oceanic regions (Fig. 2). These areas of elevated suitability predictions largely aligned with previous site-specific investigations of whale shark ecology. For example, the model predicted higher suitability offshore Utila, Honduras, in winter and spring (Fig. 2a,b,e) in line with observations from Fox et al. (2013). Similarly, increased predicted suitability offshore Gladden Split, Belize, in winter and spring (Fig. 2ab,e) reflect observations reported by Heyman et al. (2001) and Graham & Roberts (2007). Areas of increased predicted suitability on Ewing Bank and offshore of the Yucatan Peninsula in summer (Fig. 2c,e) agree with McKinney et al. (2012), Hoffmayer et al. (2021, preprint https://doi.org/10.7287/peerj.preprints.85v1), and de la Parra-Venegas et al. (2011). Within the Gulf of Mexico, habitat suitability predictions and occurrence data revealed that whale shark occurrence peaked in the northern Gulf of Mexico in the summer (Figs. 2c, 4c, & 5d,e) and autumn (Figs. 2d & 4d), consistent with previous work investigating seasonal movements in the region (Burks et al. 2006, Hueter et al. 2013, Hoffmayer et al. 2021). Seasonal peaks in suitability in the northern Gulf of Mexico, therefore, aligned with seasonal increases in suitability along the US east coast (Figs. 2e & 4c,d). Together, the simultaneous occurrence of extensive suitable habitat during the summer and autumn in the northern Gulf of Mexico and NWA suggest seasonal habitat use of each by different whale sharks, potentially by different demographic groups (e.g. age classes) among the 2 regions (Hoffmayer et al. 2021).

The presence of multiple spatiotemporal assemblages of whale sharks across seasons may reflect the ability of larger individuals to capitalize on seasonally warm and productive northern habitats during summer months. While the opportunistic nature of the sightings data precluded robust size or age estimates (Callaghan et al. 2021), our field observations suggest that both male and female whale sharks are observed in northern latitudes during summer (e.g. offshore from Cape Cod; C. Braun pers. obs.). These individuals are typically >8 m and thus are presumably mature adults based on size at maturity reported by Norman & Stevens (2007). In contrast, known aggregation sites, including Ewing Bank and areas offshore Honduras, Belize, and the Yucatan Peninsula, are typically comprised of juvenile males (Heyman et al. 2001, de la Parra-Venegas et al. 2011, Hueter et al. 2013,

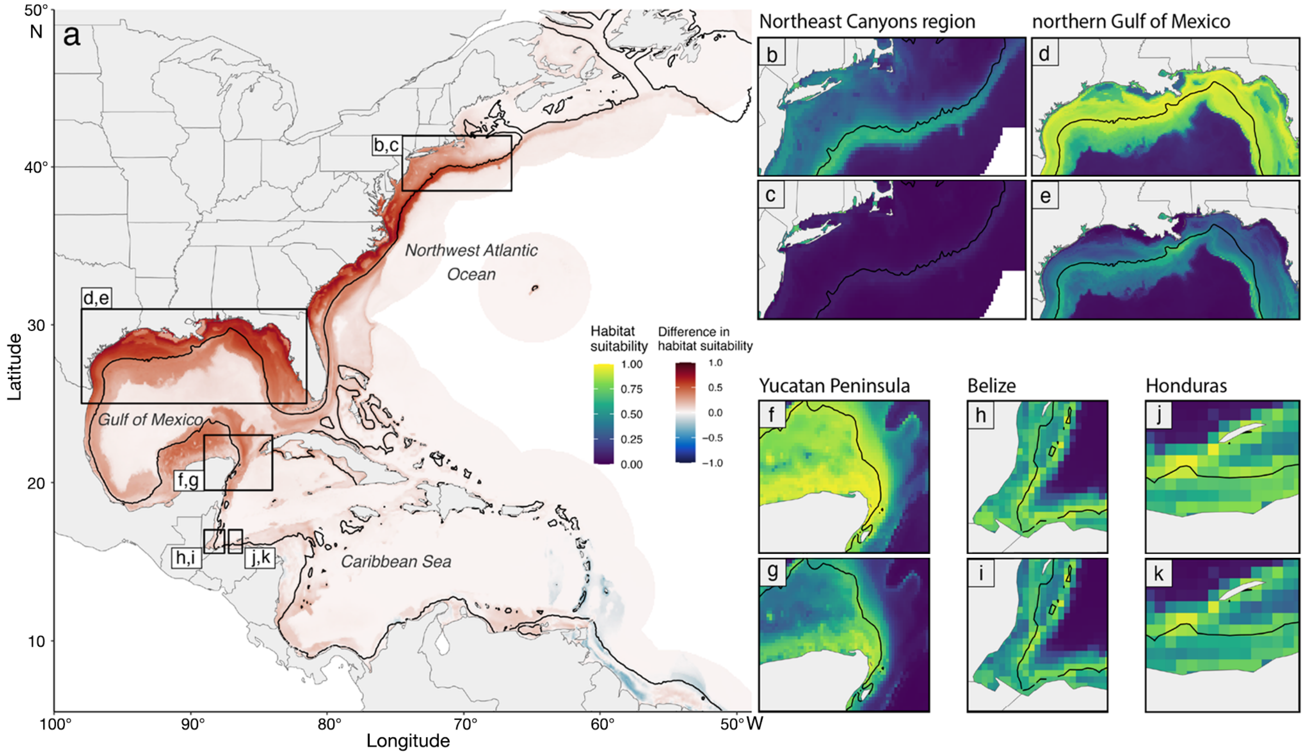

Fig. 5. (a) Difference in habitat suitability between summer (June, July, August) and winter (December, January, February) predictions, where red and blue are associated with increased and decreased levels of habitat suitability, respectively. Insets display predicted habitat suitability for summer (top) and winter (bottom) seasons in the (b,c) Northeast Canyons region, (d,e) northern Gulf of Mexico, (f,g) Yucatan Peninsula, (h,i) Belize, and (j,k) Honduras. 200 m isobath is shown in all plots

McKinney et al. 2017), while previous work suggests that juvenile and adult whale sharks of both sexes use open ocean habitat in the northern Gulf of Mexico (Hoffmayer et al. 2021). Indeed, the occurrence of multiple distinct assemblages by age across the Gulf of Mexico and NWA are reflective of previous whale shark observations. Adults have been found to occupy deeper open water (Ketchum et al. 2013, Afonso et al. 2014, Ramírez-Macías et al. 2017, Hoffmayer et al. 2021). Conversely, coastal aggregation sites are typically composed of juveniles (Rowat & Brooks 2012, Cochran et al. 2019, Hoffmayer et al. 2021). While drivers of ontogenetic

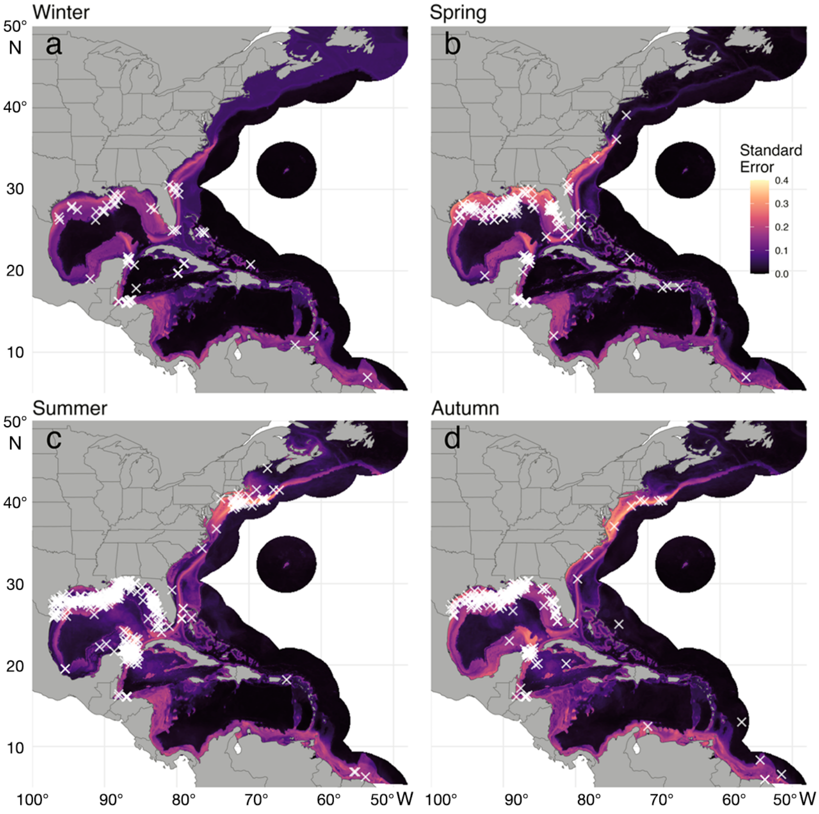

Fig. 6. Standard error of bootstrapped predicted habitat suitability by season, calculated as the standard deviation of all predictions for months included in each season, from 1993 to 2023. Presence data used to train the model are in white (n = 2010)

changes in habitat use among whale sharks are debated, they are thought to include dietary shifts (Borrell et al. 2011, Hueter et al. 2013, Hearn et al. 2016) and reproductive requirements (Ramírez-Macías et al. 2017). Thus, while the exact drivers of ontogenetic changes in whale shark habitat use remain elusive, the observation of simultaneous yet geographically distinct spatiotemporal assemblages suggests that distributional changes with age are occurring in the NWA.

Across both coastal aggregation sites and offshore oceanic regions, the observed occurrence of whale sharks and corresponding high predicted habitat suitability suggest that strong bathymetric gradients, particularly continental shelf edges, are important habitats for whale sharks in the region (Figs. 2, 4, & 5). Whale sharks are well-known to occur in areas with dynamic oceanography, such as regions of oceanic mixing. For example, in regions of oceanic upwelling, such as offshore the Galapagos Islands (Poortvliet et al. 2015), whale sharks have been observed in association with frontal gradient systems, with 80–100% of positions occurring within upwelling habitats (Ryan et al. 2017). In the mid-North Atlantic Ocean within the Azores archipelago, increased sightings of whale sharks occur in regions with greater bathymetric slope, such as near seamounts (Afonso et al. 2014). Similar to other frontal zones that often aggregate zooplankton and forage fishes (Genin et al. 2005, Lévy et al. 2012), relatively smaller-scale shelf edge upwelling in the Gulf of Mexico has been speculated to be important habitat for whale sharks (McKinney et al. 2012, Hueter et al. 2013, Hoffmayer et al. 2021). Whale sharks have also been observed throughout the Meso-American Barrier Reef system (Graham 2007, Fox et al. 2013), where meanders of the Caribbean Current in the Western Caribbean Sea and the formation of eddies may impact biological activities along the coasts of Mexico, Belize, Guatemala, and Honduras (Ezer et al. 2005, Lin et al. 2012).

Regions of high predicted habitat suitability for whale sharks in oceanic portions of the NWA, particularly in the northern extent of the Mid-Atlantic Bight offshore from Cape Cod, also coincide with strong bathymetric gradients. While the Mid-Atlantic Bight continental shelf is not considered a major upwelling region (Poortvliet et al. 2015), it is biologically productive (Zhang et al. 2023) due to nutrient-rich water that originates from land or the Arctic (Chapman & Beardsley 1989) and strong frontal gradients that differ in physical and biogeochemical properties (Hales et al. 2009). In the NWA, mesoscale eddies and meanders of the Gulf Stream interact with southwestward water from the Labrador Sea, creating smaller-scale mixing dynamics (Seidov et al. 2016) and are known to interact with the edge of the continental shelf, driving upwelling as high as 100 m d^{-1} (Forsyth et al. 2022). Similar small-scale dynamics, including continental shelf-edge upwelling and frontal convergence zones, have also been observed in the Gulf of Mexico (Zhang & Hu 2021, Qu et al. 2022). Thus, larger, mature whale sharks may be targeting these seasonally productive habitats at the northern extent of the Mid-Atlantic Bight, representing a divergence in available suitable habitat compared to tropical aggregation sites that are primarily occupied by juveniles and sub-adults.

Other dynamics, including local productivity events, may further explain the observed seasonal patterns in whale shark occurrences throughout the NWA. While we did not investigate the co-occurrence of prey species and food availability, observations included in this study encompass a range of sightings from locations where whale sharks were observed in association with prey aggregations to observations that were likely not linked to foraging opportunities. At well-studied aggregation sites, such as offshore from the Yucatan Peninsula, whale shark occurrence is likely driven by feeding on dense groupings of zooplankton in shallower waters, as well as on pelagic fish eggs farther offshore in more nutrient-poor regions (de la Parra-Venegas et al. 2011). Offshore Belize, whale sharks were observed in association with mass spawning events of *Lutjanus cyanopterus* and *L. jocu* (Heyman et al. 2001, Graham & Roberts 2007). In the northern Gulf of Mexico, whale sharks have been observed near the Mississippi River plume, where discharge creates conducive environments for plankton (McKinney et al. 2012, Hoffmayer et al. 2021), and at Ewing Bank, which is a spawning site for little tunny *Euthynnus alletteratus* (Hoffmayer et al. 2021, preprint https://doi.org/10.7287/peerj.preprints.85v1). While exact drivers of whale shark occurrence across the broad expanse of the NWA in this study remain ambiguous, local oceanographic features such as small-scale upwelling and episodic productivity events likely facilitate suitable conditions depending on geographic region, age, and sex of whale sharks.

4.2. Model performance

As a highly mobile species, research concerning whale sharks is frequently effort-intensive and spatiotemporally limited. Occurrences were concentrated in regions with strong ecotourism industries, such as offshore from the Yucatan Peninsula and Belize (Figs. 2 & 4), and uncertainties in model predictions fluctuated in conjunction with spatiotemporal variations in presence observations (Fig. 6; Fig S5). Spatial and temporal biases are common in occurrence data for highly migratory species, particularly when the primary observation mode relies on heavily skewed effort such as ecotourism (Blázquez et al. 2024) or fishing (Braun et al. 2023a, Karp et al. 2023, Liang et al. 2023). Recent work has indicated that disparate data types can be combined, such as in this study, to build more robust SDMs that draw on the broader distribution of multiple data sets (Braun et al. 2023a). In some cases, diverse data types can also be leveraged to make model predictions outside the spatial and/or temporal bounds of the training data (Stirling et al. 2016, Braun et al. 2023a). While the latest advances in ecological modeling suggest that model-based data integration may provide more ecologically realistic and skillful predictions under novel environmental conditions (such as marine heatwaves, Farchadi et al. in press), computational demand for these complex models is orders of magnitude higher than traditional approaches (Farchadi et al. 2025), highlighting the importance of model frameworks tailored to specific research objectives.

The conspicuous nature of whale sharks and associated ecotourism and offshore resource industries (e.g. fisheries, energy production) in certain regions make them a particularly suitable species for opportunistic sightings data collection through the use of citizen science (Andrzejaczek et al. 2016, Bargnesi et al. 2020, Barry et al. 2023). While these data can be readily used in SDMs (Farmer et al. 2022), the underlying spatial and temporal biases in effort are critical considerations in model development and associated inference (Hertzog et al. 2014). For example, most of the occurrences in this study originated from nearshore regions on the continental shelf and aggregation sites offshore of Belize, Honduras, and the Yucatan Peninsula at the surface. This spatial, and thus environmental, bias in the training data can directly impact predicted suitability via inflated suitability predictions in nearshore, shallow habitats. To address these biases, we used methodological choices in line with existing literature, including spatial coarsening of presences and pseudo-absences, development of pseudoabsences with background sampling (Braun et al. 2023a), and using equal numbers of presences and pseudoabsences (Barbet-Massin et al. 2012, Hazen et al. 2021). While the model indicated that nearshore habitats were consistently more suitable than open-ocean environments, model predictions captured and communicated seasonally suitable offshore habitats beyond aggregation sites and year-round suitable habitat at aggregation sites.

Future whale shark distribution analyses will benefit from more spatially and demographically representative data (DeAngelis & Yurek 2017, Williamson et al. 2022). The inclusion of satellite and acoustic telemetry data (Cagua et al. 2015, Hays et al. 2019, Shidqi et al. 2024) would help address sampling biases (Braun et al. 2023a) and are better equipped to characterize suitable habitat at depth and in the open ocean. Explicit representation of specific size or age classes may also yield more realistic results for species with expected habitat partitioning between adults and juveniles (e.g. Druon et al. 2022). When the data allow, size-specific modeling will be an important next step for whale sharks, as juveniles are hypothesized to primarily occupy nearshore aggregation sites, and adults to favor pelagic habitats (Acuña-Marrero et al. 2014, Macena & Hazin 2016).

The current study represents a valuable first step in leveraging opportunistic sightings data to better understand seasonality and broad-scale distribution of whale sharks in the NWA. These results underscore previously unknown pelagic regions conducive to high seasonal whale shark habitat suitability, particularly along the US east coast at the northern edge of the Mid-Atlantic Bight, identify extensive suitable habitat beyond known aggregations in the north Gulf of Mexico (Hoffmayer et al. 2021), and reaffirm year-round highly suitable conditions at known aggregation sites (Heyman et al. 2001, de la Parra-Venegas et al. 2011). Pulse stressors, like marine heat waves, and ongoing long-term changes in the NWA have already been shown to redistribute highly migratory species (Braun et al. 2023b, Farchadi et al. 2024). These ongoing changes highlight the importance of SDM frameworks, like the one presented here, that can account for the fluid and complex nature of changing ocean conditions and distributions of highly migratory species as new data become available (Lewison et al. 2015, Maxwell et al. 2015, Hazen et al. 2018).

5. CONCLUSIONS

Here, we assembled the most extensive occurrence data set for whale sharks in the NWA to understand their movement ecology and seasonality (Sequeira et al. 2014, Pierce & Norman, 2016). We used an SDM to link diverse observation data with environmental characteristics. The model indicated that whale shark habitat suitability was largely driven by bathymetry, SST, and SSH, which led to several areas of high, model-predicted habitat suitability outside of known aggregation sites. We present the first quantitative evidence of model-predicted suitable oceanic habitats at temperate latitudes in the NWA, such as along the continental shelf edge offshore from Cape Cod. Given rapid climate-induced changes to ocean ecosystems in this region, additional research is needed to understand the functional role and importance of these seasonal habitats within the broader life history and ecology of whale sharks in the NWA.

Acknowledgements. This work was supported in part by NSF REU OCE2150401. The present work was part of H.M.M.'s undergraduate thesis. H.M.M. thanks committee members A. Roles and J. Gleditsch for their support and feedback in improving the quality of this work. We thank those who contributed data to this project, including the Normandeau Associates Consultation Team under the Remote Marine and Onshore Technology Project completed for the Bureau of Ocean Energy Management, Equinor Wind, and the New York State Energy Research and Development Authority. We also extend our gratitude for data contribution from the North Atlantic Right Whale Consortium, the University of Southern Mississippi's Northern Gulf of Mexico Whale Shark Sightings Survey, and the MarAlliance-Marine Megafauna Program Satellite Tracking and Analysis Tool. Data for this work also used Wildbook for Whale Sharks, directed by Jason Holmberg, an online mark–recapture database operated by the non-profit scientific organization Wild Me with support from public donations and the Qatar Whale Shark Research Project. Much of the data used for this project originated from the Global Biodiversity Information Index and the Ocean Biodiversity Information System biodiversity databases. Additional thanks to those who compiled or contributed to the above-described data, including Bob Kenney at the North Atlantic Right Whale Consortium, Orla O'Brien at the New England Aquarium, and Simon Pierce and Jesse Cochran for facilitating and assisting with the Wildbook for Whale Sharks data. M.C.A. was supported by the WHOI President's Innovation Fund. We thank B. Schumaker for endless hours searching for whale sharks over the Gulf of Mexico and the associated group of experienced spotters, including T. Collins, D. Abrams, M. Sturdivant, J. Moran, G. Gray, and J. Green.

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Editorial responsibility: Jana Davis,
Annapolis, Maryland, USA
Reviewed by: 2 anonymous referees

Submitted: December 20, 2024
Accepted: May 16, 2025
Proofs received from author(s): August 4, 2025