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Distribution of breeding humpback whale habitats and overlap with cumulative anthropogenic impacts in the Eastern Tropical Atlantic

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Abstract

Aim: Species distribution modelling is a useful tool for determining important habitats. By accounting for specific animal behaviour in the model, it is possible to identify finer-scale patterns of habitat use. Together with spatially explicit data on anthropogenic activities, models can be used to assess human impacts and inform conservation management. This study used observations of breeding behaviour to identify fine-scale breeding habitats of humpback whales (*Megaptera novaeangliae*), as well as potential overlap of these habitats with cumulative anthropogenic impacts.

Location: Eastern Tropical Atlantic, West Africa.

Methods: Maxent was used to model humpback distribution using pertinent environmental predictors and an integrated dataset of humpback whale occurrences filtered for breeding-specific behaviours. In conjunction with multiple anthropogenic activities, a subsequent cumulative utilization and impact analysis assessed the degree of overlap between predicted breeding habitat and potential anthropogenic impacts.

Results: Greatest habitat suitability occurred in warm coastal waters of Gabon, and other highly suitable areas occurred off Equatorial Guinea (Bioko Island), Cameroon and Angola. Sea surface temperature and height contributed most to the model. Highest overlap between humpback whales and potential impacts from anthropogenic activities occurred off Gabon, Equatorial Guinea (Bioko Island), Cameroon and Angola. Impacts associated with oil and gas development (where oil and gas platforms serve as an indicator for industry activity) appeared to contribute most to potential cumulative impact.

Main Conclusions: Depth and sea surface temperature of predicted breeding habitats were consistent with previous studies. However, lesser known characteristics such as sea surface height and wind speed, resulting in potentially more sheltered areas for breeding whales, may also be important in delineating finer-scale habitat suitability. Identified areas of high potential cumulative impact occurred within exclusive economic zones of multiple countries and likely represent the minimum level

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of impact to humpback whales in the region, highlighting the need for additional research and effective management throughout the area.

KEYWORDS
anthropogenic activity, breeding habitat, cumulative impacts, Gulf of Guinea, humpback whale, Maxent, species distribution models

1 | INTRODUCTION

The identification of important habitats broadens our understanding of the associations between a species and its environment. Specifically, the habitat characteristics that contribute to the significance of the area for a species. Important habitats may encompass areas crucial for specific life history stages, such as feeding and breeding areas, which are critical for an individual's survival and the persistence of the population (Hoyt, 2005; Martin et al., 2015; Oviedo & Solís, 2008). In the marine environment, dynamic oceanographic processes may make important habitats seasonal or ephemeral. Some marine species respond to these environments by modifying their distributions between life history stages through regular, long-distance migrations (Redfern et al., 2006). As these habitats may not be spatially or temporally discrete, their identification can be challenging (Forney, 2000; Hoyt, 2005; Ingram & Rogan, 2002; Oviedo & Solís, 2008; Rosenbaum, Maxwell, Kershaw, & Mate, 2014). Notwithstanding these challenges, identification of important habitats and their features can help determine conservation, management and research priorities—an essential need where there are rapidly increasing or widespread anthropogenic impacts (Halpern et al., 2015b; Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000).

Species distribution modelling (SDM) is a useful method for determining the distribution and occurrence of species presence based on the quantification of presumed habitat suitability. This can then be used to prioritize research and management efforts (Elith et al., 2006; Guisan, Thuiller, & Zimmermann, 2017). SDM determines probable areas of high habitat suitability by modelling the relationship between records of occurrence and the environmental characteristics of those locations (Franklin, 2009). These models may then be used (with appropriate caution) to predict where a species may occur in areas without dedicated survey effort, thus highlighting candidate areas for future research and conservation efforts (Becker et al., 2014; Elith et al., 2006; Guisan & Thuiller, 2005). Additionally, SDMs can help identify areas where species may overlap with known anthropogenic threats and their presumed impacts (Hazen et al., 2017, 2018; Howell, Kobayashi, Parker, Balazs, & Polovina, 2008). Mixed-methods approaches that integrate multiple data types combined with SDMs are increasingly common in conservation studies, are likely to provide a better estimate of important habitats due to increased sample size and geographic coverage, and may help inform management of data-poor populations and geographic regions (Redfern et al., 2006; Stockwell & Peterson, 2002; Thiers et al., 2014).

The humpback whale (*Megaptera novaeangliae*) is a well-studied, highly migratory cetacean for which methods of data integration, modelling and determination of potential cumulative impacts can be implemented. The species is found in all the world's major ocean basins and migrates seasonally between low-latitude winter breeding areas and high-latitude summer feeding areas (Dawbin, 1966; Mackintosh, 1942). The International Whaling Commission (IWC) recognizes seven major Southern Hemisphere humpback whale breeding stocks, each of which exhibits high site fidelity to different breeding areas (IWC, 2007). Previous studies have observed general breeding habitat preferences across stocks, consisting of relatively warm, shallow and coastal waters (Craig & Herman, 1997; Ersts & Rosenbaum, 2003; Oviedo & Solís, 2008; Rasmussen et al., 2007; Rosenbaum et al., 2014; Whitehead & Moore, 1982). In addition, the humpback whale mating system is most closely associated with leks, which may influence the distribution of individuals within a breeding area (Cerchio, 2003; Clapham, 1996; Herman & Tavolga, 1980). However, Clapham (1996) noted that there is a lack of exact geographic territories of displaying males, thus developing the term “floating lek.”

Southern Hemisphere humpback whales were reduced to just a fraction of their pre-exploitation population size during the commercial whaling era (Clapham & Baker, 2002; Rocha, Clapham, & Ivashchenko, 2014; Townsend, 1935). The IWC enacted an international moratorium on commercial whaling in 1986; however, recovering humpback whale populations face a host of modern threats including increases in shipping (and associated noise), offshore industrial development, fishing (direct interaction and/or prey depletion) and climate change (Bettridge et al., 2015; Findlay, Collins, & Rosenbaum, 2006; Halpern et al., 2015b; Maxwell et al., 2013; Van Waerebeek et al., 2007). Due to the increase in multiple anthropogenic activities and overlap within important habitat areas, including breeding habitats, it is essential to identify and prioritize high-risk areas for research, conservation and mitigation efforts.

IWC Breeding Stock B (BSB) refers to the population of whales that migrate between feeding areas in the Southern Ocean and breeding areas in tropical and subtropical western Africa (Dawbin, 1966; Mackintosh, 1942; Rosenbaum et al., 2014). Genetic substructure within BSB has been observed, resulting in two distinct substocks. Humpback whales utilizing breeding areas off Gabon and Congo are termed “Breeding Substock B1” (“BSB1”), and those observed migrating and occasionally feeding off west South Africa and Namibia are termed “Breeding Substock B2” (“BSB2”) (Barendse, Best, Carvalho, & Pomilla, 2013; Findlay et al., 2017; IWC, 2011b; Kershaw et al., 2017; Rosenbaum et al., 2014, 2009). The breeding area for BSB2 is currently unknown (Barendse et al., 2013; Rosenbaum et al., 2017). The genetic distinctiveness of BSB1 is considered high, with individuals returning to the same relatively well-known breeding areas off Gabon and Congo each year. However, through satellite telemetry data, whales were observed moving directly north of Gabon during September and October (Rosenbaum et al., 2014). This is a time of year when all individuals were expected to have begun their southward migration and suggests an expansion of existing breeding areas or previously unknown use of breeding habitat further north (Rosenbaum et al., 2014). These as yet unidentified areas may include the currently unidentified breeding areas for BSB2 (Carvalho et al., 2014; IWC, 2011a, 2011b, 2005, 2003; Rosenbaum et al., 2014, 2009). These findings highlight gaps in knowledge of population structure and habitat use for a relatively well-studied breeding area (Best, 2011; Carvalho et al., 2014; Clapham, Palsbøll, Mattila, & Vasquez, 1992; Ersts & Rosenbaum, 2003; Kershaw et al., 2017; Rosenbaum et al., 2014, 2009).

This study utilized an integrated occurrence dataset of breeding-specific behaviours from three different data sources to predict the distribution of breeding habitats for humpback whales in the Eastern Tropical Atlantic. The characteristics and distribution of potentially suitable breeding habitats were modelled, and the overlap between those habitats and the presumed impacts of multiple anthropogenic activities in the region were examined. Inclusion of multiple anthropogenic activities provides a measure of the likely cumulative impact and threat to this population, and better informs research and conservation priorities for potentially high-risk areas.

2 | METHODS

2.1 | Occurrence data

A single integrated dataset of humpback whale occurrence records, filtered for breeding behaviour, was obtained from three sources: satellite telemetry data, boat-based sightings and aerial survey data (data sources summarized in Table 1). This represents a subset of the most comprehensive datasets available for this region. For satellite telemetry data, breeding behaviour was selected based on movement parameters (i.e. speed, turning angle). For boat-based sightings and aerial survey data, breeding behaviour was selected based on observed behavioural characteristics (i.e. singing, group size and composition).

Satellite telemetry data from 2002 was provided by Rosenbaum et al. (2014). Humpback whales (n = 13) were tagged with Telonics ST-Argos transmitters off the coast of Gabon in August and September of 2002 and transmitted location data for 19–104 days. Rosenbaum et al. (2014) used a behaviourally switching state-space model (SSM) to analyse individual movements (Breed, Jonsen, Myers, Don Bowen, & Leonard, 2009; Jonsen, Mills-Flemming, & Myers, 2005; Jonsen, Myers, & Mills-Flemming, 2003). Briefly (see Rosenbaum et al., 2014 for details), two Markov chain Monte Carlo (MCMC) chains were run to estimate the mean and variance of each location and behaviour parameter, resulting in two behavioural states: localized and transiting behaviours. Localized behaviour was characterized by slower movements and high rates of near 180° turning angles, which were identified exclusively within breeding and feeding areas. Locations of localized behaviour complement field observations of individuals exhibiting breeding behaviour and also complement the behaviour of competitive groups, where individuals often are jostling for the optimal position directly adjacent to the nuclear animal (Baker & Herman, 1984; Tyack & Whitehead, 1982). Transiting behaviour was characterized by faster and more directed movements, with turning angles near 0°, and was identified between feeding and breeding habitat, along migratory routes (Rosenbaum et al., 2014). To filter for breeding behaviour, satellite locations of localized behaviour within breeding areas (excluding locations of transiting behaviour and localized behaviour in feeding areas off sub-Antarctic and Antarctic regions) were retained for the model. Breeding behaviour locations were identified for nine individuals: three males, four females and two females with calves, and spanned September and October 2002 (n = 199).

TABLE 1 A summary of input data for distribution modelling. Types of occurrence data used for modelling, number of breeding occurrence points, method used to extract breeding behaviour points, temporal range of breeding occurrence points and source of original data

Data type	Number of breeding points	Selection of breeding points	Temporal coverage	Source
Satellite	199	Behaviourally switching state-space model	2002: September–October	Rosenbaum et al. (2014)
Boat	589	Singers; mother–calf–escort groups; mother–calf pairs; competitive groups	2000: August 2001 and 2002: July–September 2003 and 2004: August–October 2005: July–October 2006 and 2012: July–September	Collins et al. (2010); unpublished
Aerial	17	≥3 individuals	2002: August	Strindberg et al. (2011)

Boat-based sighting data were collected during surveys off Gabon that spanned the austral winters of 2000–2006 and 2012 (Collins et al., 2010; Collins, unpublished data). Surveys between 2000 and 2006 were focused on the collection of biopsies and photo-identification data, and thus, effort was targeted in nature and/or opportunistic (Collins et al., 2010). Surveys in 2012 used structured line transect methodology (T. Collins, personal communication, October 5, 2017). All surveys were conducted within an approximate band from the coast to 50 km offshore, and recorded depths did not exceed 100 m. When a sighting was made, the GPS location, detailed behaviour and group size were recorded. Aerial surveys were conducted in August 2002 using distance sampling (Buckland et al., 2001; Buckland, Rexstad, Marques, & Oedekoven, 2015) along a systematic zigzag survey design in August 2002, with a random starting point and a pair of observers on each side of the plane (Strindberg, Ersts, Collins, Sounguet, & Rosenbaum, 2011). The aerial survey covered a total of 2,697.14 km (1,456.34 nmi) and included areas not surveyed by boat. The GPS location and estimates of group size were recorded for each sighting.

Previous studies suggest four humpback whale behavioural categories that indicate breeding behaviour: (a) singing males, (b) mother–calf–escort group, (c) mother–calf pairs, and (d) competitive groups. Whales that were observed singing or observed in mother–calf–escort groups, mother–calf pairs and competitive groups were used to identify “breeding” behaviour in this study (Table 2). Thus, breeding habitat examined in this study reflects areas where whales exhibiting these previously described breeding behaviours were observed. Boat-based data were filtered to include only these categories deemed to be indicative of breeding activity, resulting in the selection of presence points spanning August 2000, July–September in 2001 and 2002, August–October in 2003 and 2004, July–October 2005 and July–September in 2006 and 2012 (*n* = 589). Aerial survey data, for which behaviour was not documented, were filtered by estimated group size to include only those occurrences with three or more individuals as a proxy for competitive behaviour (*n* = 17).

Boat-based sighting data were collected from the coastal waters of Gabon, a smaller area compared to aerial and satellite data, and thus, a relatively high number of records (boat: 589; satellite: 199; aerial: 17) were collected from a relatively small geographic area compared to the area being studied here. To minimize the sampling bias of the boat-based sighting data and resolve non-independence of satellite telemetry data, a nonparametric bootstrap method was used to subsample 100 random points, for both data types, 30 times (Scales et al., 2015). Each iteration of randomly subsampled data was then combined with the aerial data to obtain the complete integrated set of occurrence records.

2.2 | Environmental variables

Environmental variables previously identified as influential factors of suitable humpback whale breeding habitat were used as predictors in the Maxent model. These consisted of predictors that may influence the ability to perform breeding displays and successfully rear calves, including bathymetry (depth), distance to shore, slope of the seafloor, sea surface height (SSH, the height of the ocean's surface above sea level), sea surface temperature (SST) and wind speed (Ersts & Rosenbaum, 2003; Oviedo & Solís, 2008; Rasmussen et al., 2007; Smith et al., 2012; Whitehead & Moore, 1982). Environmental data were collated for corresponding months and years for which there were occurrence data (data sources are summarized in Table 3). Distance from shore and slope of the seafloor were calculated using the Euclidean distance estimating tool and Slope tool in ArcGIS© Spatial Analyst (v. 10.4.1). Resulting distances were converted from decimal degrees to km. SSH and SST daily values were both obtained from E.U. Copernicus Marine Service Information (Copernicus Marine Environment Monitoring Service) and averaged to represent mean SSH and SST during the period during which occurrence points were collected. SST was converted from degrees Kelvin to degrees Celsius. Wind speed (m/s) daily values were obtained from the National Centers for Environmental Information (formerly the National Climatic Data Center) of NOAA and averaged to represent the mean wind speed for the period during which occurrence points were collected.

A standard study area was used, delineated using the Large Marine Ecosystems (LME) of the World portal (Sherman & Hempel, 2009). The study extent encompasses LME 28: the Guinea Current, resulting

TABLE 2 Description of behaviours that were used to denote “breeding” for boat-based and aerial survey occurrence data

Breeding behaviour	Context	References
Singing males	Humpback whale song, observed in breeding areas, is likely sung in a reproductive context to attract mates, communicate location, sex and readiness to mate with females and engage in competitive behaviour with other males.	Tyack (1981) and Baker and Herman (1984)
Mother–calf–escort groups	Due to the "floating lek" mating system, males search widely for females in oestrus, including females with calves.	Baker and Herman (1984)
Mother–calf pairs	Mother–calf pairs are first observed on winter breeding grounds (where calves are born).	Baker and Herman (1984) and Cerchio, Jacobsen, Cholewiak, Falcone, and Merriwether (2005)
Competitive groups	Competitive groups consist of groups of three or more individuals engaged in mutual aggression. This commonly consists of breeding males competing for access to a mature female.	Tyack and Whitehead, (1982) and Baker and Herman (1984)

TABLE 3 Environmental predictors used in the model, the description of the variable, original spatial resolution of the data and original source of data

Environmental predictor	Description	Original grid resolution	Source
Bathymetry	Topography of the seafloor, depth of water mass (m)	0.017	Amante and Eakins (2009); https://www.ngdc.noaa.gov/mgg/global/
Slope	Slope (degrees) of the seafloor	0.017	Calculated using Slope in ArcMapTM from bathymetry
Distance to shore	Euclidean distance (km) from the 200-m isobath to shore	0.017	Calculated using Euclidean Distance in ArcMapTM from bathymetry
Sea surface temperature (SST)	Temperature (°C)	0.25	http://marine.copernicus.eu/ GLOBAL-REANALYSIS-PHY–001–025
Sea surface height (SSH)	Sea surface height above geoid (m)	0.25	http://marine.copernicus.eu/ GLOBAL-REANALYSIS-PHY–001–025
Wind speed	Ocean surface vector winds (m/s)	0.25	Zhang, Bates, Bates, and Reynolds (2006), Zhang, Reynolds, Reynolds, and Bates (2006) and Peng et al. (2013); https://www.ncdc.noaa.gov/

in a grid of latitudes N 15, S −20, and W −31, E 15, including the Gulf of Guinea and surrounding waters. Environmental layers were processed in RStudio to the prescribed extent and the finest scale resolution provided by the environmental layers (0.017° × 0.017°, bathymetry) in order to avoid possible inaccuracies in the data when interpolating to a lower resolution, and to provide fine-scale information for subsequent management (Nezer, Bar-David, Gueta, & Carmel, 2017; Phillips, Anderson, & Schapire, 2006; R Core Team, 2017).

2.3 | Species distribution modelling

Maxent is a SDM method that can estimate species distribution using the maximum entropy approach, whereby species presence-only data are used to estimate the occurrence by constraining each grid cell of the study area to the environmental conditions that most closely match those of known occurrence points (Phillips, Anderson, Dudík, Schapire, & Blair, 2017; Phillips et al., 2006). Maxent is ideal for modelling breeding habitat suitability of humpback whales because it requires only presence data, which is often the type of data available for migratory marine species. It is able to incorporate model complexity, while preventing overfitting, and has performed well compared to other SDM methods (Elith et al., 2006; Muscarella et al., 2014; Phillips et al., 2006, 2009).

All statistical analyses were conducted in R. The R package "ENMeval" was used to conduct Maxent models as well as model evaluation and determination of optimal model complexity (Muscarella et al., 2014). "ENMeval" allows the user to specify methods by which to partition training and testing data, as well as select a set of feature classes by which Maxent fits covariates, and regularization multipliers which smooths the model to avoid overfitting (Elith et al., 2011; Muscarella et al., 2014). Models are run across the range of custom settings, and six evaluation metrics for model performance are provided (Muscarella et al., 2014).

Each Maxent model conducted using the package "ENMeval" was run with a set of feature classes (linear, quadratic, hinge and product), a series of regularization multipliers (0.5, 1, 1.5, 2) and fivefold cross-validation. All environmental predictors were used in the model to ensure that complete information on fine-scale breeding habitat requirements was reflected in the model. Duplicate occurrence points in the same grid cell were removed so that only one point per grid cell was retained to obtain an unbiased sample. Additionally, a total of 10,000 background points were selected from within the continental shelf, which includes areas of observed breeding behaviours and thus reflects the same sampling bias as presence points to address model assumptions of random sampling (Van Waerebeek et al., 2001; Rosenbaum & Collins, 2006; Barbet-Massin, Jiguet, Albert, & Thuiller, 2012; Collins et al., 2010; Elith et al., 2011; Phillips et al., 2009; Radosavljevic & Anderson, 2014; Yackulic et al., 2013). Maxent models were restricted to the continental shelf, as both presence and background points were located within the shelf. Models were run with specified sets of feature classes and regularization multipliers, and were replicated 30 times for each bootstrapped occurrence dataset (Ainley et al., 2012).

"ENMeval" provides six model evaluation metrics (AUC_{TEST}, AUC_{DIFF}, OR_{MTP}, OR_{10} and AICc). Models with the lowest Akaike information criterion-corrected (AICc) value were selected because studies have shown that AICc performs better when selecting the optimal model for smaller sample sizes (Burnham & Anderson, 2004; Muscarella et al., 2014; Radosavljevic & Anderson, 2014; Warren & Seifert, 2011). Optimal models were averaged to produce the final results, and raw Maxent output values were converted to a complementary log-log (cloglog) output which produces an estimation of probability of presence on a scale of 0–1 (Ainley et al., 2012; Ballard, Jongsomjit, Veloz, & Ainley, 2012; Phillips et al., 2017). While the cloglog Maxent output estimates the probability of presence of a species, Phillips et al. (2017) caveat that it depends on being able to correctly estimate species prevalence and total abundance. We are currently unable to provide this information; thus, we refer to the model outputs as estimating habitat suitability rather than the probability of presence. The contribution of each environmental predictor to the final Maxent model was determined by its permutation importance, and values were normalized to percentages for more intuitive interpretation (see "A Brief Tutorial on Maxent," biodiversityinformatics.amnh.org).

The final averaged Maxent distribution model was used to produce binary presence–absence maps to more clearly delineate potential breeding areas of greater relative importance. Thresholds of 0.2, 0.4, 0.6 and 0.8 habitat suitability were applied, and the most appropriate thresholds were determined based on observations and experience of co-authors familiar with the region. Thresholds of 0.2 and 0.4 were selected, as low thresholds are most inclusive of potential suitable breeding habitats and are thus more conservative in delineating important habitats. Additionally, opting for lower threshold values takes into consideration the lack of complete information on breeding habitat in the area and surrounding waters, especially in the northern Gulf of Guinea, and the caution needed when extrapolating predicted breeding habitat suitability to the entire region. To assess potential differences in the environmental space each threshold encompasses, 10,000 random points were drawn from each appropriate threshold, and differences in environmental characteristics between thresholded areas were examined using the R package "effsize" for Cohen's *d* for each environmental predictor (Torchiano, 2019).

2.4 | Cumulative utilization and impact (CUI) analysis

A cumulative utilization and impact (CUI) analysis (Maxwell et al., 2013) was conducted to assess the extent of overlap between anthropogenic activities and potential humpback whale breeding habitat identified by the Maxent model and to estimate the relative degree to which threats associated with these activities could impact identified suitable breeding areas. Anthropogenic activities included those that previous studies have indicated may adversely affect the distribution, health and reproductive status of humpback whales. These include ocean acidification anomalies, fishing intensity (representing potential for entanglement), pollution, oil and gas platforms (as a proxy for oil and gas industry activity impacting water quality and generating noise), shipping (potential for vessel strikes and generating noise), sea-level rise (SLR) and SST anomalies (Bettridge et al., 2015; Bezamat, Wedekin, & Simões-Lopes, 2015; Blair, Merchant, Friedlaender, Wiley, & Parks, 2016; Dunlop et al., 2016; Hall et al., 2018; Ilyina, Zeebe, & Brewer, 2010; Laist, Knowlton, Mead, Collet, & Podesta, 2001; Moore, 2009; Rosenbaum et al., 2014). The CUI score was calculated per grid cell as follows:

$$\mathrm{CUI}_i = \sum_{j=1}^{n} D_i \times S_i \times u_{i,j}$$

where n is the number of anthropogenic activities, D_i is the normalized, log-transformed intensity value of an activity at location (grid cell) i, S_i is the predicted distribution of humpback whale breeding habitat produced by the Maxent model at location i, and $u_{i,j}$ is the impact weight score for activity j on humpback whales at location i (Halpern et al., 2015b; Maxwell et al., 2013).

A global map of the intensity of each anthropogenic activity used in the analysis was obtained from the National Center for Ecological Analysis and Synthesis (Halpern et al.,2015a). Nine intensity layers associated with climate change, fisheries, pollution and industrial activity (see Table 4) were obtained at a resolution of 1 km^2 and resampled by bilinear interpolation to the extent and resolution of the environmental predictors (see Halpern et al., 2008 and Halpern et al.,2015a, for detailed description of layers). Ranking of each activity's potential impact on humpback whales was determined through a review of literature published after Maxwell et al. (2013). To maintain ranking consistency, the impact weight of each activity was quantified by six measures of the anthropogenic activity: (1) frequency of the activity; (2) level of direct or indirect impact on an individual; (3) the likelihood of mortality to an individual; (4) recovery time of the individual from the impact; (5) relative impact on reproductive capacity; and (6) relative impact distributed across the population (details in Maxwell et al., 2013 Supplementary Materials). Measures (1) and (4) were ranked on a scale from 1 to 4, and all other measures were ranked on a scale of 1–3. The current literature review did not find sufficient evidence to significantly increase the impact weight values determined by Maxwell et al. (2013). However, new SLR data from Halpern et al. (2015a) warranted determination of SLR impact values on humpbacks, as SLR may impact suitable breeding areas (Table 4) (Bettridge et al., 2015). These values were normalized and summed to obtain a single weight value for each activity (Table 3) (details in supplementary materials of Maxwell et al., 2013).

TABLE 4 Anthropogenic impacts taken from Halpern et al. (2015a) include ocean acidification anomalies, fishing, pollution, oil rigs, shipping, sea-level rise (SLR) and sea surface temperature (SST) anomalies. Values to calculate the normalized impact weight include: (1) frequency of the activity, (2) level of direct or indirect impact on an individual, (3) the likelihood of mortality to an individual, (4) recovery time of the individual from the impact, (5) relative impact on reproductive capacity, and (6) relative impact distributed across the population (Maxwell et al., 2013). The influence of each activity on the overall CUI distribution was calculated using pairwise linear regressions

Activity	Normalized impact weight	Influence on CUI (R^2)
Oil rigs	0.60	0.10
Sea surface temperature anomalies	0.72	0.03
Demersal fishing bycatch	0.66	0.02
Pelagic fishing bycatch	0.66	0.02
Shipping	0.94	0.02
Ocean acidification	0.72	<0.01
Inorganic pollution	0.79	<0.01
Ocean-based pollution	0.92	<0.01
Sea-level rise	0.60	<0.01

Once CUI scores were determined across the study extent, pairwise linear regressions were conducted to determine which individual impact layer contributed most to the overall CUI distribution, which can help identify anthropogenic activities that have the greatest potential influence on humpback whales. These analyses allow identification of potential areas of high priority for directed research, conservation, and management efforts, as these areas likely encompass both high humpback whale presence and high potential impact from anthropogenic activities.

3 | RESULTS

3.1 | Humpback whale occurrences

The integrated satellite telemetry, aerial survey and boat-based sighting dataset provided presence points (*n* = 805) that were all located over the continental shelf and spanned exclusive economic zones (EEZs) of multiple countries (Figure 1). No sighting effort occurred off the coast of the mainland region of Equatorial Guinea or the northern portion of Angola and Nigeria. The majority of presence points occurred off of Gabon, which included all three types of data (satellite telemetry, boat and aerial surveys). Only satellite telemetry data occurred in the waters of Equatorial Guinea (Bioko Island), Cameroon, Nigeria and the Democratic Republic of Congo.

3.2 | Humpback whale breeding habitat distribution

Models used bootstrapped integrated occurrence datasets of between 168 and 184 points where individuals were exhibiting breeding behaviour, following the removal of duplicate records within the same grid cell. While the predicted breeding habitat suitability (compared to degree of habitat use represented by the sightings data) varies across the study extent, all areas of high suitability identified by the overall model occurred close to shore and within EEZs of multiple countries (Figure 2a). The models predicted high habitat suitability for breeding humpback whales in warm, coastal and nearshore waters (Figure 2a). Geographically, the models predicted high suitability (≥0.8) along the coast of

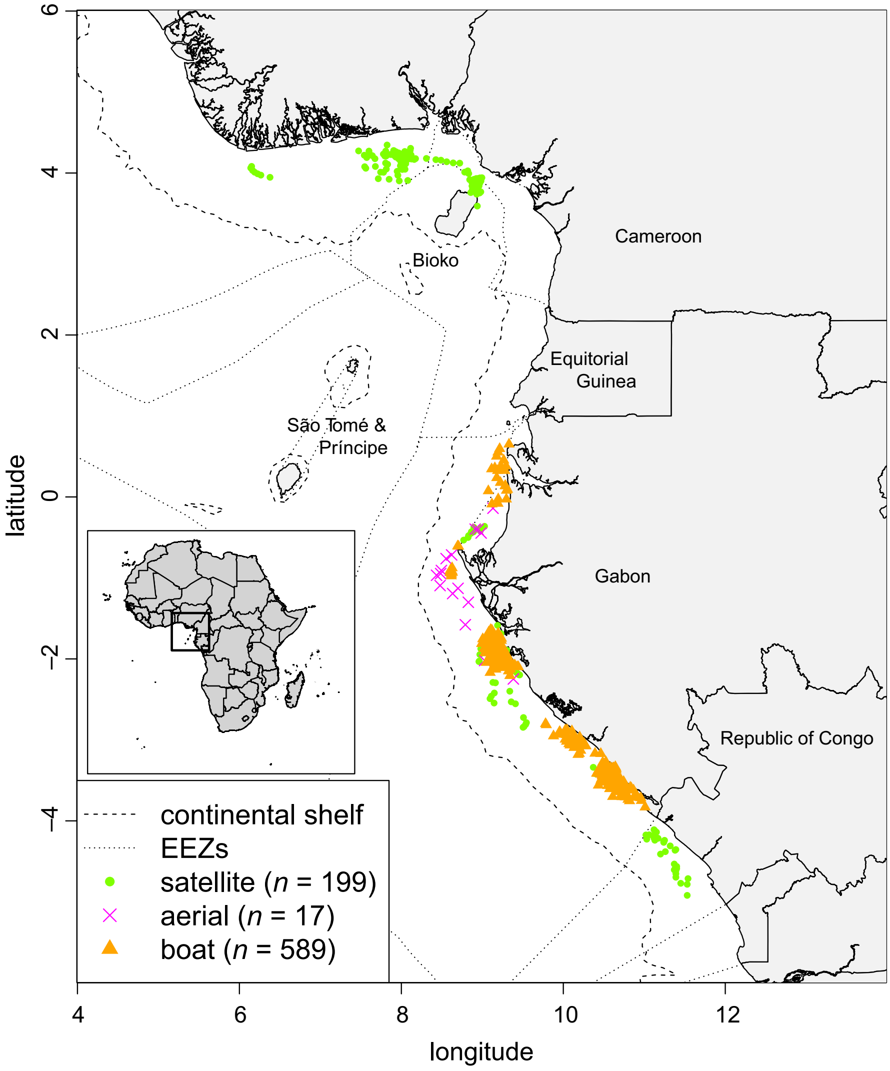


FIGURE 1 Distribution of breeding behaviour occurrences. All occurrence points used in the model of breeding behaviours from an integrated dataset of satellite telemetry, aerial survey and boat-based data for humpback whales. Green circles represent data from satellite telemetry tags (Rosenbaum et al., 2014), pink X's represent data from aerial survey data (Strindberg et al., 2011), and orange triangles represent data from boat-based sighting data (Collins et al., 2010; unpublished). Dashed lines represent the outer boundary of the continental shelf, and dotted lines represent exclusive economic zone (EEZ) boundaries

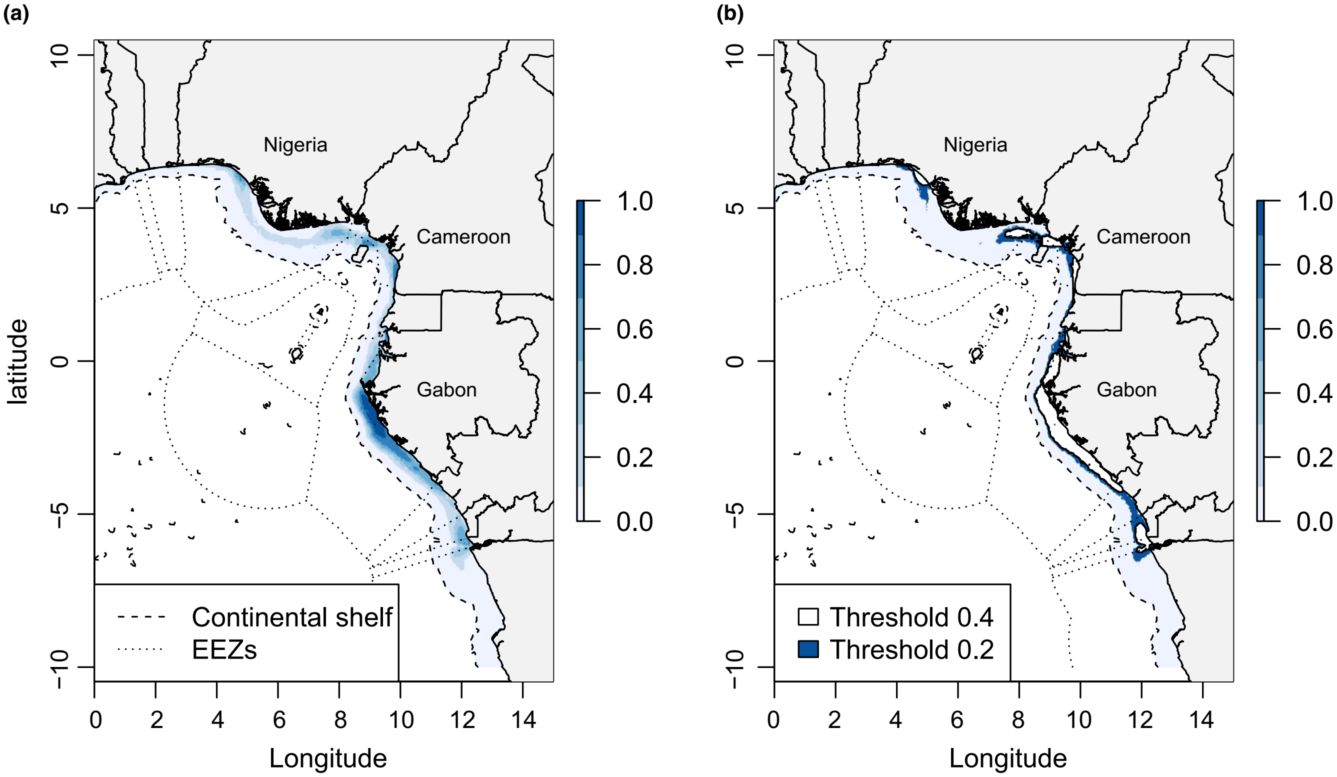


FIGURE 2 Distributions of identified suitable breeding habitat. (a) Mapped breeding habitat suitability of humpback whale breeding behaviour based on 30 Maxent model runs with environmental predictors: bathymetry, distance from continental shelf, slope, sea surface height (SSH), sea surface temperature (SST) and wind speed. Darker blue colours represent higher breeding habitat suitability. Dashed lines represent the outer boundary of the continental shelf, and dotted lines represent exclusive economic zone (EEZ) boundaries. (b) Binary map of humpback whale presence–absence derived from thresholds of breeding habitat suitability. White areas represent suitable breeding habitat defined by a threshold of 0.4, and suitable breeding habitat defined by a threshold of 0.2 is represented by the areas covered by the 0.4 threshold in addition to dark blue areas. Dashed lines represent the outer boundary of the continental shelf, and dotted lines represent EEZ boundaries

Gabon, Equatorial Guinea (Bioko Island) and southern portion of Cameroon (Figure 2a). Moderate breeding habitat suitability was identified throughout the Gabon and Cameroonian coasts, Nigeria and Angola (Figure 2a). Relatively low suitability was predicted in areas off the western coast of Congo and the mainland territory of Equatorial Guinea, and no suitable areas were predicted further north off Benin, Togo, Ghana and Côte d'Ivoire (Figure 2a). Environmental predictors that contributed most to the final model were SST (33.40%), SSH (32.25%), distance to shore (12.11%) and bathymetry (10.82%) (Figure 3).

Environmental characteristics of suitable areas identified from the random points selected within the 0.2 and 0.4 thresholds (n = 20,000) suggest that high habitat suitability for humpback whales exhibiting breeding behaviour generally occurs in shallow (−27.3 ± 42.6 m; mean ± standard deviation) and warm (24.5 ± 1.5°C) waters that are nearshore (68.2 ± 16.1 km). These areas of high breeding habitat suitability are also characterized by shallow slopes (0.2 ± 0.3°), low SSH (−0.04 ± 0.06 m) and relatively low wind speed (5.9 ± 1.3 m/s). Effect sizes were negligible for all environmental predictors between 0.2 and 0.4 thresholded areas, except for a small effect size (d = 0.2; 95% CI: 0.18–0.23) for bathymetry.

3.3 | Overlap with anthropogenic activities

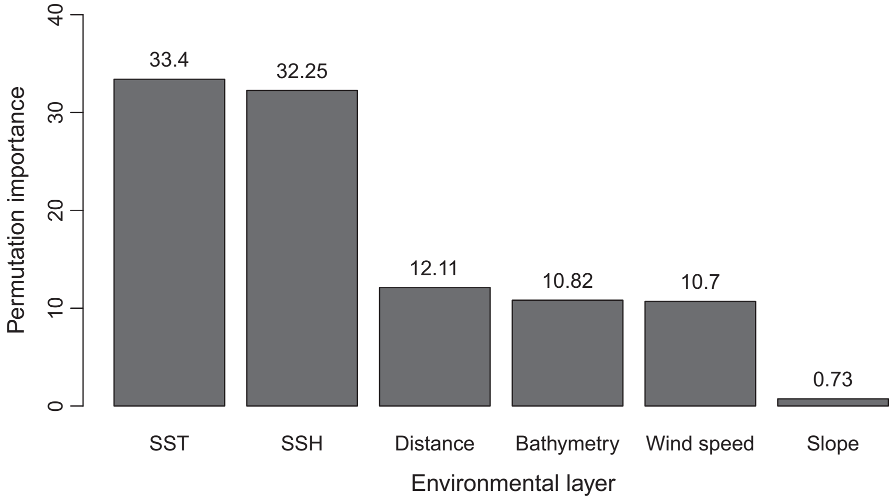
All areas of mapped cumulative impact occur within multiple EEZs. Areas with the highest cumulative threats appear to occur off the coast of Nigeria (Figure 4a). When combined with the distribution of suitable breeding habitat, highest CUI values occur in coastal waters off Gabon (Port Gentil), Nigeria (Akwa Ibom) and Equatorial Guinea (Bioko Island), southern Cameroon and Angola (Figure 4b). Moderate CUI values are estimated off the coast of Congo and northern areas of Nigeria (Figure 4b). The presence of oil platforms appeared to have the greatest contribution to the overall CUI as determined by a relatively high R^2 value (R^2 = 0.1) (Table 4). Areas where oil platforms are present are assumed to be indicative of regions where hydrocarbon exploration and development occur, which may consequently include other anthropogenic impacts.

4 | DISCUSSION

4.1 | Characteristics of suitable breeding habitat

High breeding habitat suitability was predicted in shallow, warm, nearshore waters with low SSH. This consisted of coastal waters

FIGURE 3 Permutation importance (percentage) of the environmental predictor variables used in the final Maxent breeding habitat model



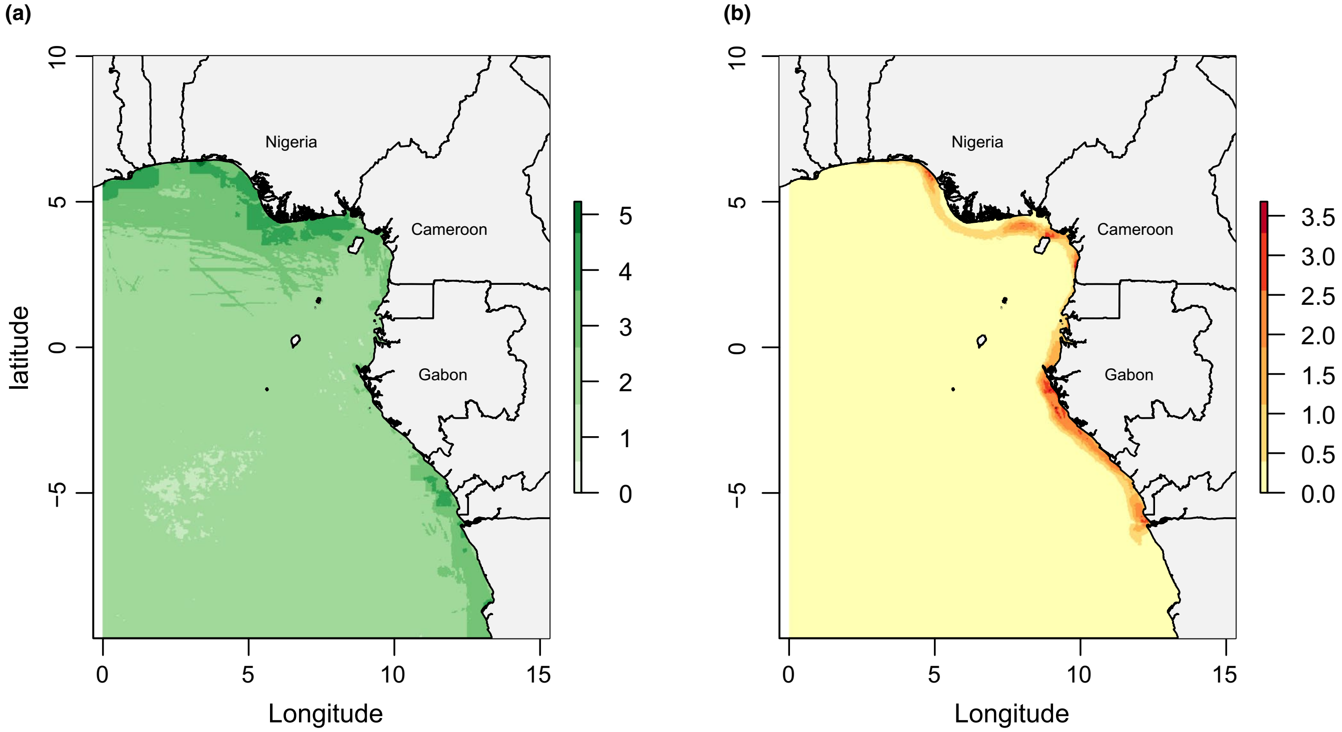


FIGURE 4 Distribution of cumulative utilization and impact (CUI). Shown for all anthropogenic activities considered, including ocean acidification anomalies, fishing, pollution, oil rigs, shipping, sea-level rise (SLR) and sea surface temperature (SST) anomalies are (a) the summation of all of each anthropogenic activity's intensity score multiplied by its impact score of each activity on humpback whales (darker green colours represent higher levels of threat and presumed impacts) and (b) the CUI distribution, which combines the breeding habitat suitability for humpback whales and cumulative impacts (warmer colours represent high use by breeding humpback whales and a higher degree of human impact). Dashed lines represent the outer boundary of the continental shelf, and dotted lines represent exclusive economic zone (EEZ) boundaries

of Gabon and southern portion of Cameroon. Moderate suitability occurred in the northern Gulf of Guinea between Nigeria and Equatorial Guinea (Bioko Island), Congo and Angola (Figure 2a). Northern areas highlight potential key areas where little empirical data exist for humpback whale BSB.

While this study was limited to 30 bootstrapped models due to available processing power, the environmental characteristics are common to those observed for other humpback whale breeding areas. Areas of high habitat suitability identified by binary maps show that breeding areas likely occur in waters with mean SSH value of approximately −0.04 m, mean depth of approximately 27.3 m, SST of approximately 24.5°C and a mean distance from shore of approximately 68.2 km (Figure 2b). Previous studies have observed humpback whales in warm waters between 21°C and 28°C, including Silver Bank (West Indies), Antongil Bay (Madagascar), the Great Barrier Reef, and Hawai'i (Ersts & Rosenbaum, 2003; Johnston, Chapla, Williams, & Mattila, 2007; Rasmussen et al., 2007; Smith et al., 2012; Whitehead & Moore, 1982). A majority of humpbacks were observed in shallow waters less than 30 m in depth in Antongil Bay, between 15 and 60 m in the West Indies, 30–58 m in the Great Barrier Reef, and between 40 and 80 m in Hawai'i (Ersts & Rosenbaum, 2003; Pack et al., 2017; Smith et al., 2012; Whitehead & Moore, 1982). Depth may have an impact on different breeding behaviours, such as needing deeper waters for mating displays or shallower waters for young calves (Ersts & Rosenbaum, 2003). We posit that warmer waters may provide some thermoregulatory benefits during the winter breeding season, when whales do not feed.

This study also examines several environmental predictors that are less well-studied, but which may be important for predicting the habitat suitability for breeding humpback whales. These include seafloor slope, wind speed and SSH. While slope contributed less than 1% to the model, wind speed and SSH contributed significantly more (wind speed contributed approximately 10% to the final distribution model, and SSH contributed approximately 32%) (Figure 3). There is a lack of knowledge on how wind speed and SSH may influence breeding habitat suitability, though both, in addition to bathymetry, may act as a proxy for sea state. Some studies have suggested that calmer conditions allow calves to remain close to their mothers with less effort and may assist with calf suckling and lower energy expenditure (Martins et al., 2001; Oviedo & Solís, 2008; Whitehead & Moore, 1982). Changes in typical SSH and wind speed may affect ecosystems that provide shallow and calm waters for breeding humpbacks (Bettridge et al., 2015). Thus, this study explores relatively novel environmental parameters for assessing suitable breeding habitats for humpback whales. Further investigation should examine differences in SSH, wind speed and humpback whale breeding behaviour occurrence over time.

4.2 | Distribution of suitable breeding habitat

While empirical sighting data from the northern Gulf of Guinea are lacking, this study used occurrence data from relatively data-rich neighbouring areas to identify potential suitable breeding habitats in the northern Gulf of Guinea. However, humpback whale sightings, strandings and song have been recorded as far north as Senegal and as far west as the Cape Verde Islands (Bamy et al., 2010; Hazevoet, Gravanita, Suárez, & Wenzel, 2011; Ryan, Romagosa, Boisseau, Moscrop, & McLanaghan, 2018; Van Waerebeek, Ofori-Danson, & Debrah, 2009). Bamy et al. (2010) suggest that the northernmost extent of humpback whale occurrence includes Sierra Leone and Liberia. While extrapolating stranding locations to actual habitat requires caution due to currents and wind, sightings and song (acoustic recorders may have limited distance from which they can detect a singing individual) provide evidence that humpback whales have been observed further north. This discrepancy between model-predicted breeding habitat and field observations may be due to differences in use of the area between concentrations of breeding animals and movements of individuals, the latter of which were excluded from this study. For example, Rosenbaum et al. (2014) tracked humpback whale movements off Ghana, but satellite tracks were classified as transiting behaviour. This highlights the need for further research and dedicated survey effort in those areas. Additionally, areas further northwest of the Gulf of Guinea are located outside the environmental envelope of our study area (the Guinea Current LME), and further analyses will be needed to determine model transferability (Lauria, Power, Lordan, Weetman, & Johnson, 2015; Mannocci et al., 2018).

This widespread distribution of potential suitable breeding habitat along the coast of central West Africa may be due to the “floating lek” mating system of humpback whales. Competitive groups are generally mobile, and there is likely a wide distribution of animals on the breeding ground as a result of factors such as the distribution of singing males and lack of predators (Clapham, 1996). Females are not restricted by males (unlike some species of pinniped which form harems) and thus can travel greater distances to find a mate or calmer waters. Likewise, males can be widely distributed in breeding areas due to mobile competitive groups, aggressive competitive behaviour or accompaniment of a mother–calf pair. At this time, data are limited for distinct breeding behaviours (e.g. competitive groups and mother–calf pairs), though with future data collection, it would be possible to investigate the differences in distribution of mating versus nursing/weaning behaviours. However, the wide distribution of predicted breeding habitat should be taken into consideration when managing these areas.

4.3 | Breeding areas of BSB1 and BSB2

Previous genetic studies indicate that the waters of Gabon and Congo are a breeding area for BSB1. There is a lack of knowledge on whether whales breeding in the northern Gulf of Guinea are distinct from BSB1 or whether that area is an extension of the same breeding region (Barendse et al., 2010; Best, 2011; Pomilla & Rosenbaum, 2005; Rosenbaum et al., 2009). While the feeding areas and migratory corridors for BSB2 include the west coast of South Africa and Namibia, the breeding areas for BSB2 remain unknown (Barendse et al., 2013; Elwen et al., 2014; Findlay et al., 2017). Satellite tracks of humpback whale females, calves and males moving into areas north of the Gulf of Guinea late in the breeding season (when whales are expected to travel south to their feeding areas) suggest these individuals may still be migrating to more northern breeding areas off of Nigeria and Ghana (Rosenbaum et al., 2014). This indicated potential breeding areas for BSB2 north of Gabon and may include the waters of Nigeria, Benin, Togo, Ghana and even countries as far north as Guinea, Guinea-Bissau and The Gambia (Van Waerebeek et al., 2013, 2001). However, Best (2011) highlighted the lack of genetic data from the northern Gulf of Guinea in helping delineate distinct breeding grounds between BSB1 and BSB2, and the apparent lack of interest in whaling further north of Gabon, suggesting a lack of mother–calf pairs further north (as mother–calf pairs were more vulnerable and attracted whalers). Additional information is needed to further delineate habitat use by different life history stages within the region.

A more directed focus on data collection for mother–calf pairs would also be useful given the particular vulnerability of those groups.

Occurrence data for the model are largely obtained from waters of Gabon and use data from breeding-specific behaviour records, perhaps explaining the spatial distribution of the highest habitat suitability values (Figures 1 and 2a). However, the model predicted suitable breeding habitat in waters north of Gabon, highlighting the utility of SDMs to inform distribution and habitat use. In conjunction with the widespread distribution of potentially suitable breeding habitats along the west coast of Africa, results appear to suggest that the breeding region of Gabon and Congo extends further north than previously assumed. Relatively fewer occurrence points were located around Equatorial Guinea (Bioko Island), and all were derived from satellite telemetry data. Additionally, genetic studies of whales sampled in the BSB2 region (west South Africa) indicated that this group of whales may represent a mixed stock comprising individuals from BSB1 and the substocks of Breeding Stock C (located on the east coast of Africa and Madagascar) (Kershaw et al., 2017; Rosenbaum et al., 2009). This supports the hypothesis that different populations may preferentially use different areas within an extended breeding region (Rosenbaum et al., 2014).

A finer-scale analysis of the spatial distributions of both substocks, integrated with further population genetic studies, is needed to further delineate breeding areas for BSB1 and BSB2. This kind of interdisciplinary approach will enhance the understanding of the potential differences in environmental space of Gabon's coastal waters and waters further north in the Gulf of Guinea experienced by these two substocks, as well as potential environmental influences on their population substructure.

4.4 | Overlap with cumulative anthropogenic activities

The CUI analysis is significant in that it is a quantitative and spatially explicit measure of anthropogenic impacts on a specific species. The CUI analysis also highlights the utility of SDMs because it incorporates the degree of habitat suitability with the degree of impact (versus a binary presence–absence), providing a more robust analysis on the potential areas of high risk to important breeding areas in the region. Combining species distributions, anthropogenic impacts and humpback whale-specific impacts contributes to the understanding of areas of spatial overlap of whales and human activities. This can, in turn, be used to inform conservation and risk management in the region. Highest impact values occurred off the coast of Congo, Nigeria, and countries further north including Togo and Ghana (Figure 4a). Identified areas of high CUI values and potential high risk occur within EEZs of Gabon, Nigeria (Akwa Ibom), Equatorial Guinea (Bioko Island), and Cameroon (Figure 4b). These also consist of high habitat suitability as identified by the binary thresholds. Thus, conservation and management efforts for this population of humpback whales should prioritize these areas to mitigate impacts from anthropogenic activities.

Areas of overlap between humpback whale breeding habitat and cumulative anthropogenic impacts are simultaneously affected by multiple anthropogenic activities. Shipping (strikes and associated noise), entanglement in fishing gear, and oil platforms (and operations associated with hydrocarbon industry activities) are of greatest concern to humpback whales. These activities are known to impact humpback whales either directly or indirectly through changes in prey availability and distribution, decrease in fitness and/or decreases in habitat quality and area, and even risk of mortality (Bettridge et al., 2015; Bezamat et al., 2015; Blair et al., 2016; Brierley et al., 2002; Cerchio, Strindberg, Collins, Bennett, & Rosenbaum, 2014; Dunlop et al., 2016; Findlay et al., 2006; Hall et al., 2018; Kawaguchi et al., 2011; Moore, 2009; Richardson, Greene, Malme, & Thompson, 1995).

Throughout the Gulf of Guinea, increasing shipping, noise, port traffic and port development increases the threat of vessel strikes and the level of noise, while increasing commercial fisheries increases the threat of entanglement in fishing gear (Chidi Ibe, 1996; Van Waerebeek et al., 2007). Additionally, unregulated fishing by foreign fleets has increased and the prevalence of vessel strikes likely occurs more frequently than acknowledged (Brashares et al., 2004; Van Waerebeek et al., 2007). Unregulated fishing and potential entanglement from active or derelict fishing gear are not included in the CUI analysis completed here (due to lack of data), and thus, areas of overlap identified by the CUI analysis may only represent the minimum impact from fishing. The development of maritime infrastructure and the promotion and development of commercial shipping in the region are increasing and could lead to an increase in humpback whale entanglement and vessel strikes. While vessel strikes and entanglement have not been formally studied in the region and were not known to significantly impact whale populations overall in the past (compared to commercial whaling, for example), current increasing trends suggest the threat is growing and may have more severe consequences in the future. Links between these stressors and increased mortality have been reported in other regions, including the unusual mortality event off the Atlantic coast of the United States, where a three- to four-fold increase in humpback whale deaths, a majority of which have been attributed to vessel strikes and entanglement, have been recorded since 2016.[1]

Oil platforms, used as a proxy for presence of hydrocarbon industry activity, were identified as the most influential anthropogenic threat in the overall CUI, indicating that hydrocarbon development may be of most risk to humpbacks in this region. The presence of industrial development, namely oil and gas exploration and production, is relatively high in these areas and is a large source of revenue for many countries in the region (Ite, Ibok, Ite, & Petters, 2013; NIMASA, 2018; Udie, Bhattacharyya, & Ozawa-Meida, 2018; ejatlas.org). Tagged humpbacks travelled through areas of oil platforms off the coast of Gabon, where the model also identified

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[1] https://www.fisheries.noaa.gov/national/marine-life-distress/2016-2019-humpback-whale-unusual-mortality-event-along-atlantic-coast

high breeding habitat suitability and high CUI scores (Figure 4b) (Rosenbaum et al., 2014). Though areas around Equatorial Guinea (Bioko Island) had moderate suitability, CUI analysis identified high CUI scores for that area (Figures 2a and 4b). High CUI areas off Nigeria, Equatorial Guinea (Bioko Island), and Gabon overlap with oil platforms identified by Halpern et al. (2015a), highlighting the importance of analysing species distributions in conjunction with cumulative impacts. Although it is unclear whether the presence of an oil platform has any particular direct consequences for humpbacks; oil platforms, as a proxy for hydrocarbon industry activities, likely involve other related anthropogenic stressors that include shipping, noise pollution from vessels and seismic surveying, and ocean-based pollutants. These have the potential to adversely affect whales in the region and surrounding waters by disrupting important behaviours, masking communication and restricting the quality of habitat (Bettridge et al., 2015; Cerchio et al., 2014; Findlay et al., 2006; Van Waerebeek et al., 2007).

Not only are the aforementioned threats and associated impacts to whales expected to increase in this region, but the cumulative threats modelled here likely only illustrate a portion of existing threats. Multiple unquantified potential impacts such as noise, biotoxins and plastic pollution in the region are unaccounted for due to lack of data and knowledge (Bettridge et al., 2015; Fossi et al., 2012; Germanov, Marshall, Bejder, Possi, & Loneragan, 2018). Also, anthropogenic impacts likely act additively and synergistically across space–time, which is difficult to assess, and are likely to be compounded over the lifetime of the animal due to their seasonal migratory behaviour and breeding site fidelity (Crain, Kroeker, & Halpern, 2008; Maxwell et al., 2013). Additionally, anthropogenic activities may impact individuals differently (a young calf may be more susceptible than a full-grown adult). Without detailed demographic information, it is difficult to draw substantial conclusions on individual-level impacts in this region. Thus, while this analysis better informs the distribution and intensity of impacts, it is likely only the minimum, and likely an underestimate, of the potential cumulative effect on humpback whales in this region.

4.5 | Conservation implications

As far as we know, this is the first study to integrate satellite telemetry, aerial survey and boat-based sighting data within a behaviour-specific distribution model for any marine mammal. While most SDM methods are conducted without taking into account the behaviour associated with occurrence records, applying SDMs to breeding-specific occurrence records provides deeper insight into how this species uses and selects breeding habitats and subsequently informs conservation policies and mitigation efforts, particularly in relatively data-poor regions such as the Gulf of Guinea and adjacent regions (Redfern et al., 2017). Furthermore, combining these types of models with the CUI analysis provides spatially explicit information on the potential distribution of high-risk areas where both the presence of humpback whale breeding behaviour and prevalence of anthropogenic activities are high. This helps target mitigation measures in locations and times where the species may be most vulnerable.

Areas that clearly delineate high breeding habitat suitability and high CUI should be prioritized to mitigate potential impacts from oil and gas activities (e.g. seismic exploration and near-shore development) and vessel strikes. Mitigation measures for seismic survey activities include the implementation of “soft start” procedures, real-time detection (visual or acoustic) of individuals in proximity to the airguns and subsequent shutdown of activities when animals are present (Weir & Dolman, 2007). Vessel speed restrictions have been successful in reducing the impact of anthropogenic underwater noise and vessel strikes to large whales (Conn & Silber, 2013; Laist, Knowlton, & Pendleton, 2014; Vanderlaan & Taggart, 2007; Wiley, Thompson, Pace, & Levenson, 2011). Further, because humpback whales are migratory, seasonal restrictions on anthropogenic activities (e.g. rerouting of maritime traffic in important areas or cessation of seismic surveys) should be considered to reduce the potential impact on humpback whales in important habitats such as these breeding areas. It is also important to note that both vessels and seismic surveys generate anthropogenic underwater noise, which is inherently transboundary. Thus, noise sources that are offshore of certain areas may impact coastal areas where high breeding habitat suitability occurred.

This study demonstrates the benefits of data integration in an area with relatively little empirical data and which is relatively difficult to access for study. In the absence of comprehensive and systematic survey work, integration of data from disparate sources can be useful for obtaining insights into the distribution of a particular population. The possibility for behaviour-specific SDMs to better predict species distributions in relatively data-poor regions is highlighted in this study, though this should not detract from the need for more research in important breeding areas. Behaviour-specific SDMs combined with CUI analysis provides important information and support for management efforts, potentially leading to more effective marine spatial planning efforts and consideration of marine protected areas in the region, as well as decisions regarding areas of high risk to humpback whales.

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DATA AVAILABILITY STATEMENT

Data can be made available upon request. Satellite telemetry data were obtained from Rosenbaum et al., 2014, boat-based data from Collins et al., 2010, and aerial survey data from Strindberg et al., 2011.

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BIOSKETCH

Emily Chou is a research assistant at the Wildlife Conservation Society and is interested in factors affecting the distribution, movement, and habitat use of marine mammals, particularly in relation to climate change and anthropogenic impacts. She is particularly interested in the bridge between science and policy, and how her work can be used for effective conservation and management efforts. This study was conducted as a part of her Master's thesis.

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