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

Emily Chou1,2 | Francine Kershaw3 | Sara M. Maxwell4 | Tim Collins1 | Samantha Strindberg5 | Howard C. Rosenbaum1,2

1Wildlife Conservation Society, Ocean Giants Program, Bronx, NY, USA
2Ecology, Evolution and Environmental Biology Department, Columbia University, New York, NY, USA
3Natural Resources Defense Council, New York, NY, USA
4School of Interdisciplinary Arts and Sciences, University of Washington Bothell, Bothell, WA, USA
5Wildlife Conservation Society, Global Conservation Program, Bronx, NY, USA

Correspondence
Emily Chou, Wildlife Conservation Society, Ocean Giants Program, Bronx, NY, USA.
Email: echou@wcs.org

Funding information
Columbia University

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...
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 sub-structure 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

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).

**KEYWORDS**

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

| 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) |

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 (\(n = 199\)).
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.

### 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 TOP, OR ID, 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:

$$CUI_i = \sum_{j=1}^{n} D_j \times S_i \times u_{ij}$$

where $n$ is the number of anthropogenic activities, $D_j$ 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 $u_{ij}$ 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 km² 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). 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 \((\geq 0.8)\) along the coast of Gabon.

**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.
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 \((-27.3 \pm 42.6 \text{ m; mean } \pm \text{ standard deviation})\) and warm \((24.5 \pm 1.5^\circ \text{C})\) waters that are nearshore \((68.2 \pm 16.1 \text{ km})\). These areas of high breeding habitat suitability are also characterized by shallow slopes \((-0.2 \pm 0.3^\circ)\), low SSH \((-0.04 \pm 0.06 \text{ m})\) and relatively low wind speed \((5.9 \pm 1.3 \text{ m/s})\). Effect sizes were negligible for all environmental predictors between 0.2 and 0.4 thresholded areas, except for a small effect size \( (d = 0.2; 95\% \text{ CI: 0.18–0.23}) \) 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 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.
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,
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 Hawaii (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 sea-floor 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 humpback whales (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; Hazaveot, Gravanita, Suárez, & Wenzel, 2011; Ryan, Romagosa, Boisseau, Moscrop, & McLanaghan, 2018; Van Waerebeek, Ofori-Danson, & Debrah, 2009). Bamy et al. (2010) suggest that the northermost 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 fourfold 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

---

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 (Redfearn 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.

ACKNOWLEDGEMENTS

The authors would like to thank the National Parks Agency of Gabon and Professor Lee White. The satellite telemetry dataset was provided as part of a collaborative effort between the Wildlife Conservation Society and Oregon State University’s Marine Mammal Institute, and we wish to thank Bruce Mate, Mary Lou Mate, Barbara Lagerquist, and Tomas Follett for all their efforts. We would also like to thank Columbia University for providing institutional and financial support for this project. J.A. Drew provided useful comments on earlier drafts of the manuscript. We are grateful to P. McKenzie and E. Glass, both of whom provided invaluable technical support. This study has been conducted using E.U. Copernicus Marine Service Information.
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.

ORCID
Emily Chou https://orcid.org/0000-0002-7862-0934
Sara M. Maxwell https://orcid.org/0000-0002-4425-9378
Samantha Strindberg https://orcid.org/0000-0002-4634-8593

REFERENCES
Ainley, D. G., Jongsomjit, D., Ballard, G., Thiele, D., Fraser, W. R., & Tynan, C. T. (2012). Modelling the relationship of Antarctic minke whales to major ocean boundaries. Polar Biology, 35, 281–290.
Amante, C., & Eakins, B. W. (2009). ETOPO1 1 Arc-Minute Global Relief Model: Procedures, data sources and analysis. NOAA Technical Memorandum NESDIS NGDC-24. National Geophysical Data Center, NOAA.
Baker, C. S., & Herman, L. M. (1984). Aggressive behaviour between humpback whales (Megaptera novaeangliae) wintering in Hawaiian waters. Canadian Journal of Zoology, 62, 1922–1937.
Ballard, G., Jongsomjit, D., Veloz, S. D., & Ainley, D. G. (2012). Coexistence of mesopredators in an intact polar ocean ecosystem: The basis for defining a Ross Sea marine protected area. Biological Conservation, 156, 72–82. https://doi.org/10.1016/j.biocon.2011.11.017
Bamy, I. L., Van Waerebeek, K., Bah, S. S., Dia, M., Kaba, B., Keita, N., & Konate, S. (2010). Species occurrence of cetaceans in Guinea, including humpback whales with southern hemisphere seasonality. Marine Biodiversity Records, 3, e48. https://doi.org/10.1017/S1755267210000436
Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? Methods in Ecology and Evolution, 3, 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x
Barendse, J., Best, P. B., Carvalho, I., & Pomilla, C. (2013). Mother knows best: Occurrence and associations of resighted humpback whales suggest maternally derived fidelity to a Southern Hemisphere coastal feeding grounds. PLoS ONE, 8, e81238. https://doi.org/10.1371/journal.pone.0081238
Barendse, J., Best, P. B., Thornton, M., Pomilla, C., Carvalho, I., & Rosenbaum, H. C. (2010). Migration redefined? Seasonality, movements and group composition of humpback whales (Megaptera novaeangliae) off the west coast of South Africa. African Journal of Marine Science, 32, 1–22.
Becker, E. A., Forney, K. A., Foley, D. G., Smith, R. C., Moore, T. J., & Barlow, J. (2014). Predicting seasonal density patterns of California cetaceans based on habitat models. Endangered Species Research, 23, 1–22. https://doi.org/10.3354/esr00548
Best, P. B. (2011). Where is the breeding ground for humpback whales from Breeding Stock B2? Paper SC/63/SH17 presented to the Scientific Committee Meeting of the International Whaling Commission, June 2011, Tromsø, Norway, pp. 8.
Bettridge, S., Baker, C. S., Barlow, J., Clapham, P. J., Ford, M., Gouveia, D., …Wade, P. R. (2015). Status review of the humpback whale (Megaptera novaeangliae) under the Endangered Species Act. NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-540
Bezamat, C., Wedekin, L. L., & Simões-Lopes, P. C. (2015). Potential ship strikes and density of humpback whales in the Abrolhos Bank breeding ground, Brazil. Aquatic Conservation: Marine and Freshwater Ecosystems, 25, 712–725. https://doi.org/10.1002/aqc.2523
Blair, H. B., Merchant, N. D., Friedlaender, A. S., Wiley, D. N., & Parks, S. E. (2016). Evidence for ship noise impacts on humpback whale foraging behaviour. Biology Letters, 12, 20160005. https://doi.org/10.1098/rsbl.2016.0005
Brashares, J. S., Arceste, P., Sam, M. K., Coppolillo, P. B., Sinclair, A. R. E., & Balmford, A. (2004). Bushmeat hunting, wildlife declines, and fish supply in West Africa. Science, 306, 1180–1183. https://doi.org/10.1126/science.1102425
Breed, G. A., Jonsen, I. D., Myers, R. A., Don Bowen, W., & Leonard, M. L. (2009). Sex-specific, seasonal foraging tactics of adult grey seal (Halichoerus grypus) revealed by state-space analysis. Ecology, 90, 3209–3221.
Brierley, A. S., Fernandes, P. G., Brandon, M. A., Armstrong, F., Millard, N. W., McPhaul, S. D., …Griffiths, G. (2002). Antarctic krill under sea ice: Elevated abundance in a narrow band just south of ice edge. Science, 295, 1890–1892. https://doi.org/10.1126/science.1068574
Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D., & Thomas, L. (2001). Distance sampling: Estimating abundance of biological populations (2nd ed.) Oxford, UK: Oxford University Press.
Buckland, S. T., Rexstad, E. A., Marques, T. A., & Oedekoven, C. S. (2015). Distance sampling: Methods and applications. Methods in statistical ecology. Cham: Springer.
Burnham, K. P., & Anderson, D. R. (2004). Multimodel Inference: Understanding AIC & BIC in model selection. Sociological Methods and Research, 33, 261–304. https://doi.org/10.1177/0094124104268644
Carvalho, I., Loo, J., Collins, T., Barendse, J., Pomilla, C., Leslie, M. S., …Rosenbaum, H. C. (2014). Does temporal and spatial segregation explain the complex population structure of humpback whales on the coast of West Africa? Marine Biology, 161, 805–819. https://doi.org/10.1007/s00227-013-2379-1
Cerchio, S. (2003). Paternity, polygyny and alternative mating tactics in humpback whales (Megaptera novaeangliae). PhD dissertation. The University of Michigan, Michigan, USA.
Cerchio, S., Jacobsen, J. K., Cholewiak, D. M., Falcone, E. A., & Merriwether, D. A. (2005). Paternity in humpback whales, Megaptera novaeangliae: Assessing polygyny and skew in male reproductive success. Animal Behaviour, 70(2), 267–277. https://doi.org/10.1016/j.anbehav.2004.10.028
Cerchio, S., Strindberg, S., Collins, T., Bennett, C., & Rosenbaum, H. (2014). Seismic surveys negatively affect humpback whale singing activity off Northern Angola. PLoS ONE, 9, e86464. https://doi.org/10.1371/journal.pone.0086464
Chidi Ibe, A. (1996). The coastal zone and oceanic problems of Sub-Saharan Africa. In G. Benneh, W. B. Morgan, & J. I. Uitto (Eds.), Sustaining the future: Economic, social and environmental change in sub Saharan Africa. Tokyo, Japan: United Nations University Press.
Clapham, P. J. (1996). The social and reproductive biology of humpback whale: An ecological perspective. Mammal Review, 26, 27–49.
Clapham, P., & Baker, C. S. (2002). Modern whaling. In W. F. Perrin, B. Wursig, & J. G. M. Thewissen (Eds.), Encyclopedia of marine mammals (pp. 1328–1332). San Diego, CA: Academic Press.
Clapham, P. J., Palsbøll, P. J., Mattila, D. K., & Vasquez, O. (1992). Composition and dynamics of humpback whale competitive groups in the West Indies. Behaviour, 122, 182–194. https://doi.org/10.1163/156853992X00507
Collins, T., Cerchio, S., Pomilla, C., Loo, J., Carvalho, I., Ngouessono, S., & Rosenbaum, H. C. (2010). Estimates of abundance for humpback whales in Gabon between 2001 – 2006 using photographic and genetic data. Paper presented to the Scientific Committee Meeting of the International Whaling Commission, June 2010, Agadir, Morocco (unpublished). Paper SC/62/SH11.
Conn, P. B., & Silber, G. K. (2013). Vessel speed restrictions reduce risk of collision-related mortality for North Atlantic right whales. Ecosphere, 4, 43. https://doi.org/10.1890/ES13-00004.1
Craig, A. S., & Herman, L. M. (1997). Sex differences in site fidelity and migration of humpback whales (Megaptera novaeangliae) to the Hawaiian Islands. Canadian Journal of Zoology, 75, 1923–1933.
Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., ... Walbridge, S. (2015b). Spatial and temporal changes in cumulative human impacts on the world’s oceans. Nature Communications, 6, 7615. https://doi.org/10.1038/ncomms8615

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D’Agorosa, C., ... Watson, R. (2008). A global map of human impact on marine ecosystems. Science, 319, 948–952. https://doi.org/10.1126/science.1149345

Hazen, E. L., Palacios, D. M., Forney, K. A., Howell, E. A., Becker, E., Hoover, A. L., ... Bailey, H. (2017). WhaleWatch: A dynamic management tool for predicting blue whale density in the California Current. Journal of Applied Ecology, 54, 1415–1428. https://doi.org/10.1111/1365-2664.12820

Hazen, E. L., Scales, K. L., Maxwell, S. M., Briscoe, D. K., Welch, H., Bograd, S. J., ... Lewison, R. L. (2018). A dynamic ocean management tool to reduce bycatch and support sustainable fisheries. Science Advances, 4, eaar3001. https://doi.org/10.1126/sciadv.aar3001

Hazevoet, C. J., Gravanita, B., Suárez, P. L., & Wenzel, F. W. (2011). Seasonality of humpback whale Megaptera novaeangliae (Borowski, 1781) records in Cape Verde seas: Evidence for the occurrence of stocks from both hemispheres? Zoologia Caboverdiana, 2, 25–29.

Herman, L. M., & Tavolga, W. N. (1980). The communication systems of cetaceans. In L. M. Herman (Ed.), Cetacean behaviour: Mechanisms and functions (pp. 149–209). Malabar, FL: Krieger Publishing Co.

Howell, E. A., Kobayashi, D. R., Parker, D. M., Balazs, G. H., & Polovina, J. J. (2008). TurtleWatch: A tool to aid in the bycatch reduction of loggerhead turtles Caretta caretta in the Hawaii-based pelagic longline fishery. Endangered Species Research, 5, 267–278. https://doi.org/10.3354/esr00096

Hoyt, E. (2005). Marine protected areas for whales, dolphins and porpoises. London, UK: Earthscan.

Ilyina, T., Zeebe, R. E., & Brewer, P. G. (2010). Future Ocean increasingly transparent to low-frequency sound owing to carbon dioxide emissions. Nature Geoscience, 3, 18–22.

Ingram, S. N., & Rogan, E. (2002). Identifying critical areas and habitat preferences of bottlenose dolphins Tursiops truncatus. Marine Ecology Progress Series, 244, 247–255.

International Whaling Commission (IWC) (2007). Annex H: Report of the sub-committee on other Southern Hemisphere Whale Stocks. Journal of Cetacean Research and Management, 9, 188–209.

International Whaling Commission (IWC) (2011a). Annex H: Report of the sub-committee on other Southern Hemisphere Whale Stocks. Journal of Cetacean Research and Management, 12, 203–226.

International Whaling Commission (IWC) (2011b). Final report on the assessment of the Southern Hemisphere humpback whale Breeding Stock B. Tromso, Norway: IWC. Paper SC/63/Rep6.

Ite, A. E., Ibok, U. J., Ite, M. U., & Petters, S. W. (2013). Petroleum exploitation and functions. Tokyo: Kyoritsu Publishing Co.

Johnston, D. W., Chapla, M. E., Williams, L. E., & Mattila, D. K. (2007). Annex H: Report of the sub-committee on other Southern Hemisphere Whale Stocks. International Whaling Commission (IWC). Tromsø, Norway: IWC. Paper SC/63/Rep6.

Jonsen, I. D., Myers, R., & Mills-Flemming, J. (2003). Meta-analysis of animal movement using state-space models. Ecology, 84, 2274–2289. https://doi.org/10.1890/02-0670

Jonsen, I. D., Mills-Flemming, J., & Myers, R. (2005). Robust state-space modelling of animal movement data. Ecology, 86, 2874–2880.

Jonsen, I. D., Myers, R., & Mills-Flemming, J. (2003). Meta-analysis of animal movement using state-space models. Ecology, 85, 2035–2036. https://doi.org/10.1890/02-0670

Kawaguchi, S. O., Kurihara, H., King, R., Hale, L., Berli, T., Robinson, J. P., ... Ishimatsu, A. (2011). Will krill fare well under Southern Ocean acidification? Biology Letters, 7, 288–291. https://doi.org/10.1098/ rbl.2010.0777

Kershaw, F., Carvalho, I., Loo, J., Pomilla, C., Best, P. B., Findlay, K. P., ... Rosenbaum, H. C. (2017). Multiple processes drive genetic structure
of humpback whale (*Megaptera novaeangliae*) populations across spatial scales. *Molecular Ecology*, 26, 977–994.

Laist, D. W., Knowlton, A. R., Mead, J. G., Collet, A. S., & Pedesta, M. (2001). Collisions between ships and whales. *Marine Mammal Science*, 17, 35–75. https://doi.org/10.1111/j.1748-7692.2001.tb00980.x

Laist, D. W., Knowlton, A. R., & Pendleton, D. (2014). Effectiveness of mandatory vessel speed limits for protecting North Atlantic right whales. *Endangered Species Research*, 23, 133–147. https://doi.org/10.3354/esr00586

Lauria, V., Power, A. M., Lordan, C., Weetman, A., & Johnson, M. P. (2015). Spatial transferability of habitat suitability models of *Nephrrops norvegicus* among fished areas in the Northeast Atlantic: Sufficiently stable for marine resource conservation? *PLoS ONE*, 10, e0117006. https://doi.org/10.1371/journal.pone.0117006

Mackintosh, N. A. (1942). The southern stocks of whalebone whales. *Discovery Reports*, 22, 197–300.

Mannocci, L., Roberts, J. J., Halpin, P. N., Authier, M., Boisseau, O., Brada, M. N., ... Vella, J. (2018). Assessing cetacean surveys throughout the Mediterranean Sea: A gap analysis in environmental space. *Scientific Reports*, 8, 3126. https://doi.org/10.1038/s41598-018-19842-9

Martin, C. S., Tolley, M. J., Farmer, E., Mcowen, C. J., Geffert, J. L., Scharlemann, J., ... Tittensor, D. P. (2015). A global map to aid the identification and screening of critical habitat for marine industries. *Marine Policy*, 53, 45–53. https://doi.org/10.1016/j.marpol.2014.11.007

Martins, C. C. A., Morete, M. E., Engel, M. H., Freitas, A. C., Secchi, E. R., & Kinas, P. G. (2001). Aspects of habitat use patterns of humpback whales in the Abrolhos Bank, Brazil, breeding ground. *Memoirs of the Queensland Museum*, 47, 83–90.

Maxwell, S. M., Hazen, E. L., Bograd, S. J., Halpern, B. S., Breed, G. A., Nickel, B., ... Costa, D. P. (2013). Cumulative human impacts on marine predators. *Nature Communications*, 4, 2688. https://doi.org/10.1038/ncomms3688

Moore, S. (2009). Climate change. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 238–241). San Diego, CA: Academic Press.

Muscarella, R., Galante, P. J., Soley-Guardia, M., Borja, R. A., Kass, J. M., Uriarte, M., & Anderson, R. P. (2014). ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for MAXENT ecological niche models. *Methods in Ecology and Evolution*, 5, 1198–1205.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858. https://doi.org/10.1038/35025051

Nezer, O., Bar-David, S., Gueta, T., & Carmel, Y. (2017). High-resolution species-distribution model based on systematic sampling and indirect observations. *Biodiversity and Conservation*, 26, 421–437. https://doi.org/10.1007/s10531-016-1251-2

Nigerian Maritime Administration & Safety Agency (NIMASA) (2018). *Nigeria's maritime industry forecast 2018–2019*. Retrieved from http://nimasa.gov.ng/pdfs/nigerian_maritime_industry_forecast.pdf.

Oviedo, L., & Solís, M. (2008). Underwater topography determines critical breeding habitat for humpback whales near Osa Peninsula, Costa Rica: Implications for marine protected areas. *International Journal of Tropical Biology*, 56, 591–602.

Pack, A. A., Herman, L. M., Craig, A. S., Spitz, S. S., Waterman, J. O., Herman, E. Y. K., ... Lowe, C. (2017). Habitat preferences by individual humpback whale mothers in the Hawaiian breeding grounds vary with age and size of their calves. *Animal Behaviour*, 133, 131–144.

Peng, G., Zhang, H.-M., Frank, H. P., Bidlot, J.-R., Higaki, M., Stevens, S., & Hankins, W. R. (2013). Evaluation of various surface wind products with OceanSITES buoy measurements. *Weather and Forecasting*, 28, 1281–1303. https://doi.org/10.1175/WAF-D-12-00086.1

Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., & Blair, M. E. (2017). Opening the black box: An open-source release of Maxent. *Ecography*, 40, 1–7. https://doi.org/10.1111/ecog.03049

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modelling of species geographic distributions. *Ecological Modelling*, 190, 231–259.

Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., & Ferrier, S. (2009). Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. *Ecological Applications*, 19, 181–197. https://doi.org/10.1890/07-2153.1

Pomilla, C., & Rosenbaum, H. C. (2005). Against the current: An interoceanic whale migration event. *Biologhy Letters*, 1, 476–479. https://doi.org/10.1098/rsbl.2005.0351

R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/.

Radosavljevic, A., & Anderson, R. P. (2014). Making better MAXENT models of species distributions: Complexity, overfitting and evaluation. *Journal of Biogeography*, 41, 629–643.

Rasmussen, K., Palacios, D. M., Calambokidis, J., Saborio, M. T., Dalla Rosa, L., Secchi, E. R., ... Stone, G. S. (2007). Southern Hemisphere humpback whales wintering off Central America: Insights from water temperature into the longest mammalian migration. *Biologhy Letters*, 3, 302–305. https://doi.org/10.1098/rsbl.2007.0067

Redfern, J. V., Ferguson, M. C., Becker, E. A., Hyrenbach, K. D., Good, C., Barlow, J., ... Werner, F. (2006). Techniques for cetacean-habitat modelling. *Marine Ecology Progress Series*, 310, 271–295.

Redfern, J. V., Moore, T. J., Fiedler, P. C., de Vos, A., Brownell, R. L., Forney, K. A., ... Ballance, L. T. (2017). Predicting cetacean distributions in data-poor marine ecosystems. *Diversity and Distributions*, 23, 394–408. https://doi.org/10.1111/ddi.12537

Richardson, W. J., Greene, C. R. Jr, Malme, C. I., & Thompson, D. H. (1995). *Marine Mammals and noise*. San Diego, CA: Academic Press.

Rocha, R. C., Clapham, P. J., & Ivashchenko, Y. V. (2014). Emptying the oceans: a summary of industrial whaling catches in the 20th century. *Marine Fisheries Review*, 76(4), 37–48.

Rosenbaum, H., & Collins, T. (2006). The ecology, population characteristics and conservation efforts for humpback whales (*Megaptera novaeangliae*) on their wintering grounds in the coastal waters of Gabon. *Bulletin of the Biological Society of Washington*, 12, 425–436.

Rosenbaum, H. C., Kershaw, F., Mendez, M., Pomilla, C., Leslie, M. S., Findlay, K. P., ... Baker, C. S. (2017). First circumglobal assessment of Southern Hemisphere humpback whale mitochondrial genetic variation and implications for management. *Endangered Species Research*, 32, 551–567.

Rosenbaum, H. C., Maxwell, S. M., Kershaw, F., & Mate, B. (2014). Long-range movement of humpback whales and their overlap with anthropogenic activity in the South Atlantic Ocean. *Conservation Biology*, 28, 604–615. https://doi.org/10.1111/cobi.12225

Rosenbaum, H. C., Pomilla, C., Mendez, M., Leslie, M. S., Best, P. B., Findlay, K. P., ... Kiszka, J. (2009). Population structure of humpback whales from their breeding grounds in the South Atlantic and Indian Oceans. *PLoS ONE*, 4, e7318. https://doi.org/10.1371/journal.pone.0007318

Ryan, C., Romagosa, M., Boisseau, O., Moscrop, A., & McLanaghan, R. (2018). Humpback whale (*Megaptera novaeangliae*) song detected at the Cape Verde Islands during boreal and austral spring. *Marine Mammal Science*, 35, 336–344.

Scates, K. L., Miller, P. I., Varo-Cruz, N., Hodgson, D. J., Hawkes, L. A., & Godley, B. J. (2015). Oceanic loggerhead turtles *Caretta caretta* associate with thermal fronts: Evidence from the Canary Current Large Marine Ecosystem. *Marine Ecology Progress Series*, 519, 195–207. https://doi.org/10.3354/meps11075
Sherman, K., & Hempel, G. (Eds.). (2009). The UNEP Large Marine Ecosystem report: A perspective on changing conditions in LMEs of the world’s regional seas. UNEP Regional Seas Reports and Studies No. 182.

Smith, J. N., Grantham, H. S., Gales, N., Double, M. C., Noad, M. J., & Paton, D. (2012). Identification of humpback whale breeding and calving habitat in the Great Barrier Reef. *Marine Ecology Progress Series*, 447, 259–272. https://doi.org/10.3354/meps09462

Stockwell, D. R. B., & Peterson, A. T. (2002). Effects of sample size on accuracy of species distribution models. *Ecological Modelling*, 148, 1-13. https://doi.org/10.1016/S0304-3800(01)00388-X

Strindberg, S., Erts, P. J., Collins, T., Sounguet, G.-P., & Rosenbaum, H. C. (2011). Line transect estimates of humpback whale abundance and distribution on their wintering grounds in the coast waters of Gabon. *Journal of Cetacean Research and Management (Special Issue)*, 3, 153–160.

Thiers, L., Louzao, M., Ridoux, V., Le Corre, M., Jaquemet, S., & Weimerskirch, H. (2014). Combining methods to describe important marine habitats for top predators: Application to identify biological hotspots in tropical waters. *PLoS ONE*, 9, e115057. https://doi.org/10.1371/journal.pone.0115057

Torchiano, M. (2019). effsize: Efficient effect size computation. R package version 0.7.6. Retrieved from https://CRAN.R-project.org/package=effsize.

Townsend, C. H. (1935). The distribution of certain whales as shown by logbook records of American whaleships. *Zoologica*, 19, 3–50.

Tyack, P. (1981). Interactions between singing Hawaiian humpback whales and conspecifics. *Behavioural Ecology and Sociobiology*, 8, 105–116.

Tyack, P., & Whitehead, H. (1982). Male competition in large groups of wintering humpback whales. *Behaviour*, 83, 132–154. https://doi.org/10.11163/156853982X00067

Udie, J., Bhattacharyya, S., & Ozawa-Meida, L. (2018). A conceptual framework for vulnerability assessment of climate change on critical oil and gas infrastructure in the Niger Delta. *Climate*, 6, 11.

Van Waerebeek, K., Baker, A. N., Félix, F., Gedamke, J., Iñiguez, M., Sanino, G. P., ... Wang, Y. (2007). Vessel collisions with small cetaceans worldwide and with large whales in the Southern Hemisphere, an initial assessment. *The Latin American Journal of Aquatic Mammals*, 6, 43–69. https://doi.org/10.5597/sajam00109

Van Waerebeek, K., Dijba, A., Krakstad, J.-O., Bilal, A. S. O., Bamy, I. L., Almeida, A., & Mbye, E. M. (2013). New evidence for a South Atlantic stock of humpback whales wintering on the Northwest African continental shelf. *African Zoology*, 48, 177–186. https://doi.org/10.3377/004.048.0120

Van Waerebeek, K., Ofori-Danson, P. K., & Debrah, J. (2009). The cetaceans of Ghana: A validated checklist. *West African Journal of Applied Ecology*, 15, 61–90.

Vanderlaan, A. S. M., & Tagart, C. T. (2007). Vessel collisions with whales: The probability of lethal injury based on vessel speed. *Marine Mammal Science*, 23, 144–156. https://doi.org/10.1111/j.1748-7692.2006.00098.x

Van Waerebeek, K., Tchibozo, S., Montcho, J., Nobime, G., Sohou, Z., Sehouhoue, P., & Dossou, C. (2001). The Bight of Benin, a North Atlantic breeding ground of a Southern Hemisphere humpback whale population, likely related to Gabon and Angola substocks. Paper presented to the Scientific Committee Meeting of the International Whaling Commission, July 2001, London. Paper SC/53/IA21.

Warren, D. L., & Seifert, S. N. (2011). Ecological niche modelling in Maxent: The importance of model complexity and the performance of model selection criteria. *Ecological Applications*, 21, 335–342.

Weir, C. R., & Dolman, S. J. (2007). Comparative review of the regional marine mammal mitigation guidelines implemented during industrial seismic surveys, and guidance towards a worldwide standard. *Journal of International Wildlife Law & Policy*, 10, 1–27. https://doi.org/10.1080/13880290701229838

Whitehead, H., & Moore, M. J. (1982). Distribution and movements of West Indian humpback whales in winter (*Megaptera novaeangliae*). *Canadian Journal of Zoology*, 60, 2203–2211. https://doi.org/10.1139/z82-282

Wiley, D. N., Thompson, M., Pace, R. M. III, & Levenson, J. (2011). Modelling speed restrictions to mitigate lethal collisions between ships and whales in the Stellwagen Bank National Marine Sanctuary, USA. *Biological Conservation*, 144, 2377–2381.

Yackulic, C. B., Chandler, R., Zipkin, E. F., Royle, J. A., Nichols, J. D., Campbell Grant, E. H., & Veran, S. (2013). Presence-only modelling using MAXENT: When can we trust the inferences? *Methods in Ecology and Evolution*, 4, 236–243. https://doi.org/10.1111/2041-210x.12004

Zhang, H.-M., Bates, J. J., & Reynolds, R. W. (2006). Assessment of composite global sampling: Sea surface wind speed. *Geophysical Research Letters*, 33, L17714. https://doi.org/10.1029/2006GL027086

Zhang, H.-M., Reynolds, R. W., & Bates, J. G. (2006). Blended and gridded high resolution global sea surface wind speed and climatology from multiple satellites: 1987–present. Presented at the 14th Conference on Satellite Meteorology and Oceanography, Atlanta, CA. American Meteorological Society. Paper 100004.

### BIOSKETCH

**Emily Chou**

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 part of her Master’s thesis.

Author contributions: H.C.R, F.K. and E.C conceived of the project; H.C.R., T.C. and S.S. collected the data; E.C., F.K., T.C. and S.M.M. analysed the data; and E.C. led the writing.

How to cite this article: Chou E, Kershaw F, Maxwell SM, Collins T, Strindberg S, Rosenbaum HC. Distribution of breeding humpback whale habitats and overlap with cumulative anthropogenic impacts in the Eastern Tropical Atlantic. *Divers Distrib*. 2020;26:549–564. [https://doi.org/10.1111/ddi.13033](https://doi.org/10.1111/ddi.13033)