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Predicting large-scale habitat suitability for cetaceans off Namibia using MinxEnt

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ABSTRACT: Knowledge of the occurrence and distribution of cetaceans is particularly important for conservation and management, but is still limited within Namibian waters. We collated 3211 cetacean records from the Namibian Exclusive Economic Zone (EEZ) for the period 2008 to 2016 and applied the principle of minimum cross entropy (MinxEnt) to predict habitat suitability. MinxEnt is a generalised form of maximum entropy modelling that allows incorporation of additional information such as sampling bias. The habitat suitability of 9 cetacean species or species groups (5 odontocete species, 2 mysticete species and 2 taxonomic groups: pilot whales *Globicephalus* spp. and balaenopterids Balaenopteridae spp.) were predicted per season, in relation to environmental variables likely to drive cetacean presence: sea surface temperature, chlorophyll *a* concentration, water depth or distance to shore, seabed slope and habitat complexity. The environmental variable which most frequently influenced habitat suitability was depth, which was the main environmental driver for bottlenose dolphin *Tursiops truncatus*, humpback *Megaptera novaeangliae* and southern right whales *Eubalaena australis*. Further, Heaviside's dolphin *Cephalorhynchus heavisidii* habitat was best predicted by distance to shore in all seasons, while common dolphin *Delphinus delphis* and the balaenopterid group habitats were best predicted by habitat complexity, and sperm whale *Physeter macrocephalus* habitats by chlorophyll *a* concentration. We identify distinct spatial patterns in habitat suitability for different species and provide baseline maps which can be used by managers of wildlife resources.

KEY WORDS: Cetacean · Dolphin · Habitat modelling · Habitat suitability · Marine protected area · Marine spatial planning · MaxEnt · Whale

1. INTRODUCTION

The southern African region is home to a high diversity of cetacean species (Pompa et al. 2011). It was previously the site of one of the world's largest whaling industries (Best 2007) and is extremely biologically productive (Shannon 1985, Shannon & Pillar 1986, Sakko 1998). At least 32 cetacean species are known, or are likely to occur, in Namibian waters, but the last study to systematically summarise the distribution of the cetacean fauna in this region was published in the early 1990s by Findlay

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et al. (1992), with some updating by Best (2007). Knowledge of cetacean presence in northern Namibian and offshore waters is particularly poor, and in this study we aim to address some of these shortcomings.

Namibia has 1570 km of coastline and is situated in the northern half of the Benguela upwelling ecosystem. The Benguela ecosystem is an eastern boundary current upwelling system, where wind regimes and oceanic currents strongly influence the temperature and primary productivity (Shannon 1985, Hutchings et al. 2009), as well as the diversity, abundance and distribution of marine species at all levels of the food web, including cetaceans (Findlay et al. 1992, Ansorge & Lutjeharms 2007). The area offshore of Lüderitz (26° 38′ S, 15° 09′ E), in southern Namibia, delineates a clear division between the northern and southern Benguela ecosystems (Ansorge & Lutjeharms 2007, Hutchings et al. 2009). This region has the strongest upwelling-favourable winds and lowest sea surface temperatures in the Benguela ecosystem (Hutchings et al. 2009), corresponding to a strong and permanent upwelling cell. The 2 sub-systems to the north and south possess dissimilar oceanographic and biological features (Shannon 1985, Hutchings et al. 2009), with the more productive northern Benguela dominated by small pelagic fish despite current stock depletion (Roux et al. 2013, Jarre et al. 2015).

Human impacts on the Benguela ecosystem date prior to 1850 with the depletion of southern right whale *Eubalaena australis* stocks by open boat whalers. The ecosystem underwent significant changes and degradation in the 20th century, due to both overfishing and environmental changes (Boyer et al. 2001, Kirkman et al. 2015). Small pelagic fish, such as sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*, have experienced a substantial biomass decline since the late 1960s (Roux et al. 2013, Jarre et al. 2015). In contrast, the biomass of horse mackerel *Trachurus capensis* and bearded goby *Sufflogobius bibarbatus* have increased (Jarre et al. 2015), and jellyfish have become prolific (Roux et al. 2013). Therefore, cetaceans are increasingly likely to suffer from resource competition with other top predators and commercial fisheries (Heymans et al. 2004). Additionally, cetaceans around southern Africa are threatened directly by various anthropogenic activities, including ship strikes, entanglement (Best et al. 2001, Meÿer et al. 2011) and seismic activities, such as oil and gas exploration (Rosenbaum & Collins 2006).

Detailed information on cetacean distributions and habitat preferences remains sparse in this region. The need for additional distribution and abundance data on humpback whales *Megaptera novaeangliae* in Namibian waters has been recognised by the International Whaling Commission (IWC) as a priority (IWC 2012). Heaviside's dolphin *Cephalorhynchus heavisidii* is endemic to the Benguela ecosystem (Best 2007), but little is known of its ecology in Namibian waters, and most research on this species originates from studies in South Africa (Elwen et al. 2006, 2009). Common species, such as the dusky dolphin *Lagenorhynchus obscurus* and pilot whales (*Globicephalus* spp.), are observed year-round in Namibian waters, although factors driving their spatial distribution remain poorly understood. Recent studies have improved our knowledge of the spatial distribution of the pygmy right whale *Caperea marginata* (Leeney et al. 2013), pygmy and dwarf sperm whales *Kogia breviceps* and *K. sima* (Elwen et al. 2013), southern right whales (Roux et al. 2015) and humpback whales (Elwen et al. 2014) in Namibian waters. However, no attempt has been made to understand the distribution of multiple cetacean species in relation to potential ecological drivers at broad spatial scales within the Namibian marine environment.

Here we investigated the spatial and seasonal distribution patterns of cetaceans in coastal and offshore Namibia, with a focus on the Namibian Islands Marine Protected Area (NIMPA). The NIMPA ranges roughly 200 km north and south of Lüderitz, and 30 km off-shore. The NIMPA was designed primarily with a focus on protecting breeding seabirds and is the largest marine protected area (MPA) in coastal continental Africa (Ludynia et al. 2012). We collated records from multiple sources, combining dedicated research sightings and opportunistic data from a range of platforms of opportunity. This approach was necessary, as research effort for offshore Namibia is low. As search effort was not systematically recorded, these records represent spatially biased 'presence-only' data, a limitation which requires specialised modelling procedures (Phillips et al. 2004, Pearce & Boyce 2006). Using a minimum cross entropy (MinxEnt) modelling approach (Merow et al. 2016), we aimed to gain a better understanding of the physical and oceanographic variables driving large-scale cetacean habitat preferences and to generate predictive distribution maps, which can be used to inform stakeholders and assist in management decisions, including those related to MPA design.

2. METHODS

2.1. Data acquisition and validation

Records of cetacean sightings were collected between 2008 and 2016, within the exclusive economic zone (EEZ) of Namibia. Data were acquired from 7 sources and associated platforms (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m619p149_supp.pdf). These include: dedicated shipboard cetacean surveys, small boat surveys in coastal waters, aerial surveys, records from observers on platforms of opportunity (Evans & Hammond 2004), including seismic surveys for hydrocarbons, and incidental sightings from a variety of sources, including citizen scientists (Newman et al. 2003, Dickinson et al. 2010). The minimum data requirements for each record to be considered for analysis included a date, location and species or taxonomic group identity. Additional descriptive data, including information on body size and shape, behaviour, group size and photographs, were often also provided and used in the data validation process (see next paragraph). As the data were collected from multiple sources, identification of sightings to species level was not always possible, and in some cases a broader taxonomic grouping was used.

Confidence in species identity was either assigned as part of the original record or post hoc, during a species validation process. During species validation, sightings were assessed for reliability on a sighting by sighting basis, using associated photographs and sighting descriptions to clarify species identity. The species identity for each sighting was assigned a ranking of definite, probable or possible. As experienced observers were involved during scientific data collection, the species identity and confidence (noted at the time of sighting in most cases) was considered high and the species designation mostly remained unchanged. However, there were cases where species identification and description appeared contradictory and, in such cases, the recording was downgraded to the more reliable broader taxonomic grouping. Records collected by untrained observers or 'citizen scientists' were scrutinised using the available evidence (sighting description, group size, behaviour, etc.), and uncertain records were downgraded to a lower taxonomic grouping or species confidence where necessary. Uncertain identifications were either re-classified under umbrella headings for which the confidence was then probable or definite, or removed from further analysis when confidence was only 'possible'. For example, a 'possible' sei whale *Balaenoptera borealis* would be re-classified as a 'probable' unidentified balaenopterid. We did not distinguish records of long-finned *Globicephala melas* and short-finned *G. macrorhynchus* pilot whales due to the difficulty of correctly differentiating these species at sea. All such sightings were reduced to pilot whale spp. (*Globicephalus* spp.); however, most of the pilot whales in this study are likely to be long-finned pilot whales, based on existing knowledge of their distribution (Best 2007). After validation, sightings records assigned with definite and probable species confirmation were used for further analysis.

2.2. Environmental variables

We used the following environmental variables to predict the habitat suitability of 9 cetacean species or species groups within Namibian waters: water depth (m), seabed slope (in degrees), habitat complexity (the rate of change of slope, in degrees of degrees), distance from shore (m), sea surface temperature (SST, °C) and chlorophyll *a* concentration (chl *a*, mg m^{-3}). The water depth layer was based on isobath data from the General Bathymetric Chart of the Oceans (GEBCO, www.gebco.net) and Natural Earth (www.naturalearthdata.com) and was created from a triangulated irregular network (TIN) dataset created using the data management TIN tool within the 3D Analyst extension of ArcGIS (ESRI, ArcMap 10.3.1). The depth layer was then converted to 'slope' and 'complexity' layers using the 'Slope' tool within the 'Spatial Analyst' extension (ESRI). The 'distance from shore' layer was created from an empty grid over the study area using the 'Create Fishnet' and 'Near' tools within the 'Data Management' and 'Analysis' extensions of ArcGIS, respectively (ESRI).

The remotely sensed oceanographic variables (SST and chl *a* concentration) were acquired from the Aqua-MODIS satellite from the NASA Giovanni portal (https://giovanni.gsfc.nasa.gov/giovanni/) at a resolution of 4 km. Monthly layers from February 2008 to August 2016 were downloaded to correspond to the sightings data collection period. Thereafter, monthly layers were used to create seasonal averages for each layer, which were used as our predictor variables. Southern hemisphere seasons were defined as summer (December to February), autumn (March to May), winter (June to August) and spring (September to November) following Jarre et al. (2015) and Tim et al. (2015). The seasonal layers were interpolated using the 'inverse distance weighted' interpolation tool within the 'Spatial Analyst' extension of ArcGIS

to fill missing values. All layers were created with the same cell size (4 km resolution) and spatial extent (latitude: 16.40–30.90° S, longitude: 8.20–17.10° W). The study area and an example of an environmental layer are presented in Fig. 1. Summary statistics of each predictor data layer are shown in Table S2 in the Supplement.

2.3. Habitat suitability modelling

The habitat of cetacean species was modelled using the minimum cross entropy principle, referred to as MinxEnt (Merow et al. 2016). MinxEnt is a generalisation of maximum entropy modelling, or MaxEnt

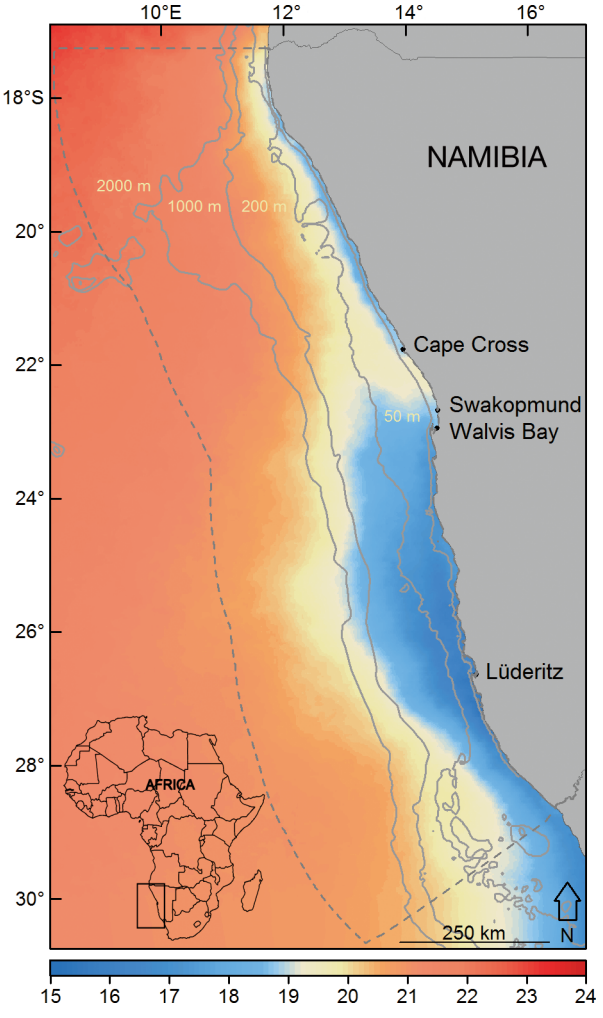

Fig. 1. Study area, showing the average summer sea surface temperature (SST, °C) calculated from satellite data generated between 2008 and 2016. The study area corresponds to the exclusive economic zone (EEZ) of Namibia and is represented by grey dashed lines. The 50, 200, 1000 and 2000 m isobaths are shown. Cold waters (blue) highlight the presence of the Benguela upwelling along the Namibian coastline

(Phillips et al. 2006). MaxEnt predicts the suitable habitat of a species by minimising the Kullback-Leibler divergence between probability densities for covariates across the entire study extent and for covariates at which the species is present (Elith et al. 2011). As such, MaxEnt relies on presence-only data and, at minimum, a large sample of covariate data across the geographical study area (termed background data) (Elith et al. 2011). The suitable habitat predicted across the landscape is not a true probability of occurrence and is referred to as the relative occurrence rate, which can be interpreted as the probability that a cell contains a presence (Merow et al. 2013). The MinxEnt approach can account for additional information on the distribution of a species, which can include sampling bias (termed nuisance effects) and additional biological information (termed informative offsets, e.g. a species' native range) (Merow et al. 2016). These offsets (also referred to as priors), in the case of sampling bias offsets, are themselves MaxEnt models and are incorporated into the MinxEnt model spatially in the form of a bias grid, which provides MaxEnt with a matrix of weights for all possible background points. Background points are then selected randomly, as per the default MaxEnt background selection strategy, but in relation to the 'bias' weight of each background cell (Merow et al. 2016).

Because the cetacean data combine different sources, and each source might have different sampling biases, we included a nuisance offset for sampling bias using the MinxEnt approach. MaxEnt does not account for sampling bias, but by incorporating nuisance offsets, MinxEnt is able to do so and has been shown to account for sampling bias and produce much better predictions of species distributions (Merow et al. 2016). We modelled spatial bias using occurrences of all species as our response variable (Merow et al. 2016) and 2 predictor variables: (1) a combined sampling intensity map and (2) the distance from start localities. We used 6 binary maps denoting surveyed (1) and un-surveyed (0) areas (Table S1) to create a combined sampling intensity map by adding the 7 survey maps together (Fig. 2). Since much of the data arose from single day or overnight trips from the 2 main harbours, Lüderitz and Walvis Bay (Fig. 2), there was a bias in effort towards these locations, so we included a continuous spatial dataset representing distance from the start localities of the 2 harbours (Table S1).

Collinearity among different variables can lead to a bias in the contribution of each variable and predictions in the model (Fielding & Bell 1997). Collinearity among environmental variables was tested

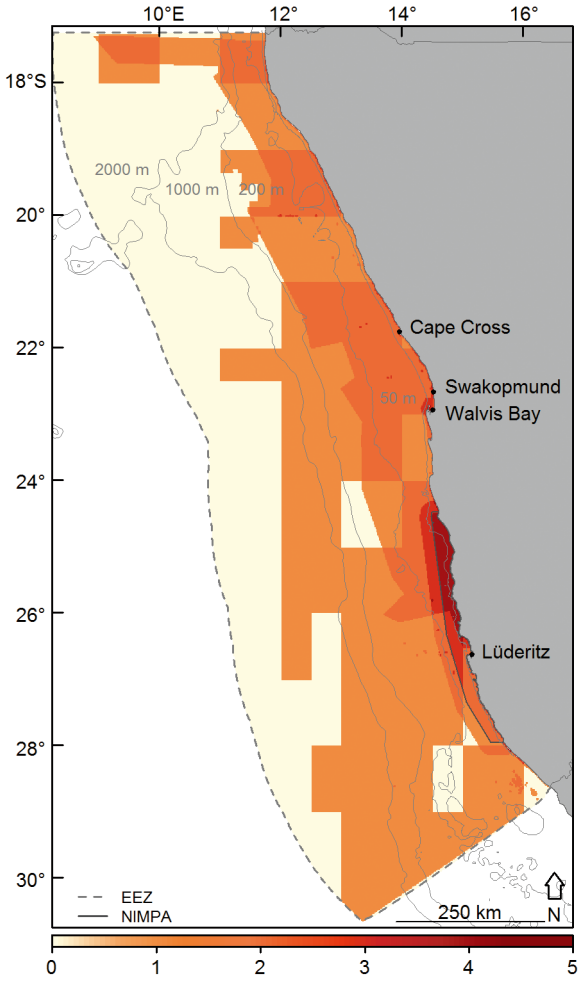

Fig. 2. Combined sampling intensity (see Section 2.3), showing the combined distribution of the 7 surveys. Warm colours (red) highlight the areas that were most sampled within the exclusive economic zone (EEZ), while the lightest colour (yellow) shows the areas not sampled. The 50, 200, 1000 and 2000 m isobaths are shown

using Pearson product-moment correlation tests of coefficients. A threshold value, for correlation coefficients >0.8, was used to identify correlated variables (Dormann et al. 2013). Distance from shore and water depth variables were highly correlated, thus a decision was made to retain the water depth variable and remove the distance from shore variable in 8 out of 9 species models. However, for Heaviside's dolphin models, distance from shore was retained as a predictor variable in place of water depth because distance to shore is assumed to be a better predictor of their behaviour (Elwen et al. 2006). The geographical study area was divided into cells following the resolution of the environmental variables. To avoid pseudo-replication in the occurrence model, each cell was assigned a presence and absence value of each species. Only species with 10 or more cells containing presence points per season were modelled. Model performance was evaluated using the area under the receiver operating characteristic curve (AUC), the sensitivity (proportion of correctly predicted presences), the specificity (proportion of correctly predicted absences) and the true skill statistic (TSS = sensitivity + specificity − 1). TSS evaluates the accuracy and performance of the predicted distribution model (Allouche et al. 2006). Models showing AUC values = 0.50 are representative of a random prediction, so models with AUC ≤ 0.70 were excluded from further analysis. Model evaluation was performed using a cross-validation approach of 100 bootstrap model runs, with a 70:30 training:testing random split of the data, and results were taken as the mean of the 100 runs. Variable importance was assessed using the permutation importance of the variables in the model, in addition to the marginal response curves. Permutation importance for each variable is calculated by randomly permuting the values of said environmental variable among its presence and background training points and measuring the change in AUC (as a percentage change from the AUC of the model using the original training point values) (Phillips et al. 2006). A large decrease in the AUC value indicates that model prediction depends strongly on that variable (Phillips et al. 2006). The marginal response curves show how each environmental variable affects the prediction using each variable in combination with the remaining variables at their mean value.

3. RESULTS

3.1. Overview

In total, 3211 sightings were recorded from February 2008 to August 2016, representing 21 cetacean species. After verification, records of 2 species were excluded, and 2 other species, Antarctic minke *Balaenoptera bonaerensis* and dwarf minke whales *B. acutorostrata*, were downgraded to 1 taxonomic group: 'minke whales', leaving data from 18 species available for analysis. The number of observations per species per season is shown in Table 1. The following 9 species or species groups had sufficient records to allow for modelling of their distributions within certain seasons: Heaviside's, dusky, common and bottlenose dolphins, and pilot, sperm, humpback, southern right and balaenopterid whales. The

Table 1. Number of records per species over the study period. The species with an asterisk are those modelled in this study

Common name	Scientific name	IUCN status	Number of sightings				
			Spring	Summer	Autumn	Winter	Total
Sei whale*	*Balaenoptera borealis*	Endangered	0	6	2	0	8
Antarctic minke whale*	*Balaenoptera bonaerensis*	Data Deficient	26	11	11	2	50
Dwarf minke whale*	*Balaenoptera acutorostrata*	Least Concern					
Bryde's whale*	*Balaenoptera brydei*	Data Deficient	0	1	0	0	1
Fin whale*	*Balaenoptera physalus*	Endangered	2	3	13	1	19
Pygmy right whale	*Caperea marginata*	Data Deficient	3	1	0	0	4
Heaviside's dolphin*	*Cephalorhynchus heavisidii*	Data Deficient	82	163	723	692	1660
Shortbeaked common dolphin*	*Delphinus delphis*	Least Concern	3	25	1	0	29
Gray whale	*Eschrichtius robustus*	Least Concern	0	0	1	3	4
Southern right whale*	*Eubalaena australis*	Least Concern	62	9	4	51	126
Pilot whales*	*Globicephala* spp.	Data Deficient	14	44	26	4	88
Risso's dolphin	*Grampus griseus*	Least Concern	0	1	0	0	1
Dusky dolphin*	*Lagenorhynchus obscurus*	Data Deficient	7	32	147	8	194
Southern right whale dolphin	*Lissodelphis peronii*	Data Deficient	0	3	2	0	5
Humpback whale*	*Megaptera novaeangliae*	Least Concern	75	40	56	225	396
Killer whale	*Orcinus orca*	Data Deficient	2	3	2	2	9
Sperm whale*	*Physeter macrocephalus*	Vulnerable	9	11	5	0	25
Striped dolphin	*Stenella coeruleoalba*	Data Deficient	0	3	0	0	3
Common bottlenose dolphin*	*Tursiops truncatus*	Least Concern	27	42	82	154	305
Balaenopterid whales*	*Balaenoptera* spp.		39	28	35	4	106
Unidentified baleonopterid*			11	7	9	1	28
Unidentified baleen whale			3	11	0	0	14
Unidentified beaked whale			0	1	0	0	1
Unidentified black fish			0	1	3	0	4
Unidentified cetacean			4	1	0	0	5
Unidentified dolphin			30	41	46	33	150
Unidentified large whale			3	2	5	20	30
Unidentified whale			10	15	23	4	52

balaenopterid group included sightings of 5 species or species groups: minke whale spp., Bryde's whale, fin whale, sei whale and unidentified balaenopterids. Sampling effort demonstrated clear temporal and spatial variability with high effort in areas within and adjacent to the northern region of the NIMPA and in Walvis Bay (Fig. 2). Moderately sampled areas included the southern region of the NIMPA and some zones between the coastline and the 200 m isobath. Offshore waters (>200 m depth) were either rarely sampled or not sampled at all (Fig. 2) because sampling effort occurred mostly from December to April when seismic surveys were conducted. The number of sightings for each month ranged from 112 to 487 (mean ± SD: 268 ± 142; Table 1). When pooled across seasons, the largest number of sightings occurred during winter (37%, n = 1200), followed by autumn (36%, n = 1161), summer (15%, n = 477) and spring (12%, n = 373) (Table 1).

3.2. Sampling bias models

The waters around Lüderitz, Swakopmund and Walvis Bay were the areas with the highest predicted sampling intensity in all seasons, followed by the coastal and shelf region (i.e. waters between the coastline and the 200 m isobath) between 22–24° S and 25.5–27.5° S (Fig. S1 in the Supplement). The AUC values of the sampling bias models were very high in winter (0.95) and spring (0.92), and fairly high in autumn (0.85) and summer (0.81), showing good accuracy of the models. Distance to launch site had the highest permutation importance in all seasons, with an importance of 100% in winter, 96.1% in summer, 94% in spring and 93% in autumn. Combined sampling intensity (i.e. sampling bias from fishing vessels, seismic vessels, research and aerial surveys) contributed to the sampling bias models with a permutation importance of 0% in winter, 3.9% in sum-

mer, 6% in spring and 7% in autumn. Thus, distance to launch site was the predictor influencing sampling bias the most.

3.3. Predicted large-scale habitat suitability for individual species

3.3.1. Heaviside's dolphin

Heaviside's dolphins were the most commonly sighted cetacean (52% of records, number of records [n] = 1660) in the database (Table 1). All sightings were recorded in water less than 125 m deep, with most sightings occurring from Walvis Bay to the southern Namibian border. AUC scores were very high in autumn (0.97), spring (0.96) and summer (0.94) and high in winter (0.85), showing good discrimination of Heaviside's dolphin habitat (Fig. 3A). The coastal waters of Namibia are suitable for this species throughout the year, especially the coastal waters between Swakopmund and Cape Cross and in the north during spring and summer and also the northern coastal areas during autumn (Fig. 3A). Distance from shore was the largest contributor to the model in spring, summer and autumn (Fig. S2 in the Supplement). In winter, distance to shore was the most important variable (48.4% permutation importance of the variable) followed by complexity (31.3%). Response curves, which characterise the relationship between habitat suitability and environmental variables, indicate that these dolphins were predicted to most likely occur in waters between the coast out to 500 m from shore in spring, summer and autumn. The winter model indicated broad habitat suitability for Heaviside's dolphins, with highest suitability at 200 km from shore.

3.3.2. Dusky dolphin

Small numbers of dusky dolphin sightings were recorded year-round (Table 1) but sample sizes were only large enough to run models for autumn (n = 147, presence cells [pc] = 94) and summer (n = 32, pc = 27). The majority of sightings were recorded in the Lüderitz area, within the NIMPA. Most of the Namibian EEZ is predicted to be a suitable habitat for dusky dolphins, especially the NIMPA and north of the EEZ in autumn (Fig. 3B). The autumn model predicted absence in waters deeper than 2000 m. AUC was high in autumn (0.85) and lower in summer (0.74). The deepest sighting of a dusky dolphin occurred at 2970 m depth and 90 km from shore. Depth was the most important predictor of dusky dolphin occurrence in summer (<250 m; 69.5%), followed by habitat complexity (30.3%). SST was the most important predictor in autumn (around 14°C; 45.4%; Fig. S3 in the Supplement), corresponding to the minimum temperature found in the study area in autumn (Table S2), followed by depth (1250 m, 38%).

3.3.3. Common dolphin

Common dolphins comprised 1% (n = 29) of the total dataset (Table 1), with most sightings recorded in offshore waters. Due to the small number of sightings, a habitat suitability model was only performed for the summer season (n = 25, pc = 24). The MinxEnt model had an intermediate AUC of 0.77, identifying offshore waters as suitable habitat for this species (Fig. 3C). The most important variables predicting habitat suitability for common dolphins in summer were low habitat complexity (49.3%) and chl *a* concentration below 0.5 mg m^{-3} (40.1%; Fig. S4 in the Supplement). This chl *a* concentration is around the minimum concentration found in Namibian waters in summer (Table S2).

3.3.4. Bottlenose dolphin

Bottlenose dolphin records comprised 9% (n = 305) of the dataset (Table 1). The majority of these records were from Walvis Bay, corresponding to high sampling effort by researchers and tour operators. MinxEnt models had high AUC values in winter (0.99), spring (0.97) and autumn (0.88) but a very low value in summer (0.46). Consequently, we excluded summer from further analysis. It appears that much of the coastal waters of Namibia provide a suitable habitat for bottlenose dolphins, notably northern Namibia in autumn and winter (Fig. 4A). The strongest predictor in all seasons was water depth, with a suggested preference for waters 0–100 m deep (Fig. S5 in the Supplement). The second most important variable was low complexity in spring, chl *a* concentration in autumn and SST in winter (Fig. S5). In winter, the model output showed high habitat suitability within the narrow temperature range of 17–18°C.

3.3.5. Pilot whales

Pilot whale records represented 3% (n = 88) of the dataset (Table 1). Sightings of pilot whales were principally recorded in offshore waters and were well

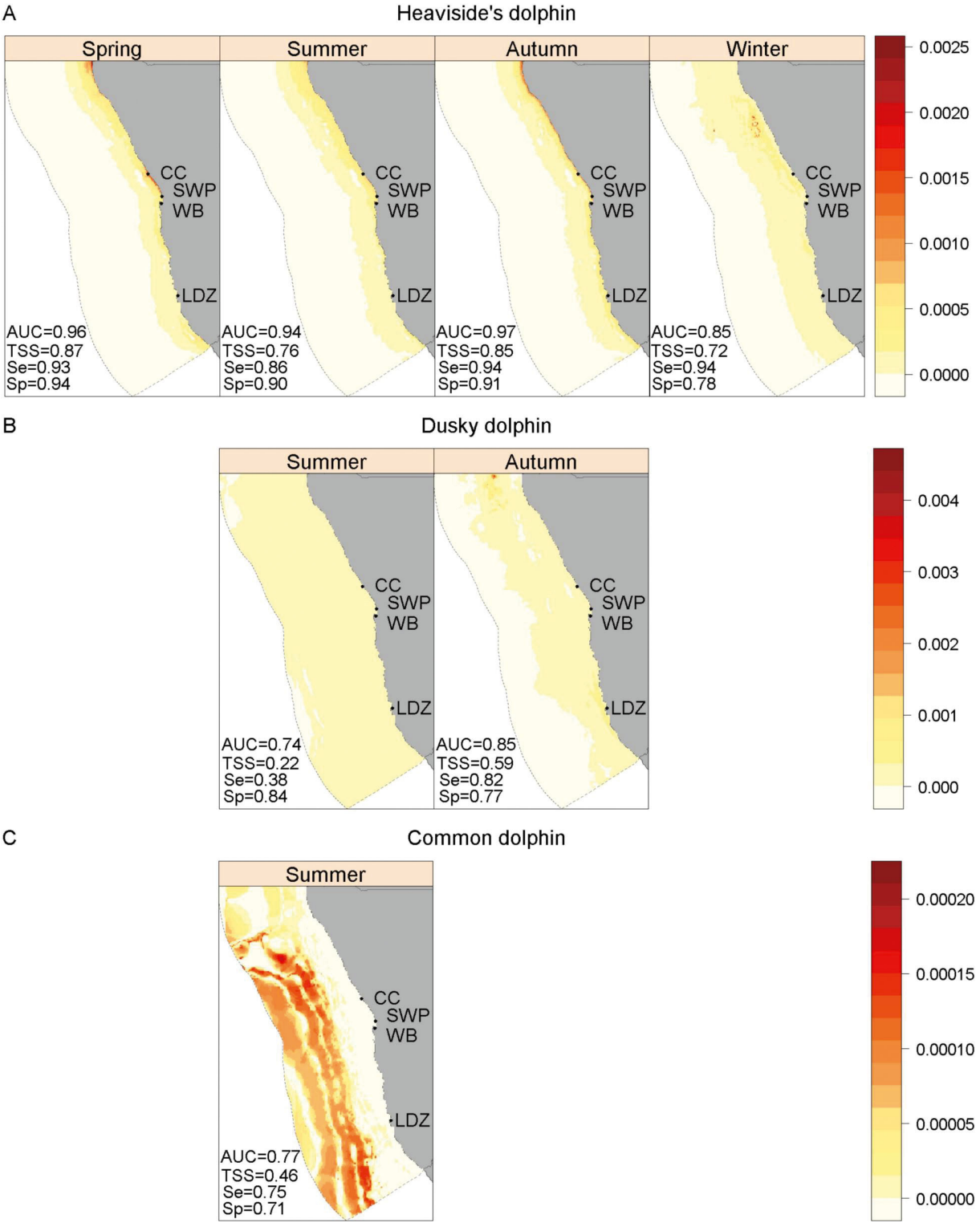

Fig. 3. MinxEnt seasonal predictions of habitat suitability for (A) Heaviside's dolphin *Cephalorhynchus heavisidii*, (B) dusky dolphin *Lagenorhynchus obscurus* and (C) common dolphin *Delphinus delphis* off Namibia. Habitat suitability is measured by the relative occurrence rate and is indicated on the maps from high to low (red to yellow). Model performance is indicated by the area under the receiver operating characteristic curve (AUC), the true skill statistic (TSS), sensitivity (Se) and specificity (Sp). Only maps for which sufficient observations were available and which had AUC values >0.70 are shown. Towns are represented by abbreviations; CC: Cape Cross, SWP: Swakopmund, WB: Walvis Bay, and LDZ: Lüderitz

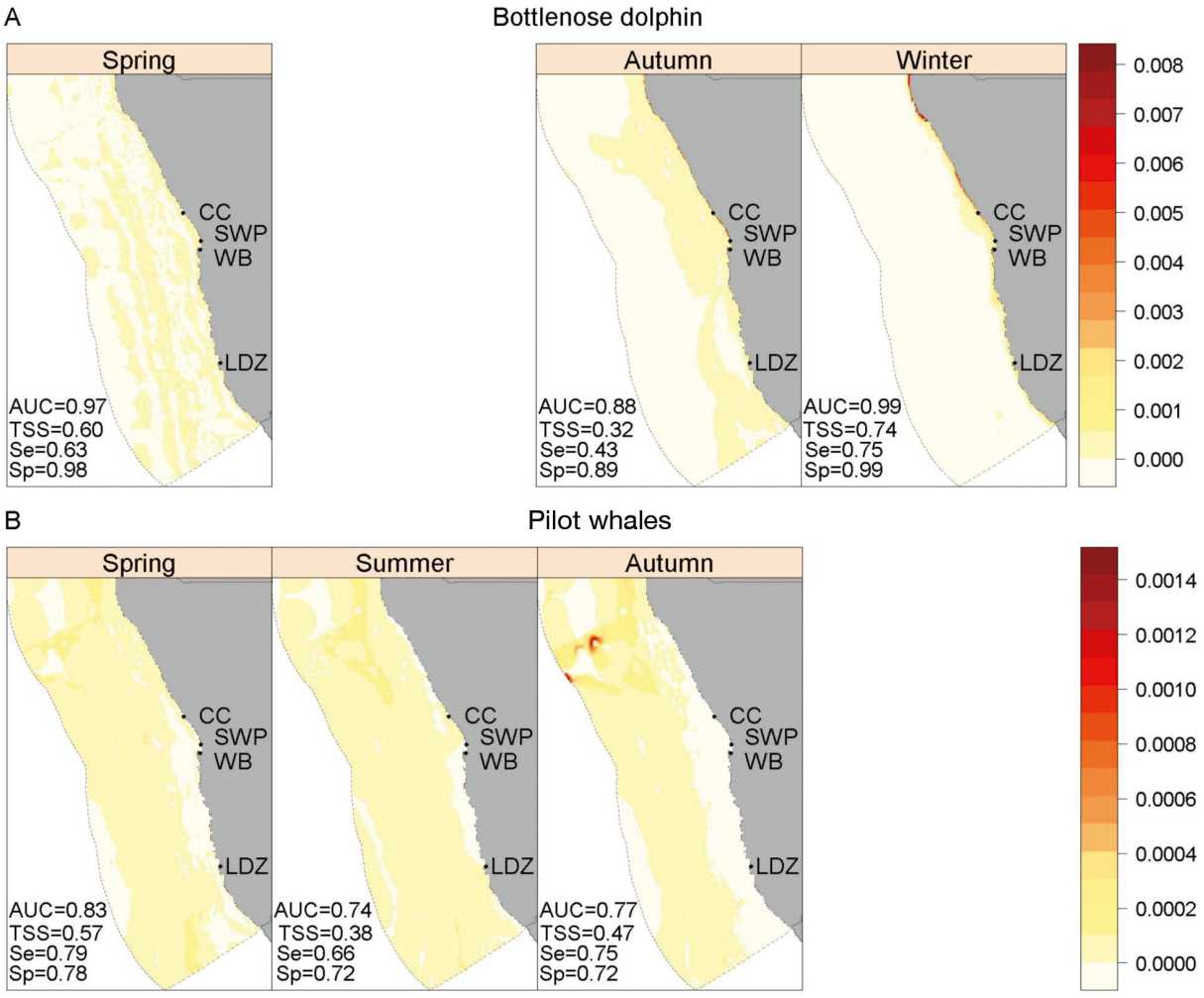

Fig. 4. MinxEnt seasonal predictions of habitat suitability for (A) bottlenose dolphin *Tursiops truncatus* and (B) pilot whales *Globicephalus* spp. off Namibia. Details and abbreviations as per Fig. 3

spread along the Namibian coastline. MinxEnt models had high AUC values in spring (0.83), autumn (0.77) and summer (0.74). Most of the EEZ provides suitable habitat for pilot whales in all seasons, with the highest habitat suitability in the north in all seasons and additionally in the south in spring (Fig. 4B). Slope was the most important predictor in spring (90°; 40%) and autumn (90°; 62%). Depth was the most important environmental variable in summer (500 m; 59.3%) (Fig. S6 in the Supplement). The second most important variable was depth in spring and autumn (highest suitability at low values) and slope in summer (90°; 19.5%; Fig. S6).

3.3.6. Sperm whale

Sperm whale sightings represented 1% (n = 25) of the total cetacean sightings (Table 1) and were only documented in offshore waters. The number of sightings was only sufficient to produce a habitat suitability prediction for summer (n = 11, pc = 11). The MinxEnt model had a high AUC value (0.82), and highly suitable areas were predicted in offshore waters with coastal waters not suitable for this species (Fig. 5A). The 2 most important variables in the model were chl *a* concentration (42.8%) and slope (37.2%) (Fig. S7 in the Supplement). Depth was the third most important predictor of sperm whale habitat preference (17.6%). Sperm whales were predicted to most likely occur in areas of low chl *a* concentrations (1 mg m^{-3}) and high slope values (90°) (Fig. S7).

3.3.7. Humpback whale

Humpback whales were observed in Namibian waters year-round, but with a seasonal peak coinciding

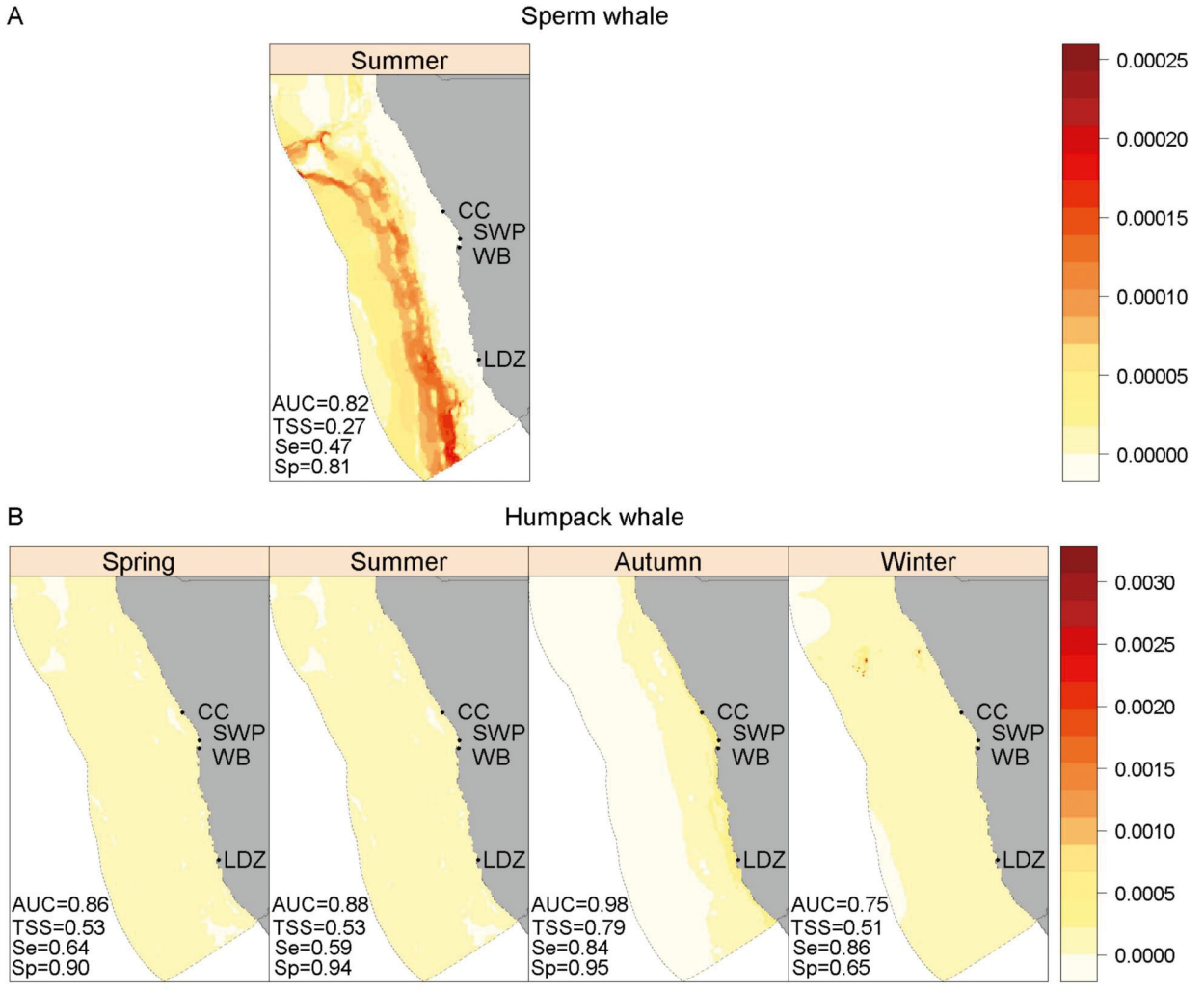

Fig. 5. MinxEnt seasonal predictions of habitat suitability for (A) sperm whale *Physeter macrocephalus* and (B) humpback whale *Megaptera novaeangliae* off Namibia. Details and abbreviations as per Fig. 3

with an annual migration between June and September. Humpback whales were the second most common cetacean found, comprising 12% (n = 396) of all records (Table 1). Humpback whales were more likely to be seen in the Lüderitz area during the summer season and were typically found in coastal waters between Walvis Bay and Lüderitz. MinxEnt modelling performed very well, with high AUC scores for autumn (0.98), summer (0.88) and spring (0.86), but not as well for winter (0.75) (Fig. 5B). The entire EEZ emerged as a suitable habitat, especially coastal waters in autumn, with depth being the most important variable in spring (<200 m; 75%), autumn (<500 m; 89.3%) and winter (2000 m; 73.4%) (Fig. 5B; Fig. S8 in the Supplement). SST emerged as the most important predictor in summer (highest suitability at low values; 43.2%). The second most important variable contributing to the model was low chl *a* in spring (highest suitability at high values; 12%) and in winter (highest suitability at high values; 21.5%), depth in summer (<200 m; 6.4%) and low SST in autumn (7.9%) (Fig. S8).

3.3.8. Southern right whale

Southern right whales comprised 4% (n = 126) of the records in the database (Table 1). Sightings of this species were mainly documented from the Walvis Bay and Lüderitz areas. The MinxEnt models had very high AUC values across all seasons (0.95–0.97). Coastal waters along the whole coastline of Namibia were identified as highly suitable habitat for southern right whales (Fig. 6A). Absence was predicted in waters deeper than 2000 m in spring. The model indicated that depth was the most important variable in

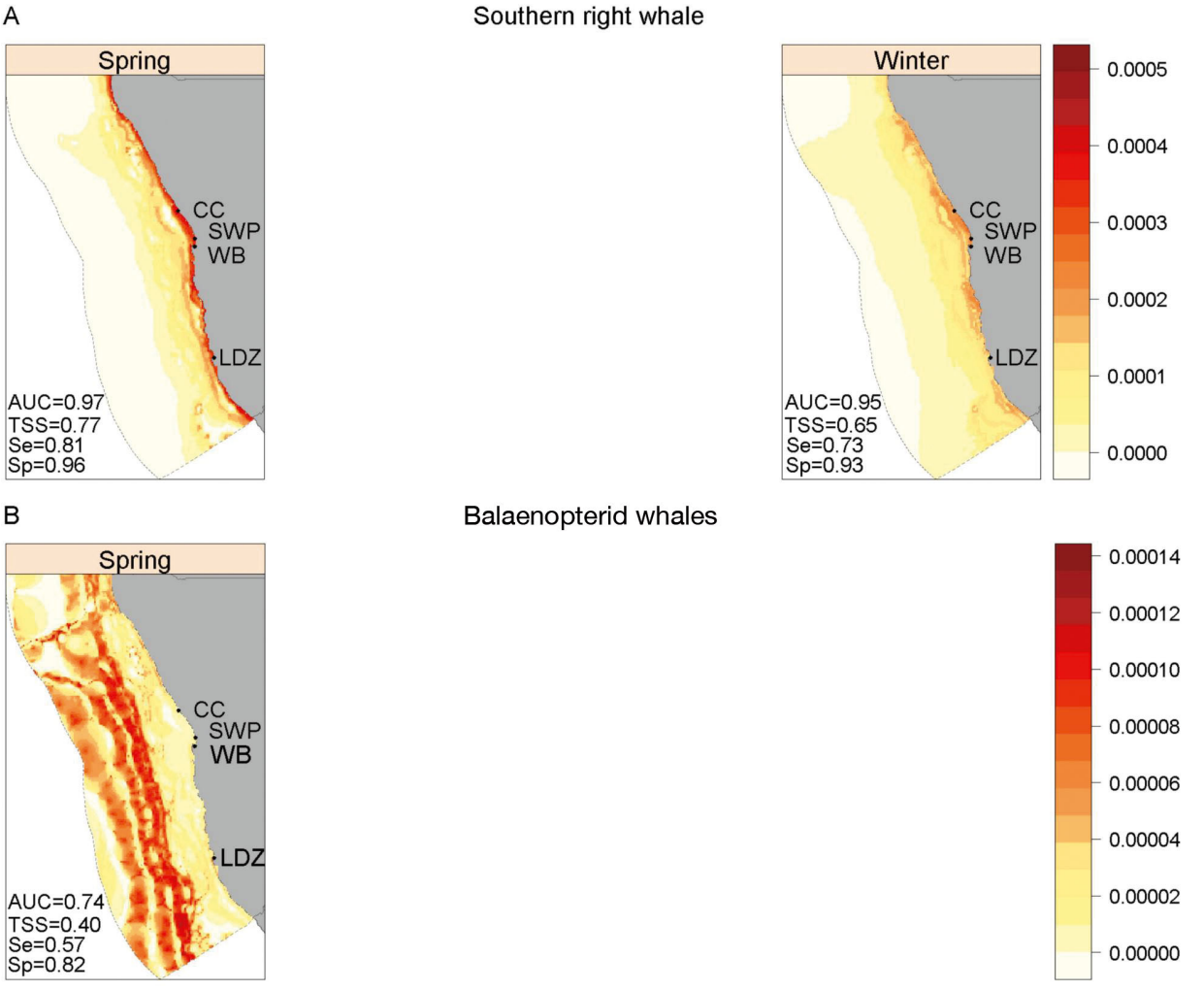

Fig. 6. MinxEnt seasonal predictions of habitat suitability for (A) southern right whale *Eubalaena australis* and (B) balaenopterid whales (Balaenopteridae spp.) off Namibia. Details and abbreviations as per Fig. 3

spring (<50 m; 97.5%) and winter (<500 m, 90.4%) (Fig. S9 in the Supplement). Variables of lesser importance were slope in spring (2.4%) and chl *a* in winter (7.5%). Highest habitat suitability was predicted to be in areas with high slope values in spring and with high chl *a* concentrations in winter (Fig. S9).

3.3.9. Balaenopterid whales

Balaenopterid whales were observed year round, and records of this group represented 3% (n = 106) of the total dataset (Table 1). Records were acquired from the Lüderitz area including within the NIMPA and from offshore waters. MinxEnt models provided a good predictor of the occurrence of balaenopterid whales in spring (0.74) but performed poorly in summer (AUC = 0.58) and autumn (AUC = 0.60), so these seasons were excluded due to poor model fit. The MinxEnt model for spring predicted almost the entire EEZ as suitable habitat for this group, with especially high suitability in waters deeper than 1000 m (Fig. 6B). Complexity was the most important environmental predictor in spring (highest suitability at low values; 49.3%) (Fig. S10 in the Supplement), with depth (<250 m; 27.4%) being the second most important variable (Fig. S10).

3.4. Summary of habitat suitability predictions

MinxEnt models performed well for the majority of species or species groups modelled for most seasons. The top performing models, i.e. those with the highest AUC and TSS values, were for bottlenose dolphins in winter (AUC = 1.00; Fig. 4), humpback

whales in autumn (AUC = 0.98; Fig. 5) and Heaviside's dolphins in autumn (AUC = 0.97; Fig. 3). The models used 21 presence cells for bottlenose dolphins (n = 154) in winter, 29 for humpback whales (n = 56) and 119 for Heaviside's dolphins (n = 723) in autumn. The least accurate models were for pilot whale and dusky dolphin habitat suitability in autumn. As AUC values of 0.5 indicate the model is no better than a random guess, models with AUC values under 0.70 were removed, which included 1 model for bottlenose dolphins and 2 models for balaenopterid whales.

3.5. Comparison between MaxEnt and MinxEnt modelling

MaxEnt modelling was performed in a comparison study for dusky and bottlenose dolphins to illustrate the ability of MinxEnt to account for sampling bias (Merow et al. 2016). However, the summer MaxEnt model for bottlenose dolphins was excluded from the analysis due to a low AUC score (0.68). MaxEnt modelling predicted very similar suitability areas to MinxEnt modelling for both species (Fig. 7). However, MinxEnt modelling tended to extend suitable habitat areas further offshore for both species, better matching the known distribution of the species (Findlay et al. 1992). Moreover, the ability of a MinxEnt approach to account for sampling bias is illustrated quite clearly for dusky dolphins in autumn (Fig. 3) where the MaxEnt model suggested high suitability around Lüderitz, a clear bias due to heavy sampling in this area (Fig. 2).

4. DISCUSSION

Species distribution models using presence-only data offer a powerful way to provide information about likely distribution patterns and potential habitat use from sparse or opportunistic data when conventional sampling methods are expensive and logistically difficult (Elith et al. 2006, Hernández et al. 2006). Here we use a novel MinxEnt modelling approach to account for sampling bias (Merow et al. 2016), to provide information on the predicted habitat suitability for 9 cetacean species or species groups, and improve on the information currently available from broad descriptions of cetacean distributions in Namibia (Findlay et al. 1992, Best 2007, IUCN 2017). This study represents the first attempt to predict likely habitat preferences for several key cetacean species within the Namibian EEZ. The results are informative for managers interested in actual and predicted species occurrence and highlight spatial and temporal gaps in species information which we hope will promote future research efforts.

The small odontocete fauna of the northern Benguela ecosystem has been described by Findlay et al. (1992) as occupying 4 main habitats: (1) deep pelagic waters off the continental shelf, (2) the continental shelf, (3) a narrow coastal band of habitat along central Namibia occupied by the coastal bottlenose dolphins and (4) a small area offshore of the Lüderitz upwelling cell associated with records of southern right whale dolphins *Lissodelphis peronii*. Due to sample size limitations, we only modelled the habitat suitability of 5 species overlapping with Findlay et al. (1992) (Heaviside's, dusky, bottlenose and common dolphins, and pilot whales), which occupy the first 3 aforementioned habitats. We also modelled habitat use of 4 large whale species or species groups for which some recent publications on distribution and habitat use within Namibia are available (Best 2007, Elwen et al. 2014, Roux et al. 2015).

We used 1 biotic (chl *a* concentration) and 5 abiotic (water depth, seabed slope, habitat complexity, distance from shore and SST) variables known from previous studies (Praca et al. 2009, Pirotta et al. 2011) to predict cetacean habitat suitability, as well as informative priors of 'survey effort' within a MinxEnt modelling frame work. Despite our best efforts, and a total sample size of 3211 records in the database, sample size and area coverage were limiting factors for all analyses, especially in offshore waters and the northern part of the study area. Water depth (or its proxy, 'distance from shore' for Heaviside's dolphins) was the most influential predictor of habitat suitability for most seasons and species. Chl *a* levels (productivity) and habitat complexity (rate of change of slope) were the second most important contributing factors in most models. Depth is the most widely used index of topographical complexity in habitat models of cetaceans and has been found to have significant relationships with the distribution of many cetacean populations, especially at broader spatial scales (Redfern et al. 2006, Bouchet et al. 2015), where its influence on current formation or localised upwelling, such as the shelf edge, may be most obvious. This interaction of depth, topography and currents results in a predictable localisation of food resources for marine animals, such as cetaceans (Cox et al. 2018).

While there are arguably more sophisticated methods to account for detectability and observer bias,

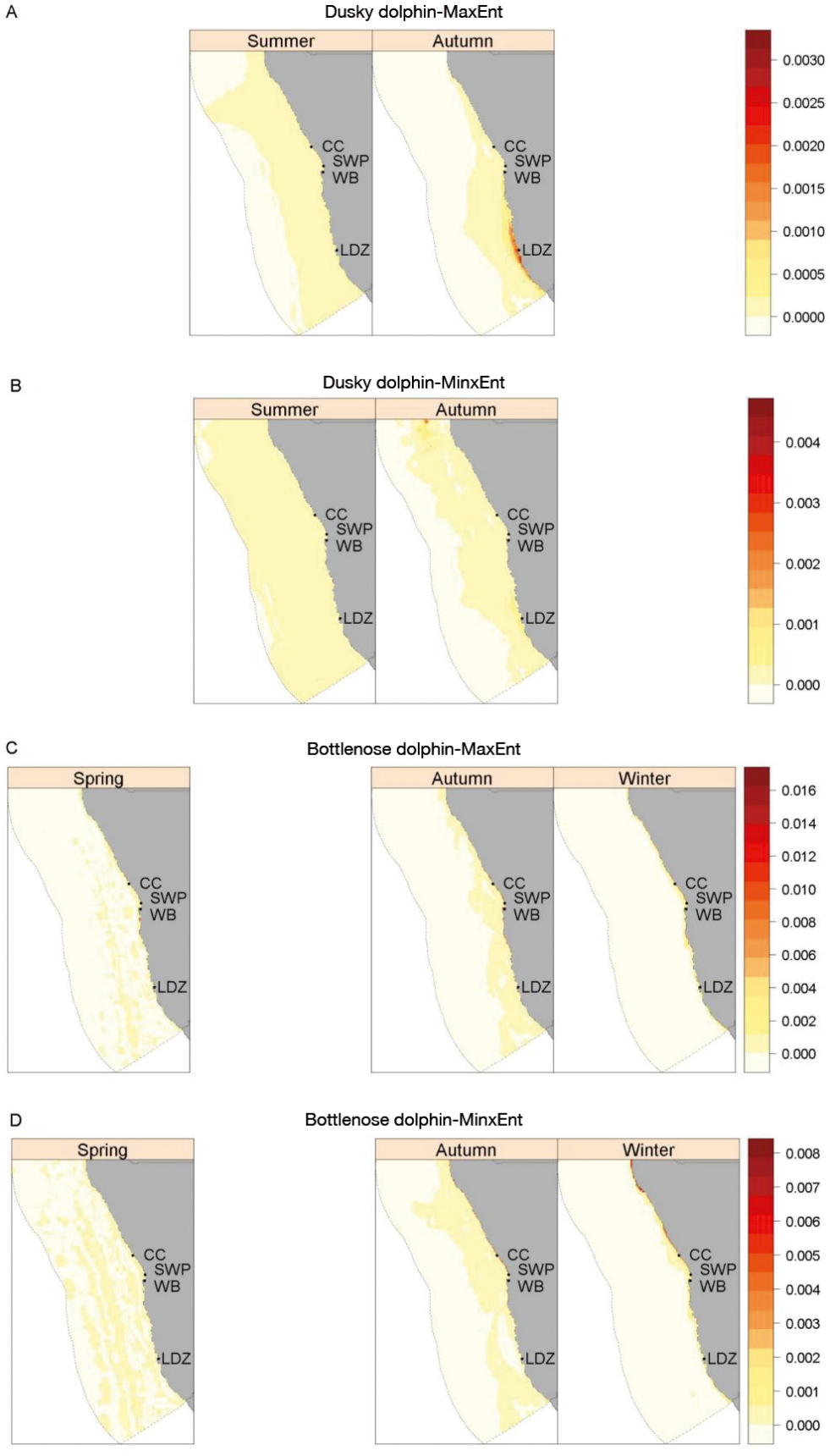

Fig. 7. Comparison of seasonal predictions of habitat suitability for dusky dolphin *Lagenorhynchus obscurus* for (A) MaxEnt modelling and (B) MinxEnt modelling, and bottlenose dolphin *Tursiops truncatus* for (C) MaxEnt modelling and (D) MinxEnt modelling off Namibia. Details and abbreviations as per Fig. 3

such as occupancy models (Kéry et al. 2010), these require much more data (i.e. repeat observations for a large number of sites) than are currently available for Namibian cetaceans. MinxEnt is a relatively novel adaptation of MaxEnt, allowing for the explicit incorporation of spatial information on, for example, sampling bias (Merow et al. 2016). Our cetacean sighting dataset represents the largest and best available for Namibia, but has a clear sampling bias (Fig. 2) because it includes a combination of opportunistic sightings and data from dedicated research surveys. This made it necessary to account for sampling bias in our predictions of cetacean distributions in Namibia. Merow et al. (2016) showed how the incorporation of a sampling bias 'prior', built using variables suspected to influence sampling bias, can provide much more reliable species predictions. Indeed, we found subtle, but clear, differences between using a regular MaxEnt model and a MinxEnt approach that suggested the latter was able to account for high sampling bias near ports such as Lüderitz (Fig. 7).

Spatial autocorrelation, the phenomenon of locations close to one another sharing similar values for environmental variables and in model residuals, is common in species occurrence data (Legendre 1993, Dormann et al. 2007). This can lead to a number of problems in species distribution modelling, including biased coefficient estimates, inflated measures of model evaluation and difficulties in transferring predictions in geographical space (Dormann et al. 2007, Guélat & Kéry 2018). Spatial autocorrelation arises from several processes, including sampling bias, environmental gradients and biotic interactions. Sampling bias is among the major causes of spatial autocorrelation in species distribution modelling (Boria et al. 2014, El-Gabbas & Dormann 2018). The MinxEnt approach incorporates prior information on the probability of observing a species (via a model of target-group samples and predictors of sampling bias), which should help to reduce sampling bias (Merow et al. 2016), as well as spatial autocorrelation (Phillips et al. 2009). We tested whether this was the case with our MinxEnt models and found that 12 out of 21 models had reduced spatial autocorrelation (as measured using Global Moran's *I*), and the other 9 had relatively similar levels of spatial autocorrelation to the MaxEnt models. However, all models still have significant levels of spatial autocorrelation, and future research should attempt to account for this. One commonly used approach to dealing with spatial autocorrelation includes spatial or environmental filtering (Veloz 2009, Boria et al. 2014, Virgili et al. 2018, Castellanos et al. 2019). However, we generally had very small datasets for each model (species occurrences within seasons; Table 1), making it difficult to use this approach. Future research could attempt to use spatial autocovariates (Crase et al. 2012) or point process models that relax the assumptions of spatial independence of observations (Renner et al. 2015).

Heaviside's dolphins have a strong diurnal onshore–offshore movement pattern throughout their range (Elwen et al. 2006, 2010, Leeney et al. 2011), reflecting a night-time movement to foraging areas located offshore where the dolphins feed on vertically migrating deep-water species such as juvenile shallow-water hake *Merluccius capensis*. The movement back inshore when not foraging is thought to reduce predation risk when not feeding (Elwen et al. 2006, 2010). Most of the records in this study arise from daytime observations of Heaviside's dolphins in nearshore waters during small-boat research studies, ship-based surveys within the NIMPA out to the 200 m isobath and from mining vessels moored in water depths of around 120 m located near the southern border of Namibia. Supporting Findlay et al. (1992), the majority of sightings were at depths less than 100 m, and MinxEnt models predicted a preference for proximity to shore and areas of potential upwelling (low mean dynamic topography). As observations were made during the day, our results are regarded as suitable daytime habitat for Heaviside's dolphins, with a data gap present overnight, when foraging offshore may shift the distribution to deeper water (Elwen et al. 2006, 2010).

Dusky dolphin distribution around southern Africa is associated with the cold waters of the Benguela current. This species has been reported to occur beyond 2000 m depth, but most observations have been made in water shallower than 500 m (Findlay et al. 1992). Observations and modelling confirmed these patterns, and most records in this study occurred within the NIMPA and on the central shelf, with only 2 records occurring in water more than 1000 m deep. Habitat modelling further suggested a preference for high habitat complexity and lower SST, both of which are more prevalent off the southern coast of Namibia within the NIMPA. Neither observation records nor modelling results confirmed the previously suggested interruption in distribution around the southern Namibian border associated with the Lüderitz upwelling cell and Orange River outflow (Findlay et al. 1992, Best 2007), but rather suggested an area of poor suitability in the warmer, deeper waters of northern Namibia, although sampling effort was particularly poor in this area.

Two morphotypes of common dolphins (short-beaked and long-beaked) or species (*Delphinus delphis* and *D. capensis*) are commonly reported around southern Africa (Best 2007), although recent genetic work suggests that all common dolphins in the Atlantic Ocean are a single species (Cunha et al. 2015). Only strandings of common dolphins and a single incidental catch have previously been reported from Namibia (Findlay et al. 1992, Best 2007). Our sightings records confirm the infrequent occurrence of this species in Namibian waters and suggest a preference for deeper waters off the continental shelf, with 23 of 26 records from waters deeper than 1000 m. However, MinxEnt model results suggest that the habitat use in these warm, deep waters offshore of the Benguela upwelling is driven by low complexity and low chl *a* levels rather than depth or surface temperature. These results are somewhat unexpected, as high chl *a* concentrations (Cañadas & Hammond 2008, Moura et al. 2012) and steep slope associated with upwelling are conditions that have been highlighted in several studies as the most important environmental drivers of common dolphin distribution (Cañadas et al. 2002, Jefferson et al. 2009, Svendsen et al. 2015). The majority of sightings took place in summer, but observer coverage in offshore waters was too low in other seasons to confirm if this is a year-round pattern, highlighting the need for additional sightings data for this species.

Of the 305 records of bottlenose dolphin sightings used in this study, 296 were in very coastal locations and 11 were in water deeper than 200 m, supporting earlier descriptions of 2 populations of the species in Namibia, one being extremely coastal (mainly <30 m depth) and the other being a pelagic offshore population (Findlay et al. 1992, Hoelzel et al. 1998, Best 2007) which is often observed in association with pilot whales (88 records in this study). The records and resultant models almost exclusively relate to the coastal bottlenose dolphin population of Namibia. This population is very small (Elwen et al. 2019) and has an extreme nearshore distribution between Lüderitz and Cape Cross (Best 2007), but its overall range is uncertain due to the difficulty to access and survey the waters north and south of these areas. Model predictions suggest that this population may inhabit areas north of Cape Cross. Sightings data from this area are sparse, as much of coastal Namibia is remote and inaccessible, and these inshore areas are not surveyed by platforms of opportunity (i.e. seismic vessels). Therefore, targeted research operations, aerial surveys or passive acoustic monitoring would be useful to confirm species presence in this area. If present, these dolphins could form a link between the Namibian bottlenose dolphin population using Walvis Bay and the population known from southern Angola (Weir 2010).

The distribution of pilot whales around southern Africa (including some sightings from southern Namibia) was described as predominantly pelagic waters near the shelf edge and generally greater than 1000 m deep (Findlay et al. 1992, Best 2007). The observations and modelling results of our study support these patterns in Namibia, with the majority (63 of 88) of pilot whale groups observed in waters deeper than 500 m, and the predicted areas of most suitable habitat being along the shelf edge (summer) and in a broad area off the shelf in northern Namibia in autumn (Fig. 5B). This offshore habitat was also associated with low chl *a* concentration and low c-omplexity.

Sperm whales usually inhabit the deep ocean and often occur along continental shelves and ridges (Best 2007, Whitehead 2009). They were historically caught during whaling operations off Namibia from shore-based catcher stations in the early 20th century (Best & Ross 1989). Seasonality of historical catches off the west coast of South Africa suggests that medium and large sized males are more abundant in winter months, while female groups are more abundant in autumn, although animals occur year round (Best 2007). This is the first study to document recent sightings of sperm whales in Namibian waters. Most sightings took place in summer, supporting historical observations. Observations and modelling results confirmed high habitat suitability in offshore waters (mostly >2000 m depth) in summer in areas with high chl *a* concentration and high habitat complexity. This supports results from other studies where complex topography (Pirotta et al. 2011, Johnson et al. 2016) and high primary productivity (Jaquet & Whitehead 1996, Praca et al. 2009) have been reported as good indicators of sperm whale distribution.

Humpback whales are thought to predominantly migrate through Namibian waters to breeding grounds further north, with 2 peaks in presence aligning with the northward (July) and southward (September) migrations, and animals may spread across the wide continental shelf with no clear 'corridor' (Elwen et al. 2014). Observations and modelling in this study support a general increase in the winter and spring periods, but there were also a significant number of records during the summer. Findlay et al. (2017) recently reported the presence of large groups of feeding humpback whales using the southern Benguela ecosystem off South Africa during summer

months, when whales are typically thought to be in the Southern Ocean feeding grounds. Regular observations of groups of humpback whales in November and December in Namibian waters, combined with observations of active feeding off Walvis Bay during the southward migration (Namibian Dolphin Project unpublished data), suggest that some whales may also be using the northern Benguela system as a foraging area.

Southern right whales in Namibia are part of a broader stock which predominantly breeds off South Africa and have shown a general increase in numbers since at least the late 1990s, thought to be associated with the overall increasing population (Roux et al. 2015). Very few calves have been reported in Namibia, and there is little evidence of the Namibian coast ever serving as a nursery ground (Roux et al. 2015). All records in this study occurred in waters less than 100 m deep, and habitat modelling indicated a strong preference for shallow waters, often with a low-relief substrate. While in their breeding grounds, such as along the South African coast, both single adults and mother–calf pairs have a preference for shallow nearshore waters with sandy bottoms, which is thought to reduce energy conservation and increase protection of their calves (Elwen & Best 2004), rather than further from shore as is typical of feeding right whales in the southern Benguela (Mate et al. 2011). The patterns observed in Namibia suggest that right whales along the Namibian coast were mostly juveniles or young adults, possibly on exploratory trips around the coast from the breeding grounds, rather than foraging animals.

The species group balaenopterid whales included 94 'definite' sightings of 5 species or species groups: minke whale spp., Bryde's whale, fin whale, sei whale and unidentified balaenopterids; and 12 further 'probable' sightings of 4 species or species groups: minke whale spp., fin whale, sei whale and unidentified balaenopterids; thus this species group contains a minimum of 4 balaenopterid species. Minke and fin whales were the most frequently observed species within this group. Each of the species in this group has its own migration and habitat use patterns, although they all show a seasonal north–south migration with a bimodal presence in Namibia, and general habitat off the shelf and in pelagic waters (Best 2007). Thus, it represents a coarse grouping of species as reflected in the wide spread of records across the shelf and into deep offshore waters. Almost the entire Namibian EEZ appeared to be a suitable habitat for balaenopterid whales, with model results suggesting that this species group is most likely to occur in waters less than 1000 m deep. Records show some seasonality, with few observations in winter (Table 1). The number of sightings of balaenopterid whales in Namibian waters highlights the importance of the northern Benguela to these recovering whale stocks and the need for more detailed information, especially in deeper waters.

Modelling of habitat suitability allows for a more formal description and better understanding of the factors driving the observed spatial and temporal patterns of animal presence. This information can be extremely useful in an applied setting when simple occurrence data are limiting. Obvious applications include environmental impact assessments (EIAs) and identification of potential conservation areas. Much of the data used in this analysis arose from marine mammal observers working on seismic survey vessels, themselves subject to EIAs by the Namibian authorities. The large number of sightings and significant role of these sightings within this dataset highlights the value of marine mammal observers and the value in sharing the resulting data with the scientific community. Namibia has an excellent conservation track record in its terrestrial environment, but the history of protection of its marine resources has been less successful. The country currently has only 1 marine protected area, the NIMPA, declared in 2009, although it is the largest one in continental Africa. Although primarily developed to protect island-breeding sea birds (Ludynia et al. 2012), the results of this study highlight the NIMPA's potential importance for protecting cetaceans and their habitat. Namibia is currently undergoing national-scale marine spatial planning initiatives to include the definition of ecologically and biologically significant areas (Bers et al. 2016). The data and model results presented in this paper can contribute to this process, in the hope that they will be integrated into protection and management of marine species.

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