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Cover image: Ngalawa (traditional dugout, outrigger canoe) being readied for a boat race in the 2018-2019 Kraken cup, Kilwa, Tanzania. © Rahim Saggaf

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Fine-scale habitat use by humpback whales (*Megaptera novaeangliae*) in Zavora Bay, Mozambique

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Abstract

Little is known about the humpback whales (*Megaptera novaeangliae*) of the East-African Coast genetic sub-unit (C1). With an estimated population size of 7000 whales, they demonstrate the resilience of the species after commercial whaling caused population numbers to decline drastically. Zavora Bay, Mozambique offers an ideal observation point of the passage of the whales during their annual migration towards the breeding ground of southern Africa and serves as an operating base to monitor this population. This study aimed at identifying the importance of Zavora Bay as part of this breeding ground and the core regions for humpback whale use within the study area. Results showed the waters off the coast of Zavora are actively used for breeding and do not merely serve as passage towards the wintering habitats. A mother-calf pair separation with a preference for shallower waters closer to shore was observed. Besides depth and distance to shore, slope also proved to have a significant influence on the distribution of adult humpback whales. Increased survey effort and more detailed investigation of the threats to humpback whales within the waters of Zavora are recommended.

Keywords: occupancy, breeding ground, geospatial, GIS, modelling probabilities, habitat use

Introduction

The humpback whale (*Megaptera novaeangliae*) is a cosmopolitan species, found in all oceans except the Arctic (Clapham *et al*., 1999; Smith *et al*., 1999; Andriolo *et al*., 2010). It has one of the largest geographical ranges in the animal kingdom, coupled with a strong annual cycle; summering in prey-abundant high latitude waters, then migrating to tropical and subtropical waters in the winter to breed and give birth (Smith *et al*., 1999; Rasmussen *et al*., 2007; Ryan *et al*., 2013). There are currently 14 different distinct populations of humpback whales worldwide (NOAA, 2018). Individuals observed in the western Indian Ocean belong to the Breeding Stock C (Rosenbaum *et al*. 2009) and in Mozambique, the East-African Coast genetic subunit (C1) has an estimated population size of 7000 individuals (Pereira *et al*., 2014).

Up until a moratorium agreed upon by the IWC (International Whaling Commission) in 1982, commercial whaling caused the population of humpback whales to decline to <10% of its estimated original size (Clapham *et al*., 1999; Tulloch *et al*., 2018). The present status of the species is difficult to determine given its wide-ranging nature and the difficulty of providing adequate sampling coverage across ocean basins (Smith *et al*., 1999; Bettridge *et al*., 2015; Gabriele *et al*., 2017). However, humpback whales are proving to be a resilient species showing strong recovery in multiple areas across the globe (Clapham *et al*., 1999; Smith *et al*., 1999; Stevick *et al*., 2003; Gabriele *et al*., 2017; Pavanato *et al*., 2017). Despite these recoveries, humpback whales still face a wide range of threats such as direct killing (Clapham *et al*., 1999; Ryan *et al*., 2013), vessel strikes (Garcia-Cegarra *et al*., 2018),

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entanglement (Johnson *et al.*, 2005), and vessel-based harassment (Corkeron, 1995; Clapham *et al.*, 1999; Andriolo *et al.*, 2010; Ryan *et al.*, 2013), resulting in lowered genetic diversity. Further, an increase in anthropogenic underwater noise can interrupt normal behaviour, driving them away from areas important to their survival (Au and Green, 2000), impede proper communication between individuals (Fournet *et al.* 2018) and cause permanent damage to their hearing (Ketten *et al.*, 1993; Maybaum, 1993).

Identifying ecologically and biologically significant areas is crucial in implementing proper marine spatial planning that facilitates economic activity and combats the degradation of marine habitats or species (Ardron *et al.*, 2008; Douvere, 2008; Agardi *et al.*, 2011). For large transient marine mammals such as humpback whales, protection of migratory corridors that link breeding and foraging grounds should be a high priority (Berger *et al.*, 2008; Douvere 2008; Pendoley *et al.*, 2013).

Abundance is a measure often used to assess species' distribution in time and space, but data to estimate abundance can be difficult to collect, require a lot of time and effort and carry a large bias in observational experience (Guillera-Arroita *et al.*, 2010; Guillera-Arroita *et al.*, 2011, MacKenzie *et al.*, 2017). Moreover, data collection for ecological research is prone to a substantial number of challenges, for example, influence of the focus species' behaviour on the data, disruptive methodologies or unpredictable weather events limiting the data collection (Barry and Elith, 2006; Guillera-Arroita *et al.*, 2011; Ruiz-Gutierrez *et al.*, 2016). Occupancy models that use presence/absence data can assess a population without the need of abundance estimates (Hall *et al.*, 2010; Sadoti *et al.*, 2013). This is done by analysing the proportion of area, patches, or sample units occupied (Guillera-Arroita *et al.*, 2010; Mackenzie *et al.*, 2003) and can be used for a wide range of purposes, such as extensive monitoring programmes, distribution, habitat selection, meta-population dynamics, species richness and interactions (MacKenzie *et al.*, 2002; Currie *et al.*, 2018).

The aim of this study was to investigate the movement of humpback whales (from the C1 population) to and from the wintering habitats of southern Africa and identify specific areas of importance within Zavora Bay. In this context, the objectives were to (i) determine the functionality of Zavora as part of a known breeding ground, (ii) assess which areas were more prone to be visited by the whales, and (iii) identify the different factors driving the absence/presence of the humpback whales within their local distribution by making use of an occupancy model. Identifying habitat preference, as well as the factors influencing their behaviour and choice of habitat, will help to improve long-term conservation and management strategies within Mozambique and along the eastern African coastline.

Material and methods

Study area

The study area is part of the continental shelf, located in Zavora Bay, Inhambane Province, Mozambique (Fig. 1). The survey area was approximately 35 km long and 20 km wide with a maximum water depth of 53 m. The bay has a shallow reef (10–20 m) and a deep reef system (35–65 m) parallel to shore with a predominant sand depression area (15–53 m) between these two reef systems. Yearly sea surface temperature ranges from 21°C to 27°C (Amone-Mabuto *et al.*, 2017).

Data collection

Data (i.e. number of individuals and groups, distribution and behaviour) were collected from 2010 to 2018, from June to October by trained volunteers. Land-based observations were made from a dune top ('whale station'), 20 m above sea level, immediately adjacent to and overlooking the study area. The maximum study area and land references were determined by collecting the GPS coordinates of the position of a 9 m long boat when this was just visible from the 'whale station'. Visual surveys were conducted from 07h00 to 17h30. Every half hour, a thorough scan from left to right of the study area was undertaken systematically, using binoculars (NIKON Aculon A211 10x50) to search for visual cues of humpback whale presence.

When a sighting occurred, the time was recorded, as well as the group size (minimum, maximum and best estimate, where the latter was further used for analysis), geographical position on a hand drawn map (based on African east coast Mozambique, 1993), primary behaviour, presence/absence of a calf, and dispersion. To identify between groups, individuals that were >100 m apart were assumed to be from different focal groups. During the sightings, environmental variables were also noted (e. g. wind speed and direction, swell, sea state, cloud cover). If whales were observed outside of the search time, it was recorded as a 'watch' rather than a 'scan' and included all the above listed variables.

Underwater temperature data were collected using two temperature sensors (STAR ODDI – Starmon mini), one on a deep reef at 32 m depth (24°33.944'S 35°16.899E) and one on a shallow reef at 16 m depth (24°28.931'S 35°14.346'E) (Fig. 1). Temperature was recorded throughout the year, with one-hour intervals.

Data analysis

All sighting data from 2010–2018 were used to determine effort. Due to inconsistency in visual surveys (e.g. incomplete coverage of the whale season), only data from 2017 and 2018 (June to October) were used for temporal relative abundance, habitat suitability and occupancy modelling.

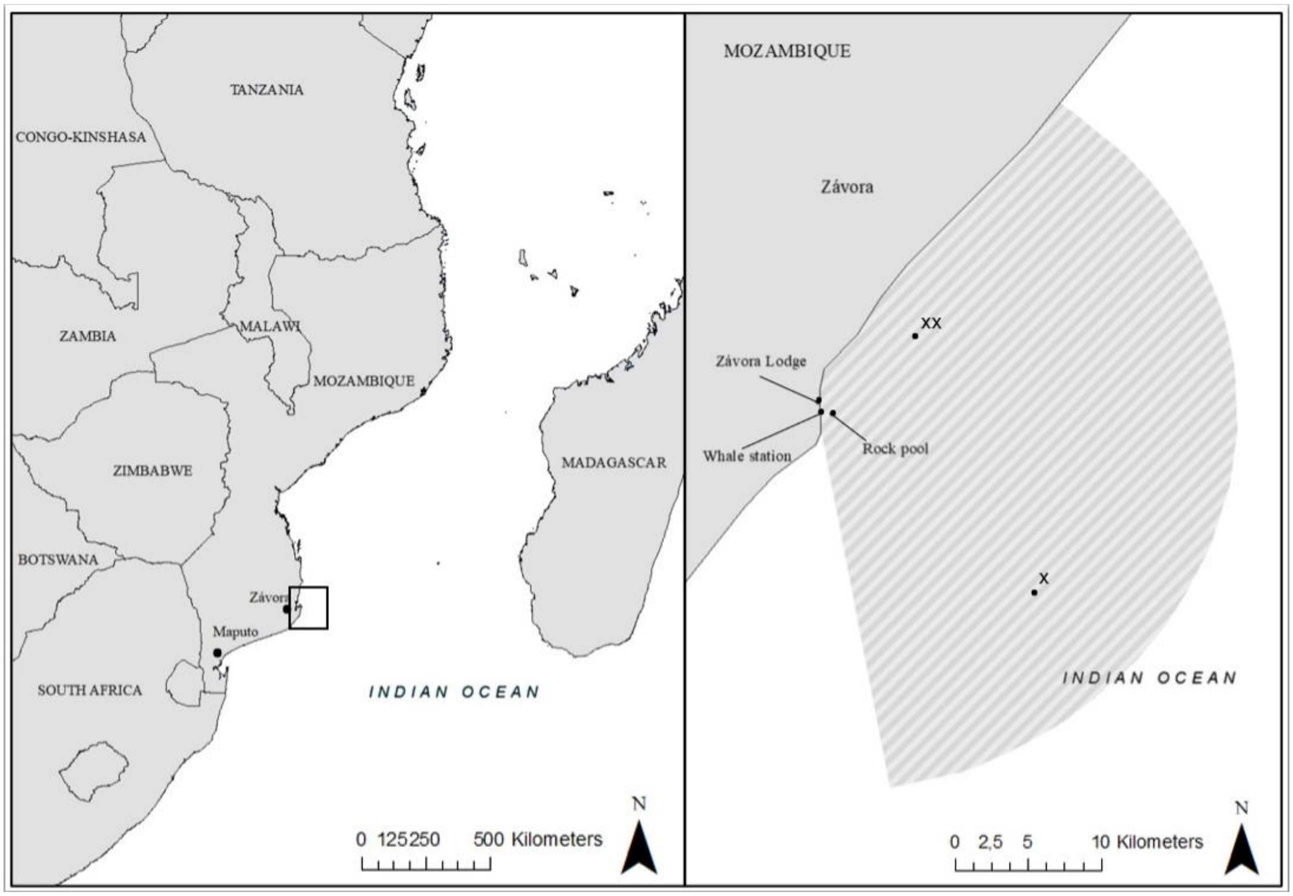

Figure 1. (a) Map of the study area located in the southern part of Mozambique. (b) Close up view of the study area, where the patterned segment highlights the area observed from the 'whale station' (observation point). The total surface covered by this study has a size of 389 km². The south-east border of the area is an approximation as the observations are limited by vegetation and land obstructions. Included are the locations of the temperature sensors (X, deep (> 30 m) and XX, shallow (< 30 m)).

For statistical analyses, R 1.1.463 was used (R development Core Team, 2010). All statistical tests were performed at the 0,05 significance level. The 'dunn.test' package was used for non-parametric post hoc tests.

Digitization of drawings

Location of each whale sighting was captured by the observers by plotting their location onto paper maps referenced with land markers. Maps were digitized, georeferenced and analysed using GIS. The JPEG output files were loaded into ArcMAP for georeferencing using GCS_WGS_1984.

Geospatial analysis

Sightings were mapped with ArcMap 10.4.1 and projected onto the UTM zone 36S coordinate system and the study area was divided into 1km x 1km grid cells. Sightings were stratified for mothers with calves and categorized according to presence of a mother with a calf, with or without escorts, and plotted correspondingly in order to identify areas of particular importance for the whales, especially for mother-calf pairs.

Occupancy model for habitat suitability

Habitat suitability was determined by applying occupancy modelling, which allows for the correction of biases inherent in opportunistic data collection, without requiring distance sampling techniques (Sadoti *et al.*, 2013). The methodology of MacKenzie (2012), MacKenzie *et al.* (2017) and Currie *et al.* (2018) was followed and adapted to the present data.

A standard single species, single season occupancy model was used to allow for the inclusion of multiple covariates and dependent surveys. Assumptions for this model were met and addressed (Table 1).

For the occupancy model, two components were defined as following:

1. Site occupancy (ψ_i) – the probability that a species occupies the sampling site *i*
2. Detectability (p_i) – the probability that a species is detected during survey *j* at site *i*

Both of these were estimated using the logit-link function (Mackenzie, 2006; MacKenzie, 2012; Currie *et al.*, 2018).

Occupancy (probability of whale use) = logit (ψ_i) = $\ln(\psi_i / 1 - \psi_i) = \alpha_0 + \alpha_1 x_{1,i} + \alpha_{2,i} x_{2,i}$

Detection probability = logit (p_{ij}) = $\ln(p_{i,j} / 1 - p_{i,j}) = \beta_0 + \beta_1 x_{1,i} + \beta_{2,} x_{2,i} + \beta_3 y_{1,ij} + \beta_4 y_{2,ij}$

Where: ln is the natural logarithm, x represents site-specific covariates, y represents survey-specific covariates, α and β are the estimated regression coefficients.

Model input was subdivided into survey-specific and site-specific covariates. Each grid cell within the survey area as defined in the geospatial analysis was given a unique ID number, to which these variables were linked. The sequence of these values per survey, per site is called the detection history (h) (MacKenzie and Bailey, 2004; MacKenzie, 2012).

Site-specific covariates

Each grid cell, for future reference referred to as 'site', was characterized by a specific depth. Bathymetry data of the survey area originated from GEBCO, sheet G.08 compiled by the Lamont-Doherty Earth Observatory (LDEO) of Colombia University and was extracted from the GEBCO Digital Atlas published by the British Oceanography Data Centre on behalf of the IOC and IHO (2014). For each site the mean slope, distance from shore, latitude and longitude were included as site covariates.

Survey-specific covariates

Data from 2017 and 2018 were grouped as one single season and the 'year' was included as an additional survey covariate. This allowed for the variance between different years to be accounted for, without addressing the change of occupancy between the two years. Other survey covariates included month of the year and temperature (°C), where temperature was split into a deep (>25 m) and a shallow (<25 m) category.

A Shapiro-Wilk test was used to test for normality of the data. Correlation between variables was assessed

Table 1. Occupancy associated assumptions and measures that were taken to meet these assumptions.

Assumption	Addressed by
The system is closed to changes in occupancy	Output was interpreted as the probability of whale 'use' rather than actual occupancy
Assumption of independence (i.e. the outcome of one survey does not depend on the outcome of another survey)	Inclusion of survey-specific covariates, which account for a so-called 'trap-response' (i.e. species is easier to detect at a site where it has already been detected) (Hines *et al.*, 2010)
Misidentification of humpback whales as a species	Excluded due to the size, nature and known distribution of humpback whales in the area
Assumption of no false positives and (site occupancy) and *p* (detectability) are constant or a function of covariates.*	Modelling was performed with finite mixture (Royle and Link, 2006)

using the Pearson correlation. In cases of non-normality in covariates, the Spearman rank correlation coefficient was used instead.

PRESENCE (Version 2.12.17) (Hines, 2006) was used to develop a candidate set of models to fit the data. First, the procedure was followed for all sightings. Secondly, only sightings with calves were tested to assess mother-calf pair separation.

The best-fit model was chosen based on the AIC criterion (MacKenzie, 2012). The estimated beta parameters from the output were used for completion of the logistic regression equations for both occupancy and detection probabilities. The final outcome displays the factors influencing both detection and occupancy of whales, in this case translated as the suitability for a site to be visited by this species.

Goodness Of Fit (GOF) of the models was assessed using a Pearson's Chi Square test (MacKenzie and Bailey, 2004).

Results

Evidence for Zavora Bay as a humpback whale breeding ground

Summary of effort and whale sightings

A total of 230 surveys were carried out between 2010 and 2018 (Table 2). Sightings were corrected and displayed in sightings per unit effort (SPUE) over time for further use. Higher sightings were found from 2012 to 2014, with 2018 having the lowest SPUE. The highest abundance of mother-calf pairs was recorded in 2013. During all years, the majority of the sightings with a calf were unescorted by adults other than the mother. Detection of pods without calves was highest in the season of 2011 and highest for pods with calves in 2013. However, relative to the observed number of groups, lowest calf abundance was recorded in 2010, followed by 2011.

Relative abundance

Relative abundance varied from a minimum average of 1.6 ± 1.5 animals/hour on the 22 October to the maximum of 25.2 ± 9.5 on 4 August during 2018. In both 2017 and 2018, whale abundance increased early/mid-July and mid/late July, respectively, and decreased at the beginning of September (Fig. 2).

Group size

To calculate group size and number of individuals, each group was only taken into account once per survey to exclude resightings and avoid overestimation of the number of whales present. During the 2017 whale season, a total of 655 groups were sighted, accounting for 1157 individual whales. The mean group size (± SD) was 1.9 (± 1.02) over the entire duration of the season. Within

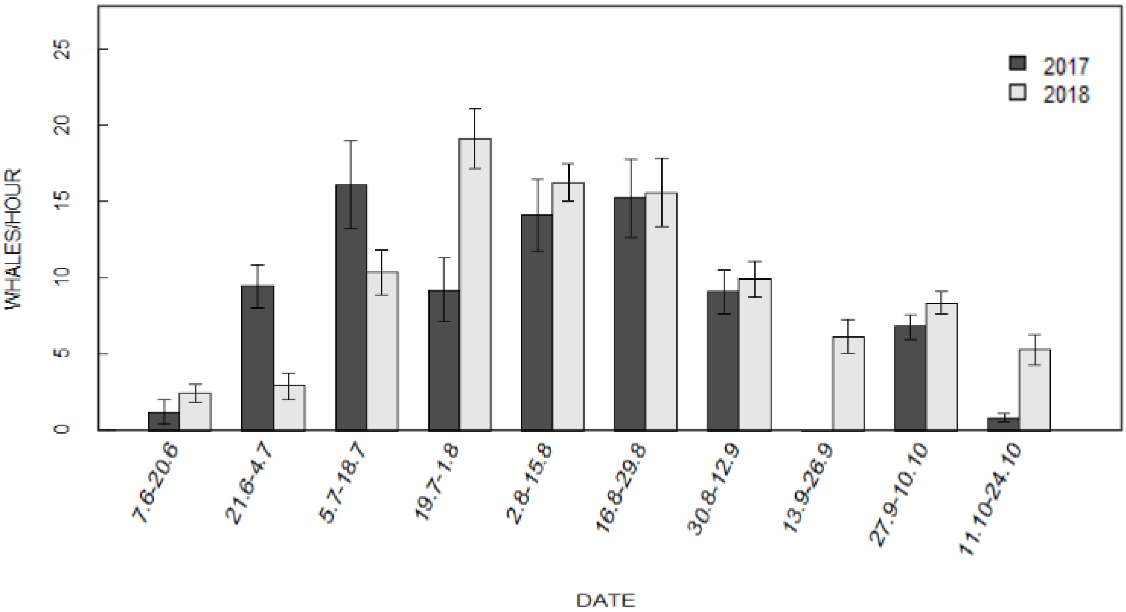

Figure 2. Seasonal changes in relative abundance of humpback whales throughout the 2017 and 2018 season. Relative abundance is represented by the average number of whales seen per hour in each two-week period (error bars represent SD, data corrected for re-sightings of the same individuals within the same hour). The two-week periodicity was chosen in the function of the survey dates, as these were inconsistent throughout the season and a two-week periodicity allowed for a nearly equal distribution of surveys. The alternative (i.e. relative abundance displayed per month), might mask potential patterns over time.

Table 2. Summary of shore-based observation effort for humpback whales at Zavora Bay, Mozambique from 2010 to 2018. Sightings were displayed in absolute numbers within brackets the number of sightings per hour spent surveying (SPUE).

	2010	2011	2012	2013	2014	2015	2016	2017	2018	Total
					Effort					
No. of obs. days	14	59	37	23	17	12	17	17	34	230
No. of scans	112	1 347	755	495	339	196	311	284	676	4 515
No. of watches	19	855	666	414	293	71	211	174	146	2 849
First day of effort	4 July	29 June	7 June	3 July	4 August	18 June	4 July	9 June	7 June	
Last day of effort	27 October	30 October	26 October	28 September	27 October	22 August	18 September	29 October	30 October	
					Sightings (SPUE)					
No. of whales	347 (5.69)	3 555 (4.80)	4 207 (9.89)	3 626 (13.71)	2 813 (14.39)	707 (6.37)	1 068 (6.40)	1 157 (7.92)	1 059 (3.39)	18 539 (7.65)
No. of groups (n>1)	104 (1.70)	971 (1.31)	1 459 (3.43)	1 260 (4.76)	861 (4.40)	225 (2.03)	304 (1.82)	297 (2.03)	348 (1.11)	5 829 (2.41)
No. of single whales	92 (1.51)	1074 (1.45)	566 (1.33)	492 (1.86)	627 (3.21)	119 (1.07)	337 (2.02)	358 (2.45)	220 (0.70)	3 885 (1.60)
Total	196 (3.21)	2045 (2.76)	2 025 (4.76)	1 752 (6.62)	1 488 (7.61)	344 (3.10)	641 (3.84)	655 (4.49)	568 (1.82)	9 714 (4.01)
No. groups with calf										
Unescorted cow-calf	0.00	67 (0.09)	33 (0.08)	238 (0.90)	177 (0.91)	35 (0.32)	48 (0.29)	90 (0.62)	63 (0.20)	751 (0.31)
Cow-calf pair escorted by one adult	0.00	13 (0.02)	6 (0.01)	114 (0.43)	37 (0.19)	13 (0.12)	12 (0.07)	16 (0.11)	18 (0.06)	229 (0.09)
Cow-calf pair escorted by two or more adults	0.00	7 (0.01)	1 (0.00)	20 (0.08)	8 (0.04)	6 (0.06)	4 (0.02)	5 (0.03)	10 (0.03)	61 (0.03)
Total	0.00	87 (0.12)	40 (0.09)	372 (1.41)	222 (1.14)	54 (0.50)	64 (0.38)	111 (0.76)	91 (0.29)	1 041 (0.43)

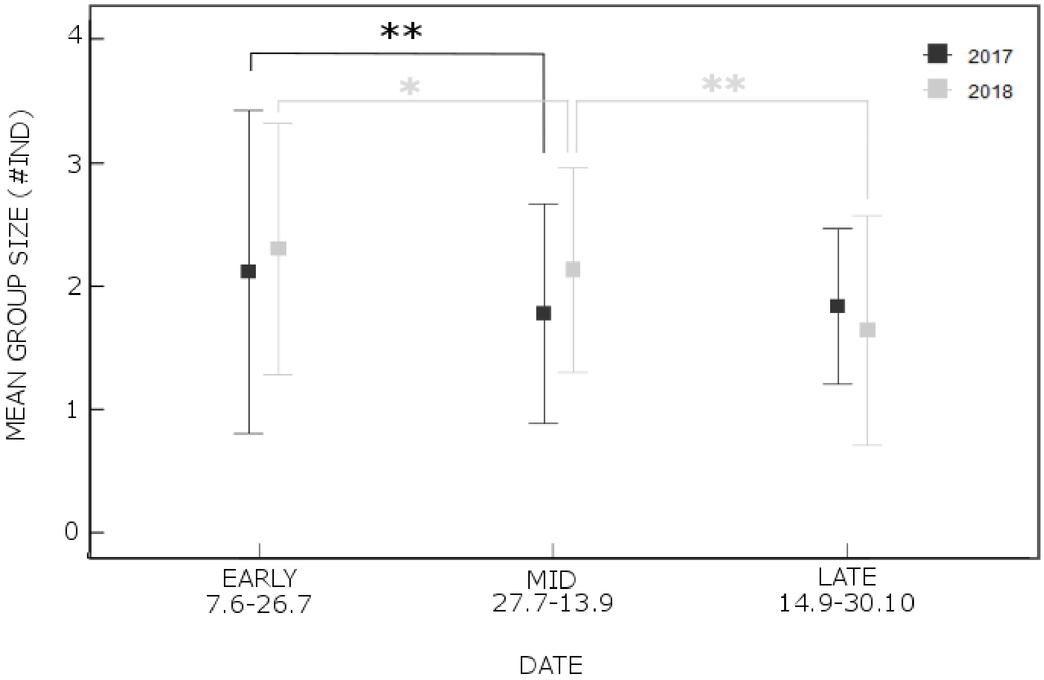

Figure 3. Seasonal changes in mean group size (±SD) for both the 2017 and the 2018 humpback whale season in Zavora, Mozambique. * indicates a significance level of 0.05, and ** indicates a significance level of 0.01.

the year, the mean group size decreased from 2.2 (± 1.3) at the beginning of the season to 1.8 (± 0.9) mid-season (Fig. 3). The mean group size at the beginning of the season was significantly higher than the group size mid-season (Kruskal-Wallis, $p < 0.05$, post hoc = Dunn Test). The difference between mid- and late season showed no significance (Kruskal-Wallis, $p > 0.05$).

In 2018, a total of 568 groups were sighted, accounting for 1059 individual whales. The mean group size was 2.1 (± 0.9) and significantly decreased from 2.3 (±1.0) in early season to 2.1 (± 0.8) mid-season and again to 1.6 (± 0.9) at the end of the season (Kruskal-Wallis, $p < 0.05$, post hoc = Dunn Test) (Fig. 3).

Modal pod size during both 2017 and 2018 was two. Sightings varied from a single individual to a maximum pod size of 10.

Presence of calves

In 2017, a total of 76.84 % of the sightings had 'undetermined' listed for calf presence. Of the remaining 23.16 % of sightings, the calf observations increased from 41.03 % in early season, to 58.82 % mid-season and again to 75.14 % late in the season. For pods with calves, a group of two signifies a mother-calf pair alone. Larger-sized pods indicate that other adult whales known as 'escorts' (Clapham, 2000) were accompanying the mother-calf pair. In the same year, 15.49 % of all sightings consisted of three or more animals. Of all sightings with calves, the most common comprised mother-calf pairs without observed escort presence (81.82 %).

Regrettably, calve presence was not recorded in a standardized manner over the years. For 2018, calf presence was recorded, however calf absence was not. Only 'undetermined' was used when no calf was sighted and thus no percentage of absence of calves could be displayed.

Identification of core areas

In the combined seasons of 2017 and 2018, both from June to October, a total of 52 surveys were conducted. Surveys were split into searches and watches, and since the effort was only consistent within and equal over all 'searches', these were the only sightings used to display the relative distribution of humpback whales (Fig. 4). The searches accounted for a total of 126.66 hours of surveying.

When SPUE included all whales (adults and calves), a north-south gradient indicating passage of the whales through the bay, as well as east-west differences showing increased abundance in areas characterized

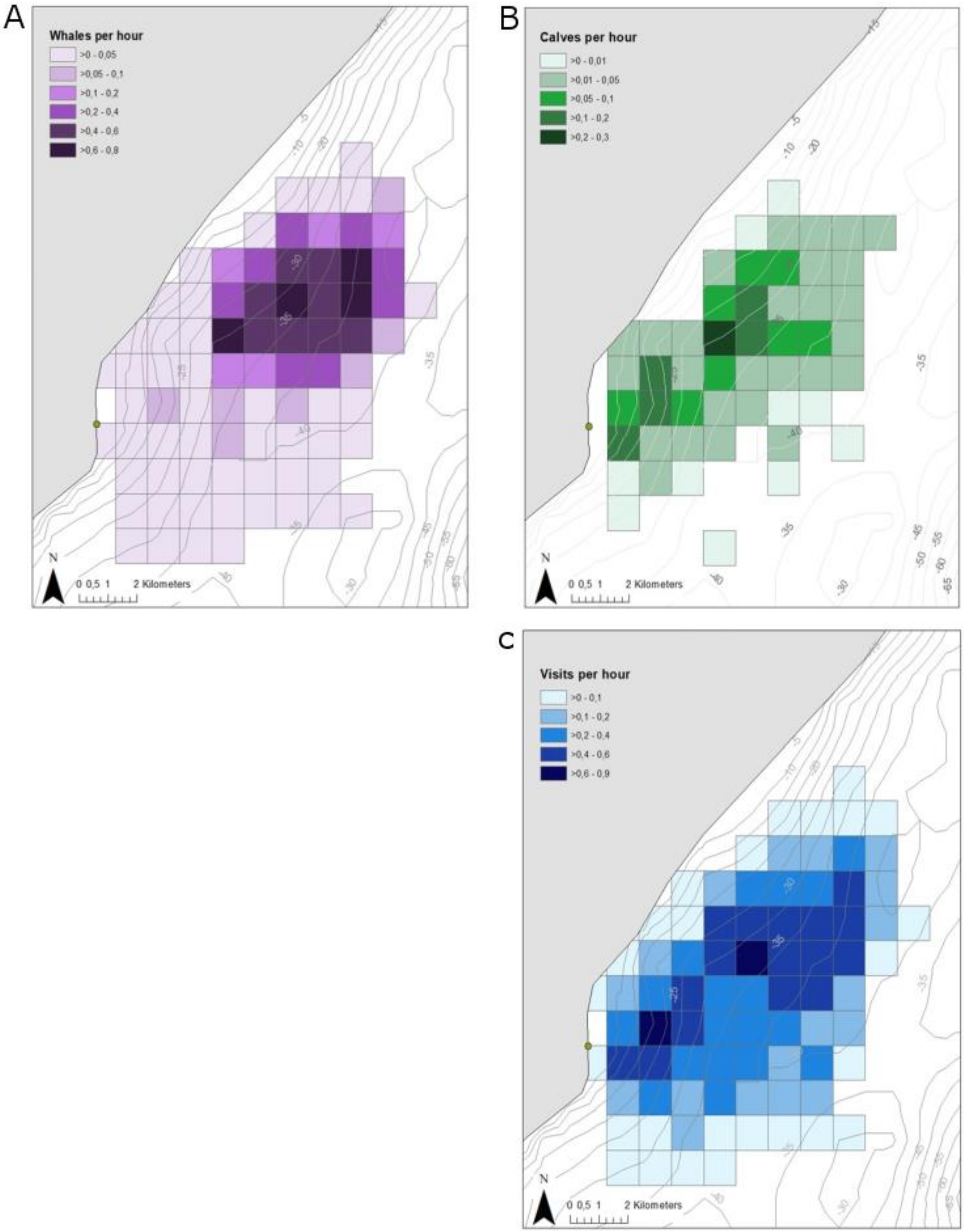

Figure 4. Relative abundance and distribution of humpback whales, with adults and calves combined (a), calves with accompanied mother only (b), and number of visits (presence/absence) per square kilometre per hour of adults and calves (c) in Zavora, Mozambique from June to October 2017 and 2018 combined. White areas lay within the survey area, but no sightings were registered in those parts of the water. The whale station is highlighted with a green dot for reference.

Table 3. Model selection results of detection probability for all humpback whale pods regardless of group size or calf presence/absence; i.e. visits of humpback whales in Zavora Bay in the combined seasons of 2017 and 2018 (June to October). Table values represent model, the change in AIC for the best model (ΔAIC), the Akaike weights (AIC_{wt}) and the number of parameters (K).

Model	K	*AIC*	*ΔAIC*	AIC_{wt}
p(month + year + temp)	5	5115.04	0.00	0.6142
p(year + temp)	4	5115.97	0.93	0.3858
p(month + temp)	4	5140.82	25.78	0.0000
p(temp)	3	5143.74	28.70	0.0000
p(year)	3	5152.25	37.21	0.0000
p(year + month)	4	5153.68	38.64	0.0000
p(.)	2	5185.71	70.67	0.0000
p(month)	3	5186.32	71.28	0.0000

by a depth of 20 to 35 meters was observed (Fig. 4a). When looking at SPUE that only included calf presence, shallower areas and those closer to the shore where of higher importance (Fig. 4b). As the observational experience was not equal over all surveys, bias is decreased by displaying the presence/absence of whales per site (Fig. 4c), instead of abundance over time. This shows that regardless the group size, the whales tend to use parts of the bay within a 10 km radius from shore, within the 35 m depth range.

Drivers of area suitability

All individuals

For the use of the occupancy model, all 2017 and 2018 sightings were grouped together, including those with calves. For all pods considered together, the model including month, year and temperature is ranked highest (Table 3). However, including month only marginally reduced *ΔAIC* (0.93). To ensure the most parsimonious model was used, the final model included only the survey covariates month and temperature.

The model output can be summarized as follows:

$$\text{logit}\ (All\_whales\ p) = 0.83 + 0.41_{year} - 0.25_{temp}$$

Whereby probability of detection decreases with increasing temperature and progression from 2017 to 2018 increases the detection probability.

Since depth and longitude were correlated (Pearson's product-moment correlation, $p < 0.05$, $r = 0.725$), depth was retained as the biologically most relevant variable for humpback whale distribution modelling and longitude was excluded from the model (Currie *et al.*, 2018).

The model including depth, slope, latitude and distance to shore was ranked highest (Table 4). Including latitude only marginally reduced *ΔAIC* (0.65). Therefore, the final model selected included covariates for depth, slope and distance to shore.

$$\text{logit}\ (All\_whales\ \psi i) = 1.12 + 0.05_{depth} - 2.31_{slope} - 22.58_{distance\ to\ shore}$$

Distance proved to be the most important variable for determining humpback whale use. Slope also showed a negative relationship in this model, where on the contrary, probability of whale use increased with increasing depth.

Given the output, the individual site estimates of the probability of use (psi per site), standard error and 95 % confidence intervals were provided as a measure of the relative suitability of the site given the model predictions.

To assess the lack of fit of the model, a significance level of 0.05 was used, whereby $p < 0.05$ was evidence of lack of fit (MacKenzie and Bailey, 2004; MacKenzie *et al.*, 2017). The Pearson's Chi-Square Goodness of Fit test showed no lack of fit for the chosen model ($p = 0.9901$). The overdispersion parameter $\hat{c}$ (0.6806) approached the value of one, which confirms the model is an adequate description of the data (MacKenzie and Bailey, 2004).

Table 4. AIC values for occupancy models describing the influence of environmental factors on the occurrence of humpback whale pods regardless of group size or calf presence/absence; i.e. visits of humpback whales in Zavora Bay in the combined seasons of 2017 and 2018 (June to October). Table values represent model , the change in AIC for the best model (ΔAIC), the Akaike weights (AIC_{wt}) and the number of parameters (K).

Model	K	*AIC*	*ΔAIC*	AIC_{wt}
p(year + temp), ψ(depth + slope + distance + latitude)	8	5092.60	0.00	0.3554
p(year + temp), ψ(depth+ slope + distance)	7	5092.71	0.65	0.2568
p(year + temp), ψ(slope + distance)	6	5094.31	2.25	0.1154
p(year + temp), ψ(slope + distance + latitude)	7	5094.50	2.44	0.1049
p(year + temp), ψ(slope)	5	5095.08	3.02	0.0785
p(year + temp), ψ(slope + latitude)	6	5096.63	4.57	0.0362
p(year + temp), ψ(slope + depth)	6	5096.79	4.73	0.0334
p(year + temp), ψ(slope + depth + latitude)	7	5098.46	6.40	0.0145
p(year + temp), ψ(distance + depth + latitude)	7	5101.08	9.02	0.0039
p(year + temp), ψ(depth + distance)	6	5103.90	11.84	0.0010
p(year + temp), ψ(distance)	5	5112.23	20.17	0.0000
p(year + temp), ψ(distance + latitude)	6	5112.45	20.39	0.0000
p(year + temp), ψ(depth)	5	5116.93	24.87	0.0000
p(year + temp), ψ(latitude)	5	5117.85	25.79	0.0000
p(year + temp), ψ(depth + latitude)	6	5118.90	26.84	0.0000
p(.), ψ(.)	2	5185.71	93.65	0.0000

Pods with calves

The model including calf sightings showed that all survey specific covariates (i.e. month, year and temperature) affected the detectability of the whales (Table 5), however including temperature only marginally reduced ΔAIC (0.64 < 1). Therefore, including only month and year gives the most parsimonious model to explain humpback whale calf habitat use.

$$\text{logit}\ (Calf\ p) = -\ 0.12 + 0.27_{month} - 0.67_{year}$$

Probability of detection increased from early whale season (June) to late whale season (October). Calf detection is characterized by a negative relationship with progression towards 2018.

The conditional models after model selection of detection probability (Table 6) show that the model including 'depth' and 'distance to shore' is best for explaining the variation in distribution of the calves (ΔAIC = 0.00).

$$\text{logit}\ (Calf\ \psi_i) = -\ 0.69 + 0.08_{depth} - 46.16_{distance\ to\ shore}$$

Probability of whale use from calves with pods is characterized by a negative relationship with distance to the shore; the further away from shore, the lower the probability of humpback whale use. This same probability of whale use however increases with depth.

The coefficient of 'distance to shore' for the calf model (46.16) is larger than the one for all sightings combined (22.58) and though the first model also includes calf sightings, this shows a stronger preference of the calves for waters closer to shore.

A Pearson's Chi-Square Goodness of Fit test showed evidence for a lack of fit ($p < 0.05$). There is also more variation in the observed data than expected by the model, as confirmed by the overdispersion parameter ($\hat{c}$ = 5.2281).

Table 5. Model selection results of detection probability for humpback whale pod sightings that include calves in Zavora Bay in the combined seasons of 2017 and 2018 (June to October). Table values represent model , the change in AIC for the best model (ΔAIC), the Akaike weights (AIC_{wt}) and the number of parameters (K).

Model	K	*AIC*	*ΔAIC*	AIC_{wt}
p(month + year + temp)	5	1720.30	0.00	0.5720
p(year + month)	4	1720.88	0.58	0.4280
p(temp + year)	4	1741.30	21.00	0.0000
p(month)	3	1741.77	21.47	0.0000
p(month + temp)	4	1742.25	21.95	0.0000
p(year)	3	1744.50	24.20	0.0000
p(temp)	3	1768.08	47.78	0.0000
p(.)	2	1769.21	48.91	0.0000

Table 6. AIC values for occupancy models describing the influence of environmental factors on the occurrence of humpback whale pod sightings with caves in Zavora Bay in the combined seasons of 2017 and 2018 (June to October). Table values represent model , the change in AIC for the best model (ΔAIC), the Akaike weights (AIC_{wt}) and the number of parameters (K).

Model	K	*AIC*	*ΔAIC*	AIC_{wt}
p(month + year), ψ(depth + distance)	6	1707.78	0.00	0.2827
p(month + year), ψ(depth+ slope + distance)	7	1707.98	0.20	0.2558
p(month + year), ψ(depth + distance + latitude)	7	1708.07	0.29	0.2446
p(month + year), ψ(depth + slope + distance + latitude)	8	1708.83	1.05	0.1673
p(month + year), ψ(slope + distance)	6	1712.89	5.11	0.0220
p(month + year), ψ(slope + latitude + distance)	7	1714.80	7.02	0.0085
p(month + year), ψ(slope)	5	1715.02	7.24	0.0076
p(month + year), ψ(slope + latitude)	6	1716.81	9.03	0.0031
p(month + year), ψ(slope + depth)	6	1716.86	9.08	0.0030
p(month + year), ψ(distance)	5	1717.09	9.31	0.0027
p(month + year), ψ(depth + slope + latitude)	7	1718.58	10.80	0.0013
p(month + year), ψ(distance + latitude)	6	1718.94	11.16	0.0011
p(month + year), ψ(depth)	5	1722.41	14.63	0.0002
p(month + year), ψ(latitude)	5	1722.58	14.80	0.0002
p(month + year), ψ(depth + latitude)	6	1723.96	16.18	0.0001
p(.), ψ(.)	2	1769.21	61.43	0.0000

Discussion

Bias and study limitation

Long-term monitoring programs are critical for understanding population trends to allow effective management measures for conservation. Nevertheless, it is particularly challenging in developing countries and even more in remote locations, where resources and experts are limited. As a result, many small organizations rely on trained volunteers to collect data which may enhance inconsistency in the data. Biases on data collection were mitigated by choosing a simple methodology, in-person training of volunteers prior to surveys, and use of a survey protocol (Lewandowski and Specht, 2014). Nevertheless, sample efforts were variable depending on the availability of volunteers. To calibrate this, for a general view of whale sightings over the years SPUE was applied, while for the determinate occupancy model only data from 2017 and 2018 was used.

Functionality as part of known breeding ground

The results from this study show that the relative abundance of humpback whales in Zavora Bay displays a pattern typical for a breeding ground (Stern, 2009), with an increase in abundance just after the arrival in June, a peak in July, followed by a decrease in September which coincides with the southern migration of the whales. A similar breeding pattern has been observed in known humpback whale breeding grounds in the South Pacific Ocean (Scheidat *et al.*, 2000), the Southern Atlantic (Martins *et al.*, 2001) and the North Atlantic (Mattila *et al.*, 1994). If the study area was merely a location along the migration route and not actively used as a breeding ground, the patterns would have displayed a bimodal distribution with a high number of whales during the migration periods, i.e. June and September (Best *et al.*, 1995; Scheidat *et al.*, 2000).

According to Craig *et al.* (2003), immature animals and late-pregnant females are the first to arrive at the breeding grounds, followed by mature males and non-pregnant females. This induces an increase of modal pod size to two and even three towards the end of the season (Scheidat *et al.*, 2000). This increase in group size is explained by mature males who seek access to reproductively active females and at the same time provide protection against predators, such as killer whales (*Orcinus orca*) (Whitehead and Glass, 1985; Pitman *et al.*, 2015). The observed decrease in mean group size from beginning to mid-season and again towards the end of the season is in contradiction with these patterns. This can partially be explained by the limitations of the 2018 calf data where no distinction between 'absent' or 'undetermined' was made, likely causing an underestimation of calves. However, the mean group size ranged from 1.6 (± 0.9) to 2.2 (± 1.3) individuals, so whether or not a statistically significant decrease in these values is biologically meaningful is debatable. It is more likely that the group size stagnated to a modal size of 2 individuals and considering that there were groups with up to 10 individuals, the presence of escorts accompanying the mother-calf pairs is patent. Available data on calf presence from 2017 show an increase in calf numbers towards the end of the season. Non-standardized data from 2014 and 2015 also support this finding.

Competitive groups, often associated with breeding seasons and ovulating females, arise due to males seeking access to single mature females (Tyack and Whitehead, 1982; Oña *et al.*, 2017), leading to aggressive surface-active behaviour (Tyack, 1981; Clapham *et al.*, 1992; Kavanagh *et al.*, 2017). Likewise, escorts accompanying a mother-calf pair display a similar array of behavioural events (i.e. breaching, repetitive slapping of the pectoral fins and flukes) in an attempt to protect the rest of the focal group. This form of close-range communication within and between groups (Kavanagh *et al.*, 2017) was observed in Zavora every year.

Additionally, singing was heard on almost every SCUBA dive throughout the season (Cullain, *pers. comm.*). Humpback whale singing is traditionally heard in breeding areas (Oña *et al.*, 2017), although some vocalization patterns have been observed in feeding areas (Vu *et al.*, 2012). Though systematic acoustic research was not conducted, the presence of singers further exemplifies the area as an important reproduction ground, but a further understanding of the song production within the study area is recommended.

Areas of preference and driving factors for habitat suitability

Models are an attempt to simplify complex distributional patterns with a reduced set of predictor variables and contain a degree of bias and mismatch between the predictions and the reality they describe (Barry and Elith, 2006). The occupancy model as described by MacKenzie (2003) is designed to model distributional patterns and accounts for a large part of this mismatch, by allowing for imperfect detection (MacKenzie, 2006). This method provides a flexible modelling framework for the incorporation of both covariate information and missing observations (MacKenzie, 2006).

Detection probabilities were slightly influenced by temperature. This lends support to the hypothesis that humpback whale seasonal migration is driven by energetic demands (Burns, 2010). Calves are born in warmer waters so that they are able to conserve more energy, which can then be used for growth and development, leading to higher reproductive success than if they were born in colder waters (Clapham, 2001; Burns, 2010). Additionally, the year of the survey influenced the detection rate of the whales, which can be explained by the survey effort that was twice as high in 2018 compared to 2017. Though corrected for in the relative distribution maps, this was not accounted for in the model and must be remembered when interpreting the results. Further studies applying a multi-annual approach, with the use of a multi-season occupancy model are recommended and would enable the estimation of colonization, extinction and persistence (MacKenzie *et al.*, 2003). The increased calf sightings with progression towards the end of the whale season (the covariate 'month' is positively related to increased calf observations), can be related to the fact that as the breeding season progresses, more mothers will have birthed their calves, demonstrating temporal segregation (Scheidat *et al.*, 2000; Pack *et al.*, 2017; Trudelle *et al.*, 2018).

Continuing with the model that best explains the detectability of the humpback whales, the probability of occupancy (probability of whale use in this case) was predicted. These results confirm the observations from the distribution maps, where the whales are more or less equally distributed throughout the continental shelf waters. This conforms to what is observed in other breeding grounds (Félix and Botero-Acosta, 2011; Bortolotto *et al.*, 2017; Gonçalves *et al.*, 2018; Trudelle *et al.*, 2018). Areas most often visited by the whales have two parameters in common, namely depth and distance to shore, which are undoubtedly connected to each other (Ersts and Rosenbaum, 2003; Burns, 2010) and have shown to be driving factors for humpback whale distribution (Ersts and Rosenbaum, 2003; Currie *et al.*, 2018; Gonçalves *et al.*, 2018). The limited role of the depth of the bay might be explained by the fact that the bathymetry within Zavora Bay region is not highly complex and only consists of two reef systems with different depths, with no steep gradient separating these areas from each other. This helps to understand why on a fine scale depth plays a rather limited role, but distance to shore has a greater influence, though both variables cannot completely be interpreted independently from each other (Ersts and Rosenbaum, 2003; Burns, 2010).

Incorrect recordings of calf sightings might explain the results of the GOF test, in which the overall model including all sightings proved a good fit for the data, where the calf model was not. However, in combination with the mapped distribution, both models identified key trends. One of them being the mother-calf pair separation. The distribution of mother-calf pairs is usually much higher in shallow waters, and simultaneously much closer to shore (Bruce *et al.*, 2014; Mattila *et al.*, 1994; Smultea, 1994; Félix and Botero-Acosta, 2011). This might be biased due to the distance between the observer and the deeper reefs associated with rough sea conditions which might hinder their occupancy and detection due to the size of the calves (Ryan *et al.*, 2013); nevertheless anecdotal boat observation in Zavora does suggest a higher abundance of mother-calf pairs closer to shore. Their distribution might be a strategy to avoid interactions with competitive groups (Martins *et al.*, 2001) or potential predators such as sharks or killer whales (Chittleborough, 1953; Smultea, 1994). At fine spatial scale, this avoidance strategy ensures energetically expensive associations with multiple male groups are minimized. Calves are then protected from accidental injury (Trudelle *et al.*, 2018) in these calm sea conditions and provided with shelter from strong ocean currents (Trudelle *et al.*, 2018). Females have also been shown to decrease their active swimming speed in these sheltering areas characterized by a lower current speed (Trudelle *et al.*, 2016), which allows them to make more localized movements related to the breeding activity (i.e. searching, pairing, mating and resting). The distribution of whales can also be related to the bottom topography (Hastie *et al.*, 2003) since courting males seek deeper waters to avoid collision with the sea floor or reef structures (Mattila *et al.*, 1989), explaining why the slope of the ocean floor influenced occupancy by adult whales in this study. The preference of courting whales for deeper waters explains why escorted mother-calf groups can be found further away from shore compared to unescorted mother-calf pairs as male escorts are assumed to be prospecting for potential mating opportunities (Trudelle *et al.*, 2018).

Preference of mother-calf pairs for near-shore, shallow regions makes them more vulnerable to human related disturbances (Ersts and Rosenbaum, 2003; Félix and Botero-Acosta, 2011; Pack *et al.*, 2017) and the progression of coastal development forces these whales to expand their range to new habitats (Andriolo, 2010). Management should aim to avoid critical human-animal conflicts and protect the habitat important for successful calf rearing (Smultea, 1994). Several action plans for the conservation of marine systems and fisheries of the southwestern Indian Ocean, including Zavora, have been developed in order to establish regional marine protected areas and to implement sustainable coastal management measures (Trudelle *et al.*, 2018). Therefore, the data and conclusions from this research can provide important information on the distribution and habitat patterns of humpback whales in Mozambique and further assist with future regional coastal management plans.

Latitude and longitude were included as site specific covariates, as they are characteristic for each predetermined site and might identify importance of areas based on hidden covariates or variables which were not recorded. Cloud cover, sea state and swell were factors that initially were expected to impact the detection probability of the whales (Findlay *et al.*, 2011), however, earlier research in Zavora (Allen, 2016) shows that environmental variables did not affect the ability to survey whales when sea state is below Beaufort Scale 4, except for the effect of glare – a confounding factor in the ability to detect cetaceans. Therefore, these environmental variables were discarded from the occupancy model. Marine vessel presence was not recorded in a standardized way and therefore not included in the model. It is recommended that data on marine vessel presence as described in Bas *et al.* (2017) is included in future surveys.

Further, investigating different uses of the bay, as well as anthropogenically induced mortalities of the whales could be mapped to identify areas of concern where anthropogenic use conflicts with the humpback whale habitat use. Results from this study show the significance of the area for humpback whales and can be used as a baseline to determine the habitat suitability of regions along the Mozambican coastline for these whales.

Conclusions and future implications

This study attempted to collate all of the existing survey data on humpback whales passing through Zavora Bay, Mozambique, and, for the first time, provide clarification of their habitat choice in these waters. Both reproductive behaviour and the observation of young calves, as well as the pattern of relative abundance throughout the season, provide evidence that the area off the coast of Zavora serves as a reproductive area for humpback whales as part of the larger scale breeding ground of southern Africa. Remaining uncertainties concerning population estimates and breeding ground affinity can be reduced by an increased effort in photo-identification processes and the comparison of catalogues of different sites and regions along the coastline. This is necessary in order to raise understanding of the migration routes and the distribution of breeding grounds throughout the region. For the humpback whales in the Zavora Bay area, a new photo-identification catalog was created (Fluke Matcher V.4.21) using photos assembled through the open resource platform called www.mozwhales.org. However, the current effort in photo-identification remains low and more data is needed to draw adequate conclusions about this population.

Areas characterized by a depth no greater than 35 m, within 10 km from shore are most probable to be used by the whales visiting Zavora Bay. A mother-calf pair separation from other adult pods was observed, with a preference for waters closer to the shore. Model outcomes predict the detection rates to be determined by temperature of the water, year and month. Considering the possibility of imperfect detection, depth and distance from shore were identified as main factors determining the suitability of the sites in the bay. After optimization of the model, these findings can be used to project to surrounding areas and further map the distribution of humpback whales. This macroecological study is the first to provide baseline information on the spatial distribution and habitat preferences of humpback whales in Zavora Bay. Further research to enhance our knowledge on priority areas for protection, management and conservation measures is recommended.

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