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Habitat selection of two island-associated dolphin species from the south-west Indian Ocean

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ABSTRACT

Identifying suitable habitats of protected species is an essential question in ecology and conservation planning. Modelling approaches have been widely used to identify environmental features that contribute to a species' ecological requirements and distribution. On Reunion Island, a fast-growing French territory located in the south-western Indian Ocean, anthropogenic impacts are mainly concentrated along the coast, representing a potential threat for Indo-Pacific bottlenose (*Tursiops aduncus*) and spinner (*Stenella longirostris*) dolphins, two resident coastal species. Beside coastal development, commercial and recreational dolphin-watching are growing, particularly along the west coast. To promote effective local management, habitat modelling was applied using presence-only data collected from 2008 to 2012 on the west coast of the island. Ecological Niche Factor Analyses were used to investigate the effect of physiographic variables on the distribution of these two dolphin species and delineate suitable habitats. It was found that the core habitat of Indo-Pacific bottlenose dolphins was mainly restricted by depth and confined to coastal waters ranging from 4.7 to 75.8 m deep. The species preferentially used soft substrates (sand and mud) and tended to be ubiquitous in terms of substrate type/color used. Foraging activities were significantly related to soft substrates. The diurnal core habitat of spinner dolphins was confined to one discrete area, on the flat portion of the insular shelf, between 45.1 m and 70.7 m of depth. Suitable habitat was mainly related to soft and light-colored substrates, with a clear avoidance of dark-colored substrates. The core habitats of both species were very restrained spatially and therefore vulnerable to human activities. The fine scale habitat mapping achieved in this study represents baseline data to conduct ad hoc impact assessment and support conservation actions.

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1. Introduction

Hutchinson (1957) defined the "ecological niche" as a hypervolume with *n*-dimensions where all environmental conditions are gathered to ensure population survival. *N*-niche dimensions are often classified into three main approaches, these being "habitat" (spatial distribution), "seasonality" (temporal distribution), and "resources" (trophic relationships). In practice, assessing all the *n*-dimensions that make up a niche is extremely challenging, especially for large and mobile species such as marine mammals and only part of an ecological niche is commonly assessed when investigating the factors driving a species' distribution. Generally, only available environmental data that are assumed to play an important role in a species' ecology, are taken into account. The most common variables used to assess cetacean habitat preferences are abiotic factors that have either a direct or indirect influence on distribution (e.g. depth, slope and distance from shore, temperature, salinity, etc.), mainly because they are fixed parameters that can be accurately and systematically measured (Cribb et al., 2008; Embling et al., 2010; Gannier and Petiau, 2006; Mannocci et al., 2015; Praca and Gannier, 2008; Praca et al., 2009; Roberts et al., 2016). Based on remote sensing data, biotic factors such as chlorophyll-a concentration are sometimes used as a proxy of productivity and prey abundance at a large spatial scale (Mannocci et al., 2015; Panigada et al., 2008; Praca et al., 2009; Roberts et al., 2016). Thus, despite being considered as one of the main forces driving a species' distribution, prey availability and predation risk are rarely considered in predictive models (Eierman and Connor, 2014; Heithaus and Dill, 2002; MacLeod et al., 2004; Torres et al., 2008), especially due to the complex nature of the data and their spatio-temporal variability. Instead, few studies have investigated seabed influence on cetacean distribution as this factor may have an effect on prey distribution and may affect predator detection (MacLeod et al., 2004; Thorne et al., 2012;

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Torres et al., 2008; Tyne et al., 2015).

Identifying and quantifying key habitats for cetaceans is crucial for management and conservation planning and can provide scientific bases to mitigate the impact of human activities. Coastal development can have a significant impact on cetacean habitat through chemical pollutants (Mwevura et al., 2010; Pierce et al., 2008), acoustic pollution (Borggaard et al., 1999; Dähne et al., 2013), and non-degradable litter such as plastic debris (Simmonds, 2012). Vessel traffic and whale- or dolphin-watching activities have also been shown to affect animal behavior and are believed to have an impact on breeding and fitness if resting periods are disturbed (see Parsons (2012) for a review). In Reunion Island, a French overseas territory located in the south-west Indian Ocean, human activities and their impacts on coastal marine habitats are intensifying as a result of population growth. Coastal planning and project developments in the marine environment (e.g. harbor extension, embankment, road construction, renewable energy, etc…) are increasing. Whale/dolphin-watching is growing on the west coast of the island and no specific legislation regulates this activity, although a code of conduct is in place (http://www.glo bice.org/02_Charte.htm). To date, knowledge on habitat requirements of coastal cetacean species are lacking to conduct ad hoc impact assessment and support conservation actions.

Among the 21 cetacean species recorded in Reunion (Dulau-Drouot et al., 2008; Globice, unpublished data), the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) and the spinner dolphin (*Stenella longirostris*) are the most commonly encountered year-round in coastal waters. Indo-Pacific bottlenose dolphins are observed all along the coast in waters 22 m deep on average (Dulau-Drouot et al., 2008). Spinner dolphins use a larger depth range (3–720 m), and, their spatial distribution can overlap with *T. aduncus* in the morning (Dulau-Drouot et al., 2008). In general, spinner dolphins are known to undertake daily movements between sheltered bays and reefs, used for resting and social activities in the morning, and offshore waters reached in the late afternoon for nocturnal feeding purposes (Norris et al., 1994; Tyne et al., 2014). Off Reunion, spinner dolphins appear to not favor sheltered and enclosed bays for resting, but rather occur in deeper waters over insular shelf waters (Dulau-Drouot et al., 2008).

This study aimed at using a presence-only modelling approach to describe habitat preferences of Indo-Pacific bottlenose and spinner dolphins off Reunion, using fine scale bathymetric and sedimentary data. An Ecological Niche Factor Analysis (ENFA), which provides a measure of the realized niche within the available habitat (Hirzel and Arlettaz, 2003; Hirzel et al., 2002, 2006) was used in order to produce habitat suitability maps and to identify core habitats for both species. Presence-only models have the advantage of discarding potential biases associated with absence data (Gu and Swihart, 2004). For highly mobile marine mammals, it is indeed very difficult to discriminate true absence data from false absence data (i.e. areas used by a species but no sightings made during the survey), especially when survey efforts are insufficient or uneven. ENFA has been tested and proved to be robust to describe cetacean habitats (Hirzel et al., 2001; MacLeod et al., 2008; Praca and Gannier, 2008; Praca et al., 2009; Skov et al., 2008a), and has also been used for other marine species (McKinney et al., 2012; Skov et al., 2008b; Stewart et al., 2014) and more generally for mobile mammals (Mertzanis et al., 2008).

2. Materials and methods

2.1. Data collection

Presence data were collected from 2008 to 2012 off Reunion Island (55°33′E, 21°07'S). Boat-based surveys were conducted up to 12 nautical miles offshore, in good weather conditions (Beaufort < 3), and at an average speed of 6 knots. Daily surveys lasted between 3 and 6 h and were conducted both in the morning and the afternoon. Effort spatial distribution was constrained by general weather conditions, port location, and boat availabilities. The west coast was surveyed on a regular basis, while the north and south coasts were covered to a lesser extent. The east coast was poorly surveyed, mostly due to its exposure to rougher sea conditions (Fig. 1).

Search efforts were recorded along the survey tracks by reporting time, GPS positions and sea state conditions every 15 min. When cetaceans were detected, sighting positions were recorded together with the group's estimated size and main activity according to four categories: socializing, resting, travelling, and foraging.

2.2. Environmental variables

Ecological Niche Factor Analyses (ENFA) were performed using Biomapper 4.0 software (Hirzel et al., 2002, 2004) to model habitat
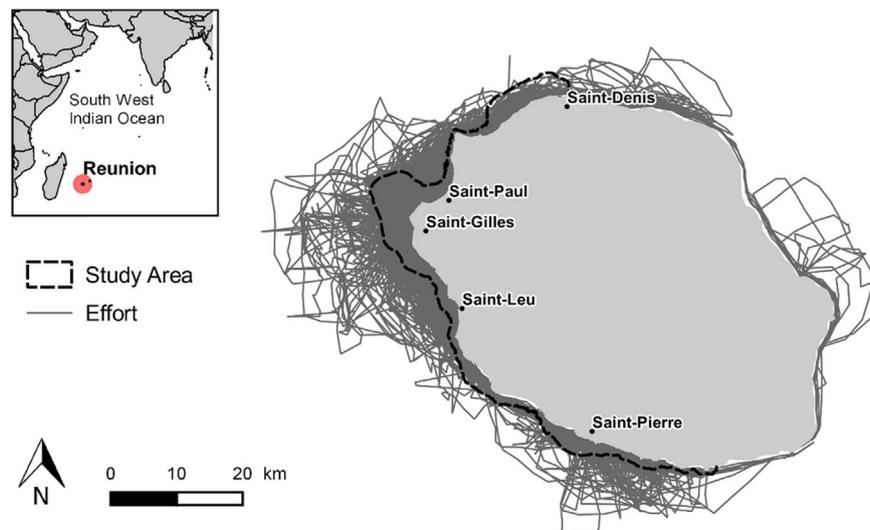

Fig. 1. Searching effort conducted during boat-based surveys around Reunion in 2008–2012 and the study Area used to run the ENFA model, delineated by the 100 m depth contour, on the west coast of the island.

suitability. Based on this model, Biomapper linked presence-only data to environmental predictor variables called Eco-Geographical Variables (EGV). The EGVs used were depth, slope, distances to the shore, to the reef and to different seabed categories (Table 1), to assess their influence on dolphin coastal distribution. Seafloor depth and slope were interpolated with MapInfo's *Grid Analyzer* extension from Digital Elevation Model points provided by the French Naval Hydrographic and Oceanographic Service (SHOM). Distances to the shore and to the reef were calculated using Biomapper's DistAn module. Seafloor data was available for portions

Table 1
Description of the Eco-geographical Variables (EGVs) used in the ENFA models.

| EGVs	Type
Depth (m)	–
Slope (°)	–
Distance-to-reef (m)	–
Distance-to-shore (m)	–
Distance-to-soft -substrate (m)	Basaltic sand, bio-detrital sand, muddy and bio-detrital sand, muddy and basaltic sand, muddy mixed sand, vase, mixed sand.
Distance-to-rocky-substrate (m)	Scattered rocks, single rocks, rocky areas, rocks flush with surface soil
Distance-to-dark-colored-substrate (m)	Basaltic sand, muddy and bio-detrital sand, muddy and basaltic sand, muddy mixed sand, vase
Distance-to-light-colored-substrate (m)	Bio-detrital sand
Distance-to-intermediate-colored-substrate (m)	Mixed sand, scattered rocks, single rocks, rocky areas, rocks flush with surface soil
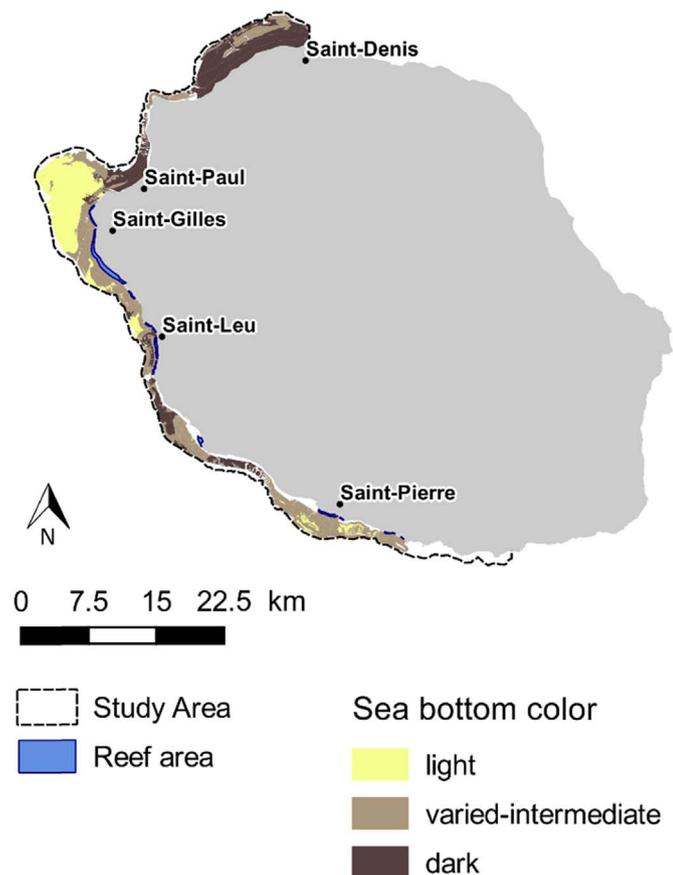
Fig. 2. Map of sea bottom color (light, intermediate and dark) around Reunion (< 100 m). Light-color bottom is of bio-detrital origin while dark bottom is of basaltic origin. Extracted from the BRGM morphosedimentary data (Guennoc et al., 2008). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
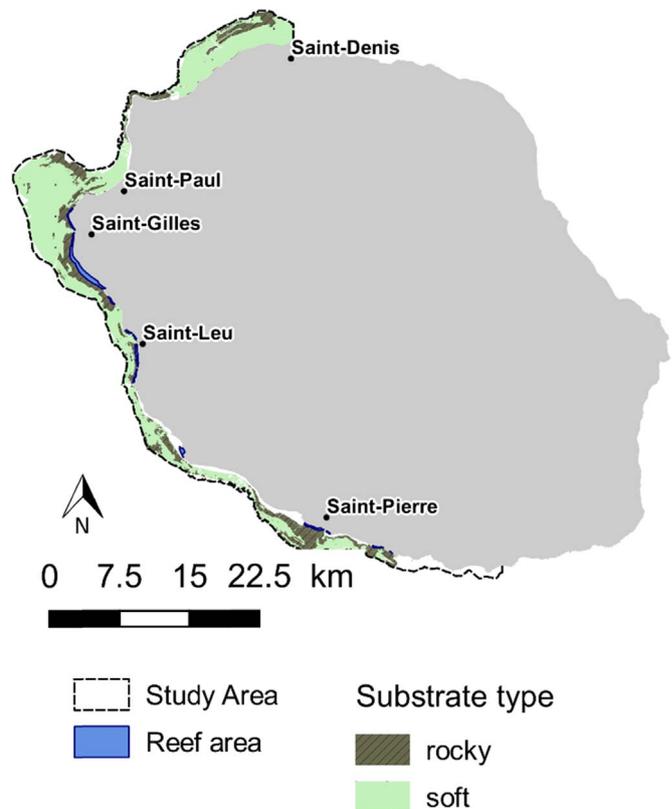

Fig. 3. Map of substrate type (rocky, soft) around Reunion (< 100 m). Extracted from the BRGM morphosedimentary data (Guennoc et al., 2008).

of the coastal waters from −20 m to −100 m (Guennoc et al., 2008). From −20 m to the coastline, the nature of the seabed was extrapolated using aerial ortho-photographs. Based on the 11 seabed types available in the initial sedimentary dataset (Guennoc et al., 2008), different seabed categories were defined (Figs. 2 and 3) according to the substrate's type ('soft', i.e. sand or mud vs. 'hard', e.g. rocks) and color ('dark', 'light' and 'intermediate'). The distance to each substrate category was calculated using Biomapper's DistAn module.

EGV collinearity was tested using a correlation matrix in Biomapper. When two EGVs were highly related (Pearson correlation coefficient > 0.75), one of them was excluded from the model. Distance to the reef was highly correlated with distance to light-colored seabeds and was therefore excluded. Distance to intermediate-colored seabed was also excluded because of its collinearity with distance to hard substrates.

2.3. Study areas and model resolution

The eastern part of the island, which was less surveyed, was discarded from the analysis in order to obtain a consistent survey effort throughout the study area. Given that substrate data were available for shallow waters only (< 100 m), the Survey Area was restricted to the 100 m depth contour to allow for a fine scale description of the continental shelf habitat (Fig. 1). Within the Survey Area, presence and environmental data were formatted in a 200 × 200 cell grid and exported in Biomapper.

2.4. ENFA model

The Ecological Niche Factor Analysis (ENFA) was run for each species separately. The ENFA compares the distribution of environmental data (EGV values) between grid cells in which the

species were observed (presence data) and cells from the entire grid (reference dataset). Each grid cell is projected within a multidimensional space using EGV values as vector components. Overall, two point clouds are projected in space: presence data and reference dataset. Information is then summarized in k factorial axes that concentrate most of the information. In this model, the value of k was chosen to summarize at least 90% of the information. For higher rates, the k number of axes was limited by broken stick methods based on the eigen-values (Hirzel et al., 2002). Among the k axes, the ENFA extracts one axis of marginality axis and several axes of specialization. The marginality axis represents the deviation of the species' mean distribution (presence dataset) from the global mean (reference dataset), and therefore identifies the preference of the species for specific conditions within the available environment. The model produce positive or negative marginality scores, which indicate directionality of trends. The specialization axes are extracted orthogonally to the marginality axis and represent the narrowness of the niche on given environmental variables. They allow to identify the species' level of specialization by comparing the reference dataset distribution's standard deviation to the species' standard deviation (Hirzel et al., 2002). The model produce specialization scores, which indicate how restrictive a species is for a given variable (absolute values are used).

Based on marginality and specialization score values, the ENFA model uses a geographical mean algorithm to compute a Habitat Suitability Index (*HSI)* for each grid cell, ranging from 0 (low suitability) to 100 (high suitability). This index was used to draw a habitat suitability map for each species (Hirzel and Arlettaz, 2003).

Given that the data came from a single data set (i.e. survey coverage for each species was similar), differences between species were could be assessed by comparing 3 overall indices: global marginality **M**, global specialization **S** and global tolerance **T**, produced by the ENFA models (Hirzel et al., 2006). **M** ranges from 0 (non-marginal habitat) to 1 (highly marginal habitat). **S** starts at 0 but do not have a superior limit and was therefore difficult to interpret. Consequently, **T**, which is the inverse of **S**, was used to assess the degree of non-specialization of the species. **T** ranges from 0 (intolerant species with a highly specialized habitat) to 1 (flexible species with no specialized habitat).

2.5. Model evaluation and habitat suitability range

The ENFA models were validated by a 10-fold cross-validation. The presence dataset was randomly divided into 10 subsamples: 9 of them were used as calibration data to compute a habitat suitability map and the left-out sample was used to validate the computed map. The process was repeated by changing the validation subsample in turn in order to evaluate the model's predictive accuracy (Hirzel and Arlettaz, 2003).

A threshold-independent method suited to presence-only models was used to evaluate the model's ability to predict suitable habitats (Hirzel et al., 2006). This method first required partitioning the *HSI* range into classes. For a class *i* with a fixed range, two frequencies were calculated: (1) *Pi,* the predicted frequency of validation presence-cells (i.e. the proportion of validation presence-cells that fall within the class *i*) and (2) *Ei,* the expected random frequency (i.e. the proportion of the overall number of cells that fall into the class *i*). The assessment of the model's reliability was based on the predicted to expected ratio: $Fi=(Pi/Ei)$. *Fi* was calculated continuously all along the *HSI* range over a moving window *i* to obtain a smooth curve named the *Fi-curve,* which represented the evolution of the *Fi*-value according to the average suitability level of class *i*. A good and discriminating model shows a monotonic increasing *Fi*-curved. The Boyce index (*B),* which is a Spearman correlation coefficient between *HSI* and

Fi, was used to test the monotonic increase of the curve and to assess the model's reliability. **B** varied between -1 (model worse than a random model), 0 (random model) and 1 (perfect model).

The 10-fold cross validation was used to compute a mean and standard deviation for **B** and for the *Fi*-curve, in order to assess the model's precision and accuracy. The higher the mean value is, the better the model's accuracy is. The smaller the variance is, the better the precision is. The shape of the *Fi*-curve also informs on the model's predictive power. A well-fitted model presents a sigmoid shape.

Based on the shape of the *Fi*-curve, four habitat categories were defined: "unsuitable", "marginal", "suitable" and "core" habitats (Hirzel et al., 2006; Praca et al., 2009). A first threshold was defined by the *Fi* random line (*Fi*=1), where the predicted frequency was equal to the expected frequency. The portion of the *Fi*-curve below the *Fi* random line was considered as "unsuitable habitat". The part close to the *Fi* random line was considered as "marginal habitat" (i.e. random and inconsistent use). "Suitable habitat" was defined as the portion of the *Fi*-curve above the *Fi* random line and showing a monotonic increase. A "core habitat" was distinguished by an exponential increase toward the highest *HSI* values. The contours of the core habitat of each species were extracted and their surface area were computed in Mapinfo (version 7.5).

To gain further insight into habitat use, the activity budget (expressed as percentage of sightings in each of the 4 activity categories: socializing, resting, travelling, and foraging) and mean group size were computed for the different substrate types/color and differences were assessed using non-parametric statistical tests.

3. Results

3.1. Sighting data

A total of 787 daily surveys were conducted in 2008–2012. Effort achieved within the Study Area was 23,698 km, representing 75% of the overall survey effort conducted off Reunion. Survey effort was evenly distributed within the 200×200 m grid, with a mean of 3.7 km (SE=0.06) achieved per cell.

A total of 517 Indo-Pacific bottlenose dolphin and 241 spinner dolphin sightings were made off Reunion during the survey period (2008–2012), of which 496 (95.75%) and 224 (92.95%) respectively occurred in the Study Area. Within the 200×200 m grid, presence of Indo-Pacific bottlenose dolphin was recorded in 382 cells and spinner dolphin in 203 cells.

Indo-Pacific bottlenose dolphins were encountered in groups ranging from 1 to 30 individuals (Table 2), with an average group size of 6.4 dolphins (SE=0.2). Mean sightings depth was 39.7 m (SE=1.5), with most sightings occurring within 19–51 m deep waters (Q1–Q3, first and third quartile respectively). Thus the Study Area (< 100 m) encompassed the entire *T. aduncus* depth range. The mean distance to the shore was 1160 m (SE=45.4) and mean bottom slope was 2.7° (SE=0.1). In the Study Area, most sightings occurred above soft substrates (80%) compared to hard substrates (20%). In terms of color, the majority (51%) of sightings occurred above intermediate-colored seabeds, followed by dark-colored seabeds (33%) and light-colored seabeds (16%) (Fig. 4).

Spinner dolphins were observed in groups ranging from 6 to 250 individuals, with a mean group size of 57 dolphins (SE=2.3). The species occurred in 75 m deep waters on average and showed a very narrow depth range with most sightings occurring between 51 and 63 m (Q1–Q3, Table 2). Sightings occurred at a mean distance of 2375 m (SE=96.6) from the coast in mean bottom slope of 1.9° (SE=0.2). In the Study Area, most sightings occurred over soft substrates (90%) and light-colored seabeds (63%). Only 4% of the

Table 2
Basic statistics of group size, bottom depth, slope and distance from shore of Indo-pacific bottlenose and spinner dolphin sightings made during 2008–2012 off Reunion.

Species		Group size	Depth (m)	Distance (m)	Slope (°)
Indo-Pacific bottlenose dolphin	**Mean**	6.42	39.72	1160	2.676
	SE	0.19	1.50	45.39	0.12
	Median	5	36	927	1.956
	Range	1–30	2–440	33–9717	0.056–20.632
	Q1–Q3	3–8.75	19–51	486–1384	1.398–2.887
	N	514	516	516	517
Spinner dolphin	**Mean**	57.16	74.75	2375	1.919
	SE	2.25	6.17	96.6	0.23
	Median	50	60	2099	0.706
	Range	6–250	5–770	129–14,448	0.019–27.808
	Q1–Q3	30–76.25	51–63	1514–2981	0.2421–3.039
	N	240	241	241	241

Table 3
Output of the Indo-Pacific bottlenose dolphin ENFA model: Marginality (Mar.) and Specialization (Spec.) scores obtained for each Eco-Geographical Variables (EGV) and proportion of information explained by each axis (in%).

EGV	Marg. (22%)	Spec. 1 (37%)	Spec. 2 (14%)	Spec. 3 (9%)	Spec. 4 (7%)	Spec. 5 (6%)
Depth	−0.573	0.051	0.427	0.476	0.229	0.481
Distance-to-light-co-lored-substrate	−0.469	0.372	0.262	0.085	0.105	0.080
Distance-to-soft-substrate	−0.397	0.709	0.247	0.570	0.442	0.335
Distance-to-shore	−0.363	0.393	0.693	0.502	0.143	0.253
Distance-to-dark-co-lored-substrate	−0.311	0.049	0.220	0.332	0.823	0.020
Slope	−0.207	0.083	0.398	0.220	0.118	0.510
Distance-to-rocky-substrate	−0.151	0.438	0.030	0.176	0.171	0.570

sightings were made on dark-seabeds and 33% on intermediate-colored seabeds (Fig. 4). The majority of sightings (99%) occurred in the morning, while only 2 sightings were made after 1:00 p.m.

The groups' main activity was determined for 60% (N=311) of all Indo-Pacific bottlenose dolphin sightings (the others were reported as "undetermined"). Among these groups, 32% were socializing, 30% were travelling, 23% were foraging and 16% were resting. Group activities differed significantly between substrate types (i.e., soft vs. hard compared to a random distribution of activities across substrate types ($X^2=18.068$; df=3; p=0.0004)). Foraging was observed in 27.3% (N=66) of the groups sighted on soft substrates (N=242), while it represented only 6% (N=3) of all group activities observed on hard substrates (N=47). Group size varied significantly according to group activity (K.W.=16.65; DF=3; p=0.0008) and seabed color (K.W.=31.3947; DF=2; p < 0.0001): larger groups were observed on dark-colored seabeds and during socializing and resting.

Spinner dolphin activities were documented for 72% (N=173) of the sightings. No significant differences were observed in the distribution of group activities across substrate types or colors compared to a random distribution. Group size did not vary significantly according to group activity.

3.2. Habitat modelling

The ENFA model retained six axes to describe the Indo-Pacific bottlenose dolphin habitat (Table 3). On the marginality axis,
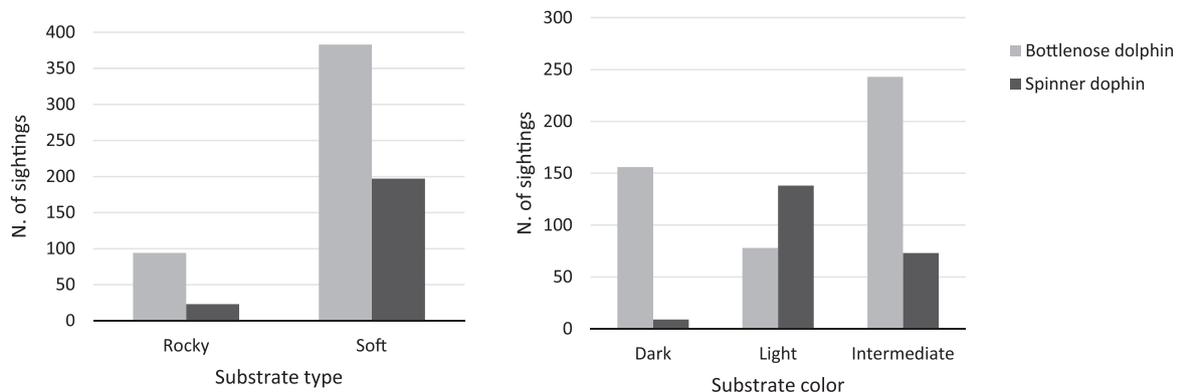
depth appeared as the most explanatory variable (−0.573). The other variables: distance to light-colored seabed, distance to soft seabed, distance from shore and distance to dark-colored seabed, also showed a certain level of marginality (−0.469; −0.397; −0.363; −0.311 respectively).

For depth and distance to the shore, a negative trend associated with high and consistent scores in the specialization axes indicated that the Indo-Pacific bottlenose dolphin tends to select shallow habitats near the coast. Based on the scores of the first specialization axis, the species appeared to be highly selective in terms of proximity to soft substrates (0.709), which was confirmed by relatively high scores in the subsequent axes. Hard substrates obtained the lowest marginal score and did not appear as a restrictive variable as the relatively high score on the first specialization axis (0.438) was not consistent with the low scores obtained on the subsequent axes. The species did not appear to be selective in terms of substrate color as marginal trends were negative for both light- and dark-colored substrates and relatively high specialization scores were obtained for both variables (Table 3).

The Boyce index was relatively high (Table 4: *B*=0.61, SD=0.32) indicated a well-fitting model, with a relative good precision. Four habitat categories were described within the Study Area thanks to the shape of the *Fi* curve (Fig. S1): (1) "unsuitable habitat" for HSI values lower than 29; (2) "marginal habitat" for values ranging from 29 to 45; (3) "suitable habitat" from 46 to 76; and (4) "core habitat" for values over 76. The resulting map (Fig. 5) showed a very narrow and coastal habitat around the island. The core habitat of *T. aduncus* covered 11% (24.6 km²) of the Survey Area, stretching along the west coast (Fig. 6). Mean depth within the core habitat was 43.4 m (SE=0.5), and ranged from 4.7 to 75.8 m. Mean distance to the shore was 1093 m (SE=16.8) for a

Fig. 4. Distribution of Indo-Pacific bottlenose (*T. aduncus*) and spinner dolphin (*S. longirostris*) sightings according substrate type and color.

Table 4
Information on the ENFA models computed for Indo-Pacific bottlenose (*T.aduncus*) and spinner dolphins (*S. longirostris*) in the Study Area. k: number of axes, rate of information and specialization explained by the k factorial axes; M: Global marginality; S: global specialization; T: global tolerance; B: Boyce Index.

Species	k	Exp. Info.	Exp. Spec.	M	S	T (1/S)	B ± SD
Indo-Pacific bottlenose dolphin	6	0.974	0.947	0.352	1.599	0.626	0.61 ± 0.32
Spinner dolphin	3	0.942	0.884	0.669	3.233	0.309	0.61 ± 0.48

maximum distance of 2629 m and mean slope was 2.2° (SE=0.04). In terms of substrate types, the core habitat comprised 75% of soft substrates and 24% of hard substrates. As for the seabed color, the core habitat encompassed 55% of intermediate-colored seabeds, 25% of dark seabeds and 19% of light seabeds.

For spinner dolphins, the ENFA model retained three axes (Table 5). On the marginality axis, slope and distance to light seabed variables showed high negative scores (−0.634 and −0.553 respectively), indicating that spinner dolphins tended to select habitats with low seabed slopes and over, or near, light-colored seabeds, compared to the study area average.
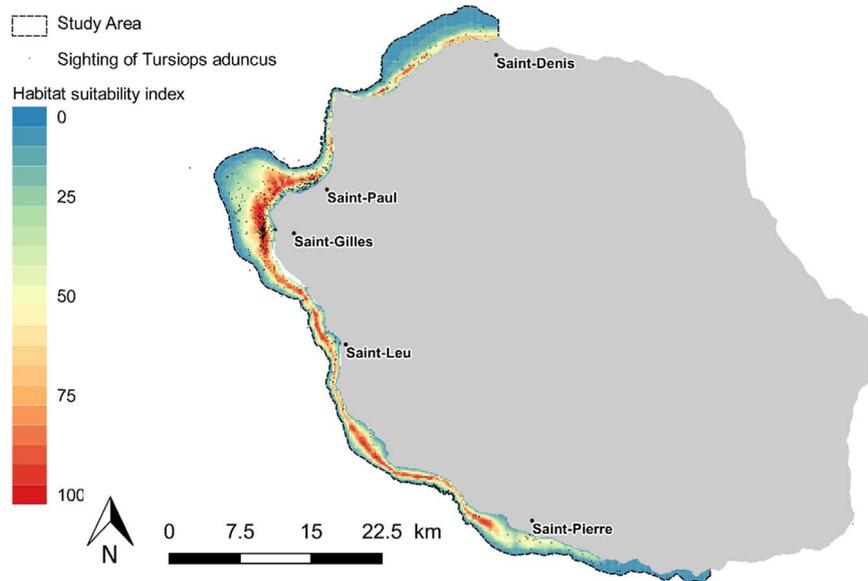

Fig. 5. Habitat suitability map based on the HSI produced by the ENFA for the Indo-Pacific bottlenose dolphin (*T. aduncus*), within the Study Area (200 × 200 m cell grid).
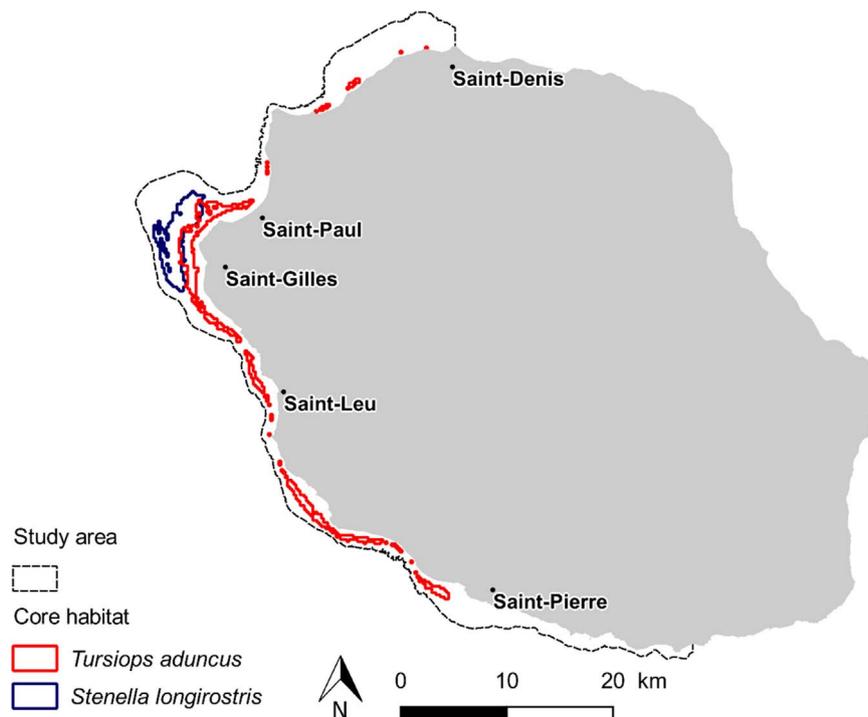

Fig. 6. Core habitat of the Indo-Pacific bottlenose (*T. aduncus*) and spinner (*S. longirostris*) dolphins within the Study Area (200 × 200 m cell grid).

Distance to the shore was associated with a positive and relatively high marginal score (0.402), indicating that the species' habitat tended to be located at the far edge of the Study Area. According to the first specialization axis, distances to soft (0.849) and light (0.461) seabed appeared to be the main specialization variables. The negative values of the corresponding marginal scores indicated that the species tends to select light-color and soft substrate habitats. On the second specialization axis, the high score (0.708) of the depth variable tended to indicate a selection of specific depth ranges (Table 5).

The Boyce index (Table 4: $B=0.61$, SD$=0.48$) indicated that the model had a good predictive accuracy but a moderate precision as indicated by the relatively large standard deviation. Similarly to Indo-Pacific bottlenose dolphins, four habitat categories were specified thanks to the increasing Fi-curve (Fig. S2): (1) "unsuitable habitat" for HSI values below 26; (2) "marginal habitat" for values ranging from 27 to 39; (3) "suitable habitat" from 40 to 63; and (4) "core habitat" for HSI values greater than 63. The resulting habitat suitability map showed that spinner dolphin core habitat was restricted to one main discrete area (Fig. 7). The core habitat was confined to the outer part of the insular shelf off Saint-Gilles and represented 8% (18.2 km²) of the Study Area. It was located in waters ranging from 45.1 to 70.7 m deep, with a mean depth of 60.4 m (SE$=0.1$), and at a mean distance of 2748 m (SE$=30.4$) from the coast. The mean slope within the core habitat was 0.38° (SE$=0.02$). Spinner dolphin core habitat was composed of 96.5% of light seabed against 2.6% of intermediate-color seabeds and 0.9%

of dark seabeds. It encompassed 1.5% of hard substrates against 98.5% of soft substrate.

The comparison of model results indicated that within the Study Area, the habitat of spinner dolphins was globally more marginal (M$=0.669$) than the habitat of Indo-Pacific bottlenose dolphins (M$=0.352$; Table 4). In this coastal area, spinner dolphins appeared to be strongly selective (i.e. a low global tolerance, T$=0.309$), whereas Indo-Pacific bottlenose dolphins were more tolerant in their habitat selection (0.626).

4. Discussion

4.1. Indo-Pacific bottlenose dolphin habitat

The modelling approach confirmed that the habitat of Indo-Pacific bottlenose dolphins is confined to coastal waters, with depth being identified as the main selective criteria. Habitat selection also relies on the proximity to the shore regardless of the slope. The map of habitat suitability showed that the species' core habitat encompassed waters shallower than 44 m and located within 1200 m from the shore. Thus, due to a steep underwater relief around the island, the core habitat of Indo-Pacific bottlenose dolphins is described as a narrow strip along the coast, restricted to very coastal waters. The preference for shallow habitats is consistent with published studies on habitat preferences of this species elsewhere in the Indo-Pacific, including insular (Stensland and Berggren, 2007; Webster, 2012), continental coasts (Browning et al., 2014; Findlay et al., 1992) and estuarine systems (Cribb et al., 2008, 2013; Fury and Harrison, 2008; Fury et al., 2013).

The ENFA model demonstrated that Indo-Pacific bottlenose dolphins show a marked preference for soft substrates compared to hard substrates, with no obvious preference for a substrate color (both light and dark-colored seabeds showed a substantial influence in the model). So far, very few studies have been conducted on seabed habitat preferences for this species. In an estuarine environment in Western Australia, Indo-Pacific bottlenose dolphins were shown to favor areas of bare sand compared to seagrass beds (Cribb et al., 2013). Preference for soft-substrates may reflect suitable foraging habitat (Hastie et al., 2004), as the majority of the groups observed on soft substrate in Reunion were engaged in foraging activities. To date, data on the diet of indo-

Table 5
Output of the spinner dolphin ENFA model: Marginality (Mar.) and Specialization (Spec.) scores obtained for each Eco-Geographical Variables (EGV) and proportion of information explained by each axis (in %).

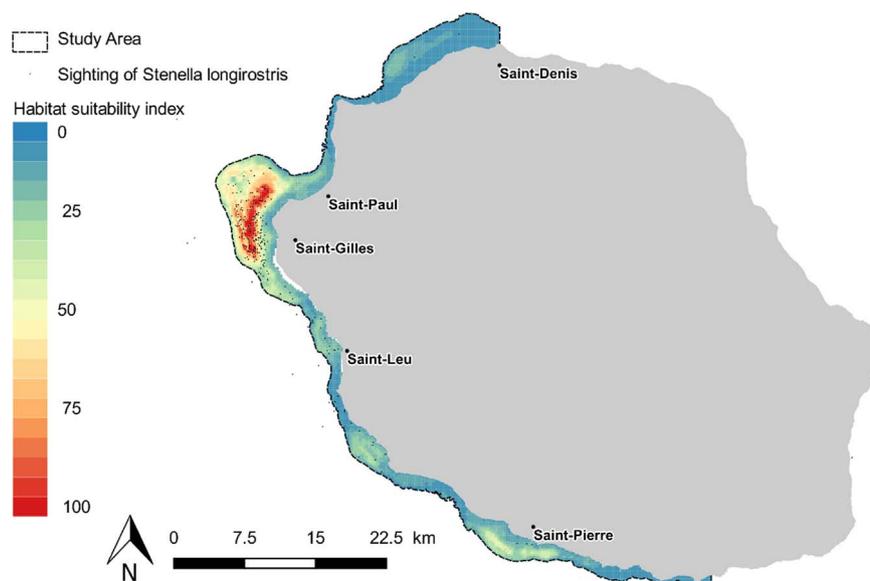| EGV	Marg. (38%)	Spec. 1 (43%)	Spec. 2 (8%)
Slope	−0.634	0.011	0.294
Distance-to-light-bottom	−0.553	0.461	0.264
Distance-to-shore	0.402	0.135	0.306
Distance-to-soft-substrate	−0.283	0.849	0.268
Distance-to-rocky-substrate	0.164	0.141	0.285
Distance-to-dark-bottom	0.107	0.066	0.319
Depth	0.106	0.157	0.703

Fig. 7. Habitat suitability map based on HSI computed by the ENFA for the spinner dolphin (*S. longirostris*), in the Study Area (200 × 200 m cell rid).

pacific bottlenose dolphins from Reunion is lacking, but in Zanzibar, the species mainly feed on the slender conger (*Uroconger lepturus)* and Kaup's arrowtooth eel (*Synaphobranchus kaupii*), inhabiting sandy and muddy seabeds (Amir et al., 2005). Other studies have showed that the diet of *T. aduncus* consisted mainly of demersal fish living on muddy or sandy seabeds from the families of Carangidae or Heamulidae (Cockcroft and Ross, 1990; Heithaus, 2001), while in Mayotte, the epipelagic needle fish (*Tylosaurus crocodilus*) also largely contribute to the diet of *T. aduncus* (Kiszka et al., 2014). In Western Australia, the Indo-Pacific bottlenose dolphin distribution was shown to be correlated to the biomass of fishes, although predation risks also appeared to have a major impact on habitat use (Heithaus and Dill, 2002 2006). In this study, group size was found to increase above dark-colored seabeds, which may suggest increased vigilance in habitat of higher intrinsic risk of predation. Further investigations on the feeding ecology and habitat use are needed to explain habitat preference of *T. aduncus* in Reunion.

4.2. Spinner dolphin habitat

Results from the model provided major information regarding spinner dolphin habitat selection in Reunion. The bottom slope was identified as the most important variable affecting spinner dolphin habitat preferences. The model also described a habitat located at the edge of the Study Area. This preference for flat areas at the outer part of the shelf, close to open waters, might be related to the species' ecological needs. Spinner dolphins generally use sheltered coastal or reef-associated habitat during the morning for resting and socializing and travels to deeper waters later in the afternoon where it forages at night (De Lima Silva and Da Silva, 2009; Gannier and Petiau, 2006; Kiszka et al., 2011; Lammers, 2004; Norris et al., 1994; Notarbartolo-Di-Sciara et al., 2008; Thorne et al., 2012; Tyne et al., 2015). It has been hypothesis that selecting resting habitat at close proximity to deep waters could be a strategy to reduce travelling time and energy costs during transit between oceanic and coastal habitats (Norris et al., 1994; Thorne et al., 2012; Tyne et al., 2015). During this study, very few spinner dolphin sightings occurred during the afternoon, so the results are believed to represent their "morning habitat", although no obvious resting activity pattern was revealed.

In terms of substrate, this study demonstrated that spinner dolphins specifically select soft and light-colored substrates corresponding to white sandy seabeds. Recent habitat modelling studies conducted in Hawaii, also demonstrated that spinner dolphins favor flat sandy seabeds, close to the 100 m isobath (Thorne et al., 2012; Tyne et al., 2015). Although few specific substrate data analyses have been undertaken, other studies in Hawaii (Norris et al., 1994), in Hawaii's Midway Atoll (Karczmarski et al., 2005), in Tahiti (Gannier and Petiau, 2006) and in Mauritius (Webster, 2012), also reported the occurrence of spinner dolphin sightings in white-sand environments. This marked preference is consistent with the hypothesis first proposed by Norris et al. (1994) that the species favors white sandy bays to improve visual detection of predators, especially during resting periods. The soft nature of the seabed might also minimize background noise and sound diffraction, resulting in more efficient echolocation and thereby may reduce predation risk (Thorne et al., 2012).

In agreement with the preference for light-colored seabed habitats, the results also suggested an avoidance of dark seabed habitats, as indicated by the low but positive marginal score of the distance to dark seabed variable. In Reunion, the spinner dolphin was shown not to use the main sheltered bays (Saint Paul, La Possession), which are made of dark sand and mud, but seemed to select a more open habitat. Avoidance of dark-colored seabed further supports that intrinsic habitat risk might be an important factor driving habitat selection for this species.

4.3. Conservation implications

This study revealed that although these two sympatric species both occurred in coastal waters, they used fairly distinct habitats as inferred from topographic and sedimentary variables. The core habitat of Indo-Pacific bottlenose dolphins was restricted to a very narrow band near the coastline and the species tended to favor sandy or muddy seabeds that were present especially in sheltered bays, and irrespective of seabed colors. Comparatively, the core habitat of spinner dolphins was located further off the coast, on the flatter and wider portion of the insular shelf. The model showed a marked preference of spinner dolphins for light-colored seabeds, thereby limiting the species' habitat range to one discrete area off Saint Gilles. The habitat partitioning observed here might reflect different ecological requirements or different strategies against predators between the two species, rather than a direct interspecific competition for space and food resources. In fact, these two species are likely to have different diets although food segregation cannot be clearly determined.

The fine scale descriptions of spinner and Indo-Pacific bottlenose dolphins core habitats achieved in this study provide useful insights for conservation. The study allowed to locate and quantify the core habitat used by both species around Reunion, which is baseline data to infer potential threats and trigger further management action. The core habitat of Indo-Pacific bottlenose dolphin, representing only 11% of the water shallower than 100 m (24.6 km^2) and stretching along the coast in a narrow band, appears as particularly vulnerable to habitat destruction and fragmentation. Project developments within the 60 m depth contour (such as road embankment, harbor extension, etc...) represent a direct habitat loss and potentially poses a barrier to movement through key habitat. Increasing underwater noise from coastal planning, vessel traffic and dolphin-watching activities might also contribute to habitat degradation and lead to changes in habitat use, with possible consequences at the population level (Bejder et al., 2006; Lusseau and Bejder, 2007; New et al., 2015; Weilgart, 2007). Furthermore, the near shore habitat of Indo-Pacific bottlenose dolphins in Reunion make them particularly vulnerable to anthropogenic pollution discharged by rivers or surface runoff compared to spinner dolphins (Dirtu et al., 2016). Given the species' conservation status around the island—described as "endangered" (UICN France et al., 2013) – it is critical to preserve its coastal habitat as a whole to ensure the population's viability for the long term.

The morning habitat of spinner dolphins was shown to be very restricted with a core habitat covering only 8% of the Study Area (18.2 km^2). Although located further away from the coast and, therefore, less vulnerable to coastal planning, concentration of the core habitat of spinner dolphins in a single main area makes the species particularly vulnerable to dolphin-watching activity, which is, to date, unregulated around the island. Most dolphin-watching tours are conducted daily off Saint-Gilles, within the species' core habitat. The species' activity budget and fitness may be affected by a continuous disturbance in its main habitat (Courbis and Timmel, 2009; Lusseau, 2003; Orams, 2004; Stensland and Berggren, 2007). Additional surveys in the eastern part of Reunion, looking at the movement of individuals around the island, are needed to confirm that the core habitat identified in this study corresponds to the main resting area of the local spinner dolphin population. Precautionary conservation measures, such as appropriate regulation including time restriction in the morning, are encouraged to reduce pressure on spinner dolphin population and ensure the sustainability of whale and dolphin-watching activities in Reunion.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.csr.2016.06.010.

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