Spatial analysis on the occurrence of inshore and offshore bottlenose dolphins (*Tursiops truncatus*) in Osa Peninsula waters and Golfo Dulce, Costa Rica

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ABSTRACT

The aim of this assessment is to advance our understanding in the spatial ecology of the resident inshore and offshore population of bottlenose dolphins in Golfo Dulce (GD) and Osa Peninsula Waters (OPW). Our approach used niche-based models (Phillips *et al.*, 2006, Thorne *et al.*, 2012, Friedlaender *et al.*, 2011), which provided details of how dolphins use coastal and oceanic habitats, describing the factors that influence their distribution in the study area and identifying the critical habitats to be considered for management and conservation. Our analyses indicate several important aspects of the distribution of these two ecotypes of bottlenose dolphins. As expected in the study area, these two ecological races occur in close proximity, but differ in the structural factors of the habitat they occupy. The inshore population uses areas close to the mouths of the rivers as critical foraging habitats, being influenced by tidal cycles and seasonal changes in water temperature and salinity. The offshore population in oceanic habitats must rely on prey species found in rare but profitable patches, therefore pelagic dolphins in the open ocean would often need to travel long distances searching for these patches. Distribution models illustrating the difference in habitat use presented in this assessment are key to effective management of the marine mammals' diversity in Costa Rica.

KEYWORDS: COMMON BOTTLENOSE DOLPHIN; PACIFIC OCEAN; HABITAT; MODELLING; DISTRIBUTION; FEEDING GROUNDS

INTRODUCTION

Bottlenose dolphins (*Tursiops truncatus*) inhabit most temperate and tropical waters around the world (Hale *et al.*, 2000; Wells and Scott, 2008; Fernandez *et al.*, 2011), including coastal inshore waters of all continents, around most oceanic islands and atolls, as well as in pelagic offshore waters, displaying strong behavioural and ecological plasticity that allows them to inhabit marine and estuarine ecosystems, even ranging into rivers. It appears that *T. truncatus* may have once or repeatedly, adapted to different environmental conditions resulting in several different forms or ecotypes (Tezanos-Pinto *et al.*, 2009). These populations exhibit notable morphological (Hersh and Duffield, 1990; Well and Scott, 2008), osteological (Perrin *et al.*, 2011), hematological (Duffield *et al.*, 1983; Hersh and Duffield, 1990) and molecular differences (Hoezel *et al.*, 1998; LeDuc *et al.*, 1999; Segura *et al.,* 2006; Perrin *et al.* 2011; Lowther-Thieleking *et al.*, 2015). Such differences are associated with their ecology (Rossbach and Herzing, 1999; Segura *et al.*, 2006; Klatsky *et al.*, 2007; Bearzi *et al.*, 2009). Therefore, they are recognised as distinct ecological races. According to Perrin *et al.* (2011), *Tursiops nuuanu* was described in the offshore eastern tropical Pacific by Andrews in 1911, and later synonymised with *Tursiops truncatus* by Hershkovitz (1966). However, the occurrence of the inshore and offshore ecotypes was first described by Norris and Prescott, (1961) in the eastern North Pacific.

According to Segura *et al.* (2006), ecological and environmental pressures can affect the evolution of phenotypic traits involved in reproductive isolation and the subsequent splitting of lineages into separate species. These phenotypic variations between the populations of *T. truncatus* throughout their geographic range have been used to characterise their distribution. Factors such as depth (pelagic forms have been reported to range primarily between the 200m and 2,000m isobaths), salinity, primary productivity, surface temperature, distance to the coast (coastal form occurs at least up to 7.5km from shore), habitat use, residence patterns and social strategies, could be the cause of these phenotypic and genetic variations (Natoli *et al.*, 2004; Natoli *et al.,* 2005; Torres *et al.*, 2005; Segura *et al.*, 2006; Querouil *et al.*, 2007; Bearzi *et al.*, 2008; Fernández *et al.*, 2011; Diaz *et al.*, 2017). According to several theoretical and empirical analyses, organisms' ecology is considered to be a driving force in speciation (Schluter, 2009). Novel ecological niches are colonised by ancestral populations that have been subjected to divergence and radiation processes. Gavrilets and Losos (2009) suggest that such processes of adaptive radiation into novel and divergent ecological niches is differentiated by a burst of phenotypic diversification, which progressively slows as available ecological niches become filled.

The territorial Pacific waters of Costa Rica are an important portion of the Eastern Tropical Pacific (ETP). They are characterised by a remarkable seascape diversity, including: coral reefs; mangrove forests; mudflats; rocky shores; sandy beaches; cliffs; seagrasses; a seasonal upwelling area; an oceanic thermal dome; an oceanic trench (more than 4,000m deep); a submarine mountain range (Coco Ridge); many coastal islands; one oceanic island

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(Coco Island); a cold seeps and even a tropical fjord (Cortés and Werhtmann, 2009; Alvarado *et al*., 2011; Alvarado *et al*., 2012). Such diversity of marine habitat is reflected in the cetacean's diversity patterns (May-Collado *et al*., 2005; Oviedo *et al*., 2015), even at different scales.

Pacheco-Polanco *et al*. (2011) documented the occurrence of the inshore and offshore ecotypes of *T. truncatus* off Osa Peninsula and Golfo Dulce respectively, Oviedo *et al*. (2015) detailed the relevance of each ecotype within the diversity pattern of the habitats they occur. In many regions of the world, however, there is insufficient evidence to distinguish between differential habitat use by individuals and true ecotype specialisation of particular *T. truncatus* genetic lineages. That is why the study of species-environment relationships can provide important information about the species' habitat use and distribution. Species' distribution models can provide quantitative predictions of geographic distribution and are useful tools for conservation purposes, as they can be used to predict locations where ecotypes are likely to occur, in areas that have not been thoroughly surveyed.

The aim of this assessment is to advance our understanding in the spatial ecology of bottlenose dolphins in Golfo Dulce and Osa Peninsula Waters (henceforth GD and OPW), test if there are dissimilar environmental variables influencing habitat suitability between the inshore and offshore ecotypes, use niche-based models (Phillips *et al*., 2006; Thorne *et al*., 2012; Friedlaender *et al*., 2011) to describe the factors that influence their distribution in the study area and identify the critical habitats to be considered for management and conservation.

METHODS

Study area

Osa Peninsula Waters: This study area was framed within a polygon limited to the East by the shorelines of Terraba-Sierpe River System, Drake Bay and Corcovado National Park to Punta Salsipuedes. The area within the polygon is the target location of whale watching boats (the platform of observation) and is characterised by a great portion of shelf waters, which progressively shrinks southward along the western coast of the Peninsula; just outside of GD's entrance, water depths reach 1,000m at less than 4nm from Cabo Matapalo. Within shelf waters, the most remarkable topographic unit is Isla del Caño (Fig. 1).

Golfo Dulce: This embayment is characterised by a deep inner basin (> 215m of maximum depth) and a shallow sill (70m), that connects the inner basin with the open ETP (Wolff *et al.* 1996; Quesada-Alpizar and Cortez, 2006; Svendsen *et al*., 2006).The total surface area is close to 750km^2. Water circulation is restricted, a characterisation of true fjords, and there is a slow, deep water renewal by occasional intrusion of dense subsurface waters. Productivity in GD is most likely subsidised by riparian discharge to the inner basin, particularly by contributions from the Esquinas, Rincón, Tigre and Coto Colorado Rivers (Fig. 1)

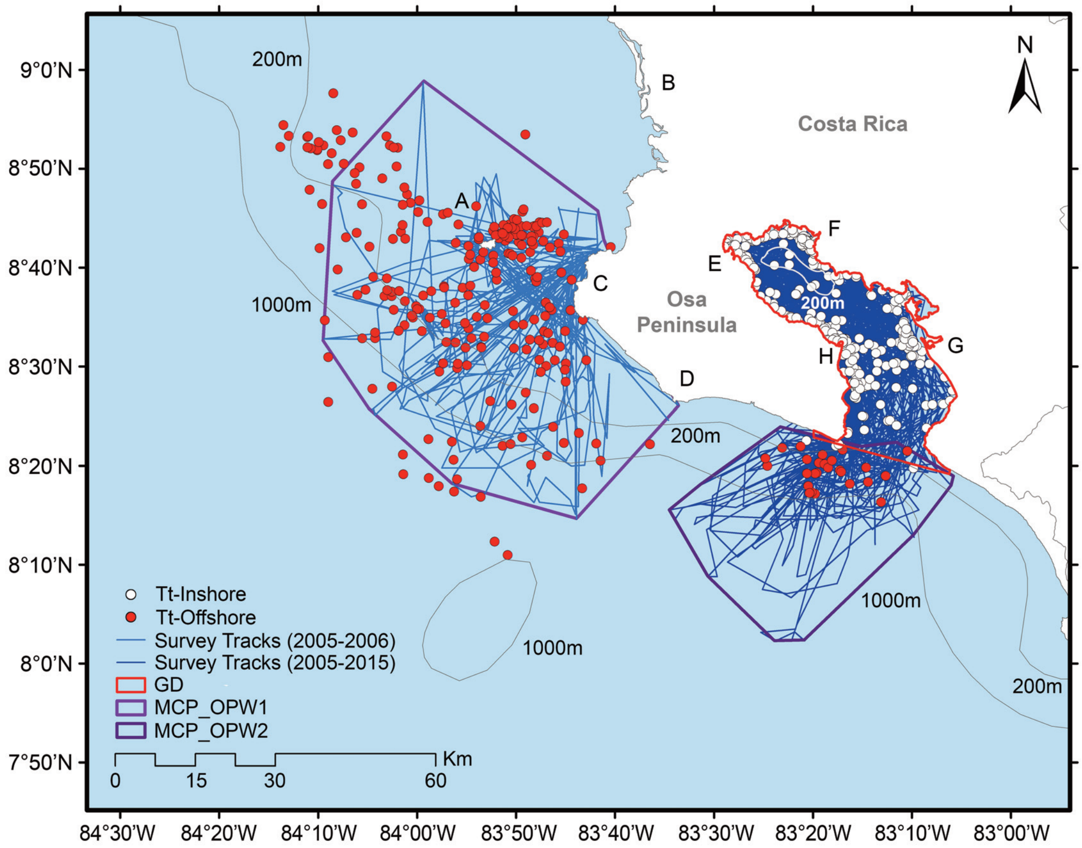

Fig. 1. Research efforts: search effort in OPW is distributed in two polygons (MCP_OPW1 and MCP_OPW2). Search effort in GD is illustrated by the tracks corresponding to 611 surveys inside GD and 165 surveys in MCP_OPW2. Encounters of inshore bottlenose dolphins (white circles) inside GD and offshore bottlenose dolphins (red circles) off OPW. Reference locations: A = Isla del Caño, B = Terraba-Sierpe River, C = Drake Bay, D = Punta Salsipuedes, E = Rincon River, F = Esquinas River, G = Coto Colorado River, H = Tigre–Platanares Rivers.

Dolphin locations

During field observations of bottlenose dolphins in the study area (GD and OPW), the putative classes of inshore and offshore ecotypes were assigned a priority by trained surveyors, following the visual and bathymetric cues described in Oviedo *et al*. (2015), which are based in those reported in Segura *et al*. (2006), Wells and Scott (2008), Perrin *et al*. (2011) and Diaz-Gamboa *et al*. (2017).

Data detailing the occurrence of bottlenose dolphin groups in the study area were derived from two databases: (1) sightings records gathered in Drake Bay-Isla del Caño and Corcovado National Park from 2001 to 2006 (Vida Marina Foundation, n = inshore: 0 sightings, offshore: 238 sightings); (2) presence-only records collected in GD from 2005 to 2015 (Centro de Investigación de Cetáceos Costa Rica CEIC, n = inshore: 450 sightings, offshore: 35 sightings). Each sighting recorded yielded information on date and location (GPS coordinates), best estimates on group size, group composition and behaviour at first encounter. Behaviour data collected in GD was more consistent and homogeneous due to the systematic utilisation of an ethogram by trained observers (LO, DHM, JDPP) and constraints related with environmental conditions and detectability (behaviour data was deemed valid when collected at a Beaufort sea condition < 3), whereas behaviour records taken in OPW during 2001–2006 were *ad libitum*.

The detection probability of the target species and subgroups are not specifically reported, however we acknowledge that detection probability would differ between locations. Dolphin encounters in GD (2005–2015) were collected using a more controlled protocol aided by the physiography of the research area; a semi-closed inner sea which facilitates a relatively high encounter rate, therefore there is a thorough documentation of the search effort. Whereas, sightings in OPW were entirely opportunistic in nature and effort tracks were only available for 2005–2006 (111 surveys), despite the search effort done since 2001 in the same sub-area (Fig. 1).

Eco-Geographic Variables (EGVs)

The variables taken into account to build the ecological niche models, were chosen according to their ecological relevance for the target species (*T. truncatus*) and availability of the data. The dataset contains three physiographic-related variables describing '*shelf tendency'* (McLeod *et al*., 2007; Bouchet *et al.,* 2015): depth, slope and curvature, which were obtained using the extracted data from the global 30 arc-second grid of the GEBCO_08 Grid dataset. Slope and curvature, a measure of the bottom topography, were processed using the *DEM tools* in the ArcGis 9.3.1 software.

Three more variables were selected for both areas (GD, OPW): the distance to the coastline, the distance to the 200m bathymetric lines and the distance to the major rivers' mouth. These variables were constructed using the *Euclidean Distance Tool* of the Spatial Analyst Toolbox in ArcGis 9.3.1. Non-physiographic variables were included in the modelling process: the mean Sea Surface Temperature (SST), Sea Surface Salinity (SSS) and the Surface Chlorophyll α (Chlor-α). Seasonal means for SST and SSS were obtained from MARSPEC dataset (Sbrocco, 2013). A 0.01-degree grid (approx. 1.6km × 1.6km) was used as resolution for the environmental layers to mimic the MARSPEC dataset original resolution. Due to the small size of GD no Chlor-α data with proper resolution was available. Chlor-α means were produced using the MODIS Aqua L2 images downloaded from Ocean Color Web (Feldman and McClain, 2012) and processed using SEADAS 7.0 (Baith *et al*., 2001). Maps were created (one for each variable) using the mean value of all the images available from 2001 to 2006 for the seascape off OPW and 2005–2015 for GD. A correlation analysis of all the variables was performed using a Pearson's correlation analysis integrated in the ENMTools (Warren *et al*., 2010). All correlated variables (significant Pearson's correlation greater than 0.5) were excluded. Selection between autocorrelated variables was done according to the field knowledge and literature existent for the species.

Modelling approach

We developed ecological niche models for bottlenose dolphins using a maximum entropy modelling approach to look at the potential distribution of these flagship species in the study area during the dry and rainy seasons, to describe differences in habitat suitability predictions and variables contribution between seasons. Maxent program (v. 3.3.3) was used in order to obtain habitat suitability (*HS*) predictions for our target ecotypes, as detailed in Phillips *et al*. (2006; 2009). Maxent estimates a target species' probability of presence by finding the probability distribution of the maximum entropy (i.e. the closest to uniform distribution), subject to a set of constraints that represent the availability of suitable habitat for the target species. In the present study, the model outputs were used as an approximation to the abiotic fundamental niche, or the species physiological range of tolerance to environmental factors in the absence of biotic interactions (Hutchinson, 1957). Due to the potential heterogeneity in detection probability in presence-only data depicting the location of bottlenose dolphins in GD and OPW, we applied a sample selection bias approach (Elith *et al*., 2010), following the recommendations in Merow *et al*. (2013) and Yackulic *et al*. (2013) to mediate an effort correction for both seasons. Two different files were constructed for each season using a Minimum Convex Polygon analysis with all the species sightings along with the effort tracks to obtain two sampled area polygons. The sample area polygons delimited the abiotic EGVs evaluated, in a way that biased variable sampling is reduced. Maxent models were run using the auto features with 100 replicates and using cross-validation to assess the model fit. To evaluate the model accuracy, we used the Area Under the Curve (AUC) metric of the Receiving Operator Characteristic (ROC) curve (Phillips *et al*., 2006). The AUC value provides a threshold-independent metric of overall accuracy; it ranges between 0.5 and 1.0. Values of 0.5 indicate that scores of specificity and sensitivity do not differ, while scores of 1.0 indicate that the distributions of the scores do not overlap. We assessed AUC values of the ROC curve of the models following the scale suggested in Hosmer and Lemeshow (1989): 0.5 indicated no discrimination; 0.5 to 0.7 represented poor discrimination; 0.7 to 0.8 indicated an acceptable discrimination; 0.8 to 0.9 indicated an excellent discrimination; and over 0.9 represented outstanding discrimination.

The permutation importance index was used to identify the most important EGVs for both ecotypes of bottlenose dolphins. This index measures the level of contribution of each EGV to the fit of the final model, in contrast to other heuristically defined metrics that depend on the path taken to obtain the models. The values of a particular variable are randomly permuted among the training points (presence and background) to measure the decrease in training AUC, a relevant decrease shows that the model is greatly dependent of such variable. The values were normalised to provide percentages (Kalle *et al.,* 2013; Svendsen *et al.*, 2015). In order to be consistent with the aim of understanding the effect of abiotic predictors in delimiting the distribution (Merow *et al.*, 2013), for both inshore and offshore bottlenose dolphins, the response curves to those variables that contributed the most to the average model (≥ 50%) were used to assess habitat suitability.

Behaviour and group size analysis

Data collected on group size and behaviours was analysed to test for differences between ecotypes. All statistical tests were performed with Statgraphics v. 2-1. We present the

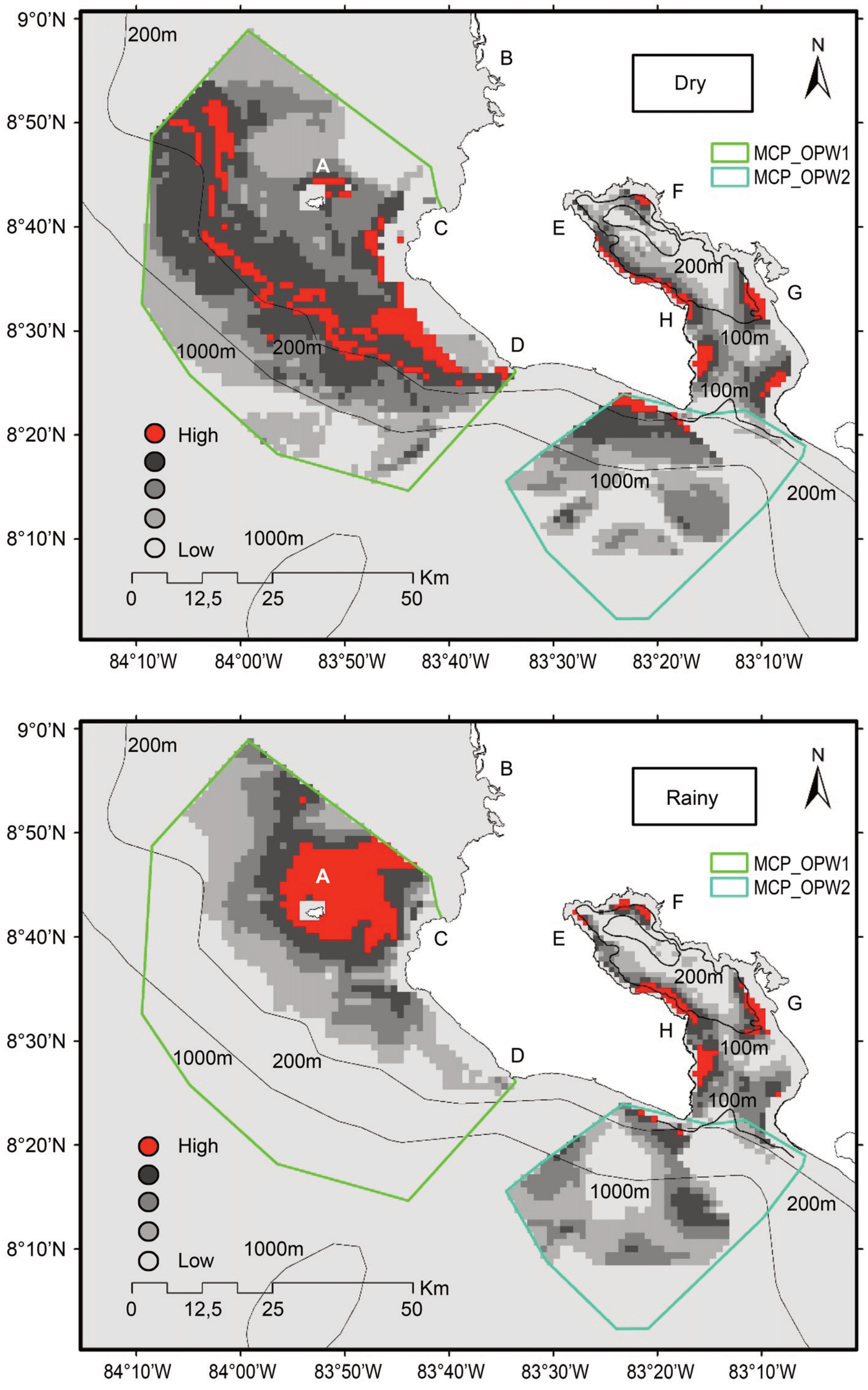

Fig. 2. Average habitat suitability model for *T. truncatus* with details in bathymetric contours in OPW (inserted polygons: OPW1 and OPW2) and GD. Reference location: A = Isla del Caño, B = Terraba-Sierpe River, C = Drake Bay, D = Punta Salsipuedes, E = Rincon River, F = Esquinas River, G = Coto Colorado River, H = Tigre–Platanares Rivers.

activity budget of both inshore and offshore bottlenose dolphins using behaviour observation at first encounter from 2010 to 2015 (*n* = 383 records) based on the ethogram used in Scheneider (1999) and modified by Garcia and Dawson (2003), which is made of five basic behavioural states: Forage, Travel, Social, Rest and Mill.

RESULTS

Survey effort was not evenly distributed between the two portions of the study area, with higher survey effort recorded in GD: a total of 775 cetaceans surveys were conducted between 2005 and 2015, including the inner basin (426 surveys ≈ 2,130hrs), the sill area (184 surveys ≈ 920hrs) and the transition to oceanic waters (165 surveys ≈ 825hrs). In contrast, earlier survey effort (2001–2006) off OPW accounted for 564 surveys equivalent to approximately 2,200hrs.

Ecological niche modelling for inshore bottlenose dolphins in GD

The average models for inshore bottlenose dolphins in GD derived from 100 replication runs are presented in Fig. 2. The major proportion of suitable habitat for *T. truncatus* in GD during the dry and rainy seasons corresponded with the coastline related to adjacent areas to the rivers' mouth, such as Esquinas and Coto Colorado, with particular reference to the sub-system conformed by the Tigre and Platanares Rivers.

The mean AUC value for the cross-validated model for inshore bottlenose dolphins in GD during the dry and rainy seasons were 0.759 (+/–0.120) and 0.775 (+/–0.076) respectively (Fig.3), which were deemed to offer an acceptable discrimination during the dry season and the rainy season. EGVs contributions to the final models of runs in GD are shown in Fig. 4. From all the set, distance to the rivers and distance to the 200m isobaths were found to be the strongest predictors during the dry season, while distance to the rivers, slope and distance to the 200m isobaths were the most influential environmental variables during the rainy season.

The seasonal model gain for GD during the dry season is notably decreased by major distance to the rivers and increased at far distance to the 200m isobaths (Fig. 5). Rainy season model gains are primarily described by distance to rivers and distance to 200m isobaths. Slope is also considered in Fig. 5 since it gains in combination with the latter and contributes by more than 50%. There is a negative

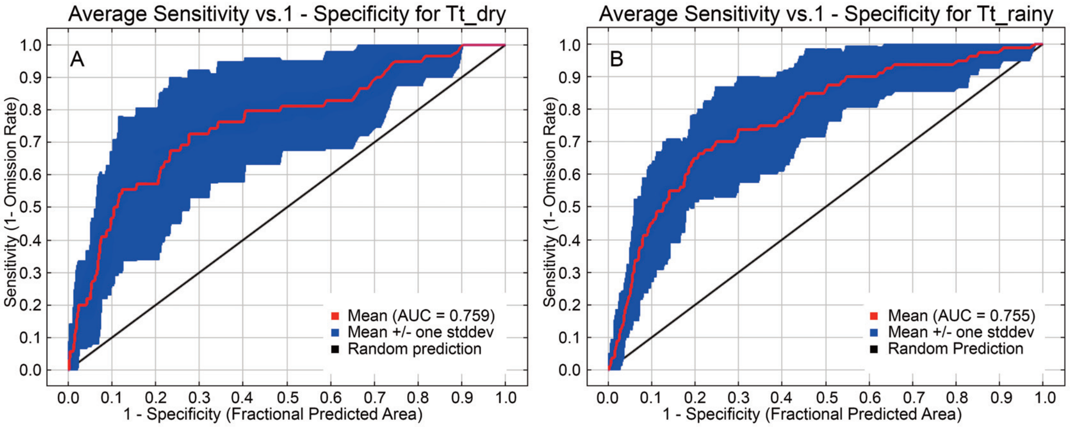

Fig. 3. Diagnostic plots for Maxent modelling of bottlenose dolphins in GD 2005–2015. Plot A indicates the receiver operator characteristic (ROC) curve for the model of the dry season (mean AUC for all the model runs equals 0.759); plot B shows the receiver operator characteristic (ROC) curve for the model of the rainy season (mean AUC for all the model runs equals to 0.775). The blue area indicates the standard deviation for the 100 model runs. The black diagonal line represents a random prediction (AUC = 0.5).

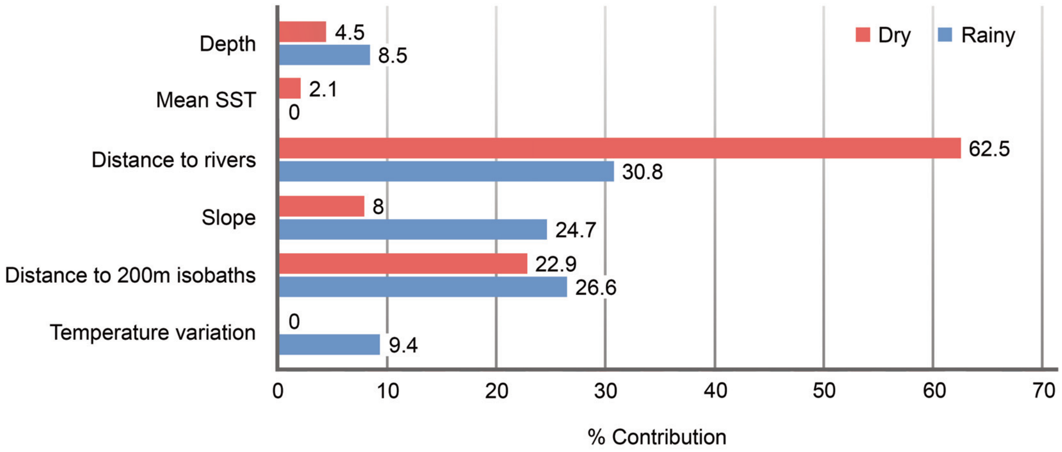

Fig. 4. Depiction for the estimates of relative contributions of the environmental variables to the Maxent model describing the abiotic fundamental ecological niche of inshore bottlenose dolphins in GD. The bars indicate the percent contribution for each variable to the overall models in the dry (blue bars) and rainy (red bars) seasons respectively, exact percentage in number at the top of each bar.

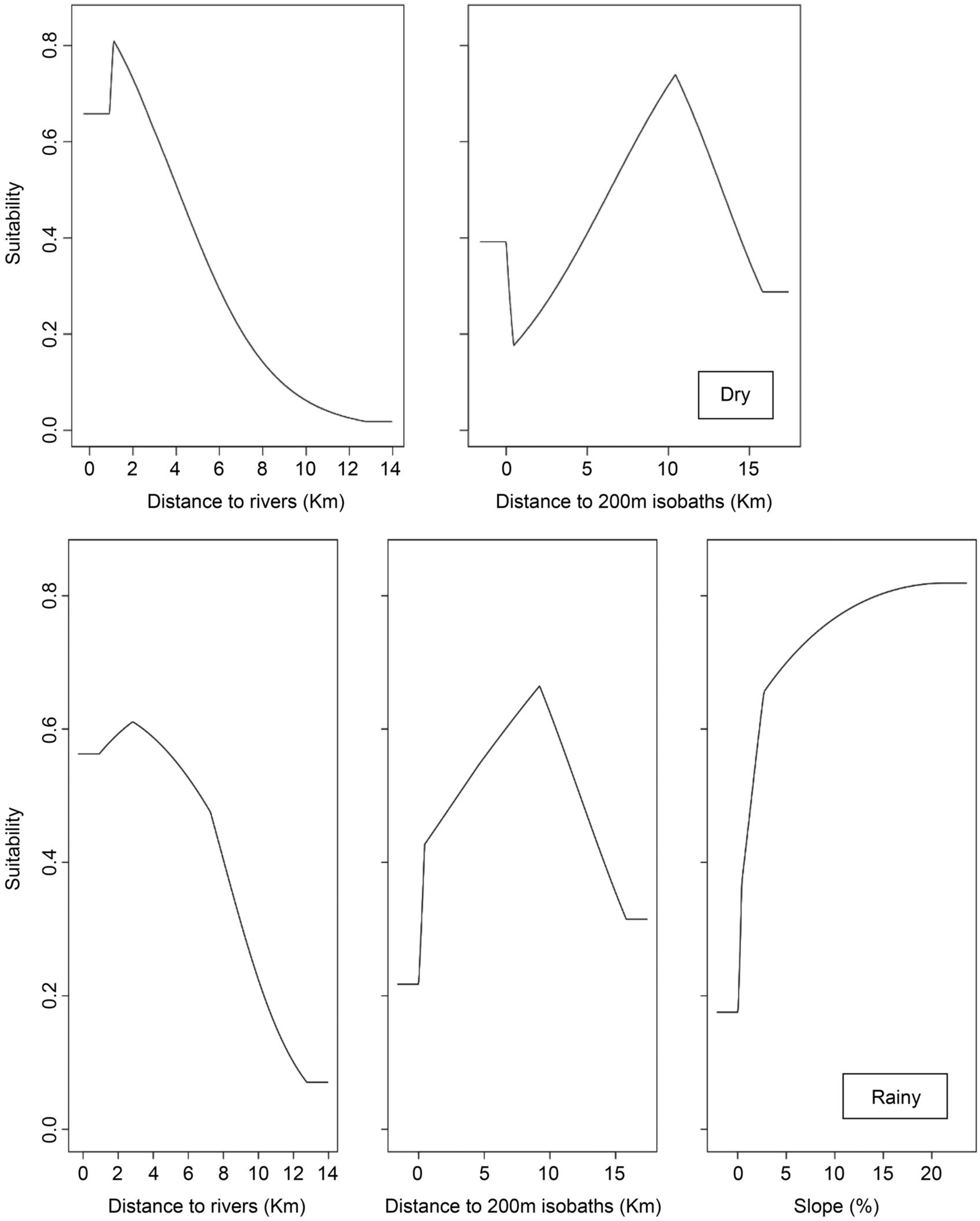

Fig. 5. Response curves for each of the main environmental variables influencing the ecological niche of bottlenose dolphins in GD during dry (distance to rivers and to 200m isobaths) and rainy (slope, distance to rivers and to 200m isobaths) seasons.

response to distance to the rivers beyond 2km, while the response associated with distance to the 200m isobaths is maximised at around 10km.

Ecological niche modelling for offshore bottlenose dolphins in OPW

The average models for OPW was obtained from 100 replication runs (Fig. 2) following the same procedure with inshore bottlenose dolphins in GD. The suitable habitat for the offshore ecotype of *T. truncatus* in OPW during the dry season is located within or close to the 200m isobaths, while in the rainy season it shifted around Caño Island and in front of the Térraba-Sierpe wetland.

Offshore bottlenose dolphins' models validation, showed a mean AUC value for the cross-validated model of the dry and rainy seasons of 0.759 (+/–0.089) and 0.888 (+/–0.098) respectively, which were deemed to offer an *acceptable discrimination* during the dry season and *excellent discrimination* for the rainy season. Plots in Fig. 6, illustrate the predictive performance of the model, highlighting low spatial autocorrelation.

The contributions of EGVs to the final models of offshore bottlenose dolphins in OPW are shown in Fig. 7. From all the set, depth and distance to the 200m isobaths were found to be the strongest predictors, both during rainy and dry seasons contributing to more than 50% to the gain in discrimination.

The seasonal models of OPW are primarily dominated by depths; during the dry season the ecological niche of bottlenose dolphins are better predicted by depths close to

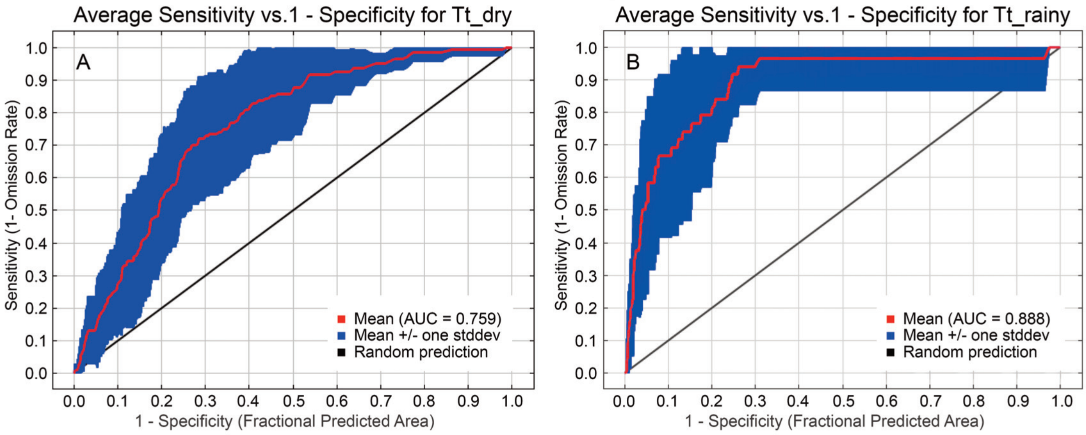

Fig. 6. Diagnostic plots for Maxent modelling of bottlenose dolphins in OPW 2001–2006. Plot A indicates the receiver operator characteristic (ROC) curve for the model of the dry season (mean AUC for all the model runs equals to 0.759); plot B shows the receiver operator characteristic (ROC) curve for the model of the rainy season (mean AUC for all the model runs equals to 0.888). The blue area indicates the standard deviation for the 100 model runs. The black diagonal line represents a random prediction (AUC = 0.5).

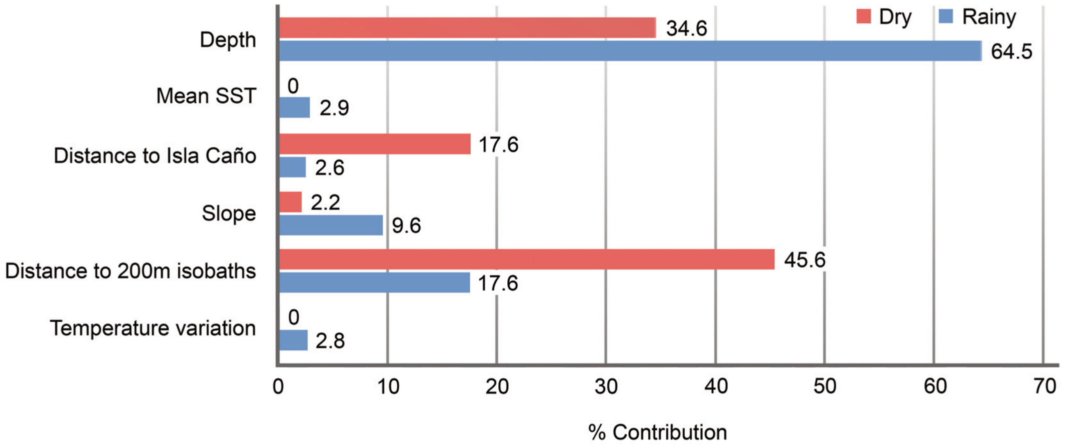

Fig. 7. Depiction for the estimates of relative contributions of the environmental variables to the Maxent model describing the abiotic fundamental ecological niche of inshore bottlenose dolphins in OPW. The bars indicate the percent contribution for each variable to the overall models in the dry (blue bars) and rainy (red bars) seasons respectively, exact percentage in number at the top of each bar.

the 200m bathymetric contour. This characteristic shifted during the rainy season to platform water depths of less than 200m. Distance to the 200m isobaths is the second best predictor of the ecological niche of *T. truncatus* in OPW. During the dry season the maximum gain is more consistent with short distances as opposed to the trend during the rainy season, where the niche is best described by distances close to 20km from this bathymetric contour (Fig. 8).

Behaviour and group size

The activity budget of inshore bottlenose dolphins showed the relevance of foraging in GD in relation to all other behaviours, while travelling is second in importance but closely associated with foraging. Dolphins will travel from one foraging spot to the other along the rivers draining in the inner basin of GD. Contrastingly, the activity budget of offshore bottlenose dolphins in the same dataset evidence the opposite trend; travelling is the most important activity for groups of the offshore ecotype of *T. truncatus*, followed by foraging as the second most important behaviour. The differences in the structure of the activity budget between putative forms is supported statistically (Kruskal Wallis test: $H(1) = 18.98$, $p < 0.05$), whereas the dissimilarities in foraging and travelling between the inshore and offshore bottlenose dolphins are not.

There was a statistically significant difference in group size between inshore and offshore bottlenose dolphins in the GD dataset (Kruskal Wallis test: $H(1) = 45.95$, $p < 0.05$), with dolphins observed in the inner basin and sill area of GD aggregated in smaller groups ($\bar{X} = 6.64$, SD = 5.93, N = 348 Range:1–30), in comparison to those documented in the transitional oceanic area off the mouth of the gulf ($\bar{X} = 43.74$, SD = 52.86, N = 35 Range 2–200), with a trend of increase in group size with oceanic depths ($r^2 = 0.346$, $p < 0.05$).

DISCUSSION

The results detailed above support the differences in distribution of inshore and offshore bottlenose dolphins in GD and OPW. Based on the environmental requirements that affect their habitat suitability and considering the dissimilarities in external morphology and behaviour, we have distinguished the abiotic environmental factors influencing the spatial ecology between these two ecotypes: in GD, the EGVs that best describe the ecological niche of

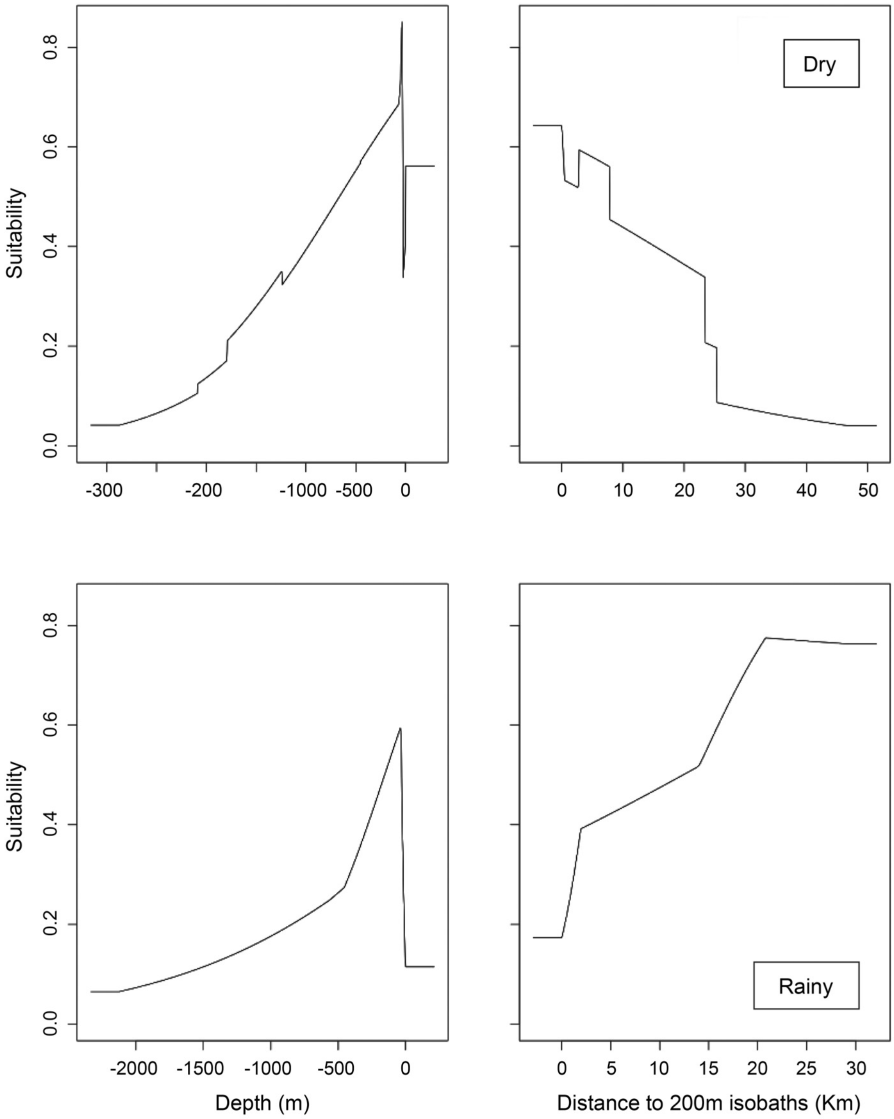

Fig. 8. Response curves for each of the main environmental variables influencing the ecological niche of bottlenose dolphins in OPW during dry and rainy seasons (depth and distance to 200m isobaths).

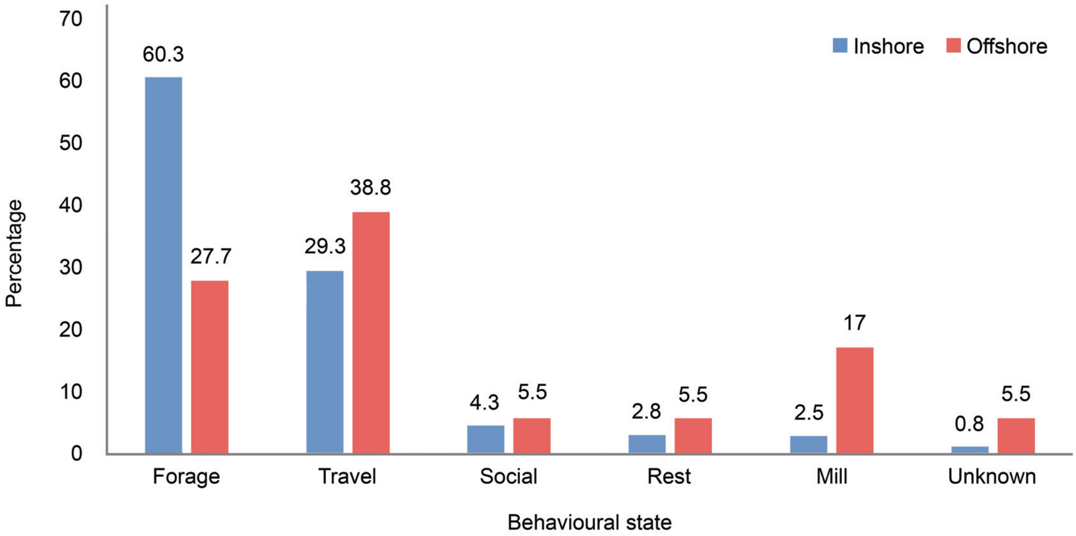

Fig. 9. Activity budget of inshore and offshore bottlenose dolphins in the study area. Exact percentage of every behaviour state on top of each bar.

the inshore form of bottlenose dolphins were distance to the rivers, distance to the 200m isobaths and slope, whereas depth and distance to the 200m isobaths were found to be the strongest predictors that describe the ecological niche of the offshore *T. truncatus* in OPW, during both seasons. Water depth, distance to the coast and distance to the 200m depth contour have been used for different authors to identify boundaries between species and ecological races in bottlenose dolphins elsewhere (Hale *et al*., 2000; Segura *et al*., 2006).

As expected in the study area, we have found the two ecological races of bottlenose dolphins to occur in close proximity, but to remarkably differ in the environmental requirements of the habitats they occupied. We do not rule out the potential for mixed encounter of both ecotypes: on 1 January 2016, we found a couple of inshore bottlenose dolphins at 10 miles from Caño Island travelling among an offshore group. We recognised the inshore ecotype individuals by the pigmentation pattern (as explained elsewhere in this study) and by the incidence of Lacaziosis Like Disease (LLD), which have been documented for the bottlenose dolphins in GD (Bessessen *et al*., 2014) and for another population off the port of Caldera at 300km north of GD (Herra-Miranda and Pacheco-Polanco, unpublished obs.). Additionally, the behaviour differentiated those inshore dolphins; even though they were travelling with a group of offshore conspecifics, they were at the periphery of the group and constantly avoided by other members within the group. We argued a confounding factor that despite the possibility for mixing, which occurs in an area where overlap between ecotypes exists, the general pattern of distribution evidencing a differential habitat use between ecotypes remains.

Based on the analysis of behavioural observations in the field, the inshore population that inhabits GD uses the areas close to the mouths of the rivers as critical foraging habitats (Herra Miranda *et al*., 2016). Estuarine habitats represent secured resources where potential prey species may be found individually, rather than in large schools. The prey species (and thus the dolphins) are being influenced by tidal cycles and seasonal changes in water temperature and salinity (Allen *et al*., 2001; Bearzi *et al*., 2008; Gowans *et al*., 2007; Perrin *et al*., 2011); hence aggregations are based in few individuals; competition at intra-specific levels for food and other factors may limit the option of forming large groups in inshore habitats (Bearzi, 2005; Pacheco-Polanco and Oviedo, 2007; Gowans *et al*., 2007; Bearzi *et al*., 2008; Oviedo *et al*., 2012; 2018). Additionally, individuals' encounter history derived from mark-capture-recapture sampling, has shown that the majority of resident dolphins are females with calves, usually gathering in the same protected locations year-round (Oviedo, 2018). In complex sheltered estuarine habitats, the dolphins can hide and notably reduce their predation risk (Gowans *et al*., 2007). According to our field observations, offshore bottlenose dolphins are usually encountered when travelling and showed an increase in group size with water depth. Likely, the offshore population in oceanic habitats would rely on prey species found in rare but profitable patches, with large areas of habitat with little to no available food sources at all, therefore, pelagic dolphins in the open ocean often would need to travel long distances searching for these patches (Gowans *et al*., 2007). Likewise, larger group sizes may benefit from cooperative feeding on patchy, rich food resources found in deeper habitats and may have a better chance of detecting predators and protecting against them. There are encounters in this spatial analysis, of fewer than five individuals, that have been assigned to the oceanic ecotype. Those smaller groups were considered as scout groups. In those instances, smaller groups, after being followed for an extended period of time, ended up being part of a major aggregation of offshore bottlenose dolphins.

Our assessment is based on presence only data, which yield several limitations regarding the inferences to be derived (Phillips *et al*., 2009). The use of a presence background algorithm (such as Maxent) limits the potential inferences to be done, as they produce different niche estimates than presence-absence models. As exemplified by Soberon and Nakamura (2009), the use of presence-absence will deliver an estimative of the occupied niche, while presence-background methods will calculate something more similar to the realised niche. A model constructed with true absences data has the potential to deliver better estimates of the actual distribution of the species studied. Nevertheless, due to the dynamic nature of the oceanic environment and the motility of the studied species, obtaining true absences might be an impossible objective when working with cetaceans. The use of methodological absences (false absences due to insufficient sampling) during the modelling process will produce incorrect distributional estimates (Lobo *et al*., 2010). Consequently, for cetaceans, it would be risky to use presence-absence algorithms, those procedures should be applied only in cases with a small area and extremely well sampled, with data in all the variety of environmental conditions available.

Opportunistic datasets, such as the ones used in this assessment, are important sources of information on distribution patterns, having the inherent potential of overcoming the caveats of presence-only data and Maxent, due to the high periodicity of the field observations in a relatively small area, which is improved by the addition of related behavioural data (Fernandez *et al*., 2018). While the inferences made from the present study might be limited due to the data available, there are several elements worth considering: (a) sightings are obtained from direct field observation using opportunistic boat-searches, therefore, instead of inferring the sampling process (as in museum collection data), the search effort during the collection of dolphin sightings, allowed for the correction of sampling bias by delimiting an effective subarea of observed records; and (b) the main drawback in modelling species distributions would not be the spatial bias in itself but the bias in the available environmental variables (Guillera-Arroita *et al*., 2015). In this assessment we established the variables that were good predictors to discern the difference in distribution of two ecotypes of bottlenose dolphins, from those variables, the fixed ones (e.g. 'shelf tendencies') which were unlikely to be misrepresented in the sample polygon, since spatio-temporally stable physical structures are easier to record or map, and require less resources to be characterised (Bouchet *et al*., 2015). Whereas those more dynamic in nature (e.g.

SST, SSS) were obtained from remote sensors, covering a much wider geographic resolution than that portrayed in the delimiting polygons.

Factors such as habitat structure, habitat boundaries, resource specialisation, and site fidelity in sheltered environments may promote phenotypic differentiation between dolphin groups like those found in OPW and GD (Natoli *et al.,* 2005; Torres *et al*., 2005; Segura *et al*., 2006; Querouil *et al*., 2007; Bearzi *et* al., 2008; Gowans *et al*., 2007; Fernandez *et al*., 2011; Pacheco-Polanco *et al*., 2011; Guevara-Aguirre and Gallo-Reynoso, 2016; Diaz *et al*., 2017). These aspects might equally have a crucial role in defining eco-morphological differences within a species. We hypothesise that the coastal habitat of GD might have stronger implications beyond the level of ecotypes, with potential localised genetic differentiation, such as that reported by Möller *et al.* (2007). Research efforts on discerning population structure are underway. We expect to couple photo-ID surveying with genetic sampling in forthcoming sampling seasons to confirm our hypothesis.

It is fundamental to understand the factors that influence the morphological differences within species, to increase our knowledge of evolutionary and ecological responses that affect a population in its natural environment, and to help us in the formulation of effective conservation measurements. The Pacific shoreline of Costa Rica is facing an increase in coastal urban-tourist development, most of which is being carried out without considering potential ecosystem effects. On the other hand, in 2010, GD was declared by the Institute for Fisheries and Aquaculture of Costa Rica (INCOPESCA) as a Marine Area for Responsible Fishery. This differs from Marine Protected Areas in goals and objectives, where the only restriction is the use of destructive fishing gear inside the Gulf. This leaves the critical foraging and calving habitats of these populations of dolphins inhabiting this embayment unprotected, defenseless and vulnerable to coastal development and degradation of their marine coastal habitats.

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