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Abstract: The aim of this assessment is to advance our understanding in the spatial ecology of the resident in-shore and off-shore population of bottlenose dolphins in Golfo Dulce and Osa Peninsula waters. Our approach use 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 on the distribution of these two ecotypes of bottlenose dolphins, as expected in the study area, we have found these two ecological races to occur in close proximity, but to differ in the ecological niche they occupied, the inshore population use 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 often would need to travel long distances searching for these patches.

INTRODUCTION

Bottlenose dolphins inhabit most temperate and tropical waters around the world (Perrin 1975, Hale *et al*. 2000, 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 behavioral and ecological plasticity that allows it 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 (Well & Scott 2008, Hersh & Duffield 1990), osteological (Perrin *et al*. 2011), hematological (Hersh & Duffield 1990, Duffield *et al*. 1983) and molecular differences (Lowther-Thieleking *et al*. 2015, Perrin *et al*. 2011, Segura *et al.* 2006, LeDuc *et al*. 1999, Hoezel *et al*. 1998), such differences are associated with their ecology (Bearzi *et al*. 2009, Klatsky *et al*. 2007, Segura *et al.* 2006, Rossbach & Herzing 1999), therefore, they are recognize as distinct ecological races. According to Perrin *et al*. (2011), *Tursiops nuuanu* was described at the offshore eastern tropical Pacific by Andrews in 1911, and later synonymized 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) the ecological and environmental pressures can affect the evolution of phenotypic traits involved in reproductive isolation and the subsequent splitting of lineages into separate species. The existence of these phenotypic variations between the populations of *T. truncatus* throughout their geographic range have been use to characterize their distribution. Factors such as deep (Pelagic forms have been reported to range primarily between the 200 and 2000 m isobaths), salinity, primary productivity, temperature, distance to the coast (coastal form occurs at least up to 7.5 km 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). According to several theoretical and empirical analyses, organism´s ecology is considered to be a driving force in speciation (Schluter 2009), novel ecological niches are colonized by ancestral populations that have been subject to divergence and radiation processes. Gavrilets and Losos (2009) suggest that such process 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, an important portion of the Eastern Tropical Pacific, are characterized by a remarkable seascape diversity, including: coral reefs, mangroves forest, mudflats, rocky shores, sandy beaches, cliffs, seagrasses, a seasonal upwelling area, an oceanic thermal dome, an oceanic trench (more than 4000 m deep), a submarine mountain range (Coco Ridge), many coastal islands, one oceanic island (Coco Island), a cold seeps and even a tropical fjord (Golfo Dulce) (Cortés & Werhtmann 2009, Alvarado *et al*. 2011, Alvarado *et al*. 2012). Such diversity of marine habitats is reflected in the cetacean's diversity patterns (May-Collado *et al*. 2005, Oviedo *et al*. 2015) even at the mesoscale.

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) details 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 specialization of particular *T. truncatus* genetic lineages, that's why the study of the 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 a useful tool for conservation purposes, as they can be used to predict locations where ecotypes are likely to occur in areas that have been poorly survey like Osa Peninsula Waters, where we only have presence-only records. Maximum entropy modeling (Maxent), is a presence-only modeling technique that has been applied to ecological studies, it estimates a species probability distribution by finding the probability distribution of maximum entropy (closest to uniform), subject to a set of constraints derived from available information about the species environmental relationships (Phillips *et al*. 2006, Friedlaender *et al*. 2011, Thorne *et al*. 2012).

The purpose of the present study is to advance our understanding in the spatial ecology of the resident in-shore and off-shore population of bottlenose dolphins in Golfo Dulce and Osa Peninsula waters (hereafter GD and OPW respectively), using niche based models (Phillips *et al*. 2006, Thorne *et al*. 2012, Friedlaender *et al*. 2011), providing details of how dolphins used 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.

MATERIALS AND METHODS

Dolphin Locations: Data detailing the occurrence of bottlenose dolphin groups in the study area derived from two data bases: 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, Fig. 1). 2) Presence only records collected in Golfo Dulce from 2005 to 2015 (Centro de Investigación de Cetáceos Costa Rica CEIC, N= Inshore: 407 sightings, Offshore: 31 sightings, Fig. 1). The specifics on the field approach are thoroughly described in Oviedo (2007), Oviedo and Solis (2008) and Oviedo *et al*. (2015).

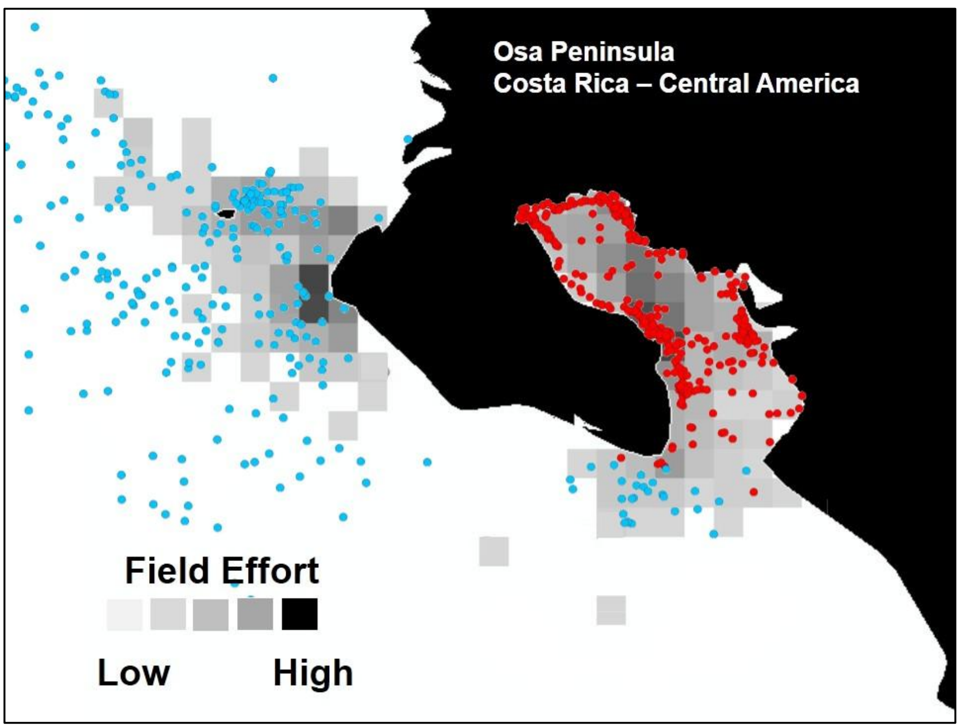

Figure 1. Research effort and encounters of inshore bottlenose dolphins (red filled circle) inside Golfo Dulce and offshore bottlenose dolphins (blue filled circles) off Osa Peninsula

Eco-geographic Variables: Several variables were taken in account in order to build the ecological niche models. The predictors were chosen due to their ecological relevance for the target specie and data availability. A 0.01-degree grid (aprox, 1.6 x 1.6 km) was used as resolution for the environmental layers. The dataset contains a group of physiographic related variables describing 'shelf tendency' (McLeod et al. 2007). Depth, slope and curvature 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 using the ArcGis 9.3.1 software. Three more variables were used in both areas: the distance to the coastline, the distance to the 200m bathymetric lines and distance to the major rivers mouth. These variables were constructed using the Euclidean Distance Tool of the Spatial Analyst Toolbox for Arcgis 9.3. Non physiographic variables were included in the modeling process, the mean Sea Surface Temperature (SST), Sea Surface Salinity (SSS) and the Surface Chlorophyll ɑ (Chlor-ɑ). Seasonal means for SST and SSS were obtained from MARSPEC dataset (Sbrocco, 2013). Due to the small size of Golfo Dulce no Chlor-ɑ data was available. Chlor-ɑ means were produced using the MODIS Aqua L2 images downloaded from Ocean Color Web (Feldman et al. 2012) and processed using SEADAS 7.0 (Baith *et al*. 2001). A 1.6 km resolution maps were created (one for each variable) using the mean value of all the images available from 2001 to 2006 for the seascape off Osa Peninsula and 2005-2015 for the Golfo Dulce. A correlation analysis of all the variables was performed using a Pearson's correlation analysis integrated in the ENMTools (Warren *et al*. 2010). All the 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 each species.

Modeling 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 the rainy season, to describe differences in the habitat suitability predictions and variables contribution between seasons. MAXENT program (version 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 probability distribution by finding the probability distribution of 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.). A sample selection bias approach (Elith *et al*. 2010) was applied in which the effort for both seasons is corrected. Two different files were constructed for each season using a Minimum Convex Polygon analysis with all the species sightings to obtain a sampled area polygon. Maxent models were run using the auto features with 10 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 0.9 represented outstanding discrimination

RESULTS

Ecological niche modeling for inshore bottlenose dolphins in Golfo Dulce

The average models for Golfo Dulce (GD) derived from 10 replication runs is presented in Figure 2. The major proportion of suitable habitat for *T. truncatus* in Golfo Dulce during dry and rainy seasons corresponded with the coastline, related with adjacent areas to the mouth of the rivers, such as Esquinas, Coto Colorado, with particular reference to the sub-system conform by Tigre and Platanares rivers. For the inshore bottlenose dolphin ecotype in GD, the mean AUC value for the cross-validated model of the dry and rainy season were 0.759 (+/- 0.120) and 0.775 (+/- 0.076) respectively, which were deemed to offer an *excellent discrimination* during the dry season and an *acceptable discrimination* for the rainy one, given our interpretation of AUC values.

There is a high level of uniformity for all replication depicting the model of the dry season according to the low value of standard deviation, in contracts with the medium level of the rainy season as indicated by the corresponding medium SD value. Plots in figure 3, illustrate the predictive performance of the model over a range of thresholds of suitable habitat, depicting details on the uncertainty associated with omission rates in the replicated models and show the replicated models performance in contrast to what a random prediction would generate. In this case the training omission a rate is close to the predicted, and do not lie well below the predicted omission line indicating low spatial autocorrelation.

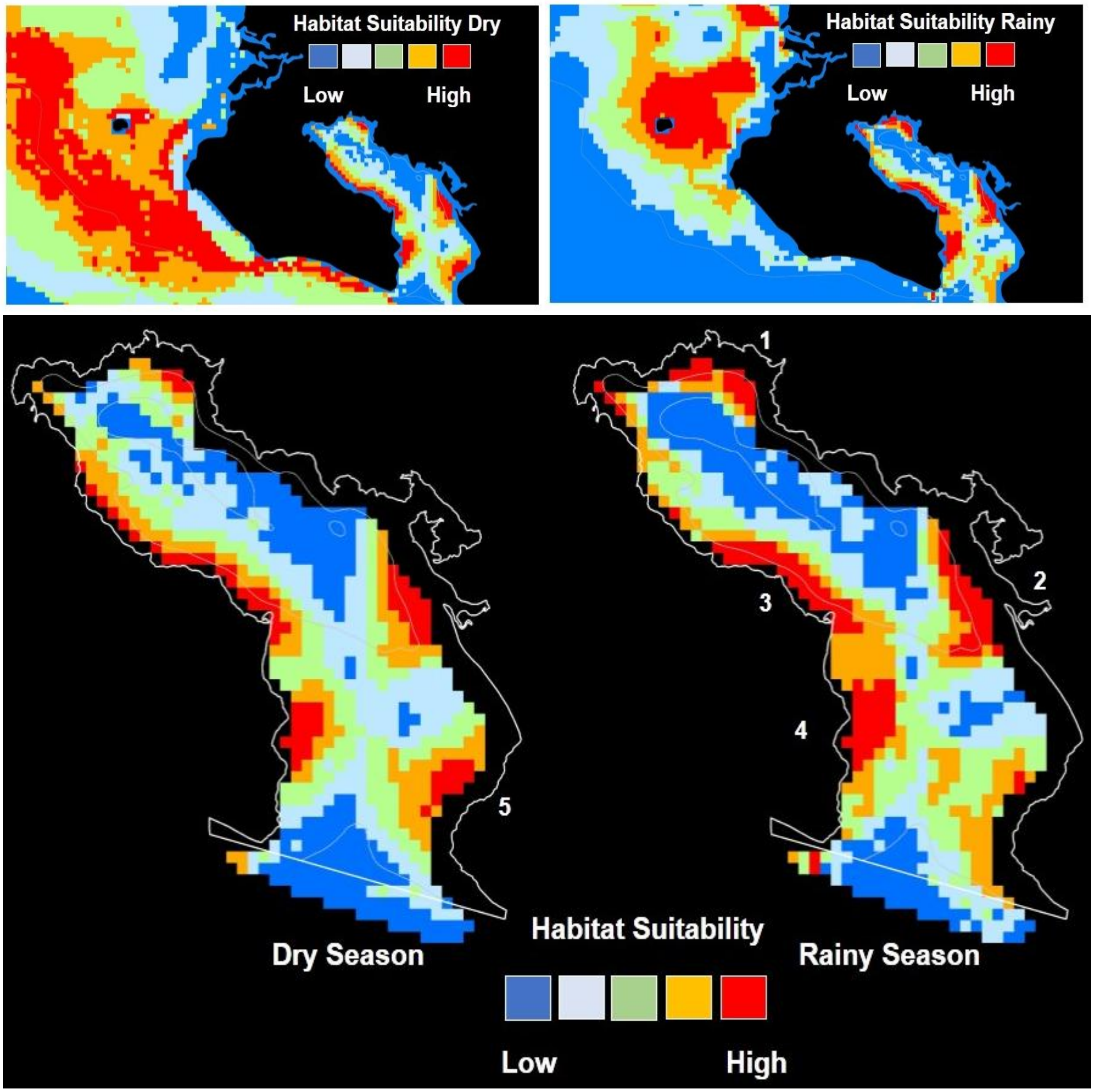

Figure 2. Average (Maxent) habitat suitability model: A) OPW offshore bottlenose during the dry season. B) OPW offshore bottlenose during the rainy season. C) Golfo Dulce inshore bottlenose dolphins: 1) Esquinas River, 2) Coto Colorado River, 3) Tigre River -Platanares River, 4) Tamales River at the sill area and 5) Pavones Beach at the sill area.

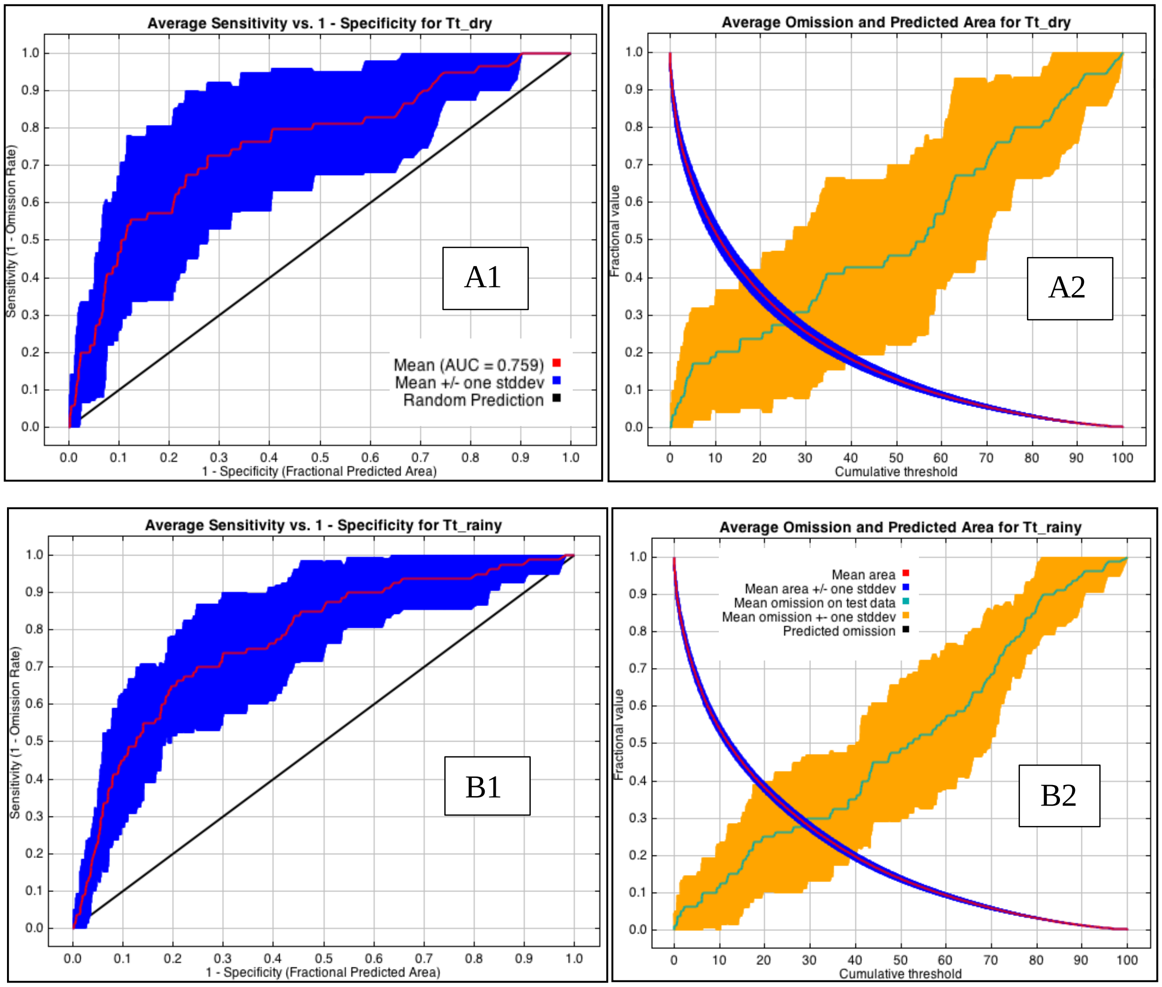

Figure 3. Diagnostic plots for Maxent modeling of bottlenose dolphins in Golfo Dulce 2005-2015. Plot A1 indicates the omission rates for the mean Maxent model and A2 the receiver operator characteristic (ROC) curve for the model of dry season. Plot B1 shows the omission rates for the mean Maxent model and B2 the receiver operator characteristic (ROC) curve for the model of rainy season.

Eco-geographical variables contributions to the final models of runs in Golfo Dulce are shown in Figure 4. From all the set, *distance to the rivers* and *distance to the 200 m isobaths* were found to be the strongest predictors during dry season, while *distance to the rivers*, *slope* and *distance to the 200 m isobaths* were the most influent environmental variables, during rainy season. Physical variables such as bathymetry, and variation on sea surface temperature were relatively weak predictors.

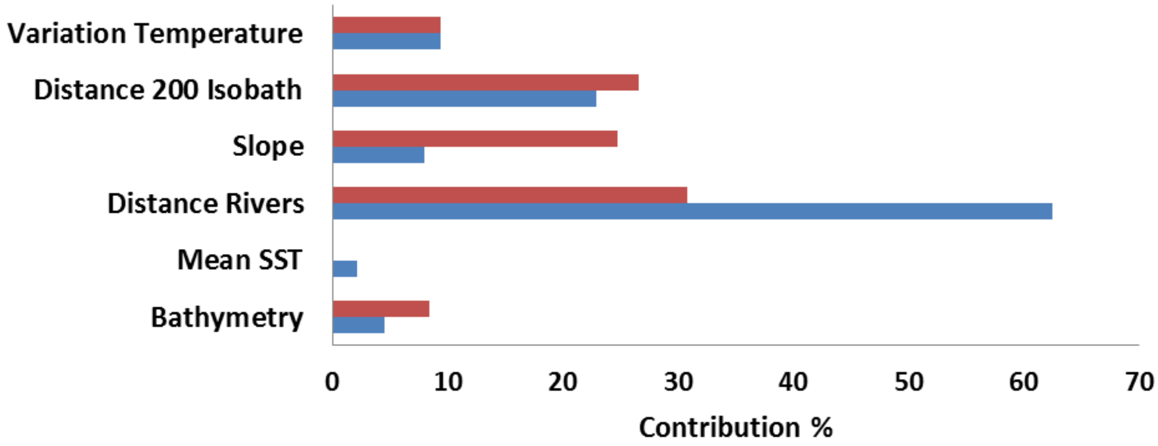

Figure 4. Eco-geographic variables describing the ecological niche of bottlenose dolphins in Golfo Dulce. The bars indicate the percent contribution for each variable to the overall models in Dry (blue bars) and Rainy (red bars) seasons respectively.

Maxent model responses to the most important predictor eco-geographical variables are shown in figure5 and figure 6 for dry and rainy seasons respectively. The seasonal model gain for Golfo Dulce during dry season is notably decrease by distance to the rivers and increase with the distance to the isobaths of 200 m (Figure 5).

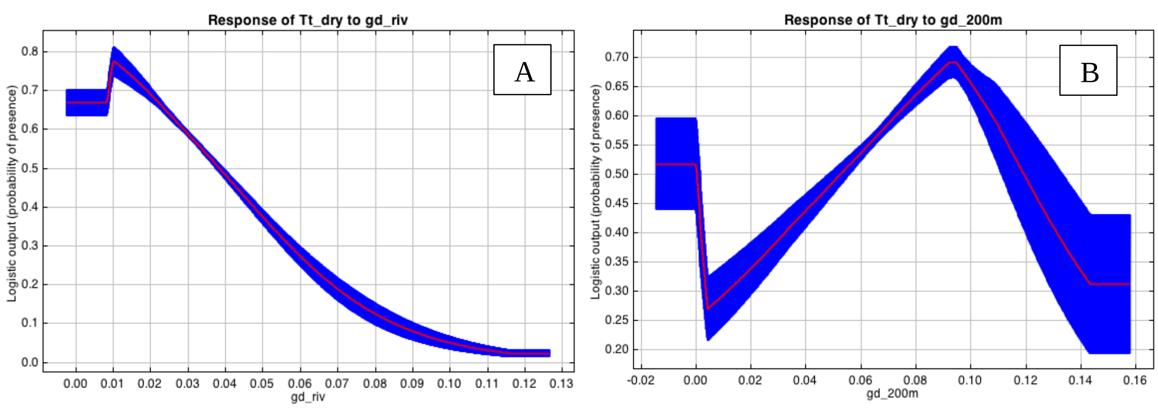

Figure 5. Eco-geographic variables response describing the ecological niche of bottlenose dolphins in Golfo Dulce during dry season: a) distance to rivers, b) distance to 200 m isobaths

Rainy season model gains are primarily described by the negative response to distance to the rivers beyond 4.45 Km, while distance to the 200 m isobaths gains are associated with distances close to 8 km (Figure 6). Additionally the model during rainy season showed a solid gain at a rather flat slope below 2 degrees.

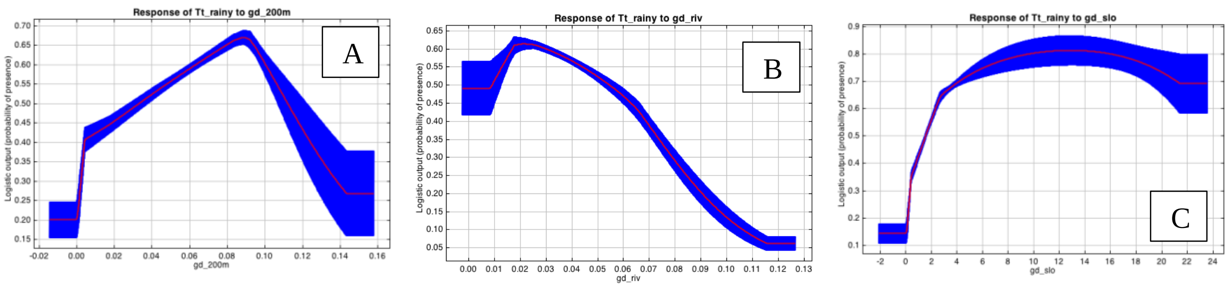

Figure 6. Eco-geographical variables describing the ecological niche of bottlenose dolphins in Golfo Dulce during rainy season: a) distance to 200 m isobaths, b) distance to rivers, c) slope

Ecological niche modeling for offshore bottlenose dolphins in Osa Peninsula waters

As in the case of Golfo Dulce, the average models for Osa Peninsula Waters (OPW) was equally obtained from 10 replication runs (Figure 2a and 2b). The model illustrates the ecological niche of bottlenose dolphins in Osa Peninsula waters. The suitable habitat for *T. truncatus* off-shore ecotype in Osa Peninsula waters during dry season is located within or close to the 200 m isobaths, while in the rainy season it shifted around Caño Island and in front Térraba-Sierpe wetland. For OPW the mean AUC value for the cross-validated model of the dry and rainy season were 0.759 (+/- 0.089) and 0.888 (+/- 0.098) respectively, which were deemed to offer an *excellent discrimination* during the dry season and *acceptable discrimination* for the rainy season. Plots in figure 7 illustrate the predictive performance of the model, highlighting low spatial autocorrelation.

The contributions of eco-geographical variables to the final models of off-shore bottlenose dolphins in Osa Peninsula Waters are shown in Figure 8. From all the set, depth and distance to the 200 m isobaths were found to be the strongest predictors, both during rainy and dry seasons. Physical variables such as distance to Caño Island, slope, variation and average sea surface temperature were relatively weak predictors.

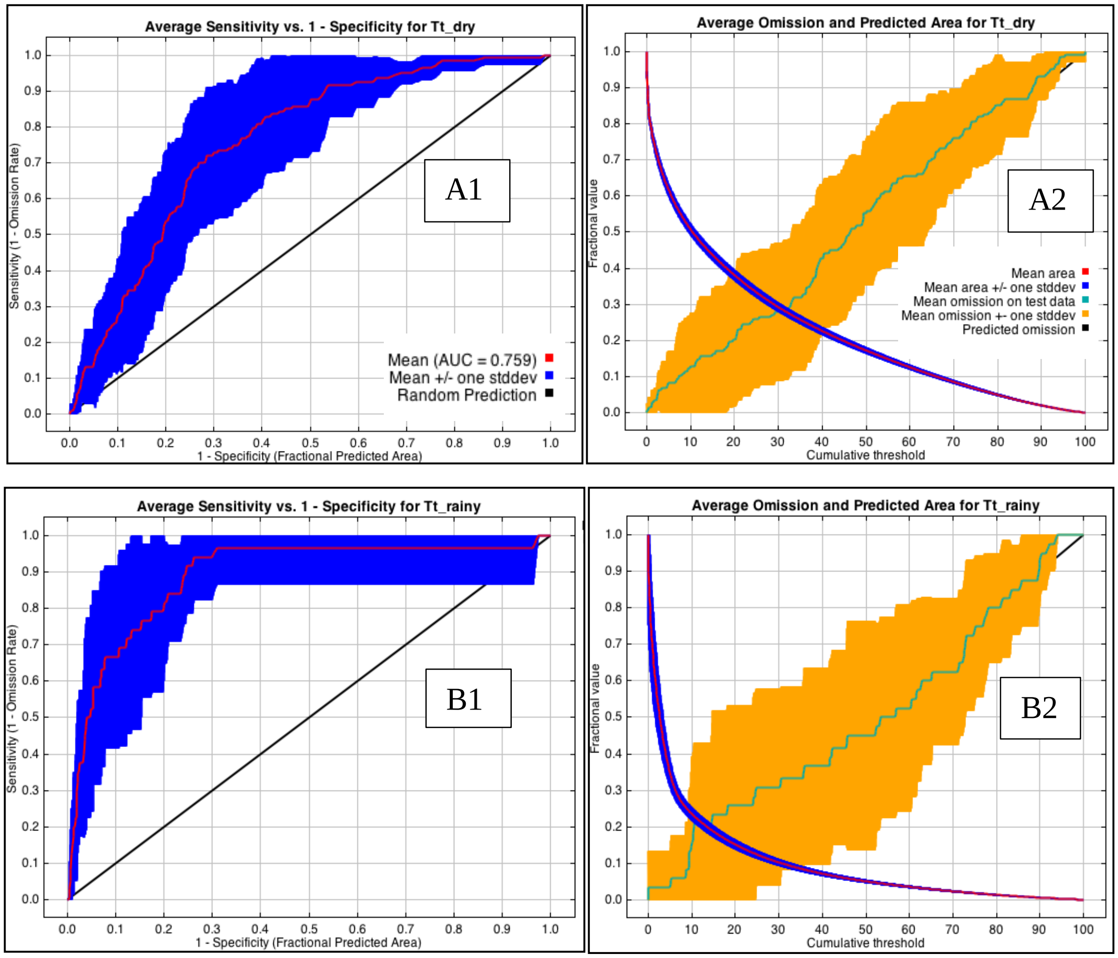

Figure 7. Diagnostic plots for Maxent modeling of bottlenose dolphin off-shore ecotype in Osa Peninsula waters 2002-2006. Plot A1 indicates the omission rates for the mean Maxent model and A2 the receiver operator characteristic (ROC) curve for the model of dry season. Plot B1 shows the omission rates for the mean Maxent model and B2 the receiver operator characteristic (ROC) curve for the model of rainy season.

The seasonal models of Osa Peninsula waters are primarily dominated by depths; during dry season the ecological niche of bottlenose dolphins are better predicted by depths close to the 200 m bathymetric contour, this characteristic shifted during rainy season to platform water depths of less than 200 m. Distance to the 200 m isobaths is the second best predictor of the ecological niche of *T. truncatus* in Osa Peninsula Waters, during the dry season the maximum gain is more consistent with very short distances as opposed with the trend during the rainy season, where the niche is best described by distances close to 16 km from this bathymetric contour.

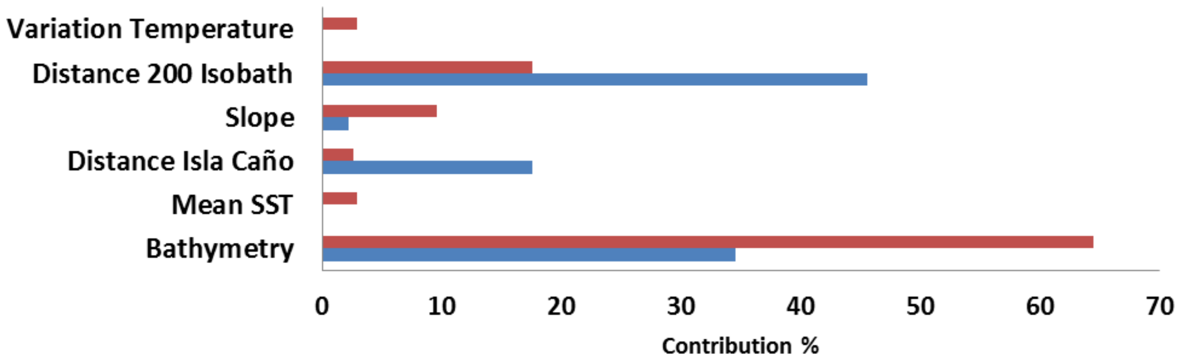

Figure 8. Eco-geographical variables describing the ecological niche of bottlenose dolphin off-shore ecotype in Osa Peninsula waters. The bars indicate the percent contribution for each variable to the overall models in Dry and Rainy seasons respectively.

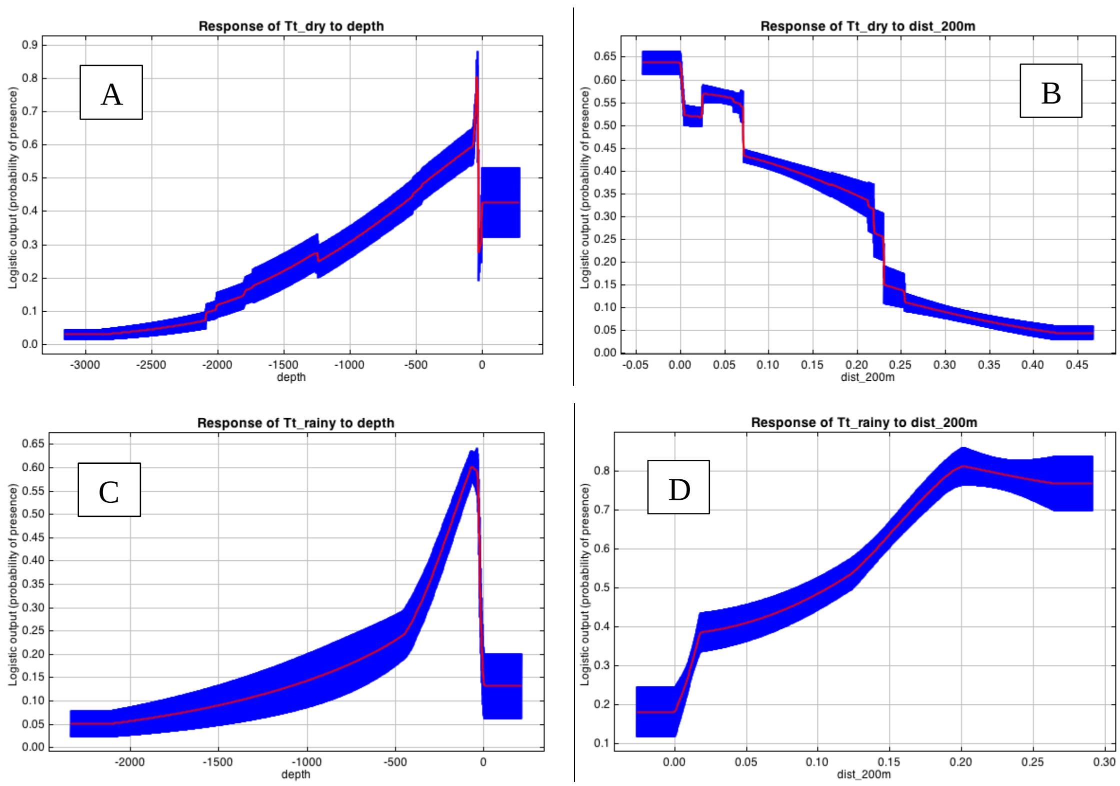

Figure 9. Eco-geographic variables response describing the ecological niche of bottlenose dolphins in Osa Peninsula waters during dry and rainy seasons respectively: a) bathymetry dry season, b) distance 200 m isobaths dry season, c) bathymetry rainy season, d) distance 200 m isobaths rainy season

DISCUSSION

The results detailed above support the occurrence of two ecotypes of bottlenose dolphins in Golfo Dulce and Osa Peninsula waters. Based on their distribution and external morphology, we have distinguished between these two ecotypes; an smaller offshore form, usually found in OPW, within or close to the 200 m isobaths, while the larger inshore race is generally found at the sill and inner basin of GD (Pacheco-Polanco *et al*. 2011). Morphologically these races corresponded with the description of the species at the Eastern Tropical Pacific (Wells & Scott 2008, Oviedo *et al.* 2015).

Differences in their morphology would be expressions of phenotype, determined by factors such as water temperature, or depth at which different populations would forage (Hale *et al*. 2000). In Golfo Dulce, the eco-geographical variables that best describe the ecological niche of the inshore form of bottlenose dolphins were distance to the rivers, distance to the 200 m isobaths and slope, whereas depth and distance to the 200 m isobaths were found to be the strongest predictors that describe the ecological niche of the offshore race of *T. truncatus* in OPW, during both seasons. Water depth, distance to the coast and distance to the 200 meter depth contour have been used for different authors to identify boundaries between them (Hale *et al*. 2000, Segura *et al*. 2006).

Presumably, the offshore form is best adapted to live in oceanic environments and to exploit mesopelagic preys, possibly found within or closed to the 200 meters isobaths, while the inshore ecotype prefers shallower inshore environments where the distribution pattern of their potential prey could be related with the distance to the mouth of the rivers that drains into the gulf. In GD, observational data on the inshore ecotype of bottlenose dolphins have allowed us to document as the main prey items, demersal and epipelagic teleostean fish such as needlefish (*Tylosurus acus pacificus*) and ballyhoo (*Hemiramphus sp*), whereas the offshore ecotype in OPW would forage on mesopelagic preys, similarly to the population of bottlenose dolphins in the Gulf of California or Mediterranean sea (Bearzi *et al*. 2008, Perrin *et al*. 2011).

Our analyses indicate several important aspects on the distribution of the two ecotypes of bottlenose dolphins, as expected in the study area, we have found these two ecological races to occur in close proximity, but to remarkably differ in the ecological niche they occupied, the inshore population that inhabits in GD, use the areas closed to the mouths of the rivers as critical foraging habitats, estuarine habitats represents secured resources, were potential prey species may be found individually rather than in large schools, 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); whereas the offshore population in oceanic habitats must rely on prey species found in rare but profitable patches, with large areas of habitat with little to not available food sources at all, therefore, pelagic dolphins in the open ocean often would need to travel long distances searching for these patches. According to our field observations, bottlenose dolphins showed an increased in group size with water depth, 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 protect against them, while in complex sheltered estuarine habitats, the dolphins can hide and reduce their predation risk. Scramble competition at intra-specific level for food and other factors may limit the option of forming large groups in coastal habitats (Bearzi 2005, Pacheco-Polanco & Oviedo 2007, Gowans *et al*. 2007, Bearzi *et al*. 2008, Oviedo *et al*. 2012).

Other factors such as habitat structure, habitat boundaries, resources specialization, and site fidelity in sheltered environments may promote phenotypic differentiation between dolphin groups like that one's 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*. 2008, Fernandez *et al*. 2011, Pacheco-Polanco *et al*. 2011). These factors might equally have a crucial role in defining eco-morphological differences within a species. We hypothesize that the coastal habitat of Golfo Dulce might have even stronger implications beyond the level of ecotypes, with potential localized 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 survey with genetic sampling in forthcoming sampling seasons to confirm our hypothesis.

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