Predicting cetacean habitat in the Colombian Pacific EEZ: challenges and recommendations

by

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April 11th, 2018

Masters project submitted in partial fulfillment of the

requirements for the Master of Environmental Management degree in

the Nicholas School of the Environment of

Duke University

Executive Summary

The study of cetaceans in the Colombian Pacific Exclusive Economic Zone has been limited to their distribution and abundance, and little is known about their habitat preferences and the ecological processes determining their range. The present study establishes a baseline habitat model for cetaceans in this area, identifying differences in habitat preferences and areas of predicted high occurrence. Four species were studied including: humpback whales (*Megaptera novaeangliae)*; bottlenose dolphins (*Tursiops truncatus*); pantropical spotted dolphins (*Stenella attenuata*, coastal and offshore forms); and the sperm whale (*Physeter microcephalus*). Presence-only data was used to model habitat suitability with MaxEnt using static and dynamic environmental variables. Models for all species except for sperm whales had AUC > 0.7 indicating acceptable model performance.

Models with static variables indicate that for humpback whales, depth was the main variable that contributed to the modeled distribution, and distance to shore was a more important contributor for the small cetaceans. Models including dynamic variables increased predictive power and fit, with AUC values higher than models employing only static variables. In the case of humpback whales, SST was a major variable contributing to the model and therefore, habitat suitability changed across months with higher predicted occurrence for the colder months. For pantropical spotted dolphins, SST had a similar effect for the offshore form but not major effects for the coastal form.

Data limitations and a lack of dedicated cetacean surveys using appropriate methodologies prevented the use of more robust modeling approaches, and therefore, make it difficult to precisely identify areas of high priority for conservation and management. Nevertheless, this study provides an initial step to analyze the best available data in the country, but it is necessary to improve methods of data collection to increase the understanding of cetacean ecology and improve management practices.

Introduction

The study of cetaceans in the Colombian Pacific Ocean has increased slowly during the past decade, thanks to their economic value for local communities as a source of ecotourism, and due to a decrease in social conflicts, making the region more accessible to researchers and environmentalists (Baptiste et al., 2017). However, due to limited resources available for research, studies of these species have been restricted largely to their distribution and occurrence (e.g., Vidal, 1990; Herrera-Carmona et al., 2011; Palacios et al., 2012). To date, at least 23 species of cetaceans are confirmed to occur in the Colombian Pacific Ocean (Palacios et al., 2012), including 17 tooth whales and six baleen whales.

Humpback whales (*Megaptera novaeangliae*), bottlenose dolphins (*Tursiops truncatus*) and pantropical spotted dolphins (*Stenella attenuata*) are the most frequently studied species in the Colombian Pacific (Ávila et al., 2013). The study of these species is facilitated by their presence in coastal areas and near islands, but little focus has been given to offshore waters due a lack of resources (Ávila et al., 2013). Initial study of offshore populations was triggered by the bycatch of pelagic dolphins during the 1970s as a consequence of the tuna purse seine fishery activities, which led to the assessment of several delphinid populations in the Eastern Tropical Pacific (ETP) by international bodies (Ferguson et al., 2006). In addition, two Colombian expeditions have investigated the distribution and relative abundance of cetaceans in the oceanic waters of the Colombian Pacific (Palacios et al., 2012).

Humpback whales have been used as umbrella and flagship species to promote broad management and conservation measures along the Colombian Pacific Coast (Flórez-González et al., 2007; Hoyt & Iñíguez, 2008). The use of such charismatic species has resulted in the creation of some Marine Protected Areas (MPAs) in this area of Colombia, and increased ecotourism (Ávila et al., 2013). Nevertheless, the study of this and other cetacean species is limited, and relatively little is known about their habitat preferences and spatial distribution in coastal or pelagic areas. Hence, it is important to identify areas where these species are likely to be found and where there is potential for improvement of management measures.

Habitat modeling is a widely used tool to predict cetacean distributions and understand the ecological processes that define such distributions (Redfern et al. 2006). Furthermore, habitat preference models can be used to assess areas of high conservation priority and identify key areas for research on cetaceans and human interactions (Bailey & Thompson, 2009). The use of advanced geospatial analysis tools will facilitate a better understand distributions of cetaceans and the environmental factors influencing these patterns in the Colombian Pacific Ocean.

Previous cetacean habitat modeling studies in the region have been conducted by the NOAA Southwest Fisheries Science Center in response to the bycatch of dolphins in the ETP tuna fishery. These studies predicted delphinid density across the ETP (Ferguson et al., 2006) and evaluated the effects of scale on dolphin-habitat relationships (Redfern et al., 2008). Furthermore, the migratory patterns of large whales along the Eastern Pacific Ocean were modeled to understand their distribution, migratory routes and critical habitat. This information was used to inform management plans to improve the protection of migratory whales from human impacts across political boundaries (CPPS/PNUMA, 2012). However, no studies have directly addressed habitat preferences of cetaceans in Colombia.

In the present study, I establish a series of baseline habitat models for cetaceans in the Colombian Pacific Exclusive Economic Zone (CP-EEZ). This baseline will identify differences in habitat preference and occurrence among cetacean species present in the area and ultimately inform management and conservation of these species in Colombia. This task is challenging given current data limitations; but, I will evaluate habitat models, discuss the difficulties of conducting such studies with limited data, and consider the implications for the management of cetaceans in this setting.

Materials and methods

Study Area

The study area is part of the Eastern Tropical Pacific Seascape (ETPS) that includes the Pacific EEZs of Costa Rica, Panama, Ecuador and Colombia. This Seascape is used to address marine conservation and management under the ideas of ecological inter-dependence and common difficulties in the countries (UNESCO, n.d.). The present study will focus on the Colombian EEZ and cetaceans found in these waters (Figure 1).

The CP-EEZ has an area of around 330,000 square kilometers, representing 36% of the Colombian national marine area (Alonso et al., 2015). This area is characterized by weak winds, high cloudiness and precipitation, warm sea surface temperatures (25- 26 ºC), and relatively low salinity (Cantera, 1993). Moreover, the Colombian Pacific is influenced by the El Niño Southern Oscillation (ENSO) events, with warmer sea surface temperatures and higher sea level during El Niño period (Wang & Fiedler, 2006).

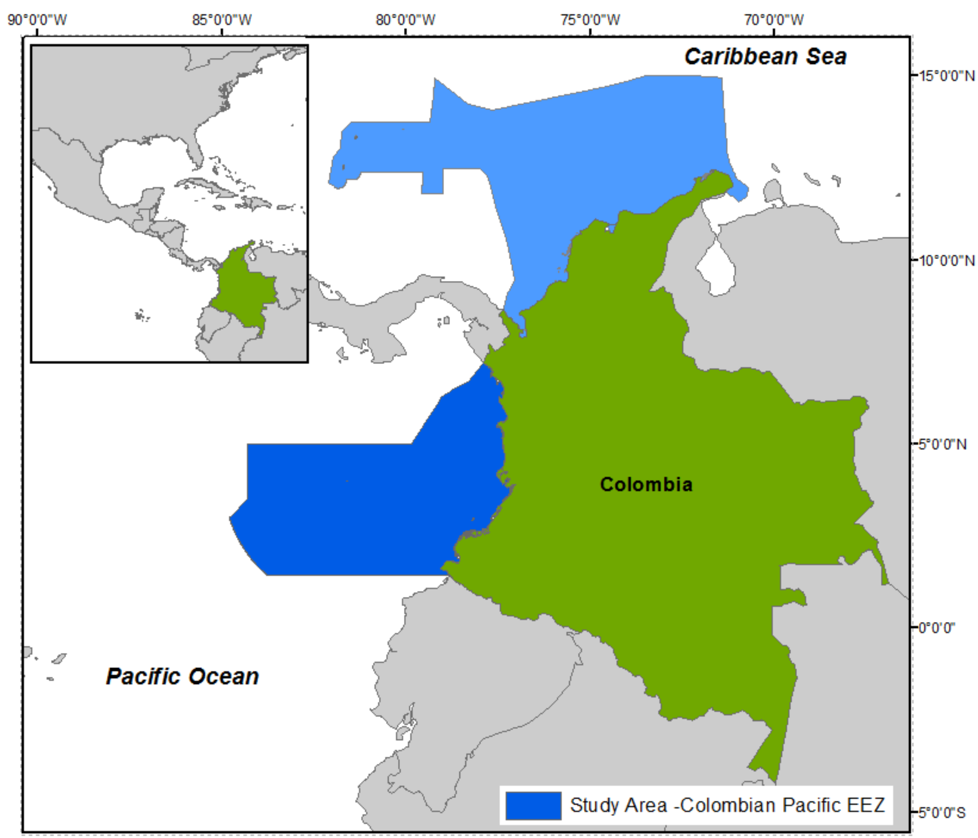

Figure 1. Colombian Pacific Exclusive Economic Zone

Occurrence data

Sightings data for cetaceans in the CP-EEZ were compiled from the Marine Environmental Information System – SIAM (http://siam.invemar.org.co) developed by the Colombian Marine Research Institute (INVEMAR), and a database developed by the Fundación Macuáticos, a local NGO. Sightings were georeferenced using datum WGS84. The dataset used for this study is presence-only, meaning that presence of a species was recorded, but absences (such as survey track lines) were not (Franklin, 2009).

Cetacean occurrences used for this study were collected from 2000 to 2017. After depurating the databases, only four species had sufficient sightings to be included in the analysis: humpback whale (n = 260), bottlenose dolphin (n = 156), pantropical spotted dolphin (n = 325) and sperm whale (*Physeter macrocephalus*, n = 106) (Figure 2).

In the case of pantropical spotted dolphin, two ecotypes or geographical forms, are recognized in the ETP: an offshore population and a coastal population (Dizon, Perrin, & Akin, 1994; Perrin, 1975). Therefore, each form was modeled independently to account for differences in their biology and ecology. A threshold of 200 km distance from shore (Dizon, Perrin, & Akin, 1994) was used to separate the coastal form (n = 129) from the offshore form (n = 196) sightings (Figure 3).

Environmental data

Environmental layers used in the model were selected after reviewing previous cetacean habitat model studies in the region (do Amaral et al., 2015; Gomez et al., 2017; Tobeña et al,2017). Due to data limitations, the analysis was performed with static variables for all four species, and a separate analysis was conducted with both static and dynamic variables for humpback whales (n = 149), and the two forms of pantropical spotted dolphins (coastal n = 77, offshore n = 102). The reasoning behind this decision is related to the reduction in the number of sightings when incorporating dynamic variables. The use of remote sensed dynamic variables is constricted by the cloudiness in the area, therefore, in many of the cases a cloud prevented to have the value of a variable for a specific time and place. This constriction reduced the number of samples that could be used for each species.

Static Variables

The static variables considered for this study included: depth; slope; distance to shore; and distance to seamounts. Distance to shelf break (using the 200-meter isobath) was not used due to the high correlation of this parameter with distance to shore (r=0.98). Variables were treated with ArcMap 10.5.1 using the model builder and a variety of different tools. The depth raster was retrieved from the General Bathymetric Chart of the Oceans GEBCO (https://www.gebco.net/). The slope was derived from the depth raster using the Slope tool from ArcMap. Shorelines were downloaded from the Global Self- consistent, Hierarchical, High-resolution Geography Database (GSHHG) Version 2.3.7 (Wessel, 2017) and the positions of seamounts were obtained from the UNEP Global Distribution of Seamounts and Knolls dataset (Yesson et al., 2011). Distance to shore and seamounts were calculated using the Near tool in ArcMap. Finally, ten thousand random background points within the CP-EEZ were used to interpolate distance to shore and distance to seamounts and create raster layers to use in the model with the IDW interpolation tool.

Dynamic Variables

Dynamic variables used in this study included remotely sensed sea surface temperature (SST) and chlorophyll-a concentration (Chl-a). I used monthly composites for these dynamic variables to conserve an acceptable sample size for humpback whales and pantropical spotted dolphins. The accuracy of the model can decline significantly due to data loss from cloudiness in some regions and, in such cases, is preferable to use aggregated environmental data for a broader temporal resolution (Scales et al., 2016; Prieto et al., 2017). The Marine Geospatial Ecology Tools (MGET) were used to access SST and Chl-a from the NASA JLP PO.DAAC and the NASA GSFC Ocean Color Group databases respectively (Roberts et al., 2010).

Rasters for both SST and Chl-a were obtained for all months between 2010 and 2017. Afterward, rasters with mean SST or Chl-a were created for the twelve months by averaging the values for each month across the years with R raster package. I used averaged values for each month to avoid No Data values caused by cloudiness in the projection raster. As a result, a raster with the mean SST and another with the Chl-a was created for each month.

In the case of humpback whales, I included only months from June to November to project predicted habitat. I used all months to project habitat suitability for the coastal and offshore form of the pantropical spotted dolphin.

Ecological niche modeling

As noted above, I used a presence only approach to model the distribution of cetacean species in the CP-EEZ. Specifically, I used MaxEnt version 3.4.1 (Phillips et al., 2017) to model the distribution of the four species. MaxEnt estimates the geographic range of a species by finding the distribution which has the maximum entropy constrained by the environmental conditions at recorded occurrence locations (Phillips et al., 2017). MaxEnt predicts environmental suitability, with better conditions represented by higher values (Phillips et al., 2006). This method tends to predict the largest possible suitable area consistent with the data (do Amaral et al., 2015). Therefore, careful consideration of the limitations and biases in the data must be taken, but MaxEnt can perform well in comparison to presence-absence models (Tobeña et al., 2016; Praca et al., 2009; MacLeod et al., 2008).

Cetacean occurrences and ten thousand random background points within the CP-EEZ were combined with the environmental layers in ArcGIS 10.5.1 producing 'sample with data' (SDW) datasets. I used the recommendations of Merow et al. (2013) as guidelines to make informed decisions about what settings and parameters to use in MaxEnt. I changed the default settings to use the linear and quadratic functions, because simpler models should be favored when there are small samples sizes and strong sample bias (Prieto et al., 2017; Merow et al., 2014).

Thirty percent of the sightings for each species were chosen randomly to serve as test data sets to evaluate the fit of the model and its predictive power. Model performance was assessed with the receiver operating characteristic (ROC) analysis and the area under the curve (AUC). AUC is useful for understanding non-random performance: values close to 0.5 indicate random predictions, AUC values between 0.7 and 0.9 indicate reasonable model performance, and values above 0.9 indicate high performance (Phillips et al., 2006;

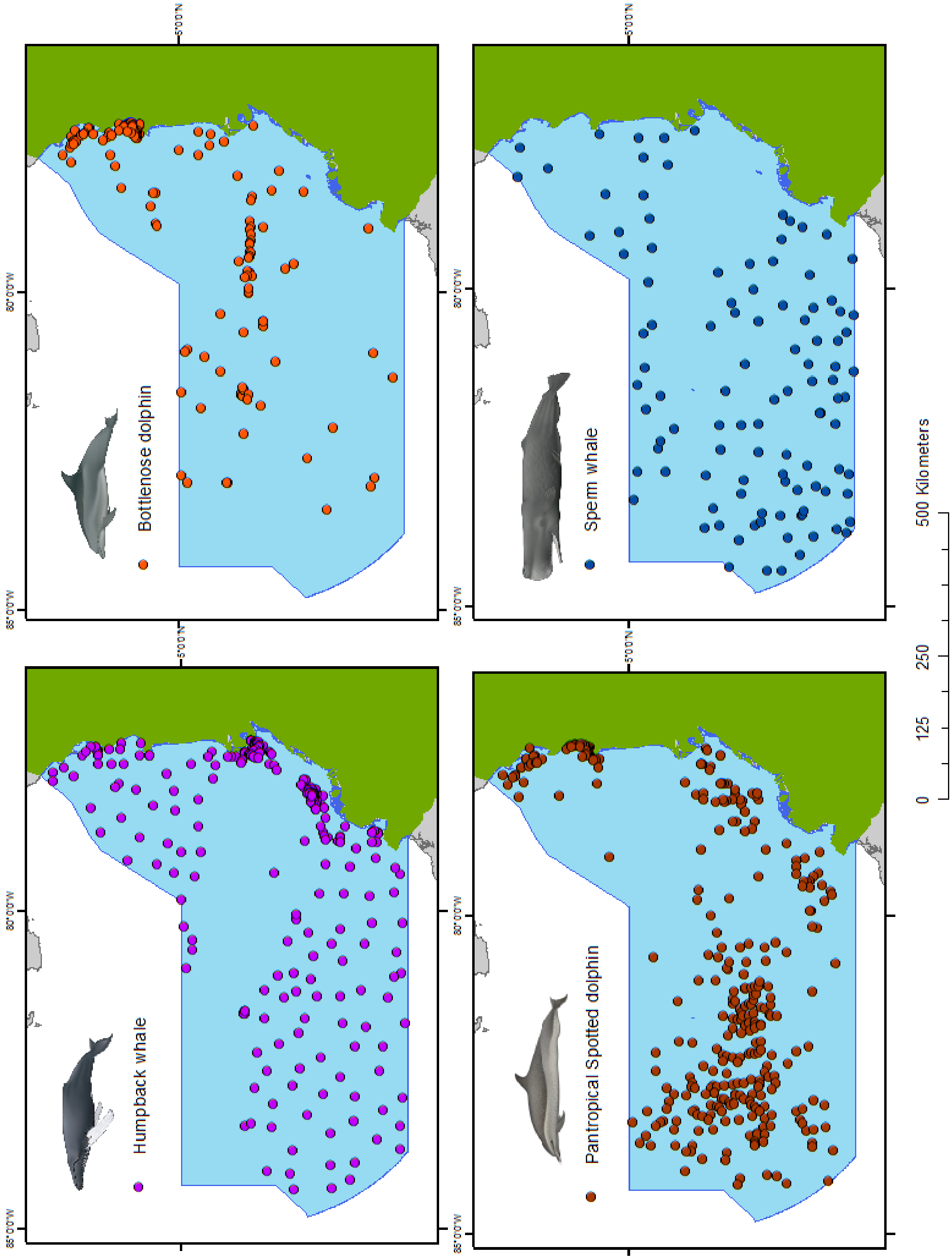

Figure 2. Distribution of sightings of the species georeferenced data used in this study.

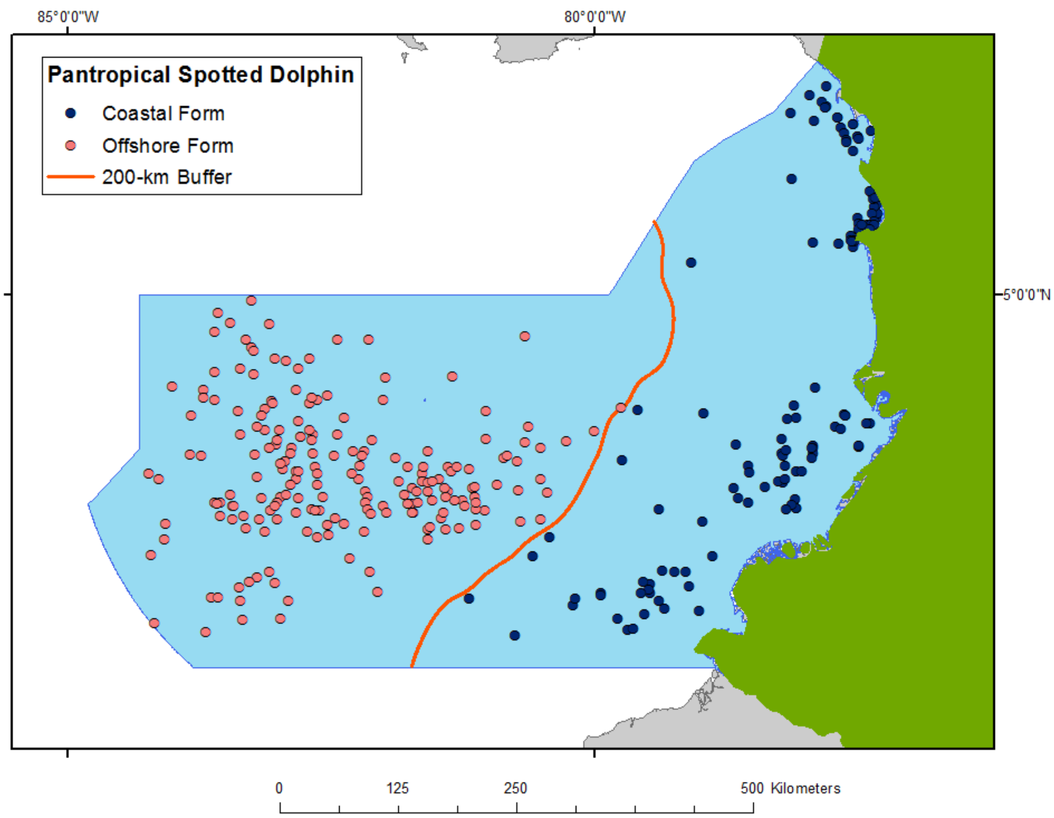

Figure 3. Sightings distribution for *Stenella attenuata* (coastal and offshore forms).

Peterson et al., 2011; Prieto et al., 2017). Maps were exported in rasterized format, and suitability scores were visualized in ArcGIS showing habitat suitability ranging from unsuitable (0) to highly suitable (1).

Results

Static Variables models

Ecological niche models generated for the four-different species returned AUC values indicating variable model performance (Table 1). The models for humpback whales, bottlenose dolphins, and the coastal form of pantropical spotted dolphins demonstrated reasonable performances. On the other hand, models for sperm whale and the offshore form of pantropical spotted dolphin performed poorly. The suitable geographical range for each species is shown in Figs. 4, 5, 6, 7 and 8.

Table 1. AUC values and relative contributions of the major environmental variables to the Maxent models.

Species	Training AUC	Test AUC	Variable Contribution (%)
Humpback whale	0.762	0.702	Depth (83.2)
			Dist Seamounts (15.3)
Bottlenose dolphin	0.762	0.702	Dist Shore (65.4)
			Depth (31.6)
Pantropical spotted dolphin (coastal form)	0.892	0.812	Dist Shore (39.6)
			Depth (36.7)
Pantropical spotted dolphin (offshore form)	0.760	0.621	Dist Seamounts (41.7)
			Depth (39)
Sperm whale	0.608	0.591	Dist Seamounts (54.1)
			Dist Shore (32.7)

<u>Humpback whale</u>

The AUC for the humpback whale model was above 0.7, indicating that the model performed well in discriminating presence and background areas (Table 1). In addition, the similar values for both test AUC and training AUC evidence that the model fit and power were high when using a different data set. The main contributor to this model was depth, showing that areas with the highest suitability for the occurrence of humpback whales (> 70%) are in shallow waters, less than 500 meters deep (Fig 4). Habitat suitability increased with decreasing depth and increasing distance to seamounts, but distance to shore and slope did not contribute much to the model.

<u>Bottlenose dolphin</u>

The bottlenose dolphin model also performed relatively well with a mean AUC above 0.7 (Table 1). Again, as with humpback whales, training and test AUC values were similar, indicating a relatively good model fit and high predictive power. Distance to shore contributed most to the bottlenose dolphin model, followed by depth and minimal contributions by slope and distance to seamounts. Suitable areas for bottlenose dolphin occurrence (> 70%) were waters less than 50 km from shore (continental and insular) and less than 1,000 m depth (Fig 5). Thus, suitability decreases with increased distance to shore and in deeper waters.

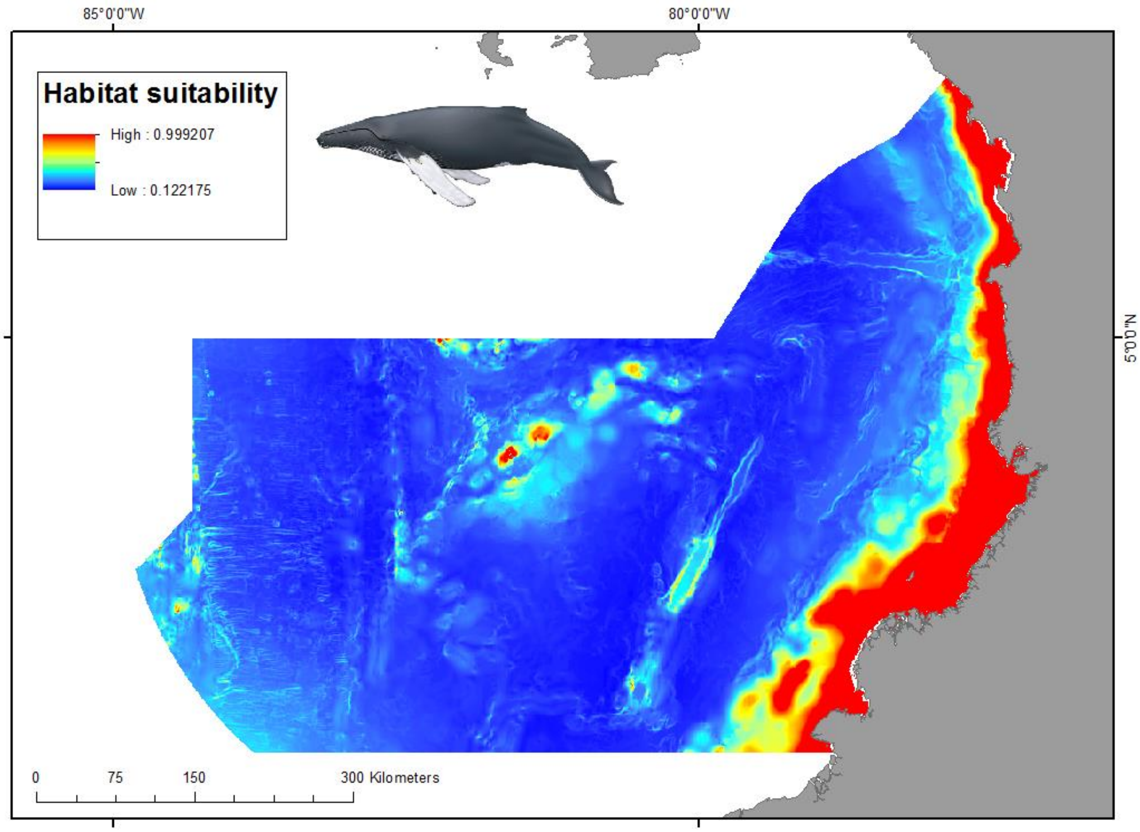

Figure 4. Potential geographic distribution for humpback whale (*M. novaeangliae*) in the CP-EEZ

Pantropical spotted dolphin – coastal form

The model for the coastal form of the pantropical spotted dolphin had the highest AUC value (> 0.8) of all models (Table 1). Both training and test AUC indicate a high model performance, with a high predictive power and model fit. Distance to shore and depth contributed the most to the coastal pantropical spotted dolphin model, with similar percentages of contribution (Table 1). Distance to seamounts had also a considerable contribution with 22%, but slope had a minor contribution. Areas with the highest suitability (>70%) were waters up to 50-60 km from shore and in less than 1,000 m of depth (Fig 6). Habitat suitability decreased with increasing depth and distance to shore, and decreasing distance to seamounts.

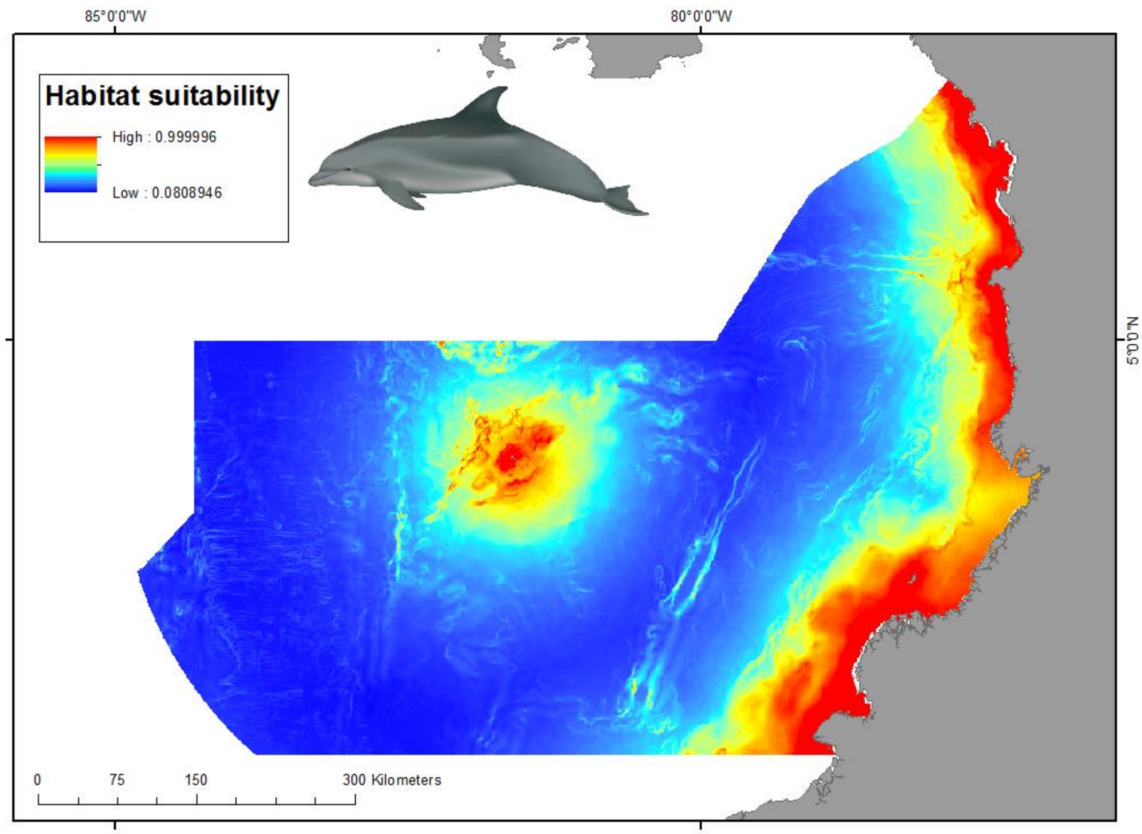

Figure 5. Potential geographic distribution for bottlenose dolphin (*T. truncatus*) in the CP-EEZ

Pantropical spotted dolphin – offshore form

This model training AUC was higher than 0.7 indicating a reasonable performance, but the test AUC value differed greatly from the training AUC, meaning that the model fit and predictive power did not perform well when using a separate set of sightings (Table 1). For the offshore pantropical spotted dolphin, the variables that contributed the most were distance to seamounts and depth (Table 1). Areas with higher suitability were those with a distance to seamounts between zero and 80 km, and depths between 2,000 and 3,000 meters (Fig 7). Habitat suitability increased with decreasing distance to seamounts and was highest with depth values between extremes.

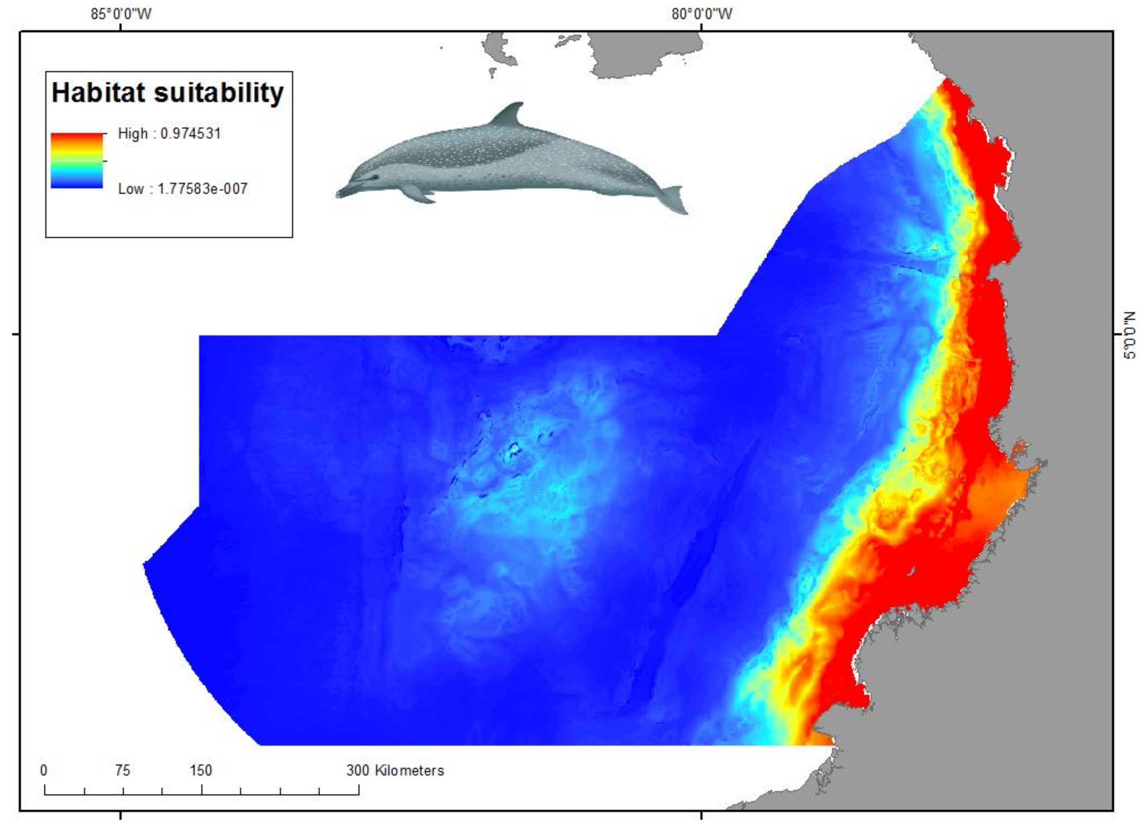

Figure 6. Potential geographic distribution for the coastal form of the pantropical spotted dolphin (*S. attenuata*) in the CP-EEZ

<u>Sperm whale</u>

The sperm whale model had the poorest performance based on both the training and test AUC values, with both below 0.7 (Table 1). Distance to seamounts contributed the most to the model, followed by distance to shore (Table 1). Areas with the highest suitability (>70%) were less than 50 km from seamounts and more than 350 km away from shore (Fig 8). Nevertheless, these results should be interpreted with caution due to the low model performance.

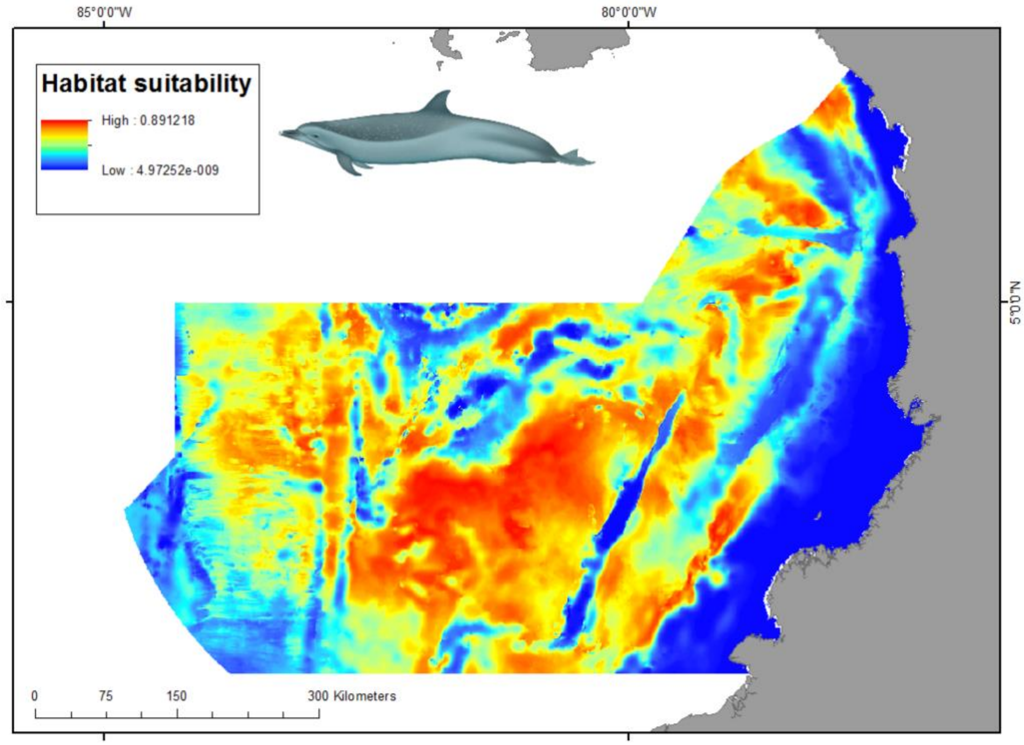

Figure 7. Potential geographic distribution for the offshore form of the pantropical spotted dolphin (*S. attenuata*) in the CP-EEZ

Dynamic and Static Variable models

Ecological niche models incorporating dynamic variables generated for both species returned AUC values higher than those using only static variables (Table 2). SST was a more important contributor than Chl-a. The model for humpback whales and the coastal form of pantropical spotted dolphins both demonstrated high performances. Similarly, the model for the offshore pantropical spotted dolphins had reasonable performance. The predicted geographical range for each species is shown in Figs. 9, 10, 11, 12 and 13.

Table 2. AUC values and relative contributions of the major environmental variables to the Maxent models with dynamic and static variables.

Species	Training AUC	Test AUC	Variable Contribution (%)
Humpback whale	0.903	0.910	Depth (53.6)
			SST (23.1)
Pantropical spotted dolphin (coastal form)	0.930	0.883	Dist Shore (30.7)
			Dist Seamounts (30.5)
Pantropical spotted dolphin (offshore form)	0.765	0.750	Dist Seamounts (49.9)
			Depth (17.2)

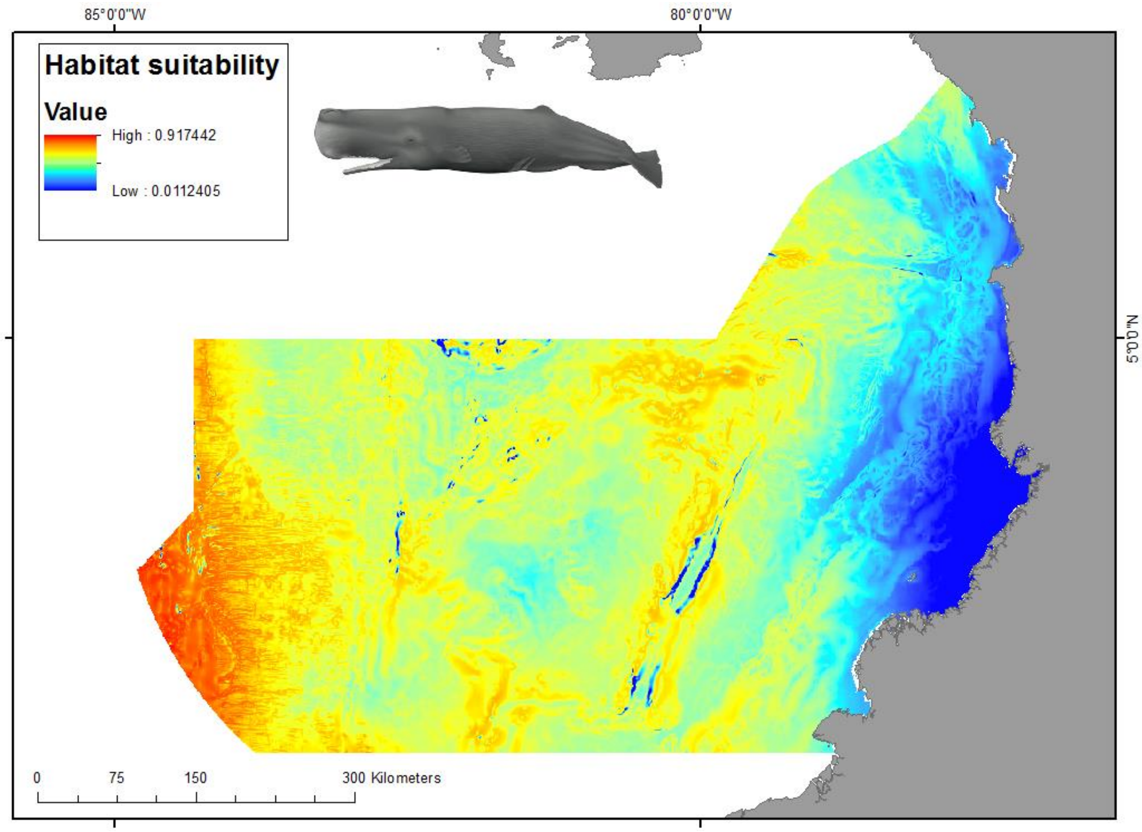

Figure 8. Potential geographic distribution for sperm whale (*P. macrocephalus*) in the CP-EEZ

Humpback whale

The model for the humpback whale had an AUC value above 0.9, indicating that the model had a high performance (Table 2). In addition, the similar values for both test AUC and training AUC evidence high fit and predictive power of the model. The main variables contributing to the model were depth and SST (Table 2).

As in the static model, suitable areas for the occurrence of humpback whales (> 70%) were in shallow waters, less than 500 meters deep. Additionally, habitat suitability was the highest with SST values between 24.5 and 26.5 ºC but decreased with greater temperatures. Furthermore, there was a larger area of habitat suitability in the southern coastal area of the CP-EZZ.

Figure 9 shows the potential geographic range for humpback whales during the months when they arrive at the tropical waters in the CP-EEZ. Predicted habitat range increases from June to November. This increase is mainly related to changes in SST, with higher temperatures at the beginning of the season and lower temperatures by the end. Although November seems the month with the most suitable habitat areas, there are few sightings of humpback whales for this month because most of them are already migrating south to their temperate and Antarctic feeding grounds (Félix & Guzmán, 2014).

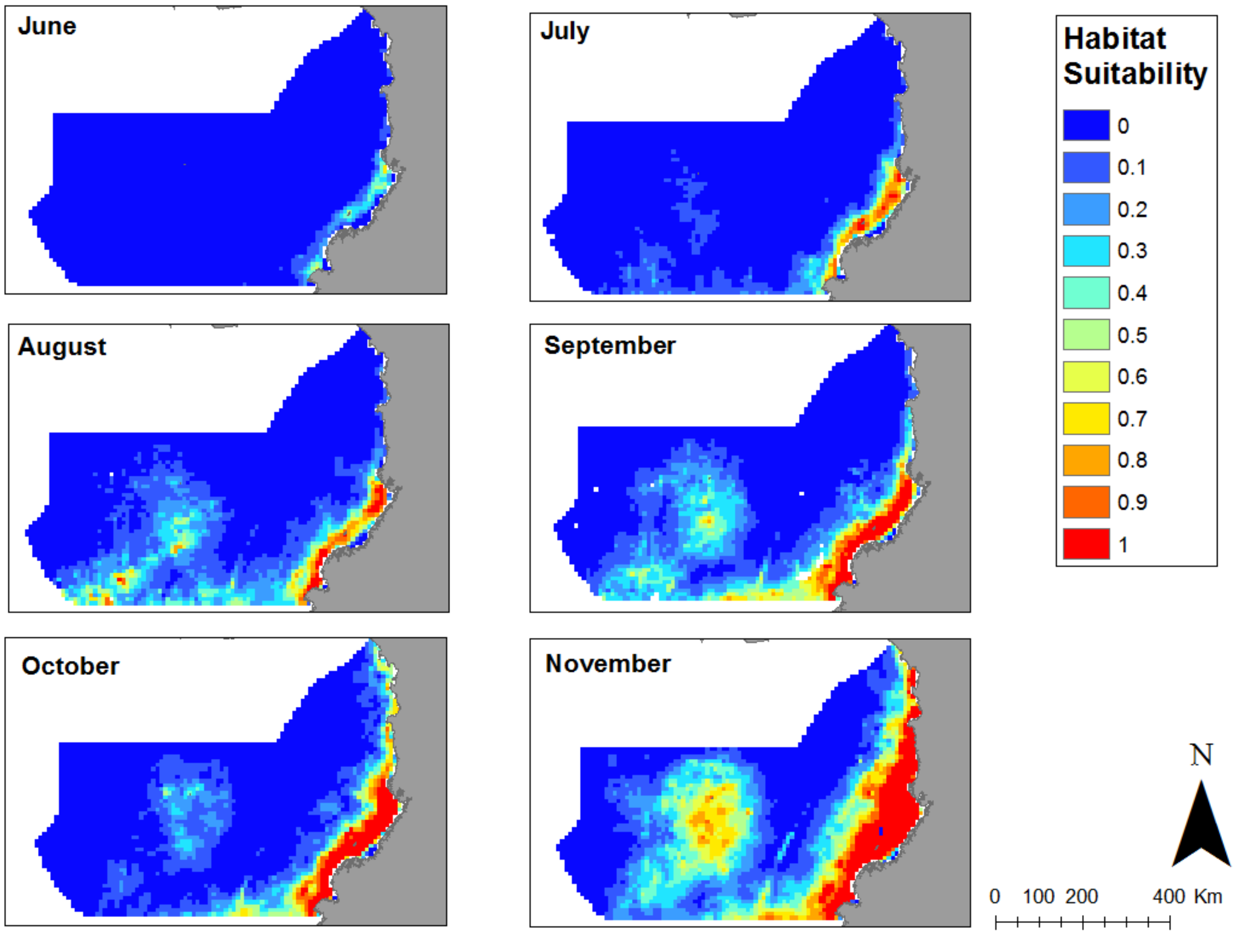

Figure 9. Potential geographic distribution for humpback whales (*M. novaeangliae*) in the CP-EEZ between June and November.

<u>Pantropical spotted dolphin – coastal form</u>

The model for the coastal form of the pantropical spotted dolphin also had a high AUC value (> 0.9), evidencing high performance (Table 2). Both training and test AUC had similar values, indicating a high predictive power and model fit. Distance to shore and distance to seamounts contributed the most to the coastal pantropical spotted dolphin model, with almost the same percentage of contribution (Table 3). Depth also had a considerable contribution with around 25%, while the other variables had minor contributions.

Areas with the highest suitability (>70%) were waters up to 50-60 km from shore and at least 200 km away from seamounts (Fig 10 & 11). Habitat suitability decreased with increasing distance to shore and decreasing distance to seamounts. Due to the low contribution of SST and Chl-a to the model, there were no major changes in habitat suitability among months for the coastal pantropical spotted dolphins (Fig 10 & 11).

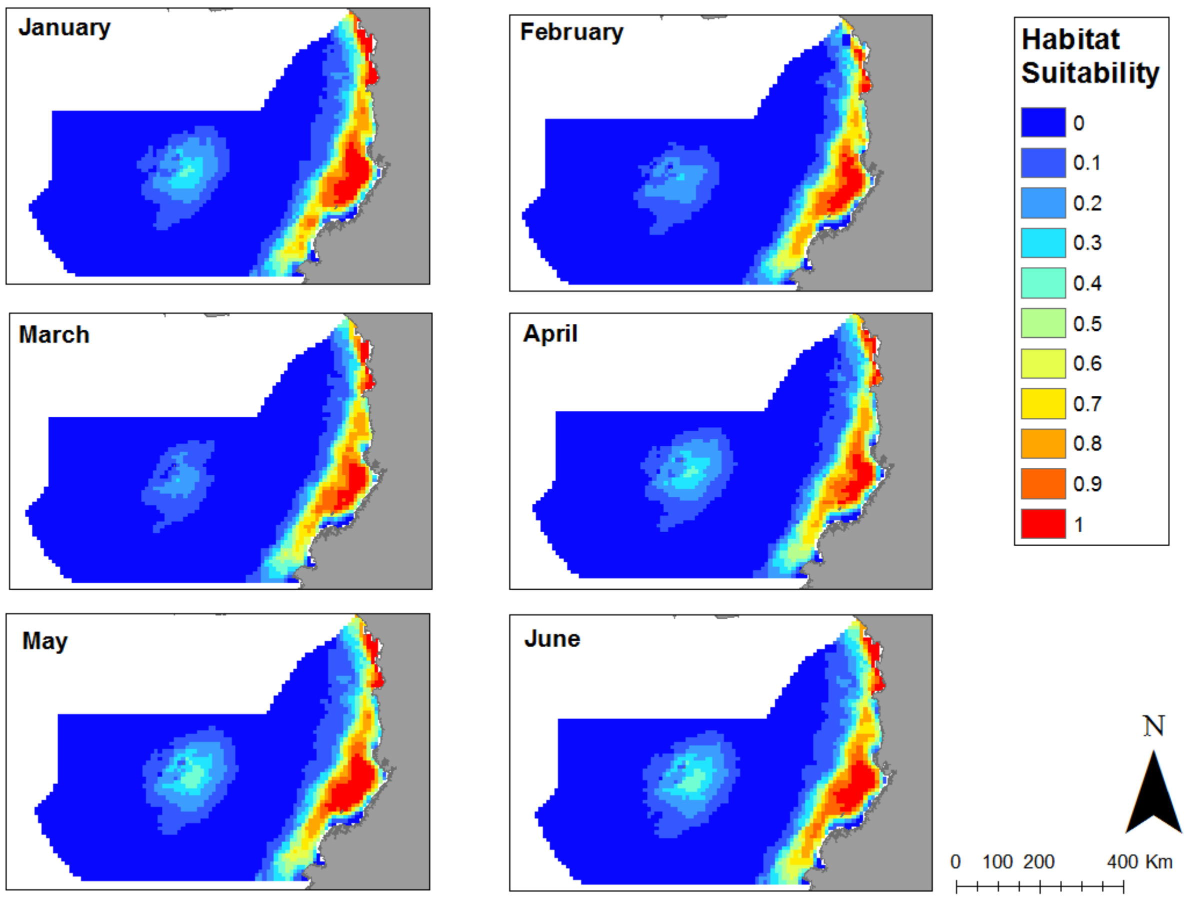

Figure 10. Potential geographic distribution for the coastal form of the pantropical spotted dolphin (*S. attenuata*) in the CP-EEZ between January and June.

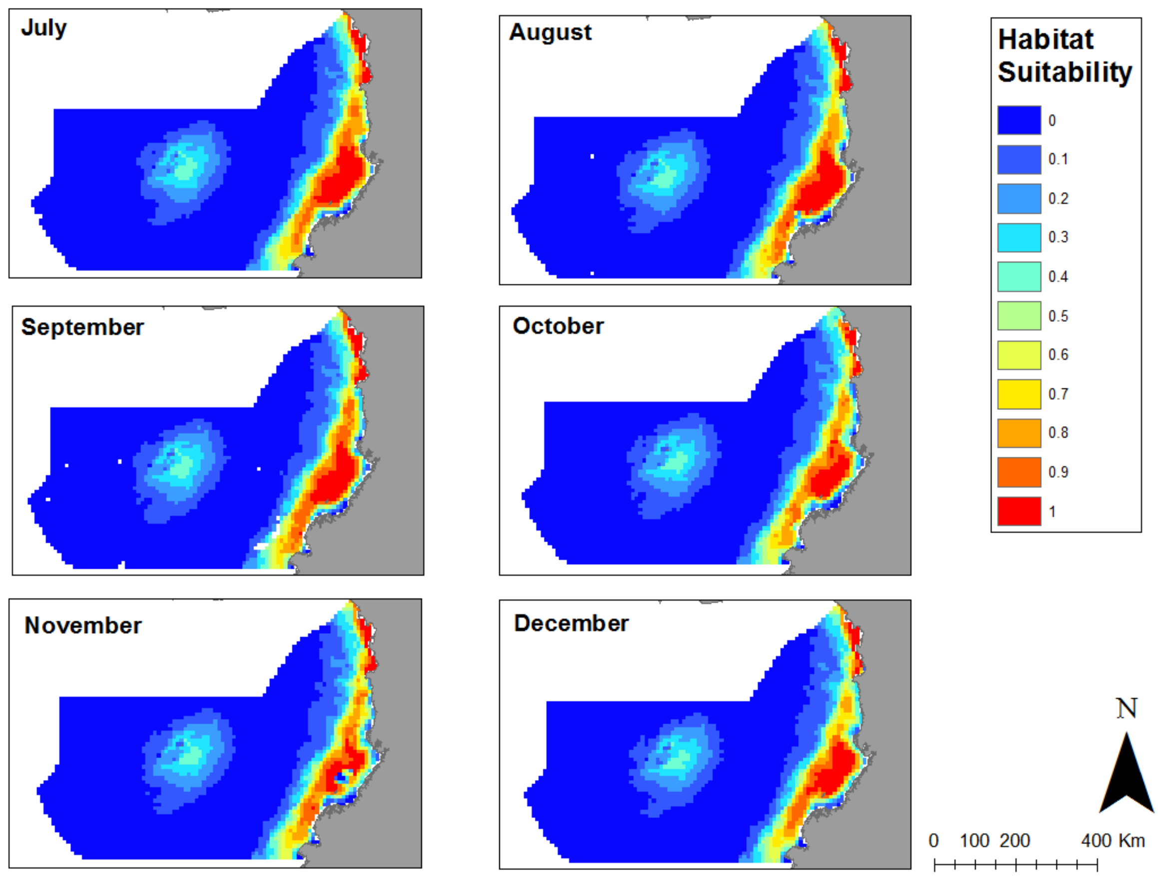

Figure 11. Potential geographic distribution for the coastal form of the pantropical spotted dolphin (*S. attenuata*) in the CP-EEZ between July and December.

<u>Pantropical spotted dolphin – offshore form</u>

This model AUC value was higher than 0.7 indicating an acceptable model performance. Additionally, similar AUC values for training and test data show high model fit and predictive power (Table 2). For the offshore pantropical spotted dolphin, the variables that contributed the most were distance to seamounts (49.9%) and depth (17.2%), followed by SST (15.9%).

Similar to the static model, higher habitat suitability was indicated in areas with a distance to seamounts between zero and 80 km, and depths between 2,000 and 3,000 meters (Figs 12 & 13). However, due to changes in SST throughout the year, February and March were the months with the highest areas of predicted occurrence, while April, May, and June had almost no areas with predicted habitat suitability above 0.7 (Fig 12). SST conditions that favor the presence of spotted dolphins in offshore waters were between 24.5 and 26.5 ºC, but habitat suitability decreased with higher temperatures

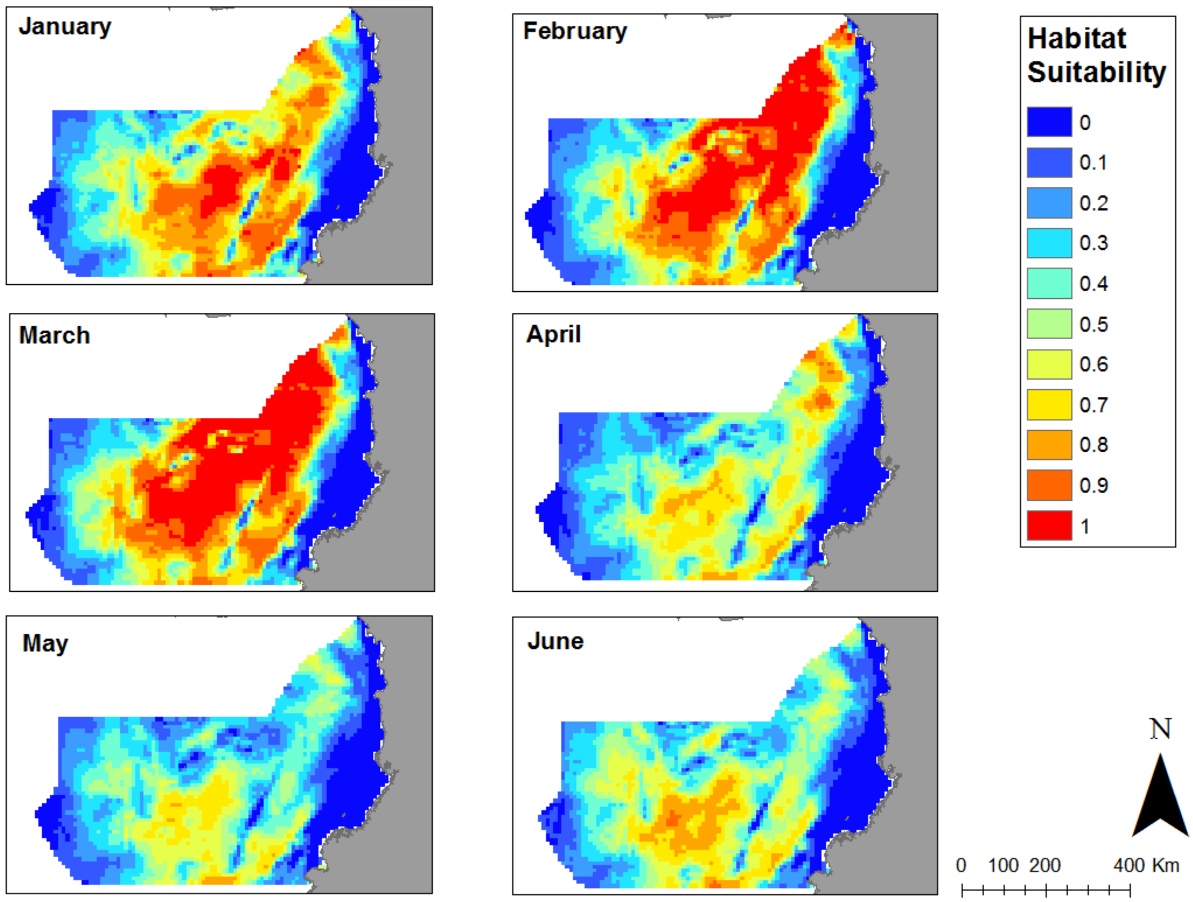

Figure 12. Potential geographic distribution for the offshore form of the pantropical spotted dolphin (*S. attenuata*) in the CP-EEZ between January and June.

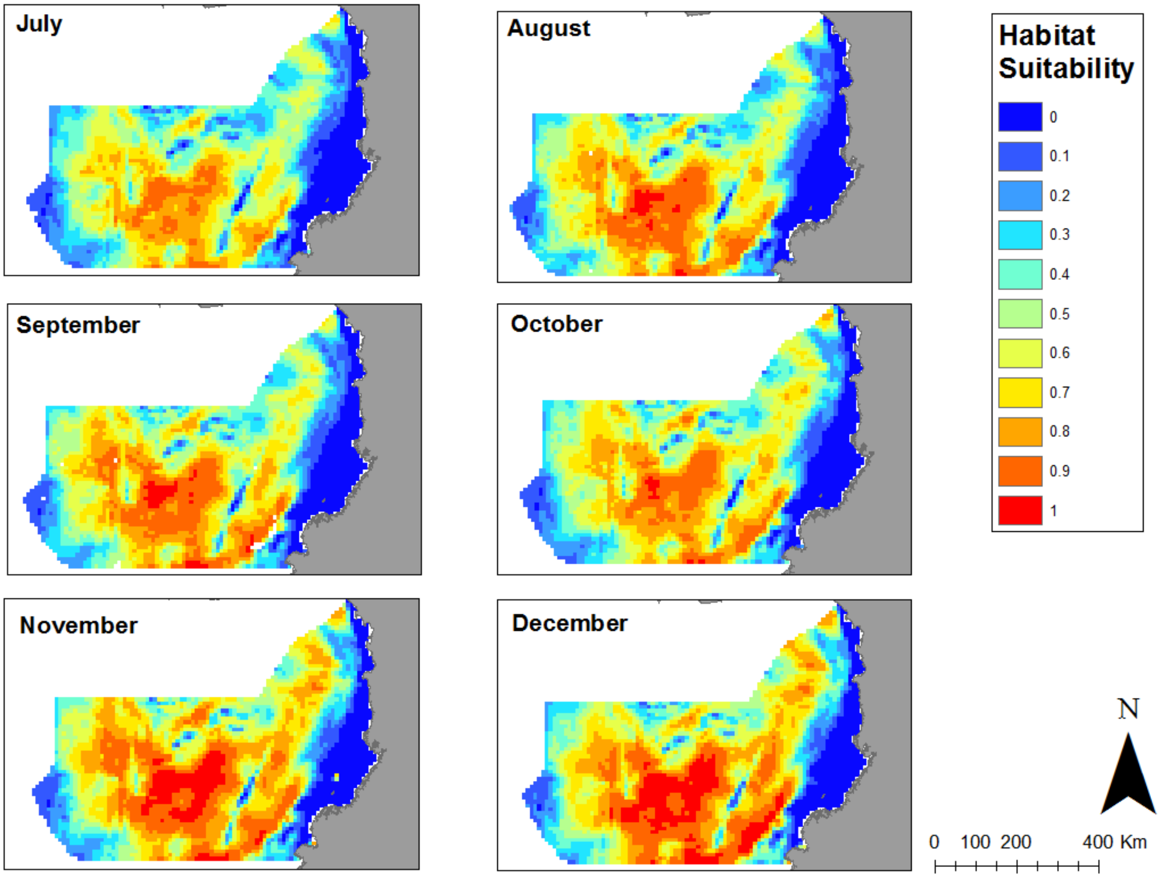

Figure 13. Potential geographic distribution for the offshore form of the pantropical spotted dolphin (*S. attenuata*) in the CP-EEZ between July and December.

Discussion

<u>Habitat models</u>

The present study established a series of baseline habitat models for humpback whales, bottlenose dolphins, pantropical spotted dolphins and sperm whales using both static and dynamic variables in a data-limited setting. To my knowledge, this is the first study which attempts to characterize the environmental niche of cetaceans in the CP-EZZ.

Humpback whales

Humpback whales are the most studied cetacean in the CP-EEZ due to their presence in coastal areas, seasonality and relevance for ecotourism (Ávila et al., 2013). Nevertheless, no previous spatial analyses have been conducted to study the habitat of humpback whales in the CP-EEZ. Humpback whales migrate from high latitudes to winter in lower latitudes where they give birth and breed (Acevedo et al., 2017; Robbins et al., 2011, Florez-González et al., 2007). The present results demonstrate that, as demonstrated in other regions of the world, depth is the most important predictor of humpback whale distribution on their breeding grounds (Guzman & Félix, 2017; Bruce et al., 2014; Craig et al., 2014 Oviedo & Solis, 2008).

The results of the present study indicate that November is the month with the largest area suitable for this species. However, the greatest numbers of humpback whales in the Eastern Tropical Pacific occur between July and September (Ávila et al., 2013; Florez-González et al., 2007; Félix & Haase, 2001). The reason why this model predicts high suitability in November is that most of the humpback whales that occur in the CP-EEZ prefer a lower temperature range (24.5 -26.5 ºC) than documented studies in the wintering areas (24-28ºC) (Trudelle et al., 2016; Rasmussen et al., 2007). Thus, the model predicts higher suitability for relatively colder months.

The occurrence of humpback whales in November is low even if the habitat is highly suitable because many whales have already started their migration southwards to their feeding grounds (Félix & Guzmán, 2014). The nature of what triggers the start of their migrations southwards is not completely understood, but it is clear that Antarctic waters provide predictably successful foraging grounds for the whales (Acevedo et al., 2006; Hucke-Gaete et al., 2013). Further studies are needed to understand the biological and ecological timing of migration with apparent suitable environmental conditions in breeding grounds.

Finally, the models show that there is a larger area of predicted habitat south of 4 ºN, which has been previously demonstrated by a higher number of sightings in the southern CP-EEZ than in the northern region (Palacios et al., 2012). This distribution pattern has been suggested to be related to the decrease of continental shelf width towards in the north of the CP-EEZ (Herrera et al., 2008). However, more studies are necessary to fully understand geographical differences in humpback whale abundance along the Colombian Pacific Coast.

Bottlenose dolphins

Bottlenose dolphins, like humpback whales, are studied relatively frequently in the CP-EEZ because of their presence in the coastal areas and high encounter rates (Palacios et al., 2012; Ávila et al., 2013). Bottlenose dolphins are a long-lived species that are found in both coastal and pelagic waters around the world (Wells & Scott, 2009), and as in other areas, the present results show that bottlenose dolphins in the CP-EEZ prefer areas close to the shore from the continent and offshore islands.

Previous studies of bottlenose dolphins' habitat preferences in different parts of the world have demonstrated that the distribution of this species distribution is highly influenced by distance to shore and depth (Milmann et al., 2017; La Manna et al., 2016; Pitchford et al., 2016; Marini et al., 2015). Furthermore, the models described here show that there is high habitat suitability for bottlenose dolphins not just close to the continental coast, but also near the offshore island of Malpelo. Sanino et al. (2005), proposed two different ecotypes of bottlenose dolphins in the Eastern Pacific: a coastal ecotype and an offshore ecotype. No samples from Colombia were used in that study, but results from Palacio et al. (2012) and the present study support the presence of these two ecotypes in the CP-EEZ.

STT and Chl-a were not included in the model for bottlenose dolphins, but future studies should include these variables because they may help to understand the seasonality of predicted presence (Gomez et al., 2017; Tobeña et al.,2017). Moreover, more research is needed to assess the existence of different bottlenose dolphin ecotypes in the Colombian Pacific waters.

Pantropical spotted dolphins

The pantropical spotted dolphin has been widely studied in the ETP due to their high incidental mortality in tuna purse-seine fishing operations in the 1970s (Escorza-Treviño, 2005; Dizon et al., 1994). Thanks to these studies, two different forms were identified in the region: a coastal form and a pelagic form (Dizon et al., 1994). In the present study, I created habitat models for both ecotypes within the CP-EEZ. The coastal form has been studied along the Colombian Pacific coast (Ávila et al., 2013), but the offshore ecotype has been studied more broadly with other ETP delphinids (Redfern et al., 2008; Ferguson et al., 2006).

The coastal spotted dolphin models with static and dynamic variables indicate that the major contributors were distance to shore, depth, and distance to seamounts. SST and Chl-a did not contribute much predictive power to the models, and as seen in the outputs from the dynamic models, there is not much variability throughout the year in predicted habitat. Further fine-scale investigations are required to better understand variability across months in coastal areas because some variation in patterns of occurrence have been reported along the Pacific Coast (Ávila et al., 2013; Valencia, 2006).

Pantropical spotted dolphins, along with humpback whales and bottlenose dolphins, occur frequently in coastal areas and thus offer a relatively high encounter rate (Ávila et al., 2013; Palacios et al., 2012). Thus, most research on this species has been focused on the coastal form within the country's Pacific EEZ. The offshore pantropical spotted dolphin has been a target of research efforts by the Southwest Fisheries Science Center from NOAA (Wade & Gerrodette, 1993; Balance et al., 2006; Redfern et al., 2008; Ferguson et al., 2006). Recent studies in the Colombian EEZ have been begun to address the distribution and relative abundance of this species in both coastal and pelagic waters (Palacios et al., 2012).

The model results for the pantropical spotted dolphin offshore form indicate that distance to seamounts and depth were the main contributors to predicted habitat in both the static and dynamic models. These results are consistent with previous studies indicating that depth is the main predictor for the distribution of spotted dolphins and other species of *Stenella* in the ETP (Cubero-Pardo, 2007) and other areas of the world (Carluccia et al., 2016; do Amaral et al., 2015, Thorne et al., 2012). However, distance to seamounts has not been identified as an important predictor of habitat in previous studies of spotted dolphins in the ETP, but the present results show that it is the most relevant contributor to habitat preferences of the offshore form. Seamounts have been typically found to be hotspots of biodiversity, productivity and biomass when compared with surrounding ocean waters (Kvile et al., 2014; Clark et al., 2010), so it is reasonable that habitat suitability of spotted dolphins is influenced by productivity and prey availability in such areas.

SST had a considerable contribution to the dynamic model, indicating that although offshore spotted dolphins are usually found in warm tropical waters (do Amaral et al., 2015, Au & Perryman, 1985; Rielly, 1990;), there is a preference for the lower temperature spectrum (24.5-26.5ºC) in the CP-EEZ and, therefore, that warmer months present lower habitat suitability. Results from the models developed in this study provide an understanding of ecological preferences of offshore pantropical spotted dolphins specific to the Colombian Pacific waters and provide evidence of regional differences when compared with the whole ETP.

Sperm whales

Sperm whales are rarely sighted in the CP-EEZ and in lower densities than in neighboring countries (Ávila et al., 2013; Palacios et al., 2012). Such low occurrences with poor survey coverage in offshore areas make it difficult to develop habitat models for this species in the study area. The results of the present study showed low model performance, so it is not possible to make precise conclusions regarding the habitat of sperm whales in the CP-EEZ. Unlike the results presented here, depth has been shown to be the main predictor for sperm whale habitat suitability in other regions (Fiori et al., 2014; Tepsich et al., 2014; Pirotta et al., 2011). Increasing survey effort is necessary to understand the ecology and habitat preferences of this species in the CP-EEZ, as well as for many other cetacean species.

Model refinement

Static variables represent a solid base to predict distribution and preferences of species (Marini et al., 2015). However, the inclusion of dynamic variables allows an assessment of the importance of temporal variation in spatial distribution of species. As witnessed in this study, incorporating variables that change with time such as SST and Chl-a can improve model performance for some species.

In the case of humpback whales, AUC increased from 0.762 to 0.903, changing model performance from acceptable to high according to general standards (Peterson et al., 2011).

Additionally, SST was the second most important variable contributing to the model. In this particular case, including the dynamic variables restrict predicted habitat to a smaller area. This change is consistent with the higher proportion of occurrences in the southern CP-EEZ than in the northern part (Palacios et al., 2012; Herrera et al., 2012).

For coastal pantropical spotted dolphins, including dynamic variables increased AUC from 0.892 to 0.930. In contrast to the model for humpback whales, the contribution from both Chl-a and SST was low, and this is reflected in the low variation in predicted habitat variability for different months of the year. Still, the inclusion of such variables improved model performance because they add a temporal scale.

Offshore spotted dolphins' training AUC were similar for the static and dynamic models, but unlike the static model, AUC values for both training and testing samples were similar in the dynamic model demonstrating better fit and model power. Furthermore, SST had a significant contribution to the predictive model, providing insights into changes in habitat suitability across months.

Limitations and implications for management

The results obtained with MaxEnt for four cetaceans in the CP-EEZ provide reasonable results that are consistent with other findings in the literature. However, the available data and the model used to predict habitat both have their limitations and sources of uncertainty, preventing precise and accurate understanding of species-habitat relationships.

In the case of the data set, some of the limitations include: major sampling efforts in some areas like Gorgona Island and Bahía Malaga compared with other parts of the CP-EEZ; most of the data was obtained from opportunistic efforts; there were no survey track lines that would allow to understand the geographical distribution of survey effort; and not all surveys data were included in the database because not all research groups or NGOs shared this information.

Due to these data restrictions, I decided to use MaxEnt because it allows modeling species distribution that lacks sampling effort records and does not require independent data (Phillips et al., 2006). Presence-only models like MaxEnt have produced comparable results to presence-absence models (Tobeña et al., 2016; Praca et al., 2009; MacLeod et al., 2008), but the latter are recognized to have higher explanatory and predictive power (Tepsich et al., 2014; Brotons et al. 2004). Therefore, future studies should involve systematic surveys where cetacean presences and absences are recorded as well as survey effort, favoring the use of more robust modeling techniques like Generalized additive models GAM (Redfern et al., 2006).

Data scarcity has prohibited the study of occurrence patterns and habitat use for marine mammal species in many areas of the world that are inaccessible or understudied (Kaschner et al. 2006). The case of Colombia is an example of such situation, and although efforts have increased to advance marine mammals research, there is still a big gap in knowledge to improve management of such species. This is of great importance considering the different threats that cetaceans face in the CP-EEZ, such as bycatch, ship collisions, increased whale watching tours and construction of megaprojects (Ávila et al., 2013).

Limited understanding about cetaceans in the CP-EEZ prevents the development of strategic and realistic management measures. Species Distribution Models (SDMs) are a practical management tool that help to identify critically important areas for species conservation (Pitchford et al., 2016; Guisan et al., 2013; Redfern et al., 2006), and future efforts to increment studies in this area are necessary to make informed decisions about cetacean conservation in Colombia.

Conclusions

Habitat models are tools that allow to predict and understand occurrence of species based on environmental variables and quantify habitat requirements. Here, I developed the first cetacean habitat models for the Colombian Pacific Exclusive Economic Zone, which contribute to a better understanding of these species in the region. Although the methodology used in this study could be improved, general trends and habitat preferences of the studied species improve our understanding the habitats that are used more frequently, the environmental features that determine their distribution, and, finally, inform management and conservation practices.

Given the increasing human threats to cetaceans within the Colombian Pacific, a greater understanding of habitat preferences is imperative to protect cetacean populations occurring in the region. Future studies should include systematic surveys of cetaceans both on the coastal and offshore areas. With the appropriate data collection methods, better and more realistic models can be constructed to predict cetacean habitats and prioritize areas for conservation. Furthermore, research should expand to other cetacean species that are least studied, but that occur in the CP-EEZ, as well as focusing on human threats differences throughout the area.

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