

Habitat Suitability of Juvenile Smooth Hammerhead Shark (*Sphyrna zygaena*) off northern Peru

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Statement of Work

The design and collection of the data was done by a Peruvian local NGO, ProDelphinus, that since 2003 has been collecting fishery information of threatened and commercial marine species from small-scale fisheries. During 2015 and 2016, I participated as an onboard observer in the collection of these data. In addition, while in ProDelphinus, I co-lead a project that aimed at understanding the trophic ecology of elasmobranchs. The findings of this project complement my minor project research, and the samples of this former project are related to the samples used for my minor project.

I was assisted in the pre-processing of the satellite data in the software ArcGis by Natalia Gonzalez-Pestana, who is currently in her last semester of geography. I developed the conception of the work and its organization, analysis of the data, prepared figures and tables, the interpretation of results and wrote the report. My advisor assisted me, specially, in the revisions of the report.

ABSTRACT

The smooth hammerhead shark (*Sphyrna zygaena*) is one of most captured shark species by southeastern Pacific fisheries. Their distribution and habitat use is poorly understood hindering the identification of critical habitats for their conservation and the possible impacts of environmental change on species distribution. The aim of this research was to predict the spatial distribution of smooth hammerheads based on habitat suitability from the Northern Humboldt Upwelling System (NHUS) off northern Peru. (06°S-11°S). To achieve this, three analyses were performed: i) characterize their population structure, ii) identify environmental factors that affect their distribution, and iii) predict their spatially and environmentally suitable habitat under current La Niña and El Niño scenarios and projected to a future scenario of ocean warming between the years 2040-2050. Between the years 2009 and 2017, 7485 sharks were measured and georeferenced obtained from a small-scale driftnet fishery. Their ecological niche was modelled using the program MaxEnt. The results indicate that neonate and juvenile smooth hammerheads are the dominant life-stage in the northern part of NHUS where this area probably represents a nursery area. The spatial distribution of sharks varies according to their ontogeny, and at seasonal and El Niño Southern Oscillation (ENSO) conditions. Sharks were closer to the coast during warmer (summer and El Niño conditions) periods. Four environmental variables were identified as important predictors of species distribution: depth, sea surface temperature (SST), chlorophyll-a, as a proxy of prey availability-, and, to a lesser degree, salinity. During current conditions, the highest suitable habitat was predicted in the central-offshore and shifted to northern-coastal part of the study area (close to the ecotone zone; 6°S) in La Niña and El Niño conditions- respectively- as the coastal upwelling area, during El Niño warm conditions, offers the coolest environment and the highest productivity. Unique bathymetric conditions are associated with these areas (i.e. shelf break, marine canyons, narrow continental shelf, and coastal topography) generating oceanographic conditions (i.e. marine fronts, upwelling) which result in zones of exceptional high marine productivity. Under future climate change scenarios, the habitat suitability of smooth hammerheads will shift to a more coastal distribution. To enhance the conservation of smooth hammerheads and their supporting ecosystem, these areas of high suitability should be a priority for fishery management and under future scenarios of climate change, their coastal distribution could increase their catchability. Furthermore, these areas of highest suitability should be considered as candidates for a dynamic pelagic marine protected area.

Key words: ecological niche, distribution, ENSO, El Niño, Eastern Pacific, climate change

INTRODUCTION

The smooth hammerhead shark (*Sphyrna zygaena*) is a relatively common and widespread pelagic shark with an amphitemperate distribution (Compagno 1984, Fowler et al. 2005). It is rare in tropical oceans, unlike other large species of hammerheads that occur most frequently in tropical waters. Worldwide, the presence of juvenile smooth hammerheads has been identified in the coasts of eastern and western south Australia, northern New Zealand, South Africa, Gulf of Guinea, Uruguay, southern Brazil, Pacific Mexican, Ecuador and Peru (McAuley and Simpfendorfer 2003, Dudley and Simpfendorfer 2006, Bornatowski et al. 2007, Doño 2008, Bizzarro et al. 2009, Bolaño 2009, Salomon-Aguilar et al. 2009, Diemer et al. 2011, Francis 2016, Wray-Barnes 2016, Casaca 2017, Gonzalez-Pestana et al. 2017). Larger individuals are more commonly found in offshore oceanic waters (Smale 1991, Sucunza et al. 2015, Casaca 2017). However, gravid females have been reported in coastal waters where they probably come close inshore to give birth (Bass et al. 1975, Francis, 2016). Smooth hammerheads are highly migratory and adults can travel significant distances. Their longest recorded migration is 6600 km (Casaca 2017). The distribution and habitat use of the smooth hammerhead shark is poorly understood globally. This hinders the identification of critical habitats for their conservation and understanding of impacts of environmental change (Casper et al. 2005).

Hammerhead populations from large species (i.e. *S. zygaena*, *S. lewini*, *S. mokarran*) have declined between 76-99% in various ocean basins, such as, Mediterranean Sea, northwest and western central Atlantic, South Africa and eastern Australia (Baum et al. 2003, Casper et al. 2005, Myers et al. 2007, Ferretti et al. 2008, 2010, Bensley et al. 2009, Baum and Blanchard 2010). Since catches of hammerhead sharks are often grouped together under a single category, few species-specific data are available to assess population trends (Casper et al. 2005). However, in most of these locations, *S. zygaena* outnumbers *S. lewini* (Casper et al. 2005, Dudley and Simpfendorfer 2006, Diemer et al. 2011, Reid et al. 2011). In other regions, such as the Mexican Pacific, some hammerhead species (e.g. *S. zygaena*), might have disappeared due to fishing pressure (Perez-Jimenez 2014). In addition, hammerhead sharks exhibit extremely specialized traits and complex behaviors that have increased their vulnerability to human exploitation (Gallagher et al. 2014 a,b), making them disproportionately vulnerable to even low levels of fishing pressure (Ferretti et al. 2010). As a result, the smooth hammerhead is decreasing globally and the species is classified as vulnerable in the Red List of Threatened Species of the International Union for the Conservation of Nature (IUCN) (Casper et al. 2005). As of September 2014, the species has been included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (<https://cites.org/eng/app/appendices.php>) as its fins are one of the most valuable

and often traded internationally (Abercrombie et al. 2005, Clarke et al. 2006 a,b).

Peru reports the highest historical shark landings in the eastern Pacific Ocean (Gonzalez-Pestana et al. 2016), making it one of the 20 most important elasmobranch fishing nations in the world (Fowler et al. 2005). The smooth hammerhead is identified as the third most captured shark species by fisheries in Peru and the most frequently captured shark species off northern Peru, with gillnet the most common fishing gear used (de la Puente 2013, Gonzalez-Pestana et al. 2016). Smooth hammerhead fins are prized in Asian markets and sharks are increasingly targeted in some areas (Abercrombie et al. 2005, Clarke et al. 2006 a,b) where Peru is one of the top 12 countries that supply shark fins to Asian markets (Anon 2001, Cheung and Chang 2011). In the eastern Pacific little information exists about the biology and ecology of smooth hammerheads where most studies have focused on its trophic ecology (Castañeda and Sandoval 2004, Estupiñán-Montaña and Cedeño-Figueroa 2005, Bolaño, 2009). Northern Peru has been identified as an important feeding area, with jumbo flying squid (*Dosidicus gigas*) and the Patagonian squid (*Doryteuthis gahi*) as their main prey (Gonzalez-Pestana et al. 2017). Yet, no study in the eastern Pacific has yet characterized their niche by identifying the environmental variables that affect their distribution, predict their suitable habitat or their response to changing environmental conditions such as inter-annual climate anomalies (e.g. La Niña and El Niño) and climate change.

Ecological niche models (ENMs) are used to predict species distribution by characterizing the environmental conditions suitable for the species, and then project such a model onto geographic space to identify the areas that fulfil those conditions. ENMs focus in the Grinnellian niche, which can be defined by fundamentally non-interactive (scenopoetic) variables and environmental conditions on broad scales, relevant to understanding coarse-scale ecological and geographic properties of a species (Soberon 2007). For successful ENM development, the selected environmental predictors should best describe ecological needs and preferably have a direct influence on the physiology of the targeted species (Austin et al. 2002, Anderson 2013). ENMs have also been used to estimate impacts of climate change on species distributions (Anderson 2013). Climate change is predicted to influence distribution and habitat use of sharks due to changes in temperature and productivity (Chin et al. 2010, Dambach et al. 2011, Hazen et al. 2013a, Sequeira et al. 2014). As a result, individuals will move to locate a suitable habitat resulting in contractions or shifts in their habitat range (Dambach et al. 2011, Hazen et al. 2013a; Sequeira et al. 2014). For the smooth hammerhead shark, only one previous study has identified environmental factors that drive species distribution (Wray-Barnes 2016); and no study has yet predicted its distribution for current and future scenarios of climate change. Peru presents a unique environment to assess this because it is strongly influenced by warm (El Niño event) and cold (La Niña event) periods that can drastically change

the oceanographic condition and consequently cause habitat alterations and changes in food availability (Fiedler 2002).

Areas of high habitat suitability are strong candidates for spatial management, such as marine protected areas or time-area closures (Norse, 2010; Graham et al., 2016), where the conservation of pelagic ecosystems is underrepresented (Game et al., 2009). Identifying these areas is relevant for the conservation and management of smooth hammerheads and their supporting pelagic ecosystem, since smooth hammerheads are heavily exploited in Peruvian waters, fisheries lack robust monitoring and management (Gonzalez-Pestana et al., 2016), and species biology and ecology remain poorly understood, both locally and worldwide (Fowler et al., 2005). The overall purpose of this research was to predict the spatial distribution of the smooth hammerhead shark based on habitat suitability in the Northern Humboldt Current Large Marine Ecosystem (NHUS) for current and future scenarios. In order to accomplish this, first the population structure of smooth hammerheads in NHUS was characterized by analyzing sex ratio and body size distribution, both spatially and temporally. Then, environmental factors that affect their distribution were identified. Finally, their spatial habitat suitability was predicted in current La Niña and El Niño scenarios and then projected to future scenarios of ocean warming. These findings could contribute to the design and implementation of local and regional management plans for this species and its ecosystem.

MATERIALS AND METHODS

Study area

The study area covered ~241 000 km² in the southeast Pacific Ocean, along 700 km of coastline off north-central Peru (06°S–11°S) in the Northern Humboldt Upwelling System (NHUS) (Figure 1). The continental shelf has a width of 27-125 km in this area, becoming wider closer to 06°S. Along the Peruvian continental margin, the area between 5°15'–7°30'S has the highest number of marine canyons, and in the study area four main canyons occur (Gutierrez et al. 2009). Eleven islands are also located in this area. The study area is within the NHUS which is part of one of the world's four Major Eastern Boundary Upwelling Ecosystems (EBUE's). These EBUE's are characterized by coastal upwelling and high productivity (Chavez and Messie 2009), with the HCLME one of the most productive ocean ecosystems (Chavez et al. 2008, Pennington et al. 2006). Within the NHUS, the study area is located in the Warm Temperate Southeastern Pacific Marine Province (WTSP-MP) (Spalding et al. 2007, Figure 1). The northern limit of the WTSP-MP is a transitional or ecotone area (4°15'S–6°S; Hooker et al. 2013, Ibañez 2016) with a strong influence of the Tropical East Pacific Marine Province (Spalding et al., 2007). In this ecotone area, cool-upwelled waters encounter warm tropical waters forming the Equatorial Front (Chavez and Messie 2009). Interannual variability is relatively strong in the NHUS

due to the natural cycle of the ocean-atmosphere system called the El Niño Southern Oscillation (ENSO) (Fiedler 2002). These regime shifts are caused by periods of warm (El Niño event) or cold (La Niña) temperature anomalies related to the approach or retreat of warm subtropical oceanic waters to the coast of Peru and Chile.

Extent of the study area

The criteria used to define the extent of the study area was based on three aspects: i) delimitation of marine provinces, ii) area sampled and, iii) dispersal abilities of the focal species. The first criteria was used as an ecological criterion because different marine provinces present different environmental conditions. As a result, individuals might be adapted to a specific marine province and this adaptation might cause potentially different populations with niche differentiation. Many niche modelling studies assume that no niche differentiation exists across a species' range (Anderson 2013); yet, some studies have found that genetic variation among populations corresponds to traits that directly affect range boundaries (Pelini et al. 2009). Therefore, to prevent treating different populations as one, only occurrences of individuals present in the WTSP-MP were included in the analysis. The second criteria for defining the extent of the study area was the area sampled which has been defined by the fishery area in the time period where the occurrence records were taken. Therefore, data from this fishery area can be used as background environmental data. The third criteria, assessing the dispersal abilities of focal species, has been highlighted as an important factor in accurately predicting species distribution (Barve et al. 2011, Peterson and Soberon 2012, Anderson 2013), since movement is a major factor for determining the occupied area. Yet, this factor is seldom included in modeling efforts or not considered explicitly (Anderson and Raza 2010, Barve et al. 2011). Movements of the focal species determines the area of comparison, since this is the area within which presences may exist and within which absences are meaningful. This background area has been "tested" by the species for suitability, but not occupied (Barve et al. 2011). The smooth hammerhead shark is a highly mobile species (Francis 2016, Casaca 2017). Casaca (2017) estimated that their average distance travelled per day was 33.5 km. Therefore, we assume that the extension of the whole study area is accessible to the shark due to its dispersal capacities. The best model performance occurs when dispersal is not a limitation; this occurs when all the inhabited areas are accessible (Saupe et al. 2012).

Species' occurrence records

Samples were obtained from a small-scale driftnet fishery between the years 2009 and 2017. Nets in this fishery have an average length of 1.7 ± 0.6 km and are typically set at sunset and retrieved the following morning with an average set length of 14 h (Alfaro-Shigueto et al. 2010). The exact position of each capture, which was taken when the net was initially set and when it was retrieved, was determined with a handheld Global Positioning System (GPS) unit, obtaining

longitude and latitude at 0.1° precision. The occurrence record of each shark was an average between the initial and final position of the net. Sharks were measured (total length and/or fork length), and sex was determined by the presence of claspers in males. For few individuals that only fork length was measured, this was converted to total length using the length-length relationships of Mas et al. (2014). Samples came from a fishery that lands in four sites: Mancora, Bayovar, San Jose, and Salaverry. The highest quantity of landings of smooth hammerheads in Peru are located in San Jose, Salaverry and Mancora (de la Puente 2013, Gonzalez-Pestana et al. 2016). Therefore, our study area is located in the area of highest capture and presumably in the area of highest abundance of smooth hammerheads in Peru.

Characterization of the population structure

Sex ratio was calculated against the null expectation of 1:1 using chi square contingency tables in which sharks were grouped in three categories: i) all sharks, ii) neonates and juveniles, and iii) adults. Sharks are considered adults if they are larger than 230 cm TL for females, and 210 cm TL for males. According to Compagno (1984), females become sexually mature when they reach an approximate length of 240 cm TL; yet, in Peru, the smallest gravid female measured 230 cm TL (Castañeda 2001). Therefore, for females, we used Castañeda (2001) for a proxy of sexual maturity (230 cm TL) in Peruvian waters, and for males we used the body size (210 cm TL) of Compagno (1984). At birth, neonates measure 50–61 cm TL (Compagno 1984). In Mexico, neonates measure 56 cm TL (Salomon-Aguilar et al. 2009), and in northern Peru they measure between 43–65 cm TL (Castañeda 2001); thus, we used the lowest length for northern Peru (43 cm TL).

Body size distributions (total length) were calculated and analyzed by sex and seasons. To determine if significant differences exist in body sizes by sex, two-sample t-test was used. To determine if significant differences exist in body sizes by seasons, one-way analysis of variance (ANOVA) followed by multiple comparisons based on Tukey's HSD post hoc test were used.

The age of sharks was calculated using the parameters calculated by Falconi (2015) in Ecuadorian waters and Garza (2004) in Pacific Mexican waters using the von Bertalanffy growth model (VBGF):

$$L_t = L_{inf}(1 - e^{-k(t-t_0)})$$

where:

L_t = mean size (TL, cm) at age t (year); L_{inf} = asymptotic maximum size (TL); k = growth coefficient (year⁻¹); t_0 = theoretical age (year) at zero size. The parameters for this model were: L_{∞} = 225.49 cm TL, k = 0.09 yr⁻¹ r^2 = 0.9964 for males, and L_{∞} = 356 cm TL, k = 0.053, r^2 = 0.9848 for females (Falconi 2015), and t_0 = -2.45 cm TL for both males and females (Garza 2004).

For analysis of spatial distribution, sharks were divided into four size classes based on their diet: I (40–70 cm TL), II (71–100 cm TL), III (101–190 cm TL) and IV (191–350 cm TL) (Gonzalez-Pestana et al. 2017) since ontogenetic shifts in diet are often associated to changes in habitat (Grubbs 2010).

For each smooth hammerhead occurrence, the shortest distances to the coast was calculated with the Near tool in ArcGIS 10.2.1 using a World Equidistant Cylindrical coordinate system, and then grouped by factor (i.e. size class, sex, season and ENSO conditions). Differences in distance from the coast between factors were analyzed by using two-sample t-test (for factors that have two groups; i.e. sex) and ANOVA with a Tukey's test (for factors that have more than two divisions).

Spatial data were mapped and analyzed in ArcGIS 10.2.1, and statistical analyses were performed using RStudio, vers. 0.96.122 (RStudio, 2012) with R, vers. 3.2.2 (R Core Team, 2016).

Environmental variables

Eight climatological environmental variables were selected in order to determine which abiotic variables affect species distribution in the study area, and therefore should be included in the modelling of species ecological niche. These were: sea surface temperature (SST; °C), chlorophyll-a (chl; mg/m³), salinity (pss), pH, currents velocity (m/s), dissolved oxygen (mol/m³) and bathymetry (depth and slope, m). These variables have been recognized for their physiological or ecological relevance in marine organisms (Tyberghein et al. 2012). For these environmental variables, with the exception of bathymetry, their mean data with a 9 km² resolution were retrieved from Bio-ORACLE (Ocean Rasters for Analysis of Climate and Environment) (<http://www.oracle.ugent.be/>) (Tyberghein et al. 2012). The bathymetry data was obtained from the General Bathymetry Chart of the Oceans (GEBCO) 30 arc-second grid data set (IOC et al. 2003) and was re-scaled to a 9 km² resolution.

Collinearity amongst input variables may result in overfitting models and thus risks under-predicting the range of suitable habitats (Heikkinen et al. 2006, Cao et al. 2013). Therefore, a correlation matrix was produced in ArcGis to measure correlation amongst the 8 selected environmental variables. If two variables were highly correlated ($r > 0.7$), only one of the variables was retained for use in Maxent modelling program (Dormann et al. 2013). In the case that highly correlated variables were known to be ecologically relevant, then both of them were retained, since collinearity has not been found to greatly affect Maxent performance (Elith et al. 2011). Then an analysis of variable contributions (i.e. jackknife procedure and percent contribution values) was run in MaxEnt to determine which environmental variables contribute most to the model (Phillips

2010).

Once the most important environmental variables were selected, monthly environmental layers with a 4 km² resolution between 2009 and 2017 were retrieved from the Moderate Resolution Imaging Spectrometer Aqua (Modis-Aqua) via the Oceancolor Data Downloader (<https://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua/>). Months were grouped into four seasons: summer (I: December to February) and autumn (II: March to May). Data from winter (III: June to August), and spring (IV: September to November) were not considered since cloud cover precluded the collection of data. Then seasons were grouped into El Niña and La Niña seasons where positive SST anomalies values represent El Niño phase-like conditions and negative SST anomalies values represent La Niña phase-like conditions. To classify a season as La Niña or El Niño, monthly estimations of El Niño Coastal Index (ICEN for its acronym in Spanish, ENFEN 2012) were used. The indices estimated on the basis of sea surface temperature (SST) anomalies in the El Niño 1+2 region. Usually the Oceanic Niño Index (ONI) is used which estimates SST anomalies in the El Niño 3.4 region, and it is commonly employed to define El Niño and La Niña episodes (Smith et al. 2008). However, the ONI does not necessarily reflect local warming events occurring in the Peruvian coast. For this reason, ICEN was used. Also, monthly coastal SST anomalies in the study area were used where SST are taken daily in the landing points of San Jose, Chicama, Huanchaco and Chimbote (IMARPE) which reflects the local in situ SST anomalies. Each group of La Niña and El Niño seasons were modelled separately, due to temporal variability in smooth hammerhead distribution and environmental variables (de la Puente 2013).

Ecological niche model analysis

Maximum Entropy (MaxEnt) is a tool for generating species ecological niche models from presence-only data (Phillips et al. 2006). This method focusses on how the environment where the species is known to occur relates to the environment across the rest of the study area (the 'background'). The approach is thus to find the probability distribution of maximum entropy (the distribution that is most spread-out, or closest to uniform) subject to constraints imposed by the information available regarding the observed distribution of the species and environmental conditions across the study area (for a detailed statistical explanation of MaxEnt, see Elith et al. 2011). For this, MaxEnt 3.4.1 software was used (www.cs.princeton.edu/~schapire/MaxEnt). Feature types were set to 'autoselect' based on the sample size (e.g. number of species observations; Phillips et al. 2006) where a minimum sample size of 80 records is recommended, since fewer samples provide limited information for determining the relationships between the species and its environment (Barry and Elith, 2006, Elith et al. 2011). Then the program was set to run jackknife tests and create response curves. Such curves correspond to a graph of the species response, with a measure of

suitability on the y-axis and the variable itself on the x-axis. Cross-validation was used for evaluation where the occurrence data was randomly split into 2 separate datasets (model building and model testing). Model performance was based on the area under the curve (AUC). This value is an indicator of whether the model predicts species distribution better than random, and can be used to prove statistical significance. An AUC value of >0.5 indicates that the model performed better than random (Phillips et al. 2006). Models that perform better than random are classified as “good” when AUC values are between 0.7-0.9 and “very good” when $AUC \geq 0.9$ (Baldwin 2009, Swets, 1988). MaxEnt generated maps of habitat suitability scaled from 0 (lowest suitability) to 1 (highest suitability) (Phillips et al. 2006, Elith et al. 2011). The 10th percentile training presence threshold output by MaxEnt was used to define suitable (above the threshold) and unsuitable (below the threshold) habitats.

MaxEnt was used because presence-only models are one of the most appropriate techniques to predict the distribution of highly mobile organisms where false absences are avoided (Guisan and Thuiller 2005). Furthermore, Maxent has been shown to perform well in comparison with alternative methods (Elith et al. 2006, Hernandez et al. 2006, Pearson et al. 2007, Wisz et al. 2008). MaxEnt has previously been used to create habitat suitability models for blue sharks (*Prionace glauca*; Sousa 2009), white shark (*Carcharodon carcharias*; Dambach et al. 2011) basking sharks (*Cetorhinus maximus*; Siders et al. 2013), whale sharks (*Rhincodon typus*; Sequeira et al. 2012; Hacothen-Domene et al. 2015, McKinney et al. 2012), great hammerhead sharks (*Sphyrna mokarran*; Calich 2016), tiger sharks (*Galeocerdo cuvier*; Calich 2016), and bull sharks (*Carcharhinus leucas*; Calich 2016).

Only juvenile smooth hammerheads were included in the modelling. Adult sharks were excluded because: i) sample size was low (<30) and it is recommended that sample size should be greater than 30 for a high model performance (Wisz et al. 2008); and ii) this size class, which is dominated by females, is the most mobile (Casaca 2017) and it mainly migrates to the coasts of Peru to give birth (Castañeda 2001); therefore, adults might not be in equilibrium with environmental conditions.

Future scenarios

To project the distribution of smooth hammerhead sharks in the study area under climate change scenarios, a reconstructed mean SST and current velocity was used between the years 2040-2050 under two different representative concentration pathways (RCP) adopted by the Intergovernmental Panel on Climate Change IPCC in its fifth Assessment Report in 2014. The RCP 26 scenario shows a peak-and-decline ending on very low greenhouse gas concentration levels where temperature will increase on average 1.6°C . Meanwhile, the RCP 85 scenario shows increasing emissions over time leading

to high greenhouse concentration levels where temperature will increase on average 4.3°C. These models were retrieved from Bio-ORACLE (<http://www.oracle.ugent.be/>) (Tyberghein et al. 2012) with a 9.2 km² resolution.

Predicting habitat suitability in future scenarios implies making predictions for areas with environmental values that are beyond the range of the data used to calibrate the model (i.e. extrapolation). To minimize and evaluate extrapolation error in the projected future scenarios, MaxEnt has three resources (Elith et al. 2011). The first was the transformation of an exponential family model to a logistic model, since exponential models can behave poorly when applied to new data. The second was to reset (or “clamp”) the values that are outside the range found in the study area, so they are constrained to remain within the range of values in the training data. Third, the model calculates MESS maps (i.e., multivariate environmental similarity surfaces) that display differences between the training and prediction environments, and gives negative values for dissimilar points and maps these values across the whole prediction region. Predictions in those negative areas should therefore be treated with caution. In addition, response curves can assess the degree of confidence in the extrapolation, in which researchers should handle extrapolation with caution when a response curve is truncated (Anderson 2013).

RESULTS

Population structure

Over the 9-year period 2009 to 2017, 7485 smooth hammerheads were measured, sexed and geo-referenced in northern Peru (Figure 1). Body size (and age) ranged from 40 to 315 cm TL (0 to 48 years), with a mean size of 92 cm TL (mean age of 3.5 years) (Figure 2). The mean body size for females (n= 4088, mean= 94.1 cm TL) exceeded that for males (n= 3396, mean= 89.1 cm TL) (two-sample t test, $t_{7481} = 5.64$, $P < 0.001$).

The overall sex ratio was female biased (ratio= 1.2:1, $X^2 = 63.98$, $df = 1$, $P < 0.001$). For neonates and juveniles (<230 cm TL for females and <210 cm TL for males), the sex ratio was also female biased (ratio= 1.2:1, $X^2 = 49.53$, $df = 1$, $P < 0.001$). For adults (n=112), this skew was particularly strong (ratio=7:1, $X^2 = 63$, $df = 1$, $P < 0.001$).

In the study area, two life-stages were dominant: neonates (young-of-year) and juvenile (>1 year-old). Sharks are born in late spring and early summer seasons and they stay in northern Peru for their first year, and some sharks might stay for up to two years (Figure 3). This was inferred from size-frequency distributions between seasons, in which major peaks represent young-of-year cohort and minor peaks represent juvenile of the second year cohort (Figure 3). Only in spring three peaks were identified of which two represent young-of-year cohort

and one second year cohort (Figure 3). For young-of-year cohort, mode length of individuals captured in summer sampling was 64 cm TL, in autumn samples 78 cm TL, in winter samples 91 cm TL, and in spring samples 101 cm TL. For second year cohort, mode length of individuals captured in summer sampling was 101 cm TL, in autumn samples 126 cm TL, in winter samples 134 cm TL, and in spring samples 142 cm TL. Comparison of the data among seasons revealed significant differences in shark total length (ANOVA: $F = 663$, $P < 0.001$). Of the 6 pair-wise comparisons between seasons, 5 were significantly different (Tukey's HSD test, $P > 0.001$), and only the seasons of winter and spring were not significantly different (Tukey's HSD test, $P = 0.72$).

No significant differences were observed in the distance from the coast by sex (two-sample t test, $t_{7289} = -1.607$, $P > 0.05$). However, significant differences were observed in the distance from the coast by size classes (ANOVA: $F = 197.5$, $P < 0.001$). All pair-wise comparisons were significantly different (Tukey's HSD test, $P < 0.001$) with the only exception of the size classes III (101–190 cm TL) and IV (191–350 cm TL) which were not significantly different. Size classes I (40–70 cm TL) and II (71–100 cm TL) were closest to the coast; while size classes III and IV were furthest from the coast (Table 1). Significant differences were observed in the distance from the coast by season (two-sample t test, $t_{7291} = -6.502$, $P < 0.001$). In warmer seasons, sharks are distributed closer to the coast (range = 1–215 km, mean = 63.5 km); while, in colder seasons, they are distributed more offshore (range = 70–273 km, mean = 70.5 km).

Significant differences were observed in the distance from the coast for all four seasons between La Nina and El Nino periods (Table 2). In El Niño seasons, sharks are distributed closer to the coast; while, in La Niña seasons sharks are distributed more offshore. The most marked difference was observed in season I and IV probably because during this seasons a strong El Niño (anomaly: 1.5–2 °C) and a moderate La Niña (anomaly: 1–1.5°C) occurred, respectively. In strong El Niño events in season I (2016–I, 2017–I) and in moderate La Niña event in season IV (2010–IV and 2013–IV) when SST and SST anomalies reached the highest and lowest values respectively, distance from the coast between El Niño and La Niña seasons became more marked (Figure 4, Table 3).

Environmental variable correlation

High levels of correlations ($r > 0.7$) occurred between 8 environmental variables (Table 4). Therefore, current velocity, dissolved oxygen and pH were excluded from further analyses. Chlorophyll-a and depth, as well as, chlorophyll-a and SST were highly correlated, yet these were retained for use in Maxent, since previous research has highlighted the ecological significance of SST, chlorophyll-a and bathymetry with respect to pelagic sharks (e.g. Sousa 2009, Sequeira et al. 2012, Vogler et al. 2012, Carlisle et al. 2015, Coelho et al. 2017, Boehlert 1988, Morato 2008, Worm et al. 2013, Hazen et al. 2013b, Ward-Paige et al. 2014, Calich 2016,

Copping et al. 2018). Thus five environmental variables were retained for further analysis: SST, chlorophyll-a, salinity, depth and slope.

Environmental factors that drive species distribution

SST, chlorophyll-a and depth contributed most to the model as predictor variables of species distribution (Table 5); while, salinity and slope contributed the least. SST, chlorophyll-a and depth were retained for further detailed analysis of El Niño and La Niña seasons. Salinity was excluded for further analysis since no spatial data was available with the spatial and temporal resolution required. However, salinity would have been an interesting variable to retain due to its strong influence on shark physiology (Bernal et al. 2012) and the apparent avoidance of hammerhead sharks to low salinity levels, since few occurrence records were observed in the lowest salinity areas (Fig. Sup. 1).

Prediction of habitat suitability under current scenarios

Under La Niña scenarios, chlorophyll-a and depth contributed the most to the model; while, under El Niño scenarios, SST and depth contributed the most (Table 5). The occurrence of sharks in environmental space and the response curves showed that sharks had a narrow preference for SST and chlorophyll (Table 6, Figure 5). Furthermore, sharks were selecting habitats that had mean SST lower and mean chlorophyll concentrations higher than the mean for the entire study area (Table 6). The spatial habitat suitability of sharks changed according to seasons and ICEN values (Niño or Niña conditions) (Figure 6). In La Niña conditions, suitable habitat was predicted to occur more offshore compared to El Niño conditions. In summer, for La Niña conditions, a high nucleus of habitat suitability was found in the central part of the study area (Figure 6). Furthermore, the highest habitat suitability value (>0.8) was predicted in El Niño conditions in the northern limit of the study area (Figure 6).

Projection of habitat suitability under future scenarios

For the reconstruction of future scenarios, current velocity was also used, because in the study area this is highly correlated to chlorophyll-a (Table 4), a variable that was not available in future scenario reconstructions, assuming that in future scenarios these two variables will maintain their correlation. The model projection for the years 2040–2050, for the RCP 26 revealed that suitable habitat for juvenile hammerhead sharks will become more coastal compared with the present distribution (Figure 7, Table 5), and this pattern will increase for the RCP 85 scenario (Figure 7). In the study area, the SST will have a range of 19.4–24.9°C and 19.7–25.3°C for the RCP 26 and RCP 85, respectively, where SST will decrease closer to the coast. According to the MESS maps, only two regions in the study area have values that are outside the range present in the training data (Fig. Sup. 2). However, these regions do not affect the interpretation of the model, since these do not overlap with species occurrence records and the response curves where not truncated (Figure 5).

DISCUSSION

This study improves our general understanding of the ecological niche and distribution of juvenile smooth hammerhead sharks in the Northern Humboldt Upwelling System (NHUS) during ENSO seasonal conditions and future scenarios of climate change. It represents the first study that predicts their distribution during a climate change scenario. Modelling of presence-only data, using MaxEnt, proved a useful approach to study ecological niche and species distribution of highly mobile predators in dynamic oceanographic conditions. Further studies should focus on finer-scale patterns of species distribution incorporating biotic factors.

Characterization of the population structure

Juvenile smooth hammerheads are the dominant life-stage in the northern part of NHUS where sharks are born in December and January as indicated by the presence of adult females and the smallest body sizes (Compagno 1984, Salomon-Aguilar et al. 2009, Castañeda 2001). From these months onward, sharks increase in size. In South Africa, New Zealand and southeastern Australia, pregnant females have been reported in coastal waters during the summer where these probably come close inshore to give birth (Bass et al. 1975, Stevens 1984, Francis, 2016). In New Zealand, neonate and juvenile sharks have the smallest mode in size frequency analysis during the summer, and, as seasons progress, the mode increases (Francis 2016). Coastal juvenile areas of smooth hammerheads differ in geographic characteristics: in Peru and eastern South Africa juvenile areas are located in exposed areas (not protected enclosed areas) (Diemer et al. 2011); while, in New Zealand and southeastern Australia, these are located in protected large harbours and/or estuaries (Francis 2016, Wray-Barnes 2016).

In the NHUS, the spatial distribution of juvenile sharks varies according to their ontogeny, season and ENSO conditions: i) as sharks increase in size, they distribute farther from the coast, ii) juvenile sharks are closer to the coast in the warm season compared to the cold season, and iii) juvenile sharks are closer to the coast during El Niño conditions compared to La Niña conditions. Worldwide, smooth hammerhead adults are commonly observed in offshore waters (Smale 1991, Sucunza et al. 2015, Casaca 2017); while juveniles are observed in coastal waters (Stevens 1984, Smale 1991, Dudley and Simpfendorfer 2006, Bornatowski et al. 2007, Doño 2008, Bizzarro et al. 2009, Bolaño 2009; Salomon-Aguilar et al. 2009, Diemer et al. 2011, Wray-Barnes 2016, Francis 2016, Casaca 2017). These studies also indicate that shark presence is higher in spring and summer and this seasonal abundance might be related to seasonal changes in

SST. In this study, sharks might be closer to the coast during warmer periods (summer and El Niño conditions) because sea surface temperature decreases approaching the coast. This suggests sharks may be searching for an optimal temperature range. Another study that analyzed the distribution of smooth hammerheads in southeastern Australia, did not identify the Southern Oscillation Index (SOI) – a measure of the intensity of El Niño and La Niña events in Australia- as an important predictor (Wray-Barnes 2016). This might be explained because in Australia compared to Peru, El Niño and La Niña events do not produce strong changes in oceanographic conditions.

Environmental factors that drive species distribution

Four environmental variables were identified as important predictors of hammerhead shark distribution in northern Peru between 2009 and 2017 (in order of importance): SST, depth, chlorophyll-a, and salinity. These four environmental variables are strong predictors of marine species distribution and have been commonly used in shark species distribution modelling, with the exception of salinity (e.g. Sequeira et al. 2012; Calich 2016). Depth is an indicator of coastal (shallow) or offshore (deep) habitat, and since juveniles are associated to coastal areas, depth was a relevant predictor.

Temperature has a major effect on the physiology of sharks since most species are ectotherms (Bernal et al. 2012, Fry 1971, Lowe 2002, Bush and Holland 2002, Bernal et al. 2012) and many studies have determined that pelagic shark species have a thermal range preference (Casey and Kohler 199, Campana and Joyce 2004, Sequeira et al. 2012, Vogler et al. 2012, Carlisle et al. 2015, Coelho et al. 2017). The thermal range preference of the smooth hammerhead shark has been poorly studied. Juvenile smooth hammerheads prefer water temperatures between: 26–29°C for the northeast Atlantic Ocean (Santos and Coelho 2018), 19–22°C for South Africa waters (Diemer et al. 2011, Dicken et al. 2018), 16–23°C for Uruguayan waters (Doño 2008), 15–25°C for southeastern Australia (Wray-Barnes, 2016), 14–24°C for New Zealand waters (Francis 2016), and 18–31°C for the Gulf of California (Salomon-Aguilar et al. 2009). These studies registered SST values, with the exception of northeast Atlantic Ocean and New Zealand waters where vertical water temperatures were additionally registered. Therefore, these studies establish that juvenile smooth hammerheads are present in water temperatures of 14 to 31°C. In this study sharks occurred in SST of 19.6 to 24.8°C in which the highest suitable SST values were narrow and slightly changed according to El Niño or La Niña seasons: 21–22°C for La Niña seasons, and 21.5–23.5°C for El Niño seasons.

Chlorophyll-a concentration is an indirect indicator of primary production and could also be indicative of food abundance, as shown by several studies where a correlation exists between the distribution of elasmobranchs and chlorophyll-a (Sousa 2009, Croll et al. 2012, Calich 2016). One of the main prey of smooth

hammerheads in northern Peru, jumbo flying squid, have their largest concentrations in areas where primary productivity is high but not maximal (Nesis 1970, 1983). This is concomitant with shark occurrence, since, in this study, sharks were present in high but not maximum values of chlorophyll concentrations. This environmental predictor is very relevant since northern Peru has been identified as an important feeding area for juvenile smooth hammerheads in the eastern Pacific Ocean (Gonzalez-Pestana et al. 2017). This conclusion is supported by a number of observations: i) jumbo flying squid has been identified as one of the main prey of smooth hammerhead in the eastern Pacific (Castañeda and Sandoval 2004, Estupiñan-Montaño and Cedeño-Figueroa 2005, Bolaño 2009, Ochoa-Díaz 2009, Galvan-Magaña et al. 2013, Gonzalez-Pestana et al. 2017), ii) this squid is the most abundant cephalopod species and one of its highest concentration is found in northern-central Peru (Anderson and Rodhouse 2001, Nigmatullin et al. 2001), iii) large smooth hammerhead fishery landings in northern Peru indicate that this species is abundant (Bonfil 1994, Fischer et al. 2012, Gonzalez-Pestana et al. 2016), and iv) this is a juvenile area that might function as nursery area - although, more studies are needed to demonstrate this (Heupel et al. 2007). Therefore, previous studies and the findings in this study indicate that northern Peru plays a major role as a foraging habitat for juvenile smooth hammerhead sharks.

Salinity also has a strong influence on shark physiology (Pang et al. 1977, Bernal et al. 2012) and can influence shark distribution (Hopkins and Cech 2003, Simpfendorfer et al. 2005, Abel et al. 2007). Compared to oceanic environments, coastal environments are more exposed to salinity fluctuations due to continental freshwater runoff, especially in estuaries (Schlaff et al. 2014). In eastern Australia, the distribution of juvenile smooth hammerheads was strongly associated with estuarine habitats; however, catches increased during periods of low rainfall where there is reduced freshwater runoff within estuaries, and as a result these habitats become more saline (Wray-Barnes 2016). In this study, salinity was the least important factor, yet it had an influence on the nearshore distribution of sharks where sharks appear to avoid lowest salinity values. Therefore, further studies should consider the influence of salinity levels in nearshore habitats, especially in El Niño conditions where continental freshwater runoff increases due to an increase in rainfall (Dai et al. 2009).

Relation between environmental and bathymetric variables

A high correlation exists between the most important predictor variables of smooth hammerhead distribution, with SST inversely correlated with chlorophyll. This relation has oceanographic explanations. The study area is located in a major coastal upwelling ecosystem which is characterized by coastal winds that drive surface waters offshore. These surface waters are replaced by cool and nutrient-rich waters from below, enhancing productivity. As a result, SST and chlorophyll are indirectly correlated. Current velocity is also correlated with

chlorophyll, since current velocity drives coastal upwelling. Finally, coastal topography strongly modifies the coastal upwelling processes; coastline irregularities such as capes and bays produce variations in coastal wind where strong upwelling and horizontal advection occur at wind-exposed capes (Chavez and Messie 2009), such as, can be found at the northern limit of the study area.

Prediction of habitat suitability under current scenarios

Under La Niña scenarios, chlorophyll was an important predictor of species distribution; while, under El Niño scenarios, SST was more important. This difference in predictor importance between ENSO conditions might be a trade-off between the suitability of SST and chlorophyll, since these variables are negatively correlated. During La Niña conditions, SST might not be as much of a constraint as it is during El Niño conditions. Therefore, in La Niña conditions, chlorophyll, as a proxy of food availability, is a better predictor of shark's distribution.

Depending on ENSO conditions, two areas of highest suitability were identified: the central-coastal part of the study area during La Niña conditions and, the northern-coastal part of the study area during El Niño conditions. Positive temperature anomalies during El Niño condition might drive smooth hammerheads closer to the coast as the coastal upwelling usually offers the coolest and the most productive environment. This pattern has also been observed for the Peruvian anchovy (*Engraulis ringens*) (Alheit and Niquen, 2004), a keystone species in the NHUS.

During La Niña conditions, the highest habitat suitability was predicted in the central-coastal part of the study area. This area is above or in close proximity with the shelf break. Marine predators, including seabirds, marine mammals and large fish, aggregate and use these areas as foraging grounds (Springer *et al.*, 1996; Worm *et al.*, 2003; Roberts *et al.*, 2016) due to upwelling of nutrient-rich waters that enhance high primary production and the presence of fronts that aggregate prey produced elsewhere (Schneider, 1991; Springer *et al.*, 1996). Therefore, this coastal area represents a foraging ground for smooth hammerheads during La Niña conditions.

During El Niño conditions, the highest habitat suitability was predicted in the northern-coastal part of the study area. This area presents unique oceanographic and bathymetric conditions, as well as, unique coastal topography in which Illescas peninsula represents the second westernmost point in the southeastern Pacific coastline (Figure 1). Coastal topography strongly modifies the coastal upwelling processes; coastline irregularities such as peninsulas produce variations in coastal wind where strong upwelling and horizontal advection occur (Chavez and Messie, 2009). Also, this area is in close proximity with an ecotone zone where two marine provinces meet forming the Equatorial Front (Chavez and

Messie, 2009). Marine fronts increase turbulence resulting in the input of nutrients which can enhance biological productivity (Yoder *et al.*, 1994). Therefore, marine fronts represent favorable feeding conditions for open-ocean higher trophic-level species in which these concentrate (Worm *et al.*, 2003; Worm *et al.*, 2005), including pelagic sharks (e.g. Pereira, 2017; Queiroz *et al.*, 2016).

Furthermore, this northern-coastal area is located near marine canyons. Oceanographically, these features increased upwelling, turbulence, mixing, and mesoscale eddies that enhance local production by transporting nutrients into the euphotic zone (Fernandez-Arcaya *et al.*, 2017). Pelagic top predator, such as, cetaceans and marine birds, aggregate in these complex topographic features, since these function as feeding areas (Yen *et al.*, 2004; Moors-Murphy, 2014). Pelagic sharks, including hammerheads, are known to aggregate around islands and seamounts to feed and orient themselves (Vaske *et al.*, 2009; Hearn *et al.*, 2010). No study has yet highlighted the importance of marine canyons for pelagic sharks. Toothed whales, which feed primarily on squid, have a strong association with marine canyons (Moors-Murphy, 2014; Roberts *et al.*, 2016). Further research is needed to determine the importance of marine canyons for pelagic sharks. Along the study area, the highest concentration of marine canyons is located on the most suitable area; therefore, this seabed feature might have an influence on shark distribution.

Along the study area, the area of highest habitat suitability during El Niño conditions is located on the narrowest part of the continental shelf. Coastal areas of shallow bathymetry in close proximity to the continental slope and deeper waters tend to be areas of high marine productivity because these features enhance upwelling (Botsford *et al.* 2003, Jacox and Edwards 2011, Connolly 2013), which often drive predator aggregations (McKinney *et al.* 2012, Bouchet *et al.* 2015). A similar pattern, as shown in this study, has been observed along the east coast of South Africa where the increased abundance of *S. zygaena* in the Transkei may relate to the continental shelf which is at its narrowest point (Diemer *et al.* 2011).

Prediction of habitat suitability under future scenarios

Climate change has an impact on species habitat, and as a consequence, species are shifting their distribution to find a more suitable habitat (Walther *et al.*, 2002). Studies have shown that the distribution of temperate marine species is contracting and shifting poleward (e.g. Perry *et al.*, 2005), including pelagic species, such as cetaceans (Macleod, 2009) and marine turtles (McMahon and Hays, 2006). For pelagic sharks, few studies have investigated the impact of climate change on their distribution. In the north Pacific, top predators were predicted to shift northward where the shark guild showed the greatest risk of pelagic habitat loss (Hazen *et al.*, 2013a). Also, in the Atlantic and Indian Oceans, the habitat of whale sharks is predicted to shift poleward accompanied by an overall range contraction (Sequeira

et al., 2014). In north-central Peru, a different pattern was observed since the suitable habitat for juvenile smooth hammerheads is predicted to become more coastal compared with the present distribution. In coastal upwelling regions, climate change is predicted to impact the marine ecosystem by increasing the upwelling intensity (Gutierrez *et al.*, 2011, Bakun *et al.*, 2015). As a result, sharks might be refuging in the coolest environment.

Ecological modelling that predicts the distribution of species under climate change scenarios focuses on the identification of a species' bioclimate envelope. Yet, this approach has been questioned by pointing to the other factors that can determine species distribution under climate change which include dispersal abilities, evolutionary change and biotic interactions (Davis *et al.*, 1998; Lawton *et al.*, 2000). Dispersal ability is not a constraint for the modelling of the smooth hammerhead since this is a highly mobile species that can be expected to track the geographical position of their bioclimate envelope. Also, evolutionary change is not a constraint since sharks are not expected to be able to undergo rapid evolutionary change over the timescale studied. Biotic interactions can have an influence in predicting species distribution. The main prey of the smooth hammerhead in northern Peru are squids (Gonzalez-Pestana *et al.*, 2017); therefore, understanding the distribution of their prey under climate change scenarios is important. Yet, at a macro-scale, climatic influences on species distributions are shown to be dominant which can minimize the impact of biotic interactions (Pearson and Dawson, 2003). Therefore, the bioclimate envelope approach can provide useful results, giving a first approximation of the potentially impact of climate change on the distributions of species (Pearson and Dawson, 2003).

Limitations

An important limitation in ENM studies is that biotic factors are usually not included (Davis *et al.* 1998). The reasons why biotic factors are not included are the followings: i) conceptual and computational difficulties (Araujo and Guisan 2006, Soberon 2010), and ii) they are difficult to estimate owing to the fine spatiotemporal resolution and potentially complex nature of biotic dimensions (Engler and Guisan 2009, Anderson and Raza 2010, Soberon 2010). Still, ENMs based entirely on scenopoetic variables have demonstrated considerable predictive value (e.g. Raxworthy *et al.* 2003). To explain this apparent paradox, two possibilities have been proposed (Soberon and Nakamura 2009). First, in some cases, biotic factors may not affect distributions at the large extents and low resolutions characteristic of geographic distribution maps (Prinzing *et al.* 2002). Second, biotic factors might correlate closely with scenopoetic variables, which thus capture an important part of the biotic signature. In this study, one of the main prey of smooth hammerhead sharks in the study area, jumbo flying squid, have their largest concentrations in areas where primary productivity is high but not maximum. Tools such as satellite tracking and archival tags might

be relevant to study fine-scale relationships of environmental variables due to their recordings of in situ conditions (Simpfendorfer and Heupel 2012).

Future studies should predict habitat suitability of smooth hammerheads off northern Peru during the colder seasons (June to November). In this study, this was not possible because the environmental data was incomplete. A limitation of satellite data is the presence of clouds that impede the collection of data, and central-northern Peru presents a high presence of clouds during the colder seasons. Therefore, future studies should consider this limitation. A final major limitation and consideration was that this study predicted the suitable habitat and characterized the ecological niche of hammerhead sharks in the epipelagic surface. Yet, most pelagic sharks operate in a three-dimensional scale and can move through the water column. Previous studies have established that smooth hammerhead sharks exhibit a diel vertical movement behavior where they stay in surface waters (0- 60 m) (Francis 2016, Casaca 2017). In this way, future studies should attempt to predict vertical habitat suitability and identify environmental predictors. For example, dissolved oxygen may be an important predictor since it is an abiotic constraint for fish physiology (Sund et al. 1981, Nasby-Lucas et al. 2009, Abascal et al. 2011), especially in oceanic regions with high primary production, as in this study area, where a shallow oxygen minimum zone exists (i.e. eastern Pacific; Fiedler and Talley 2006, Prince et al. 2006).

Conservation and management implications

To improve the conservation of smooth hammerheads off Peru and their supporting ecosystem, spatial management should prioritize areas of highest suitability, and consider the implications of shark distribution under future scenarios of climate change. These areas of highest suitability are zones of exceptionally high marine productivity that sustain the core feeding habitat of the smooth hammerhead which is a top predator, and as such acts as an indicator of high biodiversity and/or biomass (Sergio *et al.*, 2008). These features are important in the selection of marine protected areas. The northern-coastal part of the study area has previously been identified as a priority area for the conservation of Peruvian marine biodiversity (Nakandakari *et al.*, 2012). Therefore, this area of highest suitability should be considered as a candidate for a pelagic marine protected area. Pelagic ecosystems are uniquely dynamic; yet many pelagic features are either spatially or temporally predictable (Game *et al.*, 2009). Pelagic protected areas should be implemented based upon these highly productive pelagic features: static bathymetric, persistent hydrographic and ephemeral hydrographic features (Hyrenbach *et al.*, 2000). In this study, the areas of highest suitability, especially the northern-coastal area, are associated with these features (i.e. static bathymetric, persistent hydrographic). Furthermore, the area of highest suitability in the northern-coastal part of the study area has previously been identified as the most important fishery area for smooth hammerheads off Peru (Carbajal *et al.*, 2007; Llanos *et al.*, 2009).

Therefore, this area should be a priority for fisheries management. During future scenarios of climate change, coastal shift in shark distribution will have impacts on their fisheries and conservation since sharks will become more vulnerable to fisheries as their catchability increases. During warmer periods, landings of smooth hammerheads increase along the Peruvian coast (de la Puente 2013); this might be related to their coastal distribution that increases their catchability. Therefore, future management actions should take this into account.

Conclusions

In the southeastern Pacific Ocean, northern Peru represents an important area for the juvenile smooth hammerheads since this region has been identified as an important feeding area and presents the highest captures of this species, and is probably the area of highest abundance. This study supports the importance of northern Peru for this species and furthers our understanding of the ecology of the smooth hammerhead in this highly dynamic and productive pelagic ecosystem. Furthermore, this study predicts for the first time the distribution of the smooth hammerhead under a climate change scenario. These areas of highest suitability should be a priority for research and fisheries management as well as a candidate for a pelagic marine protected area.

Acknowledgments

The authors thank the following institutions who funded this long-term study: DEFRA Darwin Initiative through University of Exeter, Whitley Fund for Nature, FINCYT Contrato 369 PIBA 2014. Also, Russell E. Train Education for Nature Program World Wildlife Fund and Rufford Foundation. We would like to thank fishermen who participated and supported this study, and entire ProDelphinus team.

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Tables

Table 1. Distance from the coast (km) of smooth hammerhead sharks (*Sphyrna zygaena*) by size classes in northern Peru.

Size classes	Mean	Maximum	Minimum
I (40–70 cm TL)	65	180.6	0.9
II (71–100 cm TL)	56.6	253.4	0.6
III (101–190 cm TL)	83.9	226.3	1.4
IV (191–350 cm TL)	89.1	73.9	10

Table 2. Distance from the coast (km) of smooth hammerhead sharks (*Sphyrna zygaena*) grouped by La Niña and El Niño seasons (I: December to January, II: March to May, III: June to August, IV: September to November).

ENSO	Season	Mean	Maximum	Minimum	Two-sample t test	
					T-value	P-value
La Niña	Season I	80.1	181	10	15.947	<0.0001
El Niño	Season I	54.8	215	1		
La Niña	Season II	78.1	165	1.9	25.083	<0.0001
El Niño	Season II	43.6	192	2.1		
La Niña	Season III	48.7	132.3	13.4	4.2135	<0.0001
El Niño	Season III	40.8	141.6	0.6		
La Niña	Season IV	117.6	226.3	1.1	10.986	<0.0001
El Niño	Season IV	87.1	273.9	0.9		

Table 3. Distance from the coast (km) of smooth hammerhead sharks (*Sphyrna zygaena*) grouped by moderate La Niña and strong El Niño seasons (I: December to January, II: March to May, III: June to August, IV: September to November).

ENSO	Season	Mean	Maximum	Minimum	Two-sample t test	
					T-value	P-value
La Niña	Season I	80.1	180.5	10.0	18.65	<0.0001
El Niño (strong)	Season I	43.7	178.5	1.0		
La Niña	Season II	78.1	165.2	1.8	24.28	<0.0001
El Niño (strong)	Season II	31.7	191.9	3.5		
La Niña	Season III	48.4	132.3	13.4	8.87	<0.0001
El Niño (strong)	Season III	31.3	76.4	2.4		
La Niña (moderate)	Season IV	125.8	151.2	81.9	13.124	<0.0001
El Niño (strong)	Season IV	74.4	273.8	1.4		

Table 4. Correlation coefficients (r) of environmental variables: sea surface temperature (SST; °C), chlorophyll (chl-a; mg/m³), dissolved oxygen (dis oxy; mol/m³), salinity (pss), pH, currents velocity (cur vel; m/s), depth (m) and slope (m) in northern Peru.

	Depth	Chl-a	Cur vel	Dis oxy	pH	Salinity	SST
Chl-a	0.74						
Curr vel	0.71	0.82					
Dis oxy	-0.64	-0.75	-0.76				
pH	-0.13	-0.21	-0.50	0.39			
Salinity	-0.48	-0.64	-0.78	0.57	0.81		
SST	-0.65	-0.84	-0.66	0.42	-0.08	0.48	
Slope	-0.06	0.07	0.04	0.16	-0.09	-0.15	-0.17

Table 5. (a) Sample size, (b) Jackknife test, (c) percent contribution and, (d) validation statistics and presence threshold for environmental variables for hammerhead shark distribution models. AUC: area under the receiver operating curve. I: summer (December to February) and II: autumn (March to May).

	Present					Future
	Overall	La Niña I	La Niña II	El Niño I	El Niño II	RCP 26 and 85
a) Sample size	2994	225	1030	1015	724	2994
b) Jackknife test						
SST	1.3127	1.576	1.3926	1.3503	1.3944	1.3563
Chlorophyll	1.2068	1.4881	1.4085	1.2982	1.2369	-
Depth	1.2888	1.576	1.4112	1.5853	1.4333	-
Salinity	0.845	-	-	-	-	-
Slope	0.4692	-	-	-	-	-
Current velocity	-	-	-	-	-	1.2331
c) Percent contribution						
SST	9.1	17.1	18.8	10.8	15.2	54.5
Chlorophyll	48.7	54.4	34.1	6.5	9.4	-
Depth	40.1	28.4	47	82.7	75.4	-
Salinity	7.2	-	-	-	-	-
Slope	0.6	-	-	-	-	-
Current velocity	-	-	-	-	-	45.5
d) Validation statistics						
Test AUC	0.926	0.950	0.936	0.942	0.934	0.920
10th percentile training presence	0.301	0.293	0.334	0.341	0.249	0.355

Table 6. Descriptive statistics of environmental data throughout the study area (background) and at smooth hammerhead shark occurrence records in northern Peru between 2009 and 2017. I: summer (December to February) and II: autumn (March to May).

		SST (°C)		Chl-a (mg/m ³)	
		Mean	Range	Mean	Range
La Niña I	Sharks' occurrence	21.7	20.0- 23.4	4.6	1.3 - 7.9
	Background	23.4	17.5 - 25.4	0.9	0.2 - 14.3
La Niña II	Sharks' occurrence	21.5	20.3 - 23.1	3.25	1.1 - 6.6
	Background	23.9	19.1 - 27.1	0.8	0.1 - 11.5
El Niño I	Sharks' occurrence	22.5	21.0 - 24.6	3.5	1.0 - 7.6
	Background	23.9	20.0 - 25.5	0.7	0.1 - 15.1
El Niño II	Sharks' occurrence	22.6	21.3 - 24.8	3.6	0.7 - 7.7
	Background	25	20.1 - 27.6	0.7	0.2 - 10.5

Figures

Figure 1. Location of smooth hammerhead sharks (*Sphyrna zygaena*) captured in gillnets off northern-central Peru between 2009 and 2017. Biogeographic demarcation showing the Warm Temperate Southeastern Pacific Marine Province (WTSP-MP) and Tropical East Pacific Marine Province (TEP-MP) (Spalding et al. 2009). Light grey color is the continental shelf.

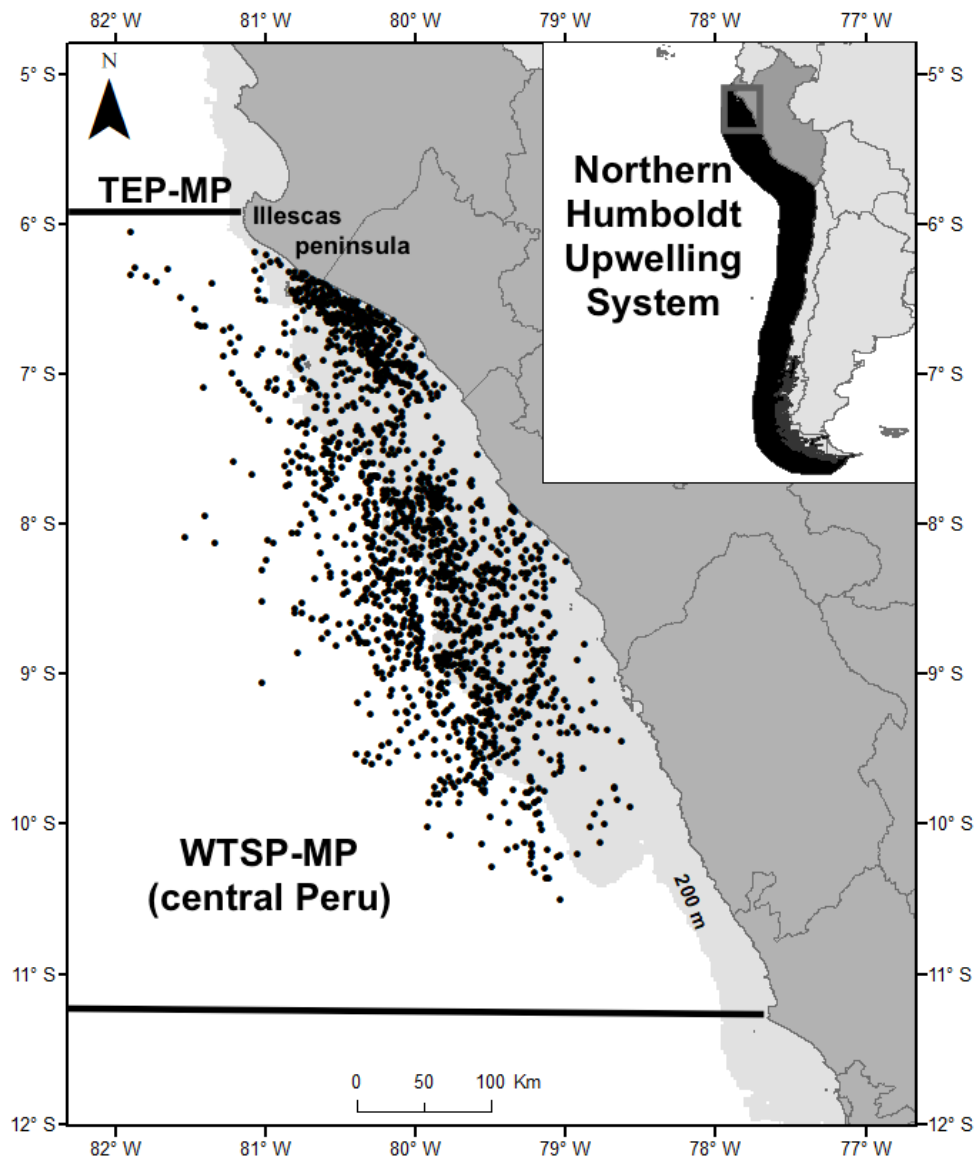


Figure 2. Size distribution (total length, cm) of smooth hammerhead sharks (*Sphyrna zygaena*) in northern Peru between 2009 and 2017. Size at maturity for females (solid vertical line) and minimum size at birth (dashed vertical line).

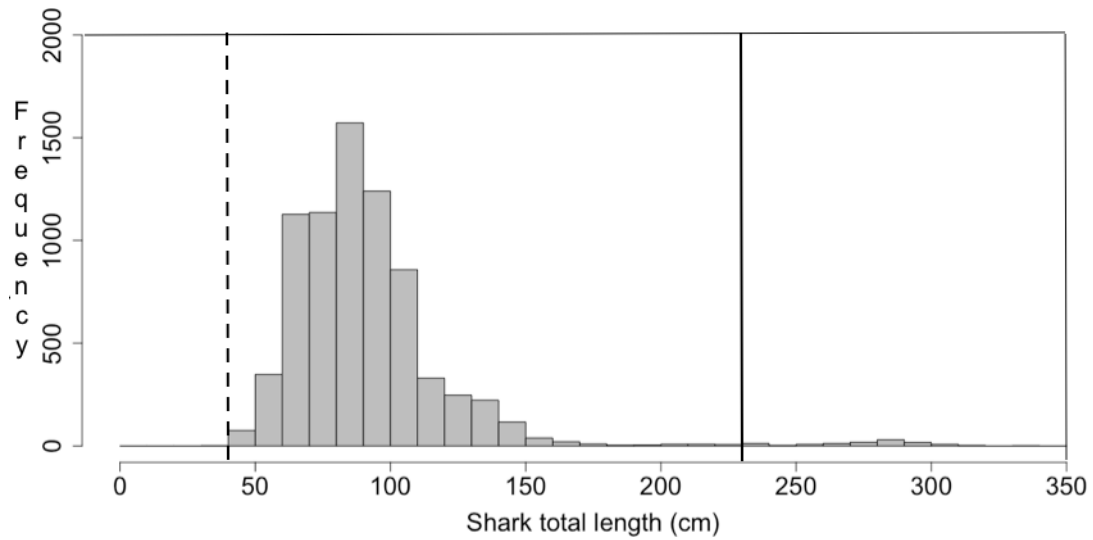


Figure 3. Smooth hammerhead sharks (*Sphyrna zygaena*) length-frequency distributions of young-of-the-year and juvenile captured in northern Peru during the four season periods between 2009 and 2017.

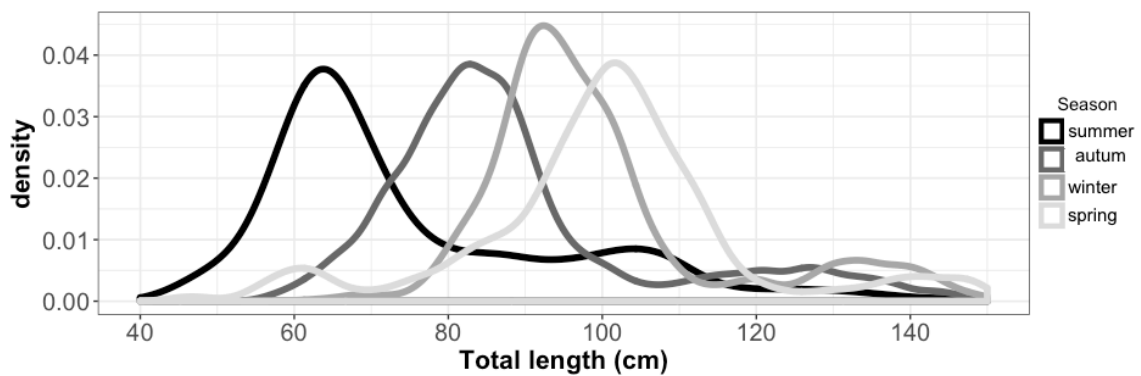


Figure 4. Occurrence of smooth hammerhead sharks (*Sphyrna zygaena*) during strong El Niño events in season I (summer) (2016-I, 2017-I) and in moderate La Niña event in season IV (autumn) (2010-IV and 2013-IV) in northern Peru between 2009 and 2017.

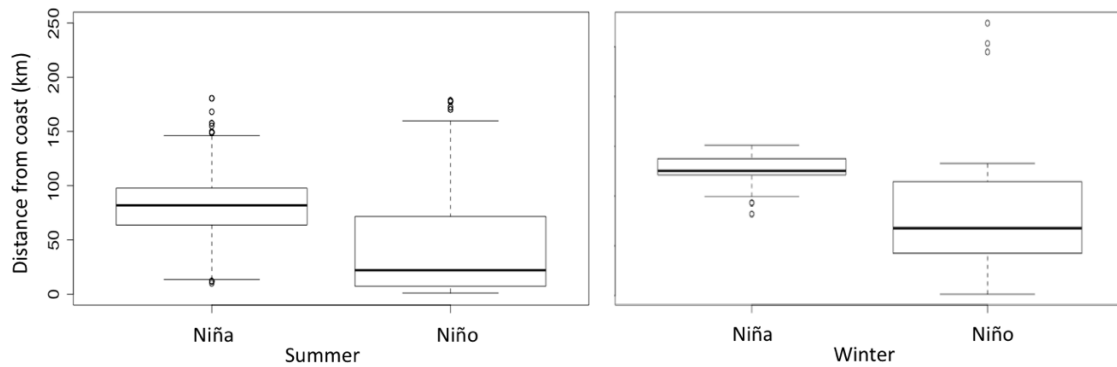


Figure 5. Response curves showing the effect of the environmental predictors on the presence of smooth hammerhead shark off northern Peru during El Niño and La Niña conditions, between 2009 and 2017, computed with Maxent 3.4.1.

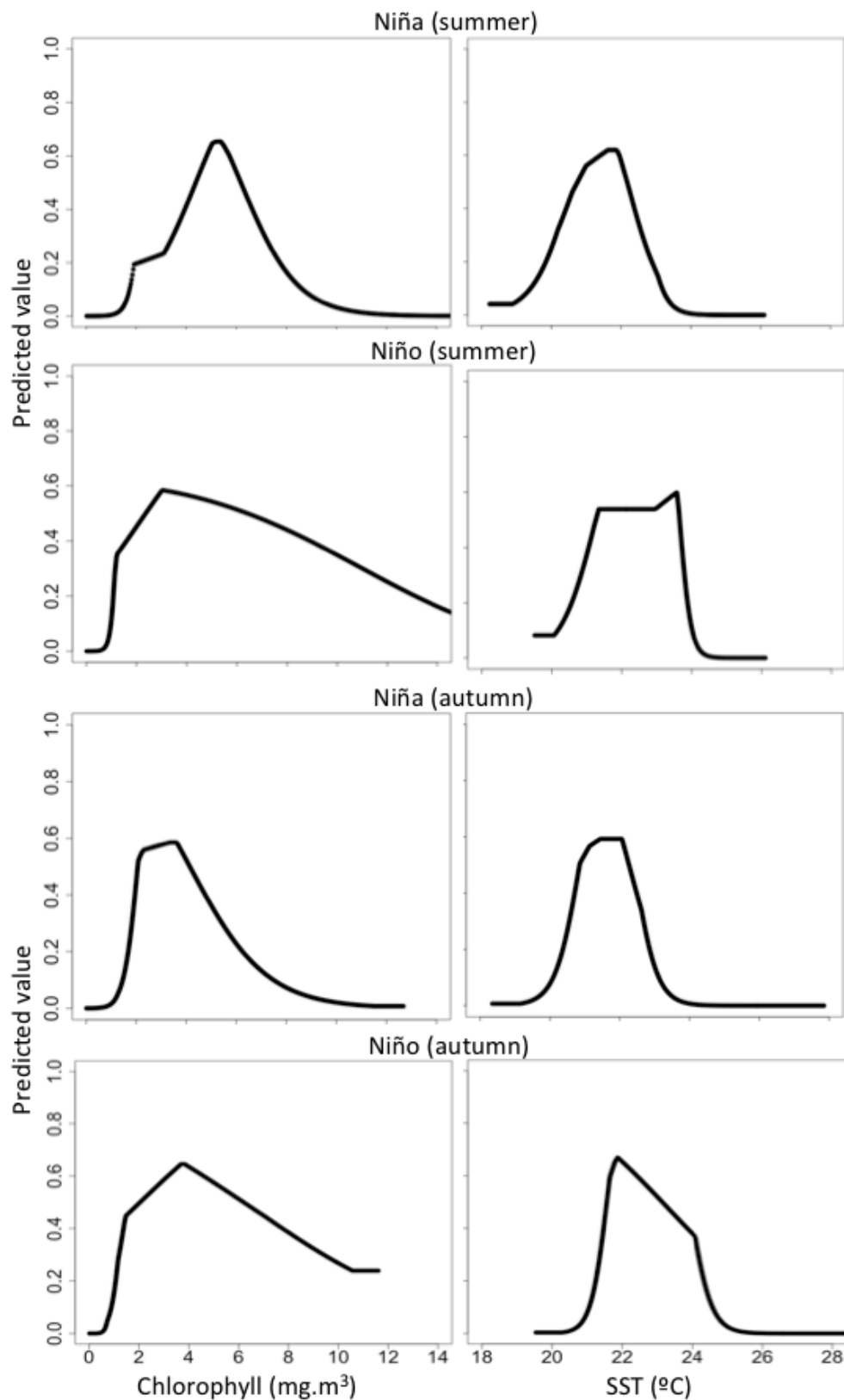


Figure 6. The current potential distribution of smooth hammerhead shark (*Sphyrna zygena*) in the Northern Humboldt Current Large Marine Ecosystem computed with Maxent 3.4.1 derived from El Niño and La Niña environmental conditions (sea surface temperature, chlorophyll-a, and bathymetry) between 2009 and 2017. Unsuitable habitat values (white colour) were determined by the 10th percentile training presence threshold output by MaxEnt (see Table 5).

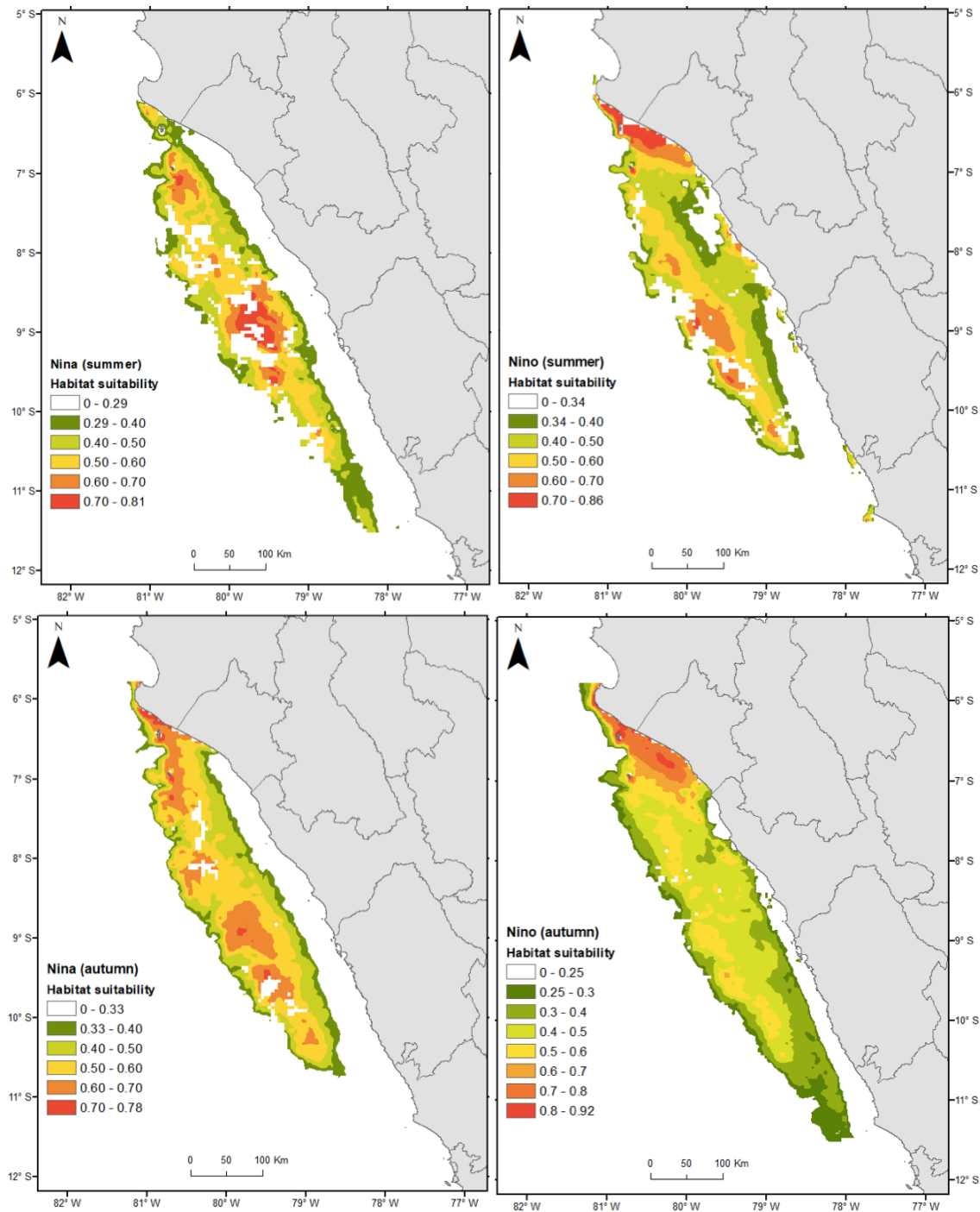
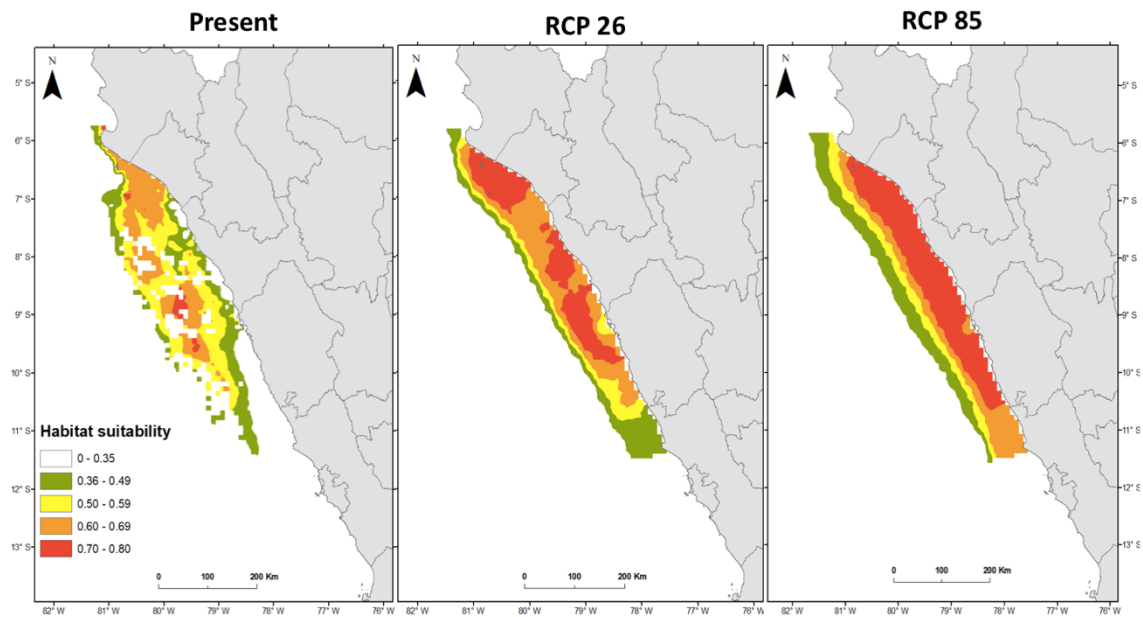


Figure 7. The future potential distribution of the smooth hammerhead shark (*Sphyrna zygena*) in the Northern Humboldt Current Large Marine Ecosystem computed with Maxent 3.4.1 derived from future environmental conditions (sea surface temperature, and current velocity) for the years 2040-2050 in RCP 26 and RCP 85 scenarios. Unsuitable habitat values (white colour) were determined by the 10th percentile training presence threshold output by MaxEnt (seeTable 5).



Supplementary material

Figure 1. Locations of smooth hammerhead sharks (*Sphyrna zygaena*) captured in gillnets off northern-central Peru between 2009 and 2017 within salinity layer (pss). Environmental data retrieved from Bio-Oracle with 9 km² resolution (Tyberghein et al. 2012).

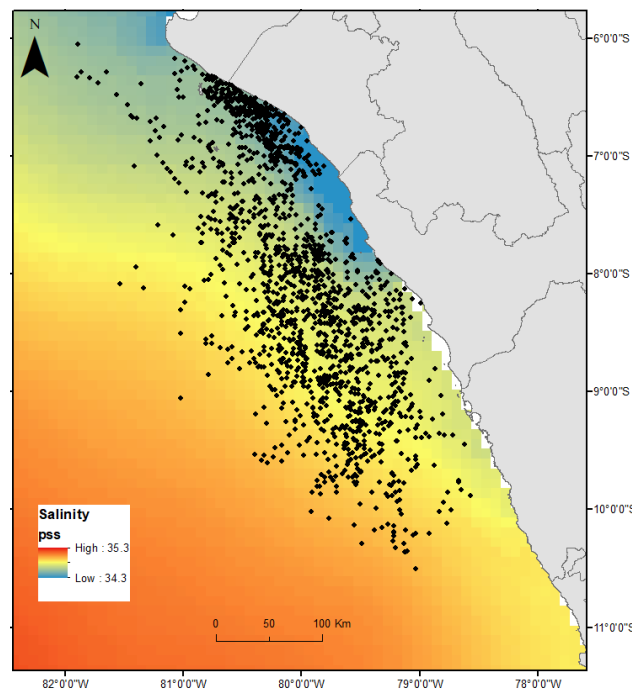


Figure 2. Multivariate environmental similarity surfaces (MESS) maps for the study area in future climate change scenarios (RCP26 and RCP85). Negative values (lighter gray) indicate dissimilar points and should be treated with strong caution.

