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Modelling common dolphin (*Delphinus delphis*) coastal distribution and habitat use: insights for conservation.

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ABSTRACT

The world's ecosystems are altered to different extents by anthropogenic activities. Marine habitats, especially coastal areas, are subjected to an increasing pressure derived from human activities on both land and ocean. Information about species distribution is fundamental to develop effective conservation and management measures and counteract negative anthropogenic impacts. The present work explores the use of species distribution models by using the Environmental Niche Factor Analysis (ENFA) to assess the habitat suitability of common dolphins (*Delphinus delphis*) in Northwest Spain, and its application to the development of effective conservation and management measures. The relationship between presence-only data and ecogeographical variables (EGV) was used to assess the potential distribution of the species. Data was collected during 273 days at sea, covering a total distance of 9 417 km between March 2014 and October 2017 with a total of 91 common dolphin encounters. This study shows that tide level and sea surface salinity are the main EGVs driving the distribution of the species in coastal areas especially in waters above the continental shelf. Additionally, this study reveals the most suitable habitats for common dolphin and outlines the need to develop conservation measures and management plans to promote the protection of this species. Findings of the study contribute to a more accurate and comprehensive understanding of the common dolphin distribution and emphasize the importance of species distribution models in the development of effective conservation and management strategies.

Keywords:

Cetaceans; Species distribution models; Environmental niche factor analysis; *Delphinus delphis*; Coastal conservation; Northwest Spain

1. INTRODUCTION

Human activities are causing a global impact on the Earth's ecosystems, affecting habitats, populations and species to different extents (Vitousek et al., 1997; Sutherland et al., 2015). As a consequence, habitat and biodiversity loss are a widespread issue (Myers et al., 2000; Brooks et al., 2002). The impact of human activities is particularly important in marine coastal ecosystems, which are being degraded by impacts such as pollution, anthropogenic noise and overfishing (Shahidul Islam and Tanaka, 2004 Halpern et al., 2008; Reynolds et al., 2009). As a result, a development of effective conservation measures coupled with an increase in scientific knowledge on the distribution, ecology and habitat use of the threatened species is needed (Brooks et al., 2002). Information on the distribution of a species, for instance, can be a very useful tool to improve its conservation (Rodríguez et al., 2007; Guisan et al., 2013). In this context, models that use environmental information to assess the distribution of a species, such as Species Distribution Models (SDMs) and Environmental Niche Models (ENMs), have been acquiring increasing importance in the different steps of spatial and conservation planning (Margules and Pressey, 2000; Rodríguez et al., 2007; Guisan et al., 2013). ENMs are based on the ecological niche concept (Hutchinson, 1957) that relates the fitness of a species to its niche. Among them, the Ecological Niche Factor Analysis (ENFA) defines the ecological niche as a hypervolume with n dimension corresponding to n ecological variables within which a species can exist and reproduce successfully (Hutchinson 1957) and combines information about a species' distribution with a set of ecogeographical variables (EGVs) to determine habitat suitability (Hirzel et al., 2002).

EGVs (biological, physical and topographical) have been used to explain species distribution (Guisan and Zimmermann, 2000; Elith and Leathwick, 2009). In the marine environment, topographical features and temporal changes in physical and biological factors are known to determine the spatial distribution of a species (Brodeur and Pearcy, 1992). Resource availability is also a crucial aspect that influences the habitat selection (Torres et al., 2008; Planque et al., 2011) and shapes the distribution of marine top predators such as seabirds, sharks and cetaceans, which are heavily influenced by the spatial movements of their prey (Hamazaki, 2002; Redfern et al., 2006; Kohler and Turner, 2008; Torres et al., 2008; Certain et al., 2011; Díaz López and Methion, 2017, 2018). Since it is difficult to obtain reliable information about prey distribution and abundance, physical and biological factors can be used as proxies to both model and make predictions about the distribution of top predators (Guisan and Zimmerman, 2000; Redfern et al., 2006; Elith and Leathwick, 2009; Pirotta et al., 2011; Díaz López and Methion, 2017, 2018).

Information about the distribution of a species can be recorded in terms of presence/absence data (Weir et al., 2012; Díaz López and Methion, 2017, 2018) or presence-only data (Moura et al., 2012; Fernandez et al., 2018). However, detection of highly mobile marine species, such as the short-beaked common dolphin (*Delphinus delphis*, hereafter referred to as common dolphin), may be challenging because they spend short periods of time at the surface (Hamazaki, 2002; Praca and Gannier, 2008). Hence, the distinction between true absences (i.e. when common dolphins are not present in the sampled location) and false absences (i.e. when common dolphins are present but could not be detected) can be challenging (Praca and Gannier, 2008; Elith and Leathwick, 2009). More specifically, it can be difficult to assess whether this small cetacean is absent in a known location because (1) the habitat is unsuitable for common dolphins, (2) the habitat is suitable, but common dolphins are not present, or (3) common dolphins are present but could not be detected. In this case models using presence-only data, such as ENFA, are recommended (Hirzel et al., 2002; MacLeod et al., 2008), and have been proved to be a robust technique to assess the habitat suitability of cetaceans (Praca and Gannier, 2008; Skov et al., 2008; Condet and Dulau-Drouot, 2016). Models based on the ENFA approach can reach high predictive accuracy with small sample sizes (Allouche et al., 2008), and are ideal to assess the habitat suitability of highly mobile and cryptic species (Reutter et al., 2003; Pracca and Gannier, 2008). Additionally, they have been used to infer potential threats to marine predator conservation, such as habitat loss or interaction with human activities, (Condet and Dulau-Drouot, 2016).

The common dolphin is a small cetacean widely distributed from tropical to cool temperate waters of both the Atlantic and the Pacific oceans (Jefferson et al., 2007). Its distribution in the Northeast Atlantic extends from Norway to the south of Spain (Mirimin et al., 2009; Murphy et al., 2013), and is the most abundant cetacean in waters above the continental shelf of the northwest Iberian Peninsula (López et al., 2002, 2003; Spyrakos et al., 2011). Despite its abundance, the species faces several threats resulting from human activities in the Northeast Atlantic (Murphy et al., 2013), where bycatch by purse-seine, gill nets and trawling fisheries is a major concern (López et al., 2003; Rogan and Mackey, 2007; Fernández-Contreras et al., 2010; De Boer et al., 2012). Although the common dolphin has been listed as Least Concern by the International Union for Conservation of Nature (IUCN), its interaction with fisheries could lead to a decline in common dolphin abundance in specific areas (De Boer et al., 2012; Saavedra et al., 2018).

To minimise these impacts and to ensure common dolphin conservation, the species has been included in several national and international agreements and conventions that cover a wide variety of aspects such as international trade, monitoring and reduction of bycatch, and habitat conservation (Murphy et al., 2013). In the European Union, the Directive on the Conservation of Natural Habitats (hereafter referred to as Habitats Directive) lists the common dolphin in Annex IV and urges governments to promote research and conservation measures to ensure that the impacts on the species are kept to a minimum, especially in the areas that include important habitats for the species ecology and reproduction (Council Directive 92/43/EEC). In Spain, common dolphins are listed as data deficient (the Atlantic population) in the Red Book of Spanish Vertebrates (Blanco and González, 1992) and in the Spanish Catalogue of Threatened Species (Real Decreto 139/2011). Additionally, common dolphins and their habitat are protected in Spain by regional and national legislations (Ley 3/2001; Ley 15/2002; Ley 42/2007; Ley 41/2010 Real Decreto 1727/2007). However, the existing legal framework is unspecific about the restrictions to be applied to reduce the impact of human activities on common dolphins. Furthermore, despite the available information concerning the threats affecting this small delphinid in Galician waters, there is a lack of studies linking the habitat suitability of the species to its conservation. A better understanding of the key habitats for the species will contribute to developing better management and conservation plans to minimise the impact of anthropogenic activities on common dolphins.

Following the above considerations, this study combines the species distribution modelling approach (ENFA) with data collected during dedicated year-round boat surveys to provide new information on the environmental variables that influence common dolphin distribution and habitat suitability. These findings were used to assess the best measures to promote the conservation of the species and evaluate the areas in which strategies would be more effective.

2. METHODS:

2.1. Study area

The present study was carried out in waters above the continental shelf of northwest Spain and beyond. The northwestern coastline of Spain is characterised by a series of drowned tectonic valleys known as rias that influence the coastal dynamics in the area (Prego et al., 1999; Evans and Prego, 2003). The study area covered approximately 2 479 km^2, and extended from Cíes Islands (42° 15’ N) in the South, up to cape Corrubedo in the North (42° 36’ N), and from the Ría de Arousa in the East (including the waters inside the inlet) up to the continental break and beyond in the West (Fig. 1). This region is characterised by a narrow continental shelf, varying from 30 to 50 km in width, with the continental break occurring between 180 and 200 metres in depth (Dias et al., 2002; Sanz Alonso, 2005). The study area includes the Atlantic Islands National Park (Fig. 1), which protects 72.85 km^2 of waters around the Cortegada, Sálvora, Ons and Cíes islands (Ley 15/2002). The park hosts different Special Areas of Conservation, Special Protection Areas for Birds and Sites of Community Importance, and was created to preserve the local marine biodiversity. Among other measures, it requires a permit to navigate in waters protected by the park and it restricts fishing activities to the artisanal fleet (Ley 15/2002).

The study area is located on the northern limit of the northwest Africa upwelling system (Gonzalez-Nuevo et al., 2014). Therefore, these coastal waters are dominated by a series of seasonal upwelling events (Torres et al., 2003), which are caused by the action of northerly winds, and are influenced by the orientation and the geographical features of the coastline (Torres et al., 2003; Álvarez et al., 2012). Indeed, upwelling events are especially common in the study area (Lavin et al., 1991; Álvarez et al., 2012) where they are important oceanographic phenomena, as they carry deep, cold and nutrient-rich waters to the photic layer, enhancing the primary productivity (Lavin et al., 1991). Upwelling episodes typically occur during spring and summer months (Torres et al., 2003; Gonzalez-Nuevo, et al., 2014); however, weaker winter upwelling episodes have also been recorded (Álvarez et al., 2012).

2.2. Data collection

Data were collected year-round by the research team of the Bottlenose Dolphin Research Institute (http://www.thebdri.com) as part of a long-term study that aims to understand the ecology of cetacean species that inhabit Galician waters (Díaz López et al., 2017, 2019; Díaz López and Methion 2017, 2018; Methion and Díaz López, 2018). Dedicated boat surveys were carried out on board a 12-m single-hulled research vessel, powered by two 180 hp inboard engines on waters above the continental shelf and beyond, between March 2014 and October 2017.

Surveys were conducted during daylight hours at a constant speed of 6 to 8 knots in adequate weather conditions (no fog, no rain and sea conditions <3 on the Douglas sea scale) (Díaz López and Methion, 2017, 2018). Observational effort was carried out by at least three experienced observers located on the flying bridge of the research vessel (4 m above sea level). Observers conducted continuous 360° scans around the research vessel searching for common dolphins at the water surface. Scans were carried out using the naked eye or 10X50 binoculars.

Environmental data were collected every 20 minutes from the beginning until the end of the survey, following Díaz López and Methion, 2017, 2018. These data collection sets (hereafter referred to as 20-minute samples) were used to summarize the environmental conditions during the survey, and to assess the presence of common dolphins. The information collected at each 20-minute sample included the time (UTC), the position of the vessel (WGS 84 latitude and longitude) and the speed (in knots), which were obtained with a hand-held GPS (Garmin eTrex 10). At the same time, the sea surface temperature (SST in degrees Celsius) was measured with a Garmin GPS-Plotter Map Sounder connected to an echo-sounder. Additionally, the sea surface salinity (SSS in parts per thousand) was measured using a portable refractometer.

The presence of common dolphins within a 1 nautical mile radius around the research vessel was recorded at the beginning of each 20-minute sample (Díaz López and Methion, 2018). Depending on its duration, a sighting of common dolphins could include more than one 20-minute sample, however, only the first 20-minute sample within the same sighting was used for the analysis.

QGIS 2.18 (QGIS Development Team, 2018), an open source Geographical Information System (GIS) software package, was used to obtain the topographical variables following Díaz López and Methion (2017). The depth (in metres) was extracted from a 30 arc second bathymetry raster of the General Bathymetric Chart of the Oceans (GEBCO, Weatherall et al., 2015) for each 20-minute sample and each sighting (presented as mean $\pm$ standard error). The same bathymetry raster was used to calculate the slope of the seafloor (understood as the rate of change between a given location and its surroundings and expressed as a percentage, hereafter referred to as Slope) and the aspect of the seafloor (compass orientation that a slope faces, hereafter referred to as Aspect) for each 20-minute sample. Additionally, the minimum distance of each 20-minute sample location to the coast (in metres) and to the 200 metres bathymetric line (in metres) was calculated with the NNJoin plugin in QGIS 2.18. The tide level (in metres) was obtained from the tide charts corresponding to the harbour of Vilagarcía de Arousa, located in the Ría de Arousa (Díaz López and Methion, 2018). Chlorophyll a data (in mg/m^3) were extracted from 1 km X 1 km daily rasters from the COPERNICUS Marine Environment Monitoring Services website (http://marine.copernicus.eu, last visited 30/11/2018). The point sampling tool in QGIS 2.18 was used to obtain the chlorophyll a value for each 20-minute sample.

2.3. Environmental Niche Factor Analysis:

In this study, ENFA was carried out using the software package Biomapper 4.0 (Hirzel et al., 2004), which takes into account the density of observations for any given species in the multidimensional EGVs space to create a habitat suitability map (Hirzel et al., 2002; Hirzel and Arlettaz, 2003). The method requires two types of data: (1) geographical positions where the species has been recorded and (2) a series of EGVs measured in these locations (Hirzel et al., 2002). In this case, depth, Slope, Aspect, distance to the coast, distance to the 200 m bathymetric line, chlorophyll a, SST, SSS and tide level (Table 1) were chosen as they have been successfully used to explain cetacean distribution in previous studies (Pirotta et al., 2011; Spyrakos et al., 2011; Fernandez et al., 2017; Díaz and Methion, 2017, 2018). The[i] EGVs were divided into two categories according to their temporal variability: *persistent* and *non-persistent* variables (following Díaz López and Methion, 2017). Depth, Slope, Aspect, distance to the coast and distance to the 200 m bathymetric line were considered invariable in time and thus named *persistent variables*. On the other hand, chlorophyll a, SST, SSS and tide level were named *non-persistent*[ii] *variables* due to their temporal variability.

To compute ENFA in Biomapper, both the EGVs and the species presence data had to be transformed to raster format (Hirzel et al., 2002). To do so, a grid with hexagonal cells was used. This type of grids has been used in various studies (Birch et al., 2000; Chow et al., 2005) and has shown some advantages to the more commonly used square tessellations (Jurasinski and Beierkuhnlein, 2006; Birch et al., 2007). In this study, the hexagonal tessellation was chosen for three reasons: (1) the visual area from the research vessel is circle-shaped, thus hexagonal cells offer a better representation than square or triangular cells; (2) due to its shape, hexagonal cells have a closer perimeter-area ratio to a circle, which could potentially reduce the edge effect (Birch et al., 2007); and (3) neighbour cells are all at the same distance, hence there is the same distance between centroids of adjacent cells (Birch et al., 2007). To generate the[iii] raster files, a grid with 294 hexagonal cells (radius = 1 nm) covering the study area was created (Coordinates 42° 14.136′ N – 42° 39.270′ N, 9° 30.000′ W – 8° 46.932′ W). A 1 nautical mile radius was chosen because, given an average speed of 6-8 kn, two consecutive 20-minute samples would be located in adjacent cells. The size and shape of the hexagonal cells were conceived to adapt to both the visual area from the research vessel and the distance covered between each 20-minute sample.

QGIS 2.18 was used to create the raster files. One raster was created to show the presence of common dolphins (hereafter referred to as species map) and nine rasters were created to represent the EGVs (hereafter referred to as biogeographical maps). All rasters had the same size and contained the same number of cells (1000x1000 cells). Additionally, the plugin MMQGIS was used to create the grid with hexagonal cells. Finally, the System for Automated Geoscientific Analyses (SAGA), built in QGIS 2.18, was used to create biogeographical maps. Three different methods were used to create the maps:

Creation of the species map: A boolean raster (with values 0 or 1) was created to show the areas in which common dolphins were present. Cells with a value equal to 1 were those containing common dolphin sightings and cells with values equal to 0 were those in which the presence of the species could not be proven.

Creation of the biogeographical maps for the non-persistent variables: To take into account the variability of the non-persistent variables, the mean of the values measured at each 20-minute samples in a given cell was calculated. This procedure was repeated in all cells containing at least one 20-minute sample. The final biogeographical maps for the non-persistent variables were created by interpolating the centroids of each cell using the inverse distance weighted (IDW) interpolation. IDW is a spatial interpolation method that assumes that values of nearby points are more similar than values of more distant points (Li and Heap, 2008). Hence, it estimates values at unknown locations by giving a heavier weight to closer sampled points (Li and Heap, 2008; Lu and Wong, 2008). IDW is a computational less-demanding method that has been successfully used to predict environmental variables (Li and Heap, 2008).

Biogeographical maps for the persistent variables: The unchanging nature of the persistent variables enabled the use of the 20-minute samples to create high resolution rasters without the need to use the mean values within a grid. The IDW interpolation was used to generate the biogeographical maps for the persistent variables by directly interpolating all 20-minute sample values.

Since both biogeographical and species maps had a square shape, they included information referring to the oceanic environmental conditions and species presence in areas located on land. The clipping tool in the raster menu in QGIS 2.18 was used to cut and exclude the areas of the species and biogeographical maps that overlapped with the land. Rasters were then transformed to Idrisi format using the *raster*, *sp* and *rgdal* packages in RStudio (R Core Team, 2016) to make them suitable for Biomapper 4.0.

2.4. Data analysis

All the biogeographical maps, except for the SSS raster, were normalised using a Box-Cox transformation algorithm (Hirzel et al., 2002). The normalised SSS map contained cells with a small range of values, therefore the original raster was kept for the analysis to avoid complications in the subsequent steps (Hirzel, 2004). A correlation matrix containing all EGVs was then computed using the Pearson correlation coefficient r to check for collinearity. Two variables were considered highly correlated to each other when $|r| > 0.7$ (Dormann et al., 2013). In such case, one of them was removed from the analysis as it was considered to contain redundant information, and the more ecologically relevant EGVs were kept for further analysis (Dormann et al., 2013).

A factor analysis was run to generate a number of uncorrelated factors from the same amount of correlated EGVs (Hirzel et al., 2002). The first factor accounted for the marginality, defined by Basille et al. (2008) as "the difference between the conditions used on average by the species and the conditions available in the study area". Marginality varies between 0 and 1, lower values meaning that the species uses similar conditions that the average available conditions and high values, close to 1, meaning that the species occupies a specific habitat within the study area (Hirzel et al., 2002). The specialisation, which can be considered equivalent to the habitat breadth (Pracca and Gannier, 2008), explains the difference between the species variance and the global variance, and is determined by all factors (Hirzel et al., 2002). Specialisation is difficult to interpret, as it varies from 0 to infinity. However, a value higher than 1 denotes some degree of specialisation (Hirzel et al., 2002).

A broken-stick distribution was used to select the number of factors to be used to create the habitat suitability map (Hirzel et al., 2002). Furthermore, following Hirzel et al., 2006, the geometric mean algorithm was chosen to generate the habitat suitability map, as it does not make any assumption on the species distribution. This method takes into account the proximity of the species points in the environmental space and gives a higher suitability where the species points show a higher density (Hirzel and Arlettaz, 2003). In this context, both marginality and specialisation values were used to calculate a habitat suitability index (HSI), which was later used to create the habitat suitability map (Hirzel and Arlettaz, 2003). The HSI varies from 0 to 100, lower values meaning low suitability and higher values meaning high suitability.

To evaluate the prediction error of the model, a k-fold cross-validation method was used. This method splits the data in several equal-sized sets k and uses k-1 sets as a calibration of the model and the remaining set to validate it (Hastie et al., 2001). This procedure is carried out k times, each of them using a different set to validate the model. In this study a 10-fold cross-validation (k=10) was used (Hirzel et al., 2006). Furthermore, the predictive power of the model was assessed with the Boyce index (Boyce et al., 2002). The index range goes from -1 to 1, positive values showing the consistency of the model with the data set used for its assessment. Likewise, values close to 1 indicate that the calculated distribution differs from a distribution expected by chance (Hirzel et al., 2006).

From the Boyce index, a threshold-based method was developed to evaluate the capacity of the model to predict habitat suitability. To do so, the HSI range was divided into different classes, and for each of them two frequencies were calculated: (1) the *predicted frequency* (P_i), which is the number of evaluation points predicted by the model in each class, divided by the total number of evaluation points; and (2) the *expected frequency* (E_i), which divides the area of a habitat suitability class by the total study area (Hirzel et al., 2006). With this information the *predicted-to-expected ratio* (*P/E*) was calculated for each class. To evaluate the model, the *P/E* ratio was calculated all along the HSI range generating 10 continuous *P/E* curves, one for each of the sets used in the cross-validation process. Three aspects of the *P/E* curves were used to assess the accuracy of the model: (1) the variance among the curves as an indication of the robustness of the model; (2) the shape as the resolution of the model predictions; and (3) the maximum as the deviation of the model from a random expectation (Hirzel et al. 2006). The *P/E* curves were used to generate thresholds to divide the habitat into 4 different classes according to its suitability: unsuitable, marginal, suitable and optimal habitat (Hirzel et al., 2006). In this context, unsuitable habitats represented those areas in which *P/E* ratio was lower than 1. Marginal habitats were defined by *P/E* ratio close to 1. Suitable habitats were described as those areas in which the *P/E* ratio showed an exponential increase, and the areas with the highest *P/E* ratio were considered to represent an optimal habitat.

3. RESULTS:

3.1. Survey effort and presence of common dolphins:

Field work was carried out for 38 months between March 2014 and October 2017. During that period, 273 daily dedicated boat surveys were completed, covering a total distance of 9 417 km and a total of 1 015 hours at sea. During that time, 3 114 20-minute samples were recorded, 91 in presence of common dolphins (Fig. 2).

Depth at which common dolphins were spotted varied between 6 and 935 metres (mean 137 ± 13.54 metres). Of the 91 groups of common dolphins encountered during the study, 79 (87%) were found in waters above the continental shelf (between 50 and 200 metres deep). Another six groups (6.5%) were seen in shallower areas and corresponded to sightings recorded inside the Ría de Arousa, whereas the remaining six groups (6.5%) were spotted in waters above the continental break or beyond (waters deeper than 200 metres). Common dolphin presence was recorded in 55 (18.7%) of the cells of the grid that was created to assess the spatial distribution of the species (Fig. 2).

3.2. ENFA results

In a preliminary analysis, a correlation matrix was generated to assess the collinearity between the EGVs. The matrix showed that five EGVs were highly correlated to each other (Table 2). Therefore, depth, distance to the coast, distance to the 200 metres bathymetry line and SST were discarded for the final analysis and chlorophyll a was kept due to its ecological significance (Pracca and Gannier, 2008; Moura *et al*., 2012). The EGVs used in ENFA were Slope, Aspect, chlorophyll a, tide level and SSS.

Of the five factors created by the ENFA model, the first four were kept for the final analysis and they explained 89% of the total specialisation (total sum of eigenvalues). The first factor explained 100% of the marginality and 16% of the specialisation (Table 3). The scores of each EGVs for this first factor revealed that marginality was mainly influenced by tide level, chlorophyll a and SSS, showing that common dolphin presence was linked to higher tide level, higher SSS and low chlorophyll a. Aspect and Slope had a smaller effect on the marginality. The remaining factors explained the rest of the specialisation. The first specialisation factor (SF1), which accounted for almost half of the total specialisation (45%), showed that common dolphin's habitat choice was mainly influenced by SSS and Aspect (SSS = 0.741; Aspect = 0.615). The remaining specialisation factors revealed some sensitivity to chlorophyll a and SSS (SF2), and chlorophyll a and Slope (SF3). The EGV with the highest influence on the specialisation, when combining all first four factors, was SSS. Overall, marginality and specialisation calculated by the ENFA model were 0.279 and 1.268 respectively, showing that the conditions of common dolphin habitat were similar to the average conditions in the area and that the species can easily adapt to different environmental conditions.

The cross-validation (Boyce index = 0.552 ± 0.2121) and the *P/E* curves showed that the model had a good predictive power. The variance along the *P/E* curves showed a constant increase with the HSI, with a narrower confidence interval for lower HSIs, indicating that the predictive power was more accurate for low suitability areas (HSI < 40) (Fig. 3). Based on the *P/E* curves, the habitat was categorised into 4 different classes: (1) "unsuitable habitat" for HSI values lower than 35; (2) "marginal habitat" for HSI values between 35 and 40; (3) "suitable habitat" for HSI values between 40 and 69; and (4) "optimal habitat" for HSI values higher than 69. The resulting habitat suitability map for the study area is shown in Fig. 4. The map reveals that the rias and the shallower coastal waters in the southern part of the study area were not suitable for the species. Marginal habitat was linked to small specific locations around the suitable habitats. Conversely, the waters above the continental shelf and especially the areas around the 100 metres bathymetry line included the more suitable habitats for common dolphins. Although some areas beyond the continental break included suitable and even optimal habitats for the species, most of the waters deeper than 300 metres were classified as an unsuitable.

4. DISCUSSION:

Knowledge on the distribution of a species has become an important tool to develop effective management and conservation plans (Rodríguez et al., 2007; Marshall et al., 2014). Studies that assess the potential distribution of marine top predators are fundamental in areas such as the northwestern coast of Spain, where these species are highly impacted by human activities (Díaz López and Methion, 2018; Methion and Díaz López, in press). One of the aims of this study was to explore the development of conservation measures for common dolphins by getting a better understanding of their distribution and their habitat use. To do so, a novel approach was designed by combining the use of hexagonal tessellation and ENFA modelling. The hexagonal tessellation provided an adequate adaptation to the sampling effort which, along with the equal distance between adjacent cells, resulted in the development of high resolution species and biogeographical maps, as has been seen in other studies (Zimmerman et al., 1999; Birch *et al*., 2007). Additionally, the ENFA approach proved to be an adequate tool to assess the habitat suitability and the distribution of a cryptic, highly mobile marine species such as the common dolphin, for which reliable absence data is difficult to obtain. Although some authors have stressed that ecological niche models have a lower predictive accuracy when compared to other models based on presence/absence data (Segurado and Araújo, 2004; Tsoar et al., 2007), the cross-validation and the Boyce Index showed the robustness of the ENFA model and its accuracy to predict habitat suitability and distribution (Macleod et al., 2008; Praca et al., 2009; Costa et al., 2013). Furthermore, this study points out the importance of having a large and reliable presence-only data set to achieve trustworthy results. This was confirmed by the *P/E* curves used to validate the model, which showed a stronger accuracy in predicting areas unsuitable for the species (and in which common dolphins were not regularly seen) such as shallow coastal areas or the rias (Pierce et al., 2010; Saavedra et al., 2018).

In this context, the current study provides new information on common dolphin distribution by showing that waters above the continental shelf are an optimal habitat for common dolphins. Additionally, the strong predictive power of the model for areas of low habitat suitability, and more specifically inside and around the rias, confirms that the species does not show a preference for the inlets. The ENFA also shows that some areas deeper than 300 metres, especially in the southwestern part of the study area, include suitable and optimal habitats for the species in concordance with previous studies (Fernández-Contreras et al., 2010). However, this result should be considered carefully, as offshore waters were not monitored as thoroughly as other parts of the study area, due to logistical and geographical constraints. Coupled with previous studies in the area that show a high abundance of common dolphins in waters above the continental shelf (Pierce et al., 2010; Spyrakos et al., 2011; Goetz et al., 2015; Díaz López et al., 2019) and waters deeper than 200 metres (López et al., 2003; Fernández-Contreras et al., 2010), these findings contribute to a more accurate and comprehensive understanding of common dolphin distribution, and provide valuable insights for the species' conservation.

To have a better understanding of the causes influencing the distribution and habitat suitability, several EGVs were included in the analysis. However, the link between EGVs and the spatiotemporal movements of the common dolphin is not a straightforward relationship and it might be affected by the interaction among the different EGVs or the temporal lags between physical and biological processes (Redfern et al., 2006; Pirotta et al., 2011). In this context, the ENFA model showed that tide level was the main factor determining the habitat suitability of the species in waters above the continental shelf and that common dolphins showed a preference for higher tide levels. This relationship might be associated to tidal currents, which are especially important around Sálvora Island (at the entrance of the Ría de Arousa), driving oceanic water towards the interior of the inlet and nutrient-rich waters offshore (Otto, 1975; Pinho et al., 2004). These tidal currents have been found to enhance local primary productivity and promote the aggregation of small fish, attracting marine top predators (Johnston et al., 2005; Lambert et al., 2017; Díaz López and Methion, 2018). Hence, the high speeds of the tidal currents and the enhanced primary productivity linked to them, could act as a mechanism to concentrate common dolphin prey in specific areas close to Sálvora Island. These areas include suitable and optimal habitat for the species according to the ENFA model.

Another EGV showing a high influence on common dolphin habitat suitability was SSS. The importance of areas with a higher SSS may be explained by the gradient that exists between the rias and the open ocean, where the innermost waters of the inlets have a lower salinity due to the freshwater inputs (Prego et al., 1999). The model pointed out that the rias were not a suitable habitat for common dolphins, which showed a clear preference for oceanic waters with higher SSS values. Previous studies have shown that SSS has an influence on cetacean distribution, and can be used as a good predictor for it (Forney, 2000). However, rather than a direct effect, the SSS might be influencing the distribution of common dolphins indirectly, by affecting the distribution of their prey, namely blue whiting (*Micromesistius poutassou*) and, to a lesser extent, Atlantic horse mackerel (*Trachurus trachurus*) and sardines (*Sardina pilchardus*) (Santos et al., 2013, 2014). Indeed, previous findings show that SSS has an influence on the distribution of the different life stages of these species, which have a preference for areas of higher SSS (Abaunza et al., 2008; Miesner and Payne, 2017).

The findings of this study provide reliable insights on common dolphin distribution and habitat preference in coastal waters which, coupled with information on the threats that common dolphins face in the area, can be used to develop effective conservation measures. The results show that the northern area of the Atlantic Island National Park, especially the waters on the western coast of Sálvora Island, includes and borders optimal habitats for common dolphins. Fishing activities within these waters are restricted to artisanal fisheries to ensure a sustainable exploitation of the resources (Ley 15/2002). However, the waters located in the outer perimeter of the park are used by commercial fisheries, which have been shown to have an impact on this small cetacean (López et al., 2003; Fernández-Contreras et al., 2010; Goetz et al., 2014, 2015; Saavedra et al., 2018; Díaz López et al., 2019). Indeed, bycatch in pair-trawlers, gill nets and purse-seines has been documented in the study area, where common dolphins are accidentally caught in approximately 5% of pair-trawler tows, and where 23% of the stranded individuals show signs of interaction with fishing gear (López et al., 2003; Fernández-Contreras et al., 2010; Goetz et al., 2014, 2015; Saavedra et al., 2018). The high number of incidental captures might be related to the intense fishing pressure in the area given that Galicia has the biggest fishing fleet in Spain, consisting of 4 466 fishing vessels at the end of 2017, 10% of which operates in coastal waters above the continental shelf (Surís-Regueiro and Santiago, 2014; Ministerio de Agricultura, Pesca y Alimentación, 2017). Furthermore, a recent study highlighted the spatial and temporal overlap between fisheries and common dolphins, especially in areas above the continental shelf between 125 and 200 metres in depth (Díaz López et al., 2019). This overlap has been confirmed by scientists (Fernández-Contreras et al., 2010; Díaz López et al., 2019) and by fishermen, which tend to avoid areas with higher abundance of common dolphins (Goetz et al., 2014). Consequently, the coastal waters above the continental shelf, which include the suitable and optimal habitats for the species, are also impacted by fishing activities.

This work highlights the importance of understanding the spatial distribution of a species for developing management and conservation plans. Indeed, this study suggests that a reassessment of the dimensions and the protection level of the area surrounding Sálvora Island (which currently covers 23.09 km^2), could improve the conservation of this vulnerable species by reducing the spatial overlap with fisheries. This reassessment would include 4 main steps (Table 4) and should involve the cooperation between different stakeholders and the development of enforcement methods to ensure compliance with the new regulations and effectiveness of the developed measures (Agardy et al., 2010; Redpath et al., 2013). All these measures could minimise the impact of fisheries on common dolphins by reducing the actual fishing pressure in the most suitable habitats for the species and could lead to a decrease in bycatch, which is one of the major threats to common dolphins in the area (López et al., 2002 and 2003; Silva and Sequeira, 2003; Goetz et al., 2014; Saavedra et al., 2018). Furthermore, these measures could lead to a lower conflict with fisheries than other measures previously proposed such as the regulation of fishing hours or seasonal closures (Fernández-Contreras et al., 2010; Goetz et al., 2014). However, further studies would be needed to understand the potential impacts of the suggested measures in local fisheries and in other marine species (e.g., fisheries displacement to other areas).

This study stresses the applicability of SDMs, and more particularly the use of ENFA, as a comprehensive tool to expand the knowledge on the distribution and habitat use of common dolphins and to develop better management and conservation strategies. However, given the widespread distribution of common dolphins and their seasonal movement patterns in the Northeast Atlantic, a joint scientific effort covering the full distribution of the species and the involvement of the different affected stakeholders are needed to ensure that effective management plans and conservation strategies are developed throughout the common dolphin distribution range.

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Table 1

The nine ecogeographical variables (EGVs) used to create the ENFA model, showing the number of 20-minute samples used to calculate them, the mean, the standard error (SE) and the range. In bold letters the EGVs that were kept for the final model.

EGV	Type	Unit	Interpolation method	n	Mean	SE	range
Depth	Persistent	Metres	Points	3114	35	1	0 – 1050
Slope	**Persistent**	**Percentage**	**Points**	**3114**	**0.85**	**0.02**	**0.01 – 30.37**
Aspect	**Persistent**	**Degrees (compass orientation 0 - 360°)**	**Points**	**3114**	**205**	**1.79**	**4 – 359**
Distance to coast	Persistent	Metres	Points	3114	2614	90	2 – 32097
Distance to 200 m bathymetry line	Persistent	Metres	Points	3114	31402	160	44 – 45788
Chlorophyll a	**Non-persistent**	**Parts per thousand**	**Centroids from hexagonal cells**	**2029***	**3.33**	**0.07**	**0 – 17**
SST	Non-persistent	Degrees Celsius	Centroids from hexagonal cells	3017*	16.13	0.04	8.9 – 23.1
SSS	**Non-persistent**	**mg/m^3**	**Centroids from hexagonal cells**	**1389***	**34**	**0.07**	**13 – 36**
Tide level	**Non-persistent**	**Metres**	**Centroids from hexagonal cells**	**3114***	**1.88**	**0.02**	**0.13 – 4.37**

* Maps created from the mean of each surveyed hexagonal cell.

Table 2

Correlation matrix showing the collinearity between the ecogeographical variables EGVs. Two variables were considered highly correlated to each other when |r| > 0.7 (highlighted in bold).

	Depth	Slope	Aspect	Dist coast	Dist 200 m	Chlorophyll a	SST	Tide level	SSS
Depth	1								
Slope	0.167	1							
Aspect	0.155	0.046	1						
Dist coast	**0.917**	0.096	0.171	1					
Dist 200 m	**-0.83**	-0.132	-0.176	**-0.95**	1				
Chlorophyll a	**-0.825**	-0.151	-0.18	**-0.768**	**0.754**	1			
SST	**0.864**	0.125	0.181	**0.873**	**-0.867**	**-0.814**	1		
Tide level	0.282	-0.115	0.032	0.317	-0.225	-0.233	0.237	1	
SSS	0.659	0.111	0.122	0.65	-0.654	-0.689	0.555	0.183	1

Table 3.

Results of the ENFA model showing the scores of each ecogeographical variable (EGVs) in the marginality and the specialisation factors (SF), and the percentage of information explained by each of the factors. The table only shows the four SF that explained 89% of the variability.

EGV	Marginality 16%	SF 1 45%	SF2 16%	SF3 12%
Slope	-0.033	-0.12	0.262	0.534
Aspect	-0.223	0.615	0.286	0.162
Chlorophyll a	-0.494	0.201	-0.643	0.685
Tide level	0.713	-0.133	0.063	0.391
SSS	0.443	0.741	-0.657	0.258

Table 4.

Shows the 4 steps that should be considered for the reassessment of the area protected by the Atlantic Islands National Park west of Sálvora Island to improve common dolphins conservation.

Conservation problem	Measure	Definition	Justification	Parties involved
Overlap between fisheries and common dolphins most suitable habitats	Expansion of the national park	Expansion of the maritime area of the National Park around Sálvora Island to the west, as has already been suggested by other conservation organisations (Aguilar et al., 2009), to include the optimal and suitable habitats for common dolphins.	This expansion would incorporate the areas with the most suitable habitats to the Atlantic Islands National Park, extending the already existing fishing restrictions into the newly created protected area.	The design of the newly created protected area should be the result of a cooperation between marine scientists, fishermen and public administration to reach a satisfactory agreement for the different parties and to develop compensation schemes if needed.
	Designation of a SCI	The designation of the maritime area of the natural park around Sálvora Island (the already existing one and the expansion) as a Site of Community Importance (SCI).	This measures is in agreement with the Habitats Directive, as the area west of Sálvora Islands includes important habitats for common dolphins, which is listed in Annex IV of the directive.	The governments of the different countries are responsible for proposing the designation of SCI to the European Union, according to the Habitats Directive.
	Designation of a SAC	Following the designation as SCI, the designation of this area as a Special Area of Conservation and adding it to the Spanish Network of Marine Protected Areas and Natura 2000 network.	This measure is in agreement with the Habitats Directive which urges governments to promote conservation measures especially in the areas that include important habitats for common dolphin ecology and reproduction.	The governments of the different countries are responsible for proposing the designation of SAC to the European Union, according to the Habitats Directive.

Unspecific legislative framework	Improved legislative framework	The development of a clear legislative framework that unequivocally specifies the fishing pressure that can be exerted in the newly created protected area by establishing the number of fishing vessels allowed to work, the gear that would be allowed, and the fishing quotas.	The fishing restrictions and regulation that currently apply in the maritime area of the Atlantic Islands National Park are scattered in several regional and national Spanish laws and are unspecific about certain aspects. Thus a new, clear and easy to follow legislative framework should be developed.	The different public administrations (local, regional and national) should be responsible for developing this new framework.

Fig. 1. Map showing the study area surveyed in northwest Spain and the 20-minutes samples collected from March 2017 to October 2017. The red boxes with the line pattern show the area of the Atlantic Islands National Park (Cortegada island inside of the Ría de Arousa, Sálvora Island at the entrance of the ria, Ons Islands south from the entrance of the ria and Cíes islands, further south).

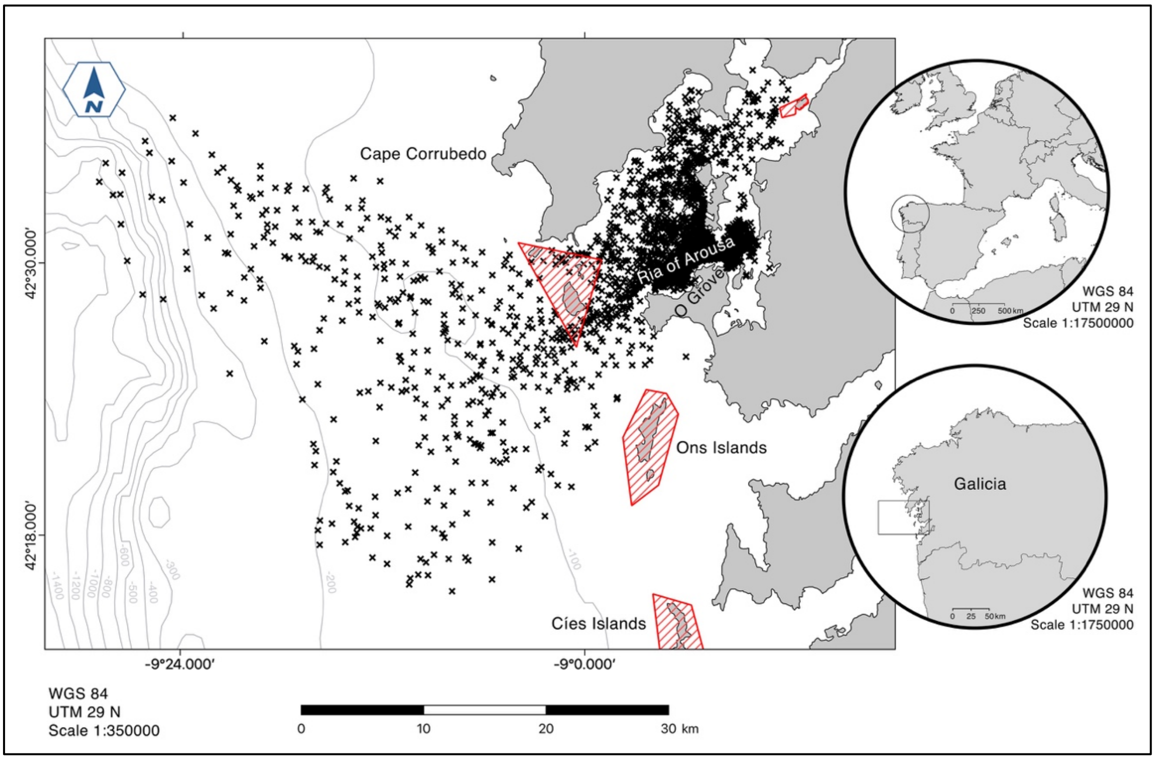

Fig. 2. Map showing the hexagonal grid used to create the species map and the biogeographical maps for the non-persistent variables and the cells with presence of common dolphins.

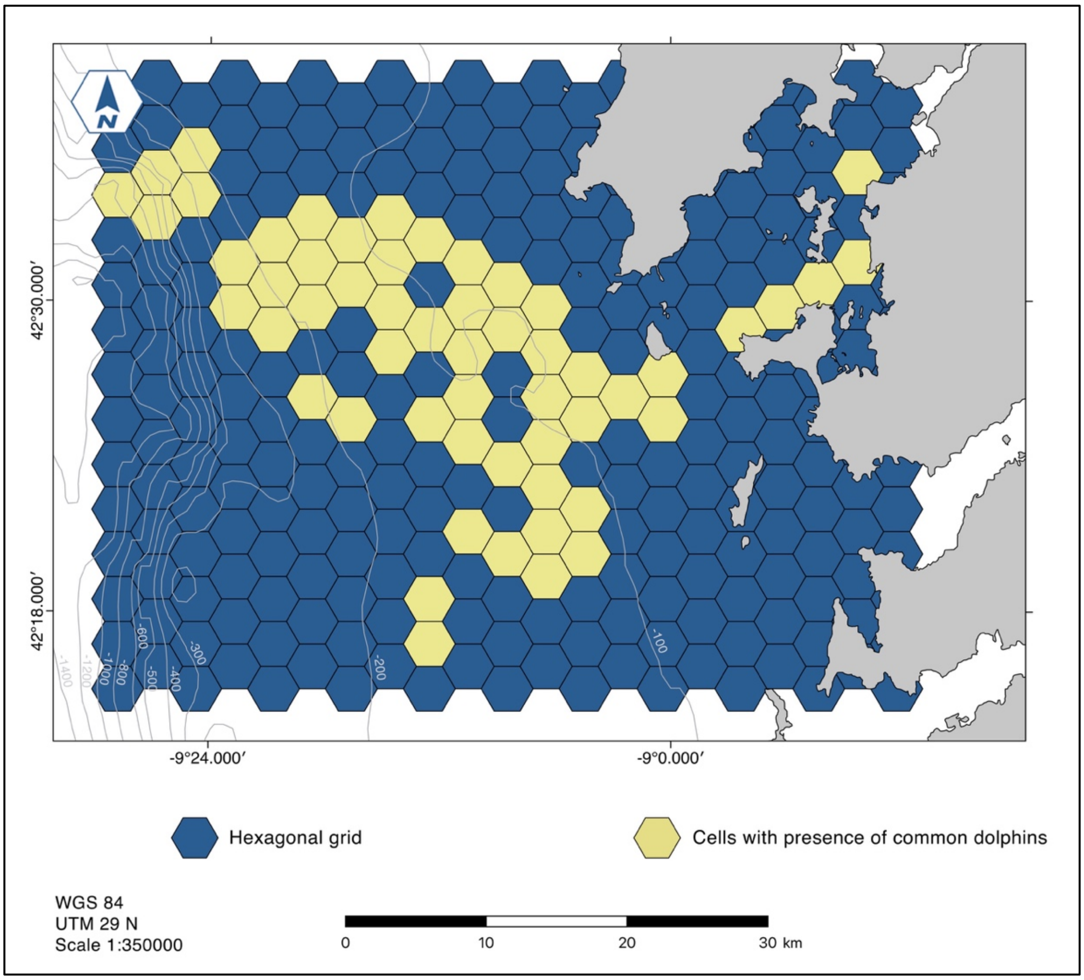

Fig. 3. Showing the mean P/E curves for the model and the 4 habitat suitability classes in which the habitat was categorized.

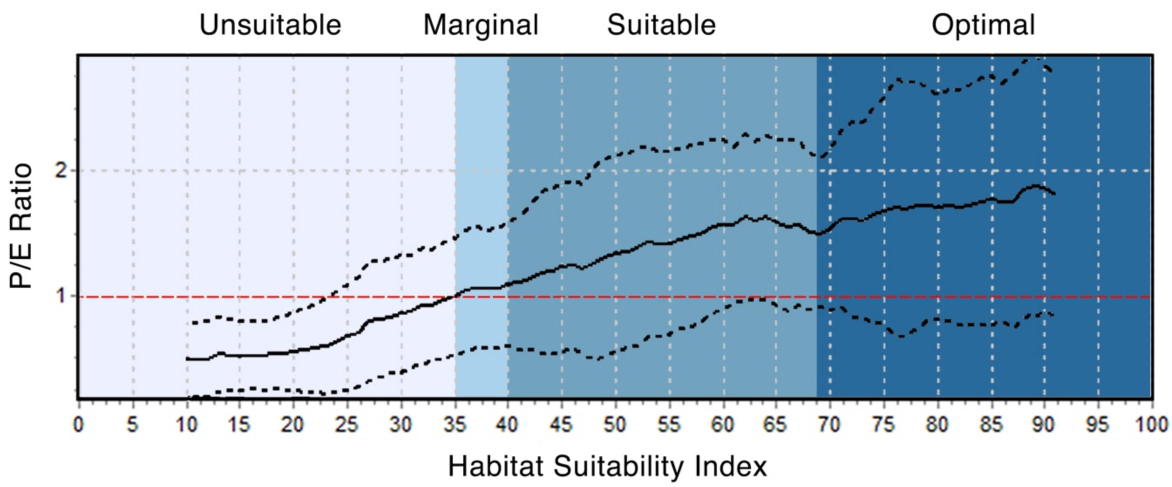

Fig. 4. Common dolphin habitat suitability map in the study area based on the habitat suitability index (HSI) calculated with ENFA. The red areas with the line pattern show the Atlantic Islands National Park, pointing out the overlap and close proximity of the northern island of the national park (Sálvora) to the most suitable habitats for common dolphins.