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Distribution and habitat modelling of common dolphins (*Delphinus delphis*) in the Eastern North Atlantic

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Abstract

*The Eastern North Atlantic (ENA) has many highly productive areas where several species of cetaceans have been recorded, with the common dolphin (*Delphinus delphis*) being one of the most frequently sighted species. However, its spatial and temporal distribution in high seas is poorly known. The study presents the results from 5 years of cetacean monitoring in the ENA (2012-2016) aboard cargo ships that follow the routes from the Continental Portugal to the Macaronesian archipelagos and the Northwest Africa. Common dolphin was the most frequently sighted cetacean with 192 occurrences registered on effort and an overall encounter rate of 0.36 sightings / 100 nmi. The species was distributed in coastal and offshore waters, but absent from Canaries and Cape Verde islands. Statistical "habitat" models were developed to describe and explain the occurrence of sightings of the species: variables affecting detection of dolphins had a small impact and there were clear spatiotemporal distribution patterns, influenced to some degree by environmental variables. Predicted probability of occurrence was highest in coastal waters of continental Portugal and around the Azores. The models, combined with maps of distribution, were useful to identify important areas for the species, which could be the focus of future conservation efforts. Common dolphin presence was related to depth, distance to coast and seamounts, seabed slope, chlorophyll concentration, sea-surface temperature and sea level anomalies; the possible ecological significance of these relationships is explored.*

Keywords: cetaceans; Macaronesia; high seas; spatial distribution; temporal distribution; ecological modelling

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INTRODUCTION

The Eastern North Atlantic Ocean (ENA) includes the four archipelagos of the biogeographic region of Macaronesia: Azores, Madeira, Canaries and Cape Verde. The region has a complex topography including seamounts, hills, banks, abyssal platforms, canyons, and a rugged coastline along European and African continents. Moreover, it is characterized by dynamic oceanographic processes: strong coastal upwelling phenomena, formation of numerous eddies and fronts, and the presence of several Atlantic oceanic currents (Caldeira *et al.*, 2002; Mason, 2009; Sala *et al.*, 2013). This complexity and diversity of habitat conditions plays a major role in the distribution of primary production, and therefore, in the distribution of biomass across the trophic levels of the marine food chain. Cetacean distribution in space and time is generally considered to be shaped by environmental factors that condition prey availability at different spatial and temporal scales (for a review, see Redfern *et al.*, 2006). Nonetheless, when looking at distribution based on observational data, it is necessary to account for factors affecting detectability in order to obtain reliable information (e.g., Pierce *et al.*, 2010). These factors include the conditions of the platform of observation, survey design, state of the weather during the survey, distance to the sighted animal(s), species detected, size of the group, and, ultimately, the ability of the observer to detect and identify the species. In the ENA, at least 36 cetacean species have been recorded, both resident and migrating, in coastal and oceanic areas (e.g., Hazevoet & Wenzel, 2000; Hazevoet *et al.*, 2010; Weir *et al.*, 2010; Carrillo *et al.*, 2010; Alves *et al.*, 2013; Hammond *et al.*, 2013; Weir & Pierce, 2013; Goetz *et al.*, 2014; Silva *et al.*, 2014; Berrow *et al.*, 2015; Correia *et al.*, 2015; Dinis *et al.*, 2016; Djiba *et al.*, 2015; Tobeña *et al.*, 2016; Jungbult *et al.*, 2017; Dinis *et al.,* 2017; Alves *et al.*, 2018; Alves *et al.*, in press). All cetaceans in European Union (EU) waters receive protection under the Habitats Directive (Council Directive 92/43/EEC) and the Marine Strategy Framework Directive (MSFD, Directive 2008/56/EC). These directives demand both monitoring of cetacean population status (e.g. distribution, abundance) and enactment of conservation measures if population status is found to be unfavourable (see Santos & Pierce, 2015, for a discussion of the application of the MSFD to cetaceans). Marine conservation in the ENA is also covered by several international organizations and agreements, including the International Council for the Exploration of the Sea (ICES, http://www.ices.dk/) the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR, http://www.ospar.org/), the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS) and the Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and contiguous Atlantic area (ACCOBAMS).

In the ENA, common dolphins (*Delphinus delphis* Linnaeus, 1758), are among the most frequently sighted cetacean species (Correia *et al.*, 2015; Goetz *et al.*, 2014; Silva *et al.*, 2014; Hammond *et al.*, 2013; Tobeña *et al.*, 2016; Jungblut *et al.*, 2017; Alves *et al.*, 2018). Their distribution and habitat characteristics have been modelled in relation to geographic, physiographic, oceanographic and fishing-related variables, and several studies have identified well-defined habitat preferences related to the abundance of prey, for example productive areas (i.e., upwelling regions), with low to medium sea-surface temperatures, mostly coastal and shallow but often deeper waters, and/or areas that concentrate their preferred prey (e.g., Cañadas & Hammond, 2008; Pierce *et al.*, 2010; Moura *et al.*, 2012; Goetz *et al.*, 2014; Correia *et al.*, 2015; Halicka, 2016; Tobeña *et al.*, 2016). Their apparently patchy distribution suggests that common dolphins, although widely distributed, have a well-defined habitat and they may be dietary specialists in the sense of feeding on schooling fish (Moura *et al.*, 2012; Marçalo *et al.*, 2018). Common dolphins usually target high energy prey and/or locally abundant pelagic schooling fish and some of their prey have high commercial value, such as sardines, blue whiting, anchovy, sprat and horse mackerel, which often results in interactions of feeding dolphins with fisheries (e.g., Meynier *et al.*, 2008; Santos *et al.*, 2013; 2014; Marçalo *et al.*, 2018). In fact, negative impacts of fishery bycatch mortality and/or prey depletion due to overfishing of common dolphin prey have been widely reported. For example, in the Bay of Biscay, bycatch has been suggested to have reached unsustainable levels, inconsistent with the maintenance of common dolphin populations at a favourable status (Peltier *et al.*, 2016). In the Mediterranean, overfishing is probably one of the causes for the estimated 50% decline in abundance of this species in the last 45 to 35 years, leading the Mediterranean sub-population of common dolphins to be listed as endangered in the IUCN Red List of Threatened Species (Piroddi *et al.*, 2011; Cañadas & Vázquez, 2017).

Common dolphin occurrence in coastal areas of the ENA (Weir *et al.*, 2010; Moura *et al.*, 2012; Hammond *et al.*, 2013; Weir & Pierce, 2013; Goetz *et al.*, 2014; Djiba et al., 2015) and around the islands of Macaronesia (Hazevoet & Wenzel, 2000; Carrillo *et al.*, 2010; Silva *et al.*, 2014; Halicka, 2016; Tobeña *et al.*, 2016; Alves *et al.*, 2018) is reasonably well reported, but in the high seas, where logistic constraints impede systematic surveys for cetacean monitoring, data are still lacking and spatial and temporal distribution of this species is poorly known (Correia *et al.*, 2015; Jungbult *et al.*, 2017). This baseline knowledge is fundamental to further assess the conservation status of the species and the impacts of human activities on its distribution, and to efficiently manage the status of common dolphins in the North Atlantic. In 2012, a monitoring project started collecting cetacean occurrence data in the ENA using cargo vessels as observation platforms of opportunity (OPOs) along routes from the Continental Portugal to the Macaronesian archipelagos and Northwest Africa (Correia *et al.*, 2015). In the present study, the occurrences recorded in the surveys from 2012 to 2016 were used to analyse the spatial and temporal distribution of common dolphins. Four different models were developed to describe (i) the influence of detectability factors (observation effects model), (ii) dolphin distribution across space and time (spatiotemporal model), (iii) the influence of topographic and oceanographic features (environmental model), and (iv) a combination of all the above (final habitat model). We evaluate the usefulness of data collected from surveys on OPOs to develop habitat models and to identify important areas for conservation across a wide area of ocean. The results are expected to contribute to status evaluations by international organizations that have responsibility or interest in the conservation of cetaceans, and to support legal instruments for the management of the area.

MATERIALS AND METHODS

Study area

As part of the CETUS Project (http://www.cetusproject.com/), data on cetacean occurrence were collected within the ENA. The study area included the coastal waters of Mainland Portugal and of Northwest Africa, the waters in between (oceanic) and within the Macaronesian archipelagos: the Azores and Madeira (Portugal) and the Canary (Spain) and Cape Verde islands (Figure 1).

From 2012 to 2016, surveys for cetacean occurrence took place during 99 round-trips aboard cargo ships belonging to TRANSINSULAR, a Portuguese maritime transport company. The cargo ships were used as OPOs and each followed one of three different routes, all starting and ending in Mainland Portugal, to the Azores, Madeira and Cape Verde respectively, with a total of 15 ports visited, 10 of them routinely (Figure 1).

Most surveys were conducted during summer months (from July to October) with favourable weather conditions for cetacean sampling, especially considering North Atlantic offshore areas where sea conditions are generally rough during the rest of the year (Table 1).

Data collection

IN-SITU

For each route, two observers were trained in use of survey protocols by the project team and then boarded TRANSINSULAR cargo ships to visually monitor cetaceans throughout the trips. Travel speed generally varied from 11 to 16 knots. Surveys were performed from sunrise to sunset, whenever weather conditions were favourable (with sea state and wind speed up to 4, on the Douglas and Beaufort scales respectively, and visibility over 1 km) and the ship was sailing outside the ports. Surveys stopped occasionally during periods when observers were not allowed at the observation stands, i.e., during safety drills, cleaning of the deck or manoeuvres. Observers stood in the navigation bridge and wings of the bridge, at an approximate height of 20 metres above sea level (depending on the loading of the ship) and searched for cetacean presence through 180 degrees, centred on the ship's heading, with and without binoculars (magnification of 7 x 50 mm, with scale and compass). When cetaceans were sighted, the species was identified and number of individuals recorded. When it was not possible to determine the exact number of individuals, a minimum and maximum number of animals was recorded, as well as the most probable number of individuals according to the observer´s perception (best estimate). Besides cetacean occurrence, data on the presence of other top predators (e.g., turtles, sharks, tuna), as well as information on weather conditions and marine traffic, were collected. For more details on sampling protocol, see Correia *et al.* (2015). Since the present paper is focused on common dolphins (*Delphinus delphis* Linnaeus, 1758), results for other species will be presented elsewhere.

REMOTE SENSING

For the statistical habitat modelling, in addition to weather conditions and spatiotemporal variables needed for both observational and spatiotemporal models, habitat variables were derived from satellite data at several temporal and spatial scales (see Table 2). Slope was derived from bathymetry data. For distance to seamounts, topographic features classified as seamounts, banks, hills, ridges and rises in GEBCO (GEBCO 2017) were delimited, using contour lines created every 50m, and defining a polygon from the outermost closed contour line around the geographic location of the top of the features. Then, the distance from the base of the seamounts and from the coastline (distance to coast) to the sightings was calculated. Both slope and distances were computed using ArcGIS 10.5 (ESRI 2016).

For dynamic variables, satellite data were used. Chlorophyll-a and sea-surface temperature are ocean products derived from the satellite MODIS – Aqua Mapped data from NASA (NASA, 2017). The algorithms return the near-surface concentration of chlorophyll-a (from in situ remote sensing reflectance) and temperature (from measured radiances). Both variables were extracted at two different temporal and spatial scales. Chlorophyll-a was extracted for the calendar month and week in which the sightings occurred but also with four different time lags (one and two weeks and months of lag). For altimetry, the mean sea level anomalies were obtained from Ssalto/Duacs multimission altimeter products provided by AVISO (AVISO, 2017). The sea level anomalies are sea-surface heights computed with respect to a twenty-year mean profile (1993-2012). When assembling data for sea level anomalies, delayed products were available only until 5^{th} of May, 2016 and, as a consequence, near-real time products were used for July-October, 2016. Near-real time final products become available six days after the date of measurement, but are less precise than delayed products, which become available around two months after collection, having been re-analysed and re-processed (AVISO, 2017). For this variable, weekly and monthly resolutions were computed by averaging daily products.

Data analysis

Total and on effort sightings of common dolphins per season of survey and route were computed, as well as the survey effort. On effort sightings are those recorded during survey effort, while total number includes off effort sightings recorded opportunistically. The group size (minimum, maximum, mean and standard deviation values) was accessed from the recorded best estimate for the number of individuals in the group (Table 1). For the remaining analyses, an individual sighting was used as the sampling unit, regardless of the group size. Encounter rates were computed as the total number of sightings on effort per 100 nautical miles (nmi) surveyed, for each season and route. Then, the spatial and temporal distributions of common dolphin occurrences were analysed for the entire study area (considering data from the three routes), computing geographical positions and monthly variation of sightings, survey effort and encounter rate.

Statistical modelling was performed using Generalized Additive Models (GAMs), which have been widely used to describe cetacean distribution and habitat characteristics. An approach based on used/available habitat was chosen (Pearce & Boyce, 2006; Elith & Leathwick, 2009; Correia *et al.*, 2015), with used (common dolphin sightings on effort) and available (survey route) habitat points combined to generate a binary (1,0) response variable. The set of available points was created as in Correia *et al.* (2015), through the creation of equidistant points (every 2.5 nmi) along all effort tracks. Using this methodology guarantees that areas that had a higher survey effort are given more points of available habitat, hence, survey effort is being taken into account in the models. The values of the variables to use as predictors in the modelling process were extracted from the set of used and available points (Table 2). For oceanographic variables, the pack of tools for ArcGIS, Marine Geospatial Ecology Tools (MGET) (Roberts *et al.*, 2010) was used.

Prior to modelling, Pearson correlation between explanatory variables was computed to avoid using highly correlated variables in the same model (threshold of 0.75) (after Marubini *et al.*, 2009). Distance to coast and depth were the only pair of variables highly positively correlated. Since both were of interest, a GAM model was fitted, with depth as predictor and distance to coast as response variable, and both depth and the residuals of this model were used as predictors in the common dolphin models (see Smith *et al.*, 2011). Moreover, multiple correlation among explanatory variables was assessed through the Variance Inflation Factor (VIF, with a threshold of 3) (Zuur *et al.*, 2010). After replacing distance to coast by the residual distance as described above, all remaining variables had VIF values <3 and no additional variables were removed.

A binomial distribution was assumed for the response variable and a maximum of four splines was used (k-fold set to 4) to limit the complexity of smoothers describing effects of explanatory variables. Model fitting mainly involved backward selection, starting from an oversaturated model (Quian, 2009; Viddi *et al.*, 2010; Correia *et al.*, 2015). However, forward selection was undertaken when choosing between the different scales of the oceanographic variables (and different time lags for chlorophyll). Interactions between spatial and temporal variables were also explored in the fitting process to account for main and interaction effects: interaction between latitude with longitude and between year with day of the year. This was done by including these pairs of variables in two dimensional smoothers and visualising the results as surface plots (in this case, the k-fold was set to 16 as to account for the interaction effect, i.e., four times four).

Following Correia *et al.* (2015), and to account for varying dolphin group size, a weight parameter was included in the models, corresponding to the best estimate of animals sighted for each observation. Given the wide range of group size and high uncertainty of the estimations, weights were attributed in categories: a small group – from one to five animals (weight = 1); a medium group – from six to 20 animals (weight = 2); a large group – more than 20 animals (weight = 3). A weight of 1 was set for points of available habitat.

Best models were selected by using the Akaike Information Criterion (AIC) as a measure of goodness of fit, choosing the model with the lowest AIC value at each step of the model fitting process, i.e. comparing otherwise identical models with or without a specific explanatory variable. If the difference in AIC values between two models was less than 2, a Chi-squared test was applied. Whenever differences between AIC values were not statistically significant (based on δAIC >2 or the chi-square test result), the simplest model was maintained (following the principle of parsimony, e.g. Burnham & Anderson, 2002). Finally, at the end of the modelling process, the models were evaluated by creating two random subsets of data: fitting and evaluating sets (75% and 25% of the data, respectively). Prediction power of the models was determined using the Area Under the Curve (AUC) metric of the Receiving Operator Characteristic (ROC) curve (Beck & Shultz, 1986).

Four different models were developed, three of these to specifically evaluate, respectively (i) variables affecting cetacean detection (observation effects model), (ii) spatiotemporal variation (spatiotemporal model) and (iii) habitat preferences (environmental model). Model iv, the final habitat model, used a combination of all the variables tested (Table 2) and was then used to predict probabilities of common dolphin occurrence at the set of used/available points along the routes. Prediction was done using all the original data values for explanatory variables. Finally, predicted probabilities of dolphin occurrence at the points were represented in a map.

Maps were created in ArcGIS 10.5 (ESRI 2016) using a Mercator projection (EPSG: 4326), graphs in Microsoft Excel 2016 and statistical modelling was carried out using R (R Development Core Team 2012) with R Studio.

RESULTS

Survey effort

Most of the survey effort was during summer months, from July to October. A total of 2073 sightings was collected and 26 species identified (at least to genus), with 17 species occurring along the Madeira route, 11 along the Azores route and 25 along the Cape Verde route. Sighted species included baleen whales, toothed whales, dolphins and porpoises, with most sightings being of dolphin species. With a total of 25475 nmi surveyed, the route to Madeira was the most sampled, being surveyed since 2012 (Table 1). Survey effort was heterogeneous across the sampled transect with some gaps due to periods of bad weather conditions as well as areas crossed during night time (Figure 2).

Spatiotemporal distribution of common dolphins

Common dolphin (*Delphinus delphis* Linnaeus, 1758) was the most frequently sighted species (283 sightings, approximately 14% of the all species total), present over a wide latitudinal range, but mostly sighted in northern latitudes within the sampled area, with fewer occurrences south of Madeira island (Table 1 and Figure 2).

There were 192 on effort sightings of common dolphins, giving an overall encounter rate of 0.36 sightings / 100 nmi (Table 1). Common dolphin groups varied in size between one and 2500 animals and encounter rates (by route and by year) ranged from 0.28 sightings / 100 nmi (2012 along Madeira route and 2015 on the Cape Verde route) to 0.54 sightings / 100 nmi (2016 on the Azores route) (Table 1). The largest group, of 2500 animals, was recorded off Dakar, in 2015 (Figure 2).

The highest monthly number of common dolphin sightings on effort (20) was in August 2016, while the highest monthly encounter rate (0.73 sightings / 100 nmi) was recorded in October, 2013, with 10 on effort sightings over 1370 nmi surveyed. No common dolphin sightings were registered in the months with the lowest survey effort (February, March and December, 2016) (Figure 3).

Modelling

Of the three initial models, the model fitted for observation effects had the lowest deviance explained (4.11%) and AUC (0.689), while the spatiotemporal model had a slightly higher deviance explained (16.5%) than the environmental model (15.5%). The final habitat model had the highest deviance explained (22.3%) and included variables from all the three models above (Table 3).

All the three variables tested, namely sea state, wind state and visibility, contributed to the observation effects model. Sea state had a positive effect over the range Douglas 2 to 4, visibility had an overall positive influence, albeit with a negative effect apparent at intermediate visibilities (range 7 to 8), and wind-state had a negative influence over the range Beaufort 1 to 3 (Figure 4).

The spatiotemporal model included latitude × longitude and year × day effects (i.e. main effects and interactions). There were positive effects at several different geographical locations within the surveyed area: northern latitudes with eastern longitudes, corresponding to the proximities of the continental Portugal; northern latitudes with western longitudes, corresponding to Azores region; and a smaller peak at southern latitudes with eastern longitudes, along the African coast. As for the temporal variables, the surface of the year × day of year plot varies along the day of year axis with the same pattern seen across all years. A peak is observed in the beginning of the survey season (July), sightings rate decreasing thereafter and with a smaller peak at the end (October) (Figure 5).

The environmental model included seven environmental variables: depth, residuals from the model of distance to coast versus depth, slope, distance to seamounts, chlorophyll concentration, sea surface temperature and mean sea level anomaly. Depth had an almost linear negative correlation with common dolphin occurrence, i.e. there was a lower probability of sightings over deeper waters. As for the residuals from the model of distance to coast versus depth, GAM results indicate that, for a given depth, there is a positive influence of proximity to coastal areas. In relation to seabed slope, there was a peak in sightings probability at approximately five degrees of slope, with predicted dolphin presence then decreasing over steeper slopes. Distance to seamounts had a negative effect up to 300 km and then a positive effect towards areas most distant from seamounts. Both chlorophyll and sea-surface temperature had a broadly negative effect, while for mean sea level anomaly there was a negative correlation between 0.07 cm and 0.15 cm but also a probable positive correlation at higher anomaly values (where, however, the confidence interval is wide). While sea-surface temperature and mean sea level anomalies had the highest explanatory power at the finest spatial and temporal resolutions (8-day for both and 4 km for sea-surface temperature), chlorophyll presented a strong relationship with sightings at the lowest resolution, both spatially and temporally, and with no lags (Figure 6).

The final habitat model, where all the variables were tested during the fitting process, included ten variables with two interactions among variables, namely the spatial (latitude with longitude) and temporal (day of the year with year of survey) variables. By introducing the dynamic variables, chlorophyll and sea-surface temperature, the total number of observations decreases (from 192 to 165), and consequently the number of available habitat points also decreases, as these variables were collected from satellite data and presented several data gaps (Table 3). While combining all predictors, the effects illustrated by the smooth curves for the variables included remain similar to their forms in the previous models. Dolphin presence was negatively and linearly related to chlorophyll concentration. The relationship between sightings and depth was approximately linear and also negative. The other variables had non-linear fits, with more complex relationships with the response variable. In general, probability of common dolphin detection was highest with low wind speed (low values on the Beaufort scale) and very good visibility. Common dolphin occurrence was more likely in areas further than 300 km from seamounts and at locations of intermediate and high positive sea level anomalies. Occurrence varied spatially (with peaks in Portuguese and African coastal areas and Azorean islands) with a relatively consistent seasonal pattern over the years of the survey (increase in the beginning of the season and small peak at the end) (Figure 7).

When mapping probability of occurrence predicted by the final GAM habitat model, at the set of available and used points along the route, two main areas stood out as having the highest values for predicted probability of common dolphin occurrence (28% to 47%): coastal continental Portugal and the Azores archipelago. The areas of Madeira island and in the open ocean close to continental Portugal and in front of the Nouadhibou port in Mauritania had intermediate probabilities of dolphin occurrence (10% to 28%) (Figure 8).

DISCUSSION

This study presents the results from a 5-year data set on common dolphin (*Delphinus delphis* Linnaeus, 1758) occurrence from systematic surveys for cetacean monitoring in the ENA, with a great amount of effort carried out along a wide latitudinal range of about 30º latitude, mostly in poorly surveyed areas such as the high seas. Survey effort was concentrated in summer months, which is very common in marine surveys dependent on weather conditions (Redfern *et al.*, 2006; Kaschner *et al.*, 2010; Kaschner *et al.*, 2012). Hence, results here presented reflect common dolphin distribution mainly for this period and few conclusions can be drawn for the remaining months of the year.

Common dolphin was the most frequently encountered species, accounting for 14% of the sightings across 26 species. This species has been reported as being among the most abundant in the area, however most studies present data mainly for coastal areas and islands (Goetz *et al.*, 2014; Silva *et al.*, 2014; Hammond *et al.*, 2013; Tobeña *et al.*, 2016; Alves *et al.*, 2018). On the contrary, the present study sampled mostly areas in the high seas. The biggest group of common dolphin, comprising approximately 2500 individuals, was recorded off Dakar in 2015. Large pods of dolphins have been registered previously in the coastal areas of Northwest Africa

(Bowman Bishaw Gorham, 2003; Camphuysen *et al.*, 2012; Weir *et al.*, 2014; Djiba *et al.*, 2015). The group size was highly variable, which is consistent with published results for coastal areas (e.g., Djiba *et al.*, 2015), islands (e.g., Alves *et al.*, 2018) and high seas (e.g., Correia *et al.*, 2015). Group size has been correlated with the water depth and, in the case of common dolphins, larger pods, frequently with calves, often occur closer to the coast (Cañadas & Hammond, 2008).

Spatially, common dolphin occurrences were most frequently registered over the shelf of continental Portugal and around the Azores and Madeira islands. There were also sightings along the entire Madeira route, which may be a consequence of higher survey effort but also an effect of the complex topography (Schlacher *et al.*, 2010; Correia *et al.*, 2015). Along the routes to the Azores and Cape Verde, there were areas with a total absence of sightings. No sightings of common dolphin were recorded in the Canaries and Cape Verde archipelagos. Our results for the Canaries are consistent with those from Carrillo *et al.* (2010) who reported the seasonal presence of common dolphins in the Canary Islands from December to May, the species being absent from June to November.

The year to year variation in common dolphin encounter rates did not present any clear pattern, which may relate to the spatial heterogeneity of survey effort. In fact, encounter rates peaked in different seasons in different years. In 2016, no encounters were registered in the months of February, March and December, but during these months only the route to Cape Verde was monitored and effort was very low.

Putative explanatory variables were chosen for the modelling process according to the effects they may have on the presence of common dolphins (based on the literature) but also reflecting availability. Observation effects were modelled to test whether the weather conditions likely to affect detection of dolphins strongly influenced the models. While detectability factors are not always included or tested in habitat modelling, their inclusion should provide more reliable results (Pierce *et al.,* 2010). While the variables tested did significantly affect the probability of seeing common dolphins, the observational effects model (as might be expected) had the lowest deviance explained of all the models (4.11%). Contrary to what was expected, sea state was positively correlated with common dolphin occurrence with probability of sighting increasing with higher wave height, at least in the range Douglas 2 to 3. This is probably due to the fact that common dolphins tend to surf down the leading edge of waves (possibly to save energy) and thus may be visible at the surface for longer if the waves are higher and wider. Nonetheless, this variable was then excluded from the final habitat model as it did not significantly affect common dolphin presence when considering the effects of the remaining predictors. Although weather conditions affect the detection of cetaceans which in turn influences model results (Pierce *et al.* 2010), in this case, observation effects had a very low explanatory power; hence deviance explained in the final model is mainly related with the other predictors.

The spatiotemporal and environmental models had similar values of deviance explained, 16.5% and 15.5% respectively, likely to a large extent capturing the same variation since the best final model explained only 22.3% of deviance. Some habitat variables were excluded from the best final model while geographic location and temporal variables (days and years) were retained, presumably thus accounting for the effects of other habitat variables not being considered (Elith & Leathwick, 2009; Pirotta *et al.*, 2011; Spyrakos *et al.*, 2011; Correia *et al.*, 2015). Over three-quarters of the variation in presence remains unexplained. In part this may be because relevant habitat variables were not included but it is also likely that many of the observed animals were travelling through less-preferred habitat.

In general, common dolphin probability of occurrence was higher in continental regions (continental Portugal and African coast) and in the area of Azores. As for seasonality, there seems to be a higher probability of occurrence at the beginning and the end of the survey season (July and October). However, this temporal trend should be interpreted with caution as there was substantial temporal heterogeneity in survey effort, which may be a source of noise in the analysis. If occurrence really is lower in the middle of the survey season, the question is whether this indicates animals moving out of the survey area (or at least away from the survey trackline) or a change in behaviour (e.g. aggregation, surfacing or response to boats). Nevertheless, the surface in the temporal perspective plot shows that common dolphin presence varies through the days of the year, with a pattern that remains relatively constant between years, pointing to a seasonal pattern. Seasonality of common dolphin occurrence in the different archipelagos of Macaronesia has been reported, in general, with higher abundances in cold months and a negative tendency during the summer months: in Madeira (Halicka, 2016; Alves *et al.*, 2018), Azores (Silva *et al.*, 2014; Tobeña *et al.*, 2016) and in Canary Islands (Carrillo et al., 2010). The decrease of abundance in summer months is consistent with results presented here.

For the environmental variables, different spatial and temporal scales were tested. It has been shown that spatial and temporal scales affect model results and it is important to understand at which scale the impacts of the variable are significant for the presence of the species (Fernandez *et al.*, 2017; 2018; González *et al.*, 2018). Some of the variables included in the environmental model were dropped from the final combined habitat model during the fitting process. This probably reflects the fact that their effects are already explained by spatial and temporal variables and thus does not mean they are unimportant. However, depth, distance to seamounts, chlorophyll and sea level anomalies remained statistically significant in the final habitat model, increasing the overall deviance explained and having a clear influence in the spatiotemporal patterns.

Depth had an almost linear negative correlation with common dolphin presence. In the environmental model, the residual effect of the distance to coast (after taking depth into account) is negative, i.e. there is a preference for coastal waters. However, in the final habitat model this effect is probably being captured by longitude. A preference for shallower and coastal waters has been reported for common dolphins in several different studies, a result most likely due to the distribution of their preferred prey (Cañadas & Hammond, 2008; Meynier *et al.*, 2008; Stockin *et al.*, 2008; Moura *et al.*, 2012; Santos *et al.*, 2013; 2014; Correia *et al.*, 2015; Alves *et al.*, 2018), although strictly speaking we cannot prove whether diet choice follows from habitat choice or vice versa. Another suggestion for the coastal distribution is the presence of calves within the group (Cañadas & Hammond, 2008; Stockin *et al.*, 2008; Alves *et al.*, 2018). However, since this information was not collected in the present study, such a relationship could not be investigated. Most survey effort in previous studies was coastal, so the preferences of common dolphins could be reflecting sampled rather than preferred areas; in the present study, this is not the case as most effort was in deeper, offshore waters.

Although seamounts have a positive effect in cetacean presence, especially in the high seas where these structures act as oases of productivity in rather oligotrophic waters (Schlacher *et al.*, 2010), they did not seem to strongly influence common dolphin distribution. In fact, the model results indicate the highest probability of occurrences furthest from the seamounts (more than 300 km distance), which probably relates to the preference for coastal areas that are located furthest from the seamounts.

Sea surface temperature acts as a good indicator of upwelling phenomena that are characterized by the cold productive waters at the surface (Caldeira *et al.*, 2002; Mason, 2009). In the environmental model, an increase in sea surface temperature negatively affects common dolphin presence, pointing to a preference for colder waters. The ENA is characterized by strong coastal upwellings (Caldeira *et al.*, 2002; Mason, 2009), that are characterized by colder surface waters. This may explain the apparent preference for colder waters. The preference of common dolphins for more productive areas associated with strong upwellings has been reported before, as well as a tendency to prefer colder waters rather than warmer (sub-) tropical waters (Cañadas & Hammond, 2008; Stockin *et al.*, 2008; Jefferson *et al.*, 2009; Moura *et al.*, 2012; Halicka, 2016). However, when including all the other variables, the sea-surface temperature does not significantly affect common dolphin distribution. This is probably because the sea-surface temperature pattern in the area is related to latitude, with a decrease of temperature from north to south, and distance to coast, with an abrupt decrease of temperature during coastal upwellings.

The surveyed area is highly dynamic and habitat is influenced by several current systems (Caldeira *et al.*, 2002; Mason, 2009). The sea level anomalies reflect this dynamism, probably not fully captured by spatial and temporal variables, and are related to productivity, being affected by upwelling and downwelling phenomena and currents that aggregate or disperse prey (Davis *et al.*, 2002; Baird *et al.*, 2011; Robinson, 2011). Two different temporal scales were tested for the altimetry data, with the 8-day resolution leading to the model with highest deviance explained. The fit indicates that common dolphin presence is more strongly affected at a weekly than a monthly scale, probably due to the high dynamism in the area. This also means that models would probably benefit from a better spatial resolution for altimetry, as the one available is rather low (0.25 degrees, approximately 28 km). In the study area, there is a complex relationship between sea level anomalies and common dolphin presence, with a decrease in probability of occurrence at intermediate positive anomalies and an increase at more highly positive anomalies. This complex relationship may however indicate overfitting in the model.

In the case of the chlorophyll concentration, different temporal lags were also tested, besides the different spatial and temporal scales. The rationale is that chlorophyll is a proxy for productivity and there is a temporal) lag (and possibly also spatial displacement) between chlorophyll blooms and high abundance of common dolphin prey (Frederiksen *et al.*, 2006; Grémillet *et al.*, 2008). Nonetheless, and contrary to the result for sea-surface temperature and altimetry, the chlorophyll had the highest explanatory power at the lowest resolution, both spatially and temporally, and with zero lag. Chlorophyll negatively affected common dolphin presence, contrary to what was expected (Cañadas & Hammond, 2008; Moura *et al.*, 2012; Halicka, 2016; Tobeña *et al.*, 2016). However, the influence of chlorophyll reflected in these results has to be interpreted with caution, partly due to the wide confidence limits around the fitted line but mostly because, as with all the explanatory variables, we are describing partial effects, once effects of all other variables in the model have been taken into account. Also, most of the survey is in the high seas, comprising mostly oligotrophic areas, with a low representation of effort in coastal areas which leads to a highly heterogeneous distribution of records within the range of chlorophyll values. In previous studies that reported positive relationships between chlorophyll and common dolphin presence, survey effort was mostly concentrated in coastal areas, thus providing a wider range of chlorophyll values, making this a good proxy for productivity (Cañadas & Hammond, 2008; Moura *et al.*, 2012; Halicka, 2016; Tobeña *et al.*, 2016). However, in this study, a wide range of depth values was sampled while the surveys passed through mainly oligotrophic waters which resulted in a small range of chlorophyll values sampled, hence depth being a better proxy for areas of upwelling (i.e., more productive areas). Moreover, timings of the chlorophyll blooms vary across the area and common dolphin distribution may not be affected by production at certain times of the year, or in certain areas where other factors are more important. Hence, although the inclusion of chlorophyll concentration improves the overall model result, it is not very useful for the ecological interpretation of the distribution when working over such a wide area. To test the effect of chlorophyll, models would probably perform better when working in narrower areas and with a more homogeneous effort across the range of available chlorophyll values.

Maps of the predicted probabilities along the routes illustrate the model results, highlighting the areas where sighting probabilities reach the highest values: coastal continental Portugal and the Azores archipelago, with slightly lower probabilities in Madeira and in the open-ocean areas close to continental Portugal and in front of Nouadhibou port in Mauritania.

This study shows that common dolphins have core areas of occurrence, thus supporting the idea that the species is more of an ecological specialist than a generalist (Moura *et al.*, 2012; Marçalo *et al.*, 2018). The explanatory power of the models developed was relatively low (under 25%) and, in fact, we have to be realistic about how much we can expect a model to explain about the distribution of a highly mobile species in such a wide area. Moreover, we are grouping animals that are potentially using the area for different purposes (e.g., foraging or travelling). Also, we have to be aware that cetaceans spend a great amount of time underwater so that, with visual observational data, we are only getting a sample of their occurrence. Finally, we do not have a complete knowledge about all the environmental variables that may influence distribution and we cannot assume that cetaceans occurring in the area have perfect knowledge about prey distribution and its variation across seasons and years, so models based on resource selection functions will only tell us where animals are more likely to be, based on an incomplete knowledge of all the predictors involved. Nevertheless, all models performed considerably better than a random model (AUC>0.5) and provide new information on common dolphin preferences in the area between the months of July and October, especially in the high seas region. Spatial and temporal predictors had a slightly stronger influence than environmental variables on common dolphin distribution. In this wide study area, with surveys occurring over five years and with heterogeneous effort, it is likely that the spatial pattern and the seasonality of common occurrence are linked to different habitat characteristics, also reflecting the effects of several environmental variables. However further work would be needed to determine which environmental variables are involved. Hence, in this context, the models, combined with the spatial and temporal distribution of occurrences, are more successful in identifying important areas of conservation than explaining the ecological rationale for the common dolphin distribution.

This study has several limitations, mostly related with effort heterogeneity, both temporally and spatially: surveys evidently depend on the company's schedule and the surveys along the three routes began in different years, with the Madeira route starting first (2012), therefore having a higher survey effort than the other two transects. Such differences in effort along line-transects are an almost unavoidable disadvantage of using OPOs (Kiszka *et al.*, 2007; MacLeod *et al.*, 2008; Moura *et al.*, 2012; Correia *et al.*, 2015).

Nonetheless, this work shows that the use of OPOs to systematically monitor cetaceans provides important data to fill data gaps in space and time, especially in areas that are logistically challenging for dedicated surveys and where baseline knowledge is needed, i.e. the high seas. It constitutes an important contribution to the knowledge of common dolphin distribution in the ENA, with records in poorly surveyed areas and insights in habitat preferences based on a 5-year dataset of systematic surveys and a great amount of effort. However, more surveys are still needed to fill knowledge gaps, mainly in relation to seasonal variation, as results here presented mainly reflect temporal variation from July and October, failing to provide a year-round distribution of common dolphins in the area.

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FIGURE LEGENDS

Fig. 1. The study area within the Eastern North Atlantic, with surveyed transects and visited ports.

Fig. 2. Spatial distribution of common dolphin (*Delphinus delphis*) occurrences with survey effort transects represented in grey lines. Only sightings on effort are represented.

Fig. 3. Temporal variation of common dolphin (*Delphinus delphis*) occurrence, encounter rate and monthly survey effort in nautical miles (nmi). Data from the entire study area, within the Eastern North Atlantic, is summarized. Only sightings on effort are considered.

Fig. 4. GAM predicted splines of the response variable dolphin presence as a function of the explanatory variables for the observation effects model produced for common dolphin (*Delphinus delphis*). The degrees of freedom are in brackets on the y-axis. Tick marks above the x-axis indicate the distribution of observations. Dashed lines delimit the 95% confidence intervals of the spline functions and dots on the graph area represent the residuals. For parameters abbreviations, see table 2.

Fig. 5. GAM predicted perspective graphs of the response variable dolphin presence as a function of the explanatory variables for the spatiotemporal model produced for common dolphin (*Delphinus delphis*). These correspond to variables introduced as interactions in the model, spatially (latitude x longitude) and temporally (day of the year x year), and represent in a surface the variation along the two variables. The degrees of freedom are in brackets on the z-axis. Grey surfaces define the upper and lower limits of the 95% confidence interval. For parameters abbreviations, see table 2.

Fig. 6. GAM predicted splines of the response variable dolphin presence as a function of the explanatory variables for the environmental model produced for common dolphin (*Delphinus delphis*). The degrees of freedom are in brackets on the y-axis. Tick marks above the x-axis indicate the distribution of observations. Dashed lines delimit the 95% confidence intervals of the spline functions and dots on the graph area represent the residuals. resid_dist_coast – residuals from the model for distance to coast with depth as predictor. For other parameters abbreviations, see table 2.

Fig. 7. GAM predicted splines of the response variable dolphin presence as a function of the explanatory variables for the final model produced for common dolphin (*Delphinus delphis*). The degrees of freedom for non-linear fits are in brackets on the y-axis. Tick marks above the x-axis indicate the distribution of observations. Dashed lines delimit the 95% confidence intervals of the spline functions and dots on the graph area represent the residuals. Perspective graphs correspond to variables introduced as interactions in the model, spatially (latitude x longitude) and temporally (day of the year x year), and represent in a surface the variation along the two variables. In these graphs, the degrees of freedom are in brackets on the z-axis and grey surfaces define the upper and lower limits of the 95% confidence interval. For parameters abbreviations, see table 2.

Fig. 8. GAM predicted probabilities of common dolphin (*Delphinus delphis*) for the set of the response variable points.

TABLES

Table 1. Survey effort, sightings of common dolphin (*Delphinus delphis*), group size and total encounter rates, for each sampled route and season of survey. A trip is considered a round-trip starting and ending in Mainland Portugal while a survey is a leg between two ports. Survey effort is presented in nautical miles (nmi) rounded to the unit. For the group size, the minimum (min), maximum (max), mean and standard deviation (std) values presented are based on the best estimate of the number of animals per sighting on effort, accessed by the observer.

Route	Year	Season	Nr of trips / Nr of surveys	Survey effort	Total sightings / Sightings on effort	Group size min-max (mean ± std)	ER
Madeira	2012	July-October	9 / 19	5025	17 / 14	1-40 (12.21 ± 10.19)	0.28
	2013	July-October	13 / 29	5616	30 / 22	1-120 (15.91 ± 29.16)	0.39
	2014	August-October	11 / 23	3938	22 / 16	2-100 (18.31 ± 24.54)	0.41
	2015	July-October	18 / 44	6009	30 / 21	1-80 (20.95 ± 19.29)	0.35
	2016	July-October	16 / 46	4887	28 / 19	2-100 (12.95 ± 22.62)	0.39
Azores	2014	July-September	6 / 32	5556	30 / 19	2-40 (8.16 ± 9.50)	0.34
	2015	July-October	7 / 33	3444	37 / 14	3-80 (21.86 ± 20.53)	0.41
	2016	July-October	7 / 31	3920	26 / 21	1-50 (16.48 ± 15.77)	0.54
Cape Verde	2015	May-October	7 / 46	8723	29 / 24	3-2500 (168.29 ± 510.22)	0.28
	2016	February/ August-December	5 / 42	6203	34 / 22	2-40 (13.32 ± 10.58)	0.35
		TOTAL	99/ 345	53321	283 / 192	1-2500 (34.58 ± 185.04)	0.36

807 **Table 2.** Variables tested as predictors for statistical modelling and its characteristics.

Model	Variables	Source	Reference	Product name	Name used in the analysis	Spatial resolution	Temporal resolution	Unit
Observation effects	Sea-state	Sea-surveys	-	-	sea_state	-	-	Douglas scale
	Wind-state	Sea-surveys	-	-	wind_state	-	-	Beaufort scale
	Visibility	Sea-surveys	-	-	visibility	-	-	1-10 scale[a]
Spatiotemporal	Latitude	Sea-surveys (GPS)	-	-	lat	-	~10 seconds	Decimal degrees
	Longitude	Sea-surveys (GPS)	-	-	lon	-	~10 seconds	Decimal degrees
	Day of the year	Date of survey	-	-	day	-	Daily	Day
	Year	Year of survey	-	-	year	-	Yearly	Year
Environmental	Depth	GEBCO	GEBCO, 2017	bathy_30arc_second	depth	30 sec	-	Meters (m)
	Slope	GEBCO	GEBCO, 2017	-	slope	30 sec	-	Degrees (º)
	Distance to coast	-	-	-	dist_coast	-	-	Kilometres (km)
	Distance to seamounts	GEBCO	GEBCO, 2017	-	dist_sm	-	-	Kilometres (km)
	Chlorophyll	MODIS Aqua	NASA, 2017	CHL_chlor_a	CHL	4 km / 9 km	8 day / monthly	Density (mg m^{-3})
	Chlorophyll lag 1 week	MODIS Aqua	NASA, 2017	CHL_chlor_a	CHL_lag1w	4 km / 9 km	8 day / monthly	Density (mg m^{-3})
	Chlorophyll lag 2 weeks	MODIS Aqua	NASA, 2017	CHL_chlor_a	CHL_lag2w	4 km / 9 km	8 day / monthly	Density (mg m^{-3})
	Chlorophyll lag 1 month	MODIS Aqua	NASA, 2017	CHL_chlor_a	CHL_lag1m	4 km / 9 km	8 day / monthly	Density (mg m^{-3})
	Chlorophyll lag 2 months	MODIS Aqua	NASA, 2017	CHL_chlor_a	CHL_lag2m	4 km / 9 km	8 day / monthly	Density (mg m^{-3})
	Sea-surface temperature	MODIS Aqua	NASA, 2017	sst4_4_sst4	SST	4 km / 9 km	8 day / monthly	Celsius (ºC)
	Mean sea level anomalies	AVISO	AVISO, 2017	MSLA_h_DT_all_sat_merged_0.25 / MSLA_h_NRT_all_sat_merged_0.25	MSLA	0.25 degree	8 day / monthly	Centimetres (cm)
Final	All variables above							

[a] Visibility scale: 5 - 1 to 2 km; 6 - 2 to 4 km; 7 - 4 to 10 km; 8 - 10 to 20 km; 9 - 20 to 50 km; 10 - > 50 km. Below 5 (1 km of visibility), the survey stopped (off effort).

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Table 3. Best GAM model results for common dolphin (*Delphinus delphis*).

Model Parameters	Estimate	edf	se	z-value	Chi-square	p-value	Deviance explained (%)	r^2	UBRE	AUC (CI 95%)
Observation effects										
Intercept	-4.18		0.06	-68.32		<0.001				
Smoother terms										
sea_state		1.61			26.34	<0.001				
wind_state		2.92			135.44	<0.001				
visibility		2.88			11.62	0.008				
Best model (n=20388; 192 presences): CD~s(sea_state)+s(wind_state)+s(visibility)							4.11	9.41^{E-3}	-0.82	0.689 (0.619-0.758)
Spatiotemporal										
Intercept	-4.83		0.10	-49.82		<0.001				
Smoother terms										
lat, lon		14.65			464.95	<0.001				
day,year		12.33			81.95	<0.001				
Best model (n=20388; 192 presences): CD~s(lat,lon)+s(day,year)							16.5	0.06	-0.84	0.809 (0.727-0.891)
Environmental										
Intercept	-4.81		0.21	-22.52		<0.001				
Smoother terms										
depth		1.84			160.32	<0.001				
resid_dist_coast		2.75			21.34	<0.001				
slope		2.87			9.69	0.017				
dist_sm		2.80			18.27	<0.001				
CHL_9km_monthly		2.58			19.12	0.005				
SST_4km_8day		2.83			22.42	<0.001				
MSLA_8day		2.83			9.83	0.015				
Best model (n= 16706; 165 presences): CD ~ resid_dist_coast+s(depth)+s(slope)+s(dist_sm)+ s(SST_4km_8day)+s(CHL_9km_monthly)+s(MSLA_8day)							15.5	0.05	-0.84	0.744 (0.651-0.838)
Final										
Intercept	-4.73		0.10	-49.89		<0.001				
CHL_9km_monthly	-0.45		0.07	-6.09		<0.001				
Smoother terms										
wind_state		2.87			45.16	<0.001				
visibility		2.93			17.98	<0.001				
lat,lon		14.39			104.02	<0.001				
day,year		11.03			66.88	<0.001				
depth		1.04			26.54	<0.001				
dist_sm		2.84			16.17	0.001				
MSLA_8day		2.97			28.66	<0.001				
Best model (n= 19658; 189 presences): CD ~ CHL_9km_monthly+s(wind_state)+s(visibility)+s(lat,lon)+s(day,year)+ s(depth)+s(dist_sm)+s(MSLA_8day)							22.3	0.09	-0.85	0.727 (0.639-0.814)

edf, effective degrees of freedom; se, standard error; AUC, Area Under the Curve; CI 95%, 95% confidence interval for the AUC; n, total number of points (used/available) considered in the model fitting; CD, common dolphins; resid_dist_coast, residuals from the model for distance to coast with depth as predictor. For other parameters abbreviations, see table 1.

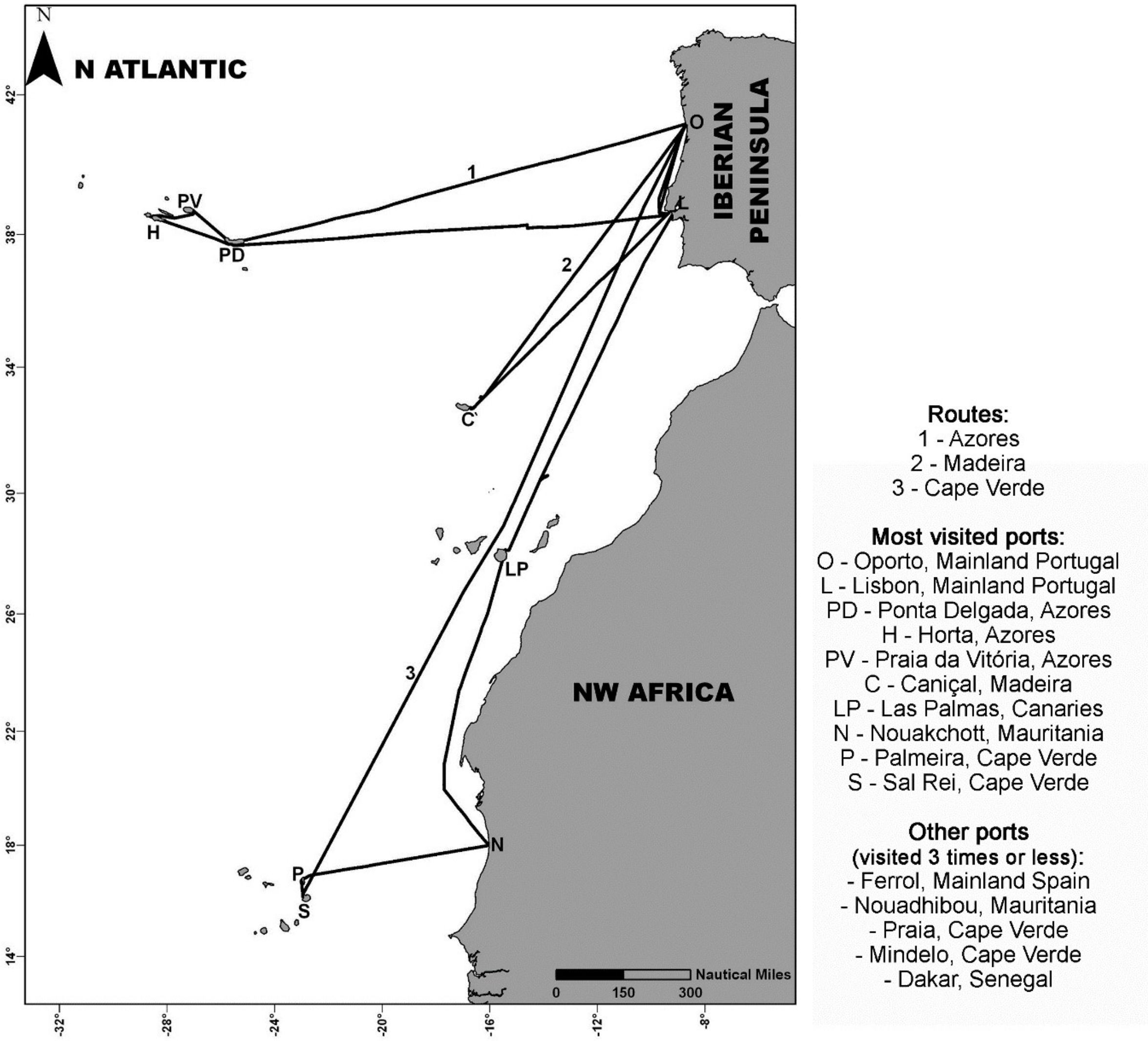

N
N ATLANTIC
IBERIAN PENINSULA
NW AFRICA
O
L
PV
H
PD
C
LP
N
P
S
1
2
3
42°
38°
34°
30°
26°
22°
18°
14°
-32°
-28°
-24°
-20°
-16°
-12°
-8°
Nautical Miles
0
150
300
Routes:
1 - Azores
2 - Madeira
3 - Cape Verde
Most visited ports:
O - Oporto, Mainland Portugal
L - Lisbon, Mainland Portugal
PD - Ponta Delgada, Azores
H - Horta, Azores
PV - Praia da Vitória, Azores
C - Caniçal, Madeira
LP - Las Palmas, Canaries
N - Nouakchott, Mauritania
P - Palmeira, Cape Verde
S - Sal Rei, Cape Verde
Other ports
(visited 3 times or less):
- Ferrol, Mainland Spain
- Nouadhibou, Mauritania
- Praia, Cape Verde
- Mindelo, Cape Verde
- Dakar, Senegal

Figure 1

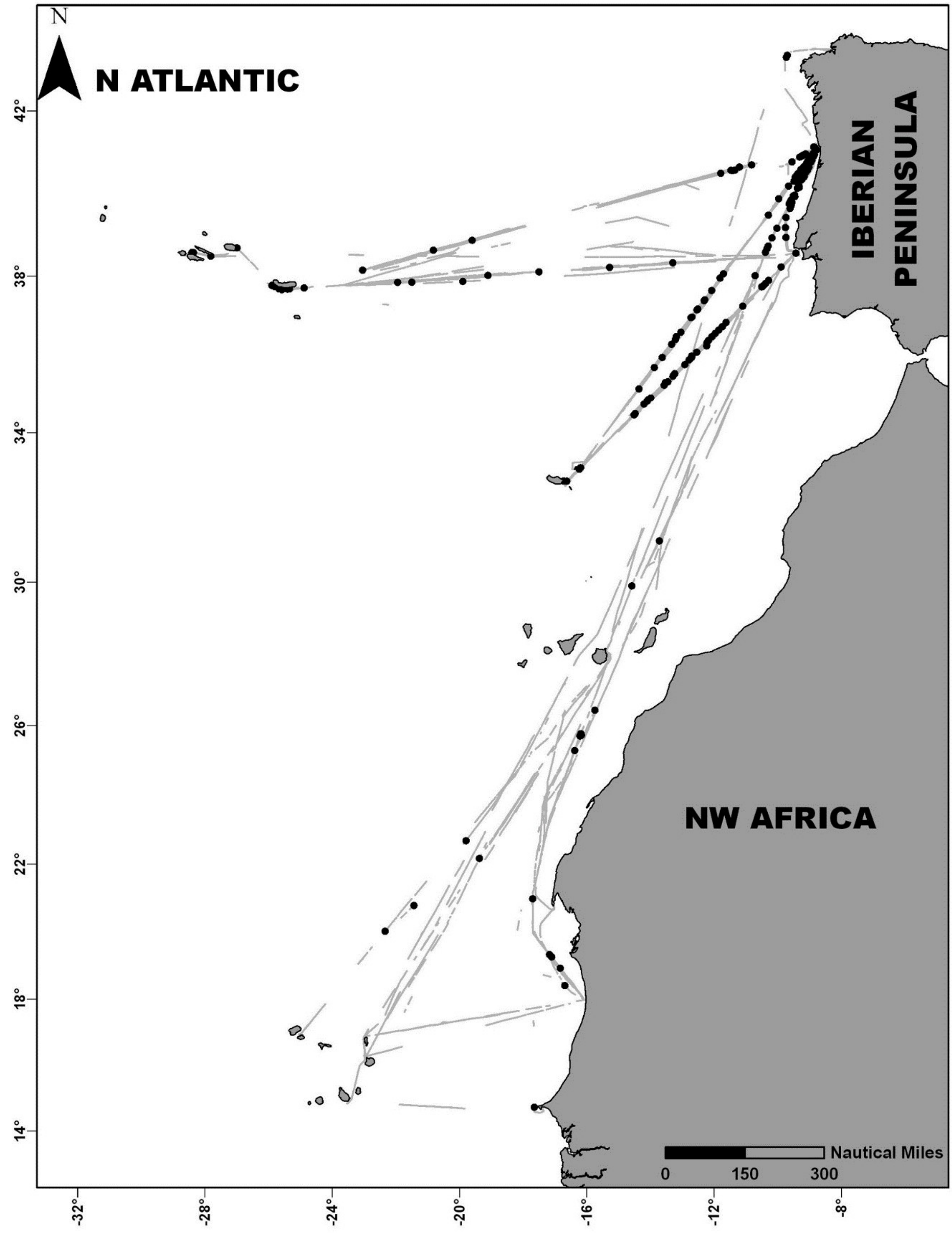
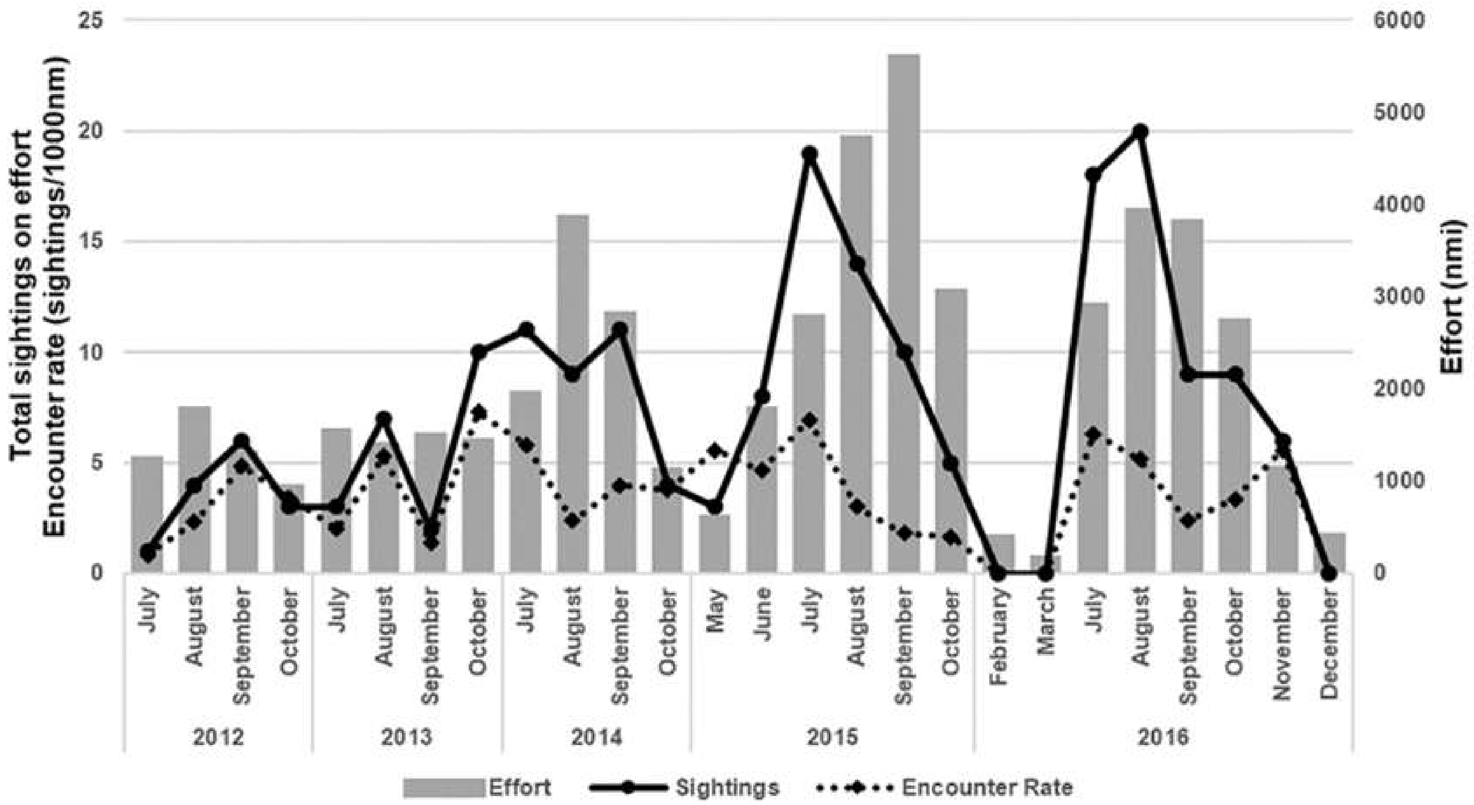

N
N ATLANTIC
IBERIAN PENINSULA
NW AFRICA
Nautical Miles
0
150
300
42°
38°
34°
30°
26°
22°
18°
14°
-32°
-28°
-24°
-20°
-16°
-12°
-8°

Figure 2



818

819 Figure 3

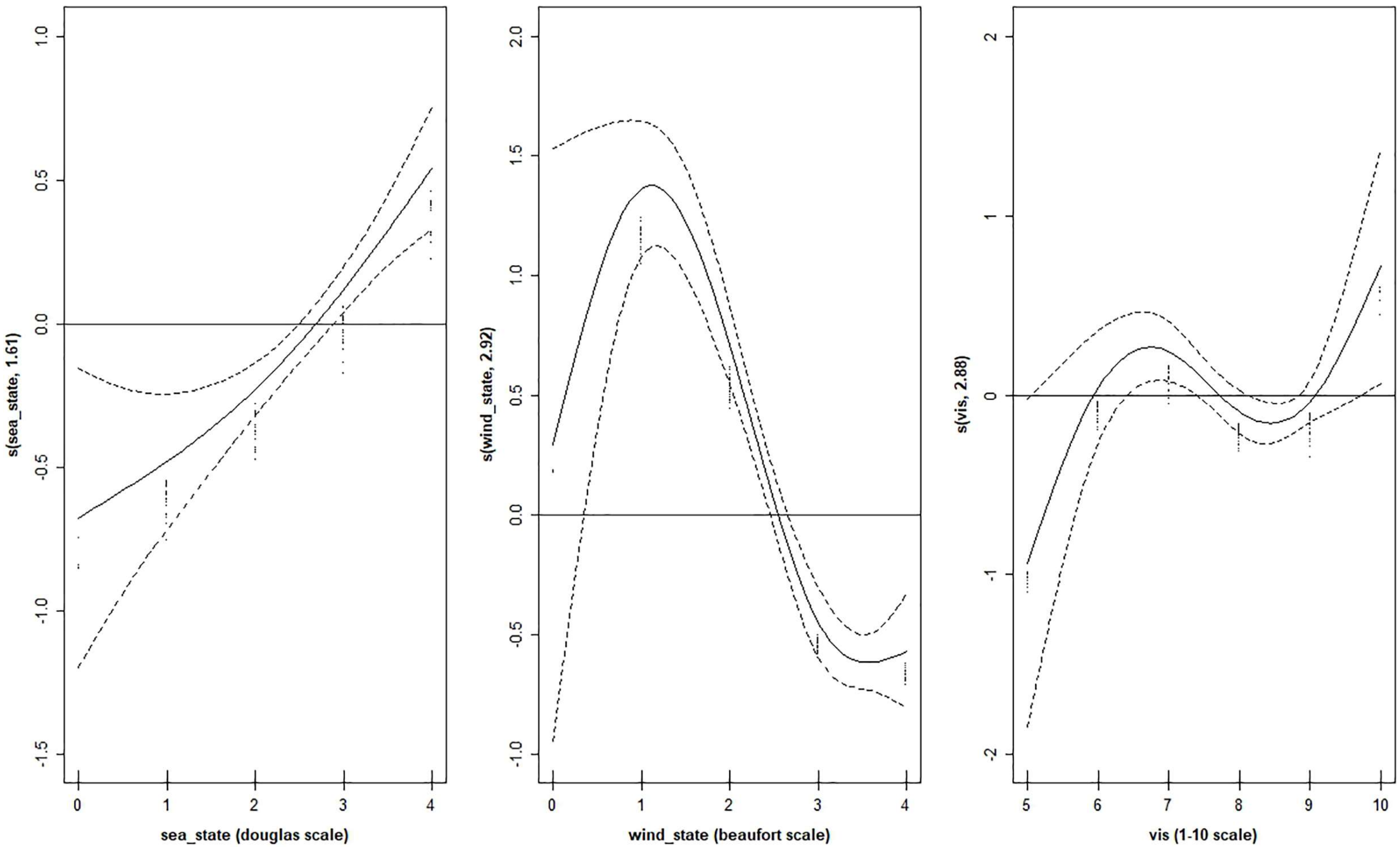

s(sea_state, 1.61)
sea_state (douglas scale)
s(wind_state, 2.92)
wind_state (beaufort scale)
s(vis, 2.88)
vis (1-10 scale)

Figure 4

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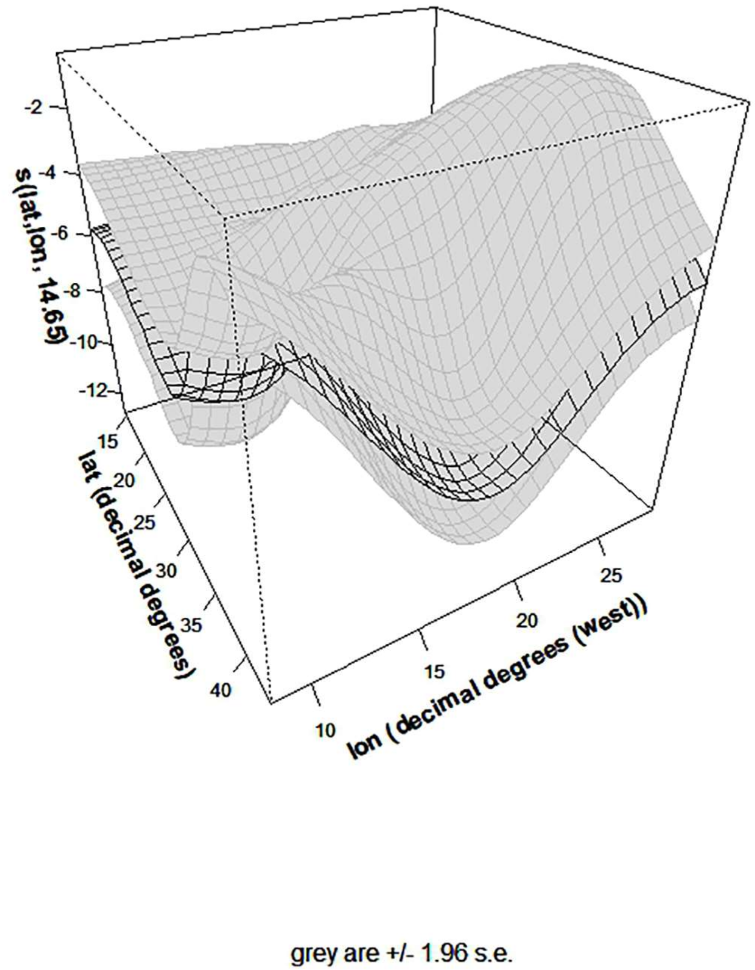
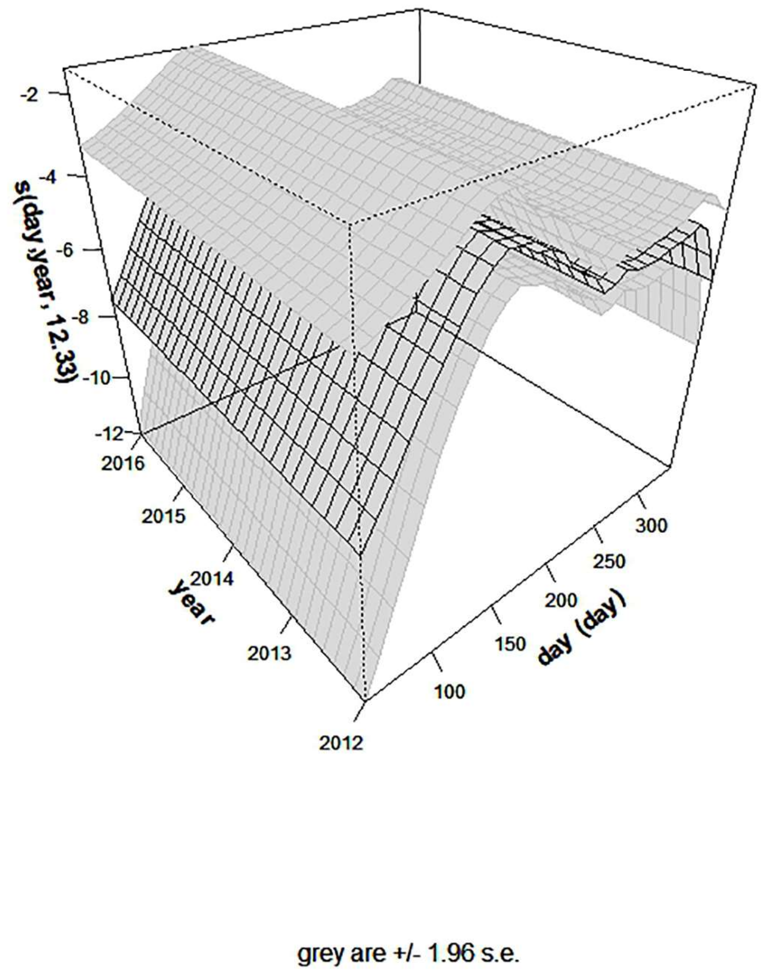




823 Figure 5

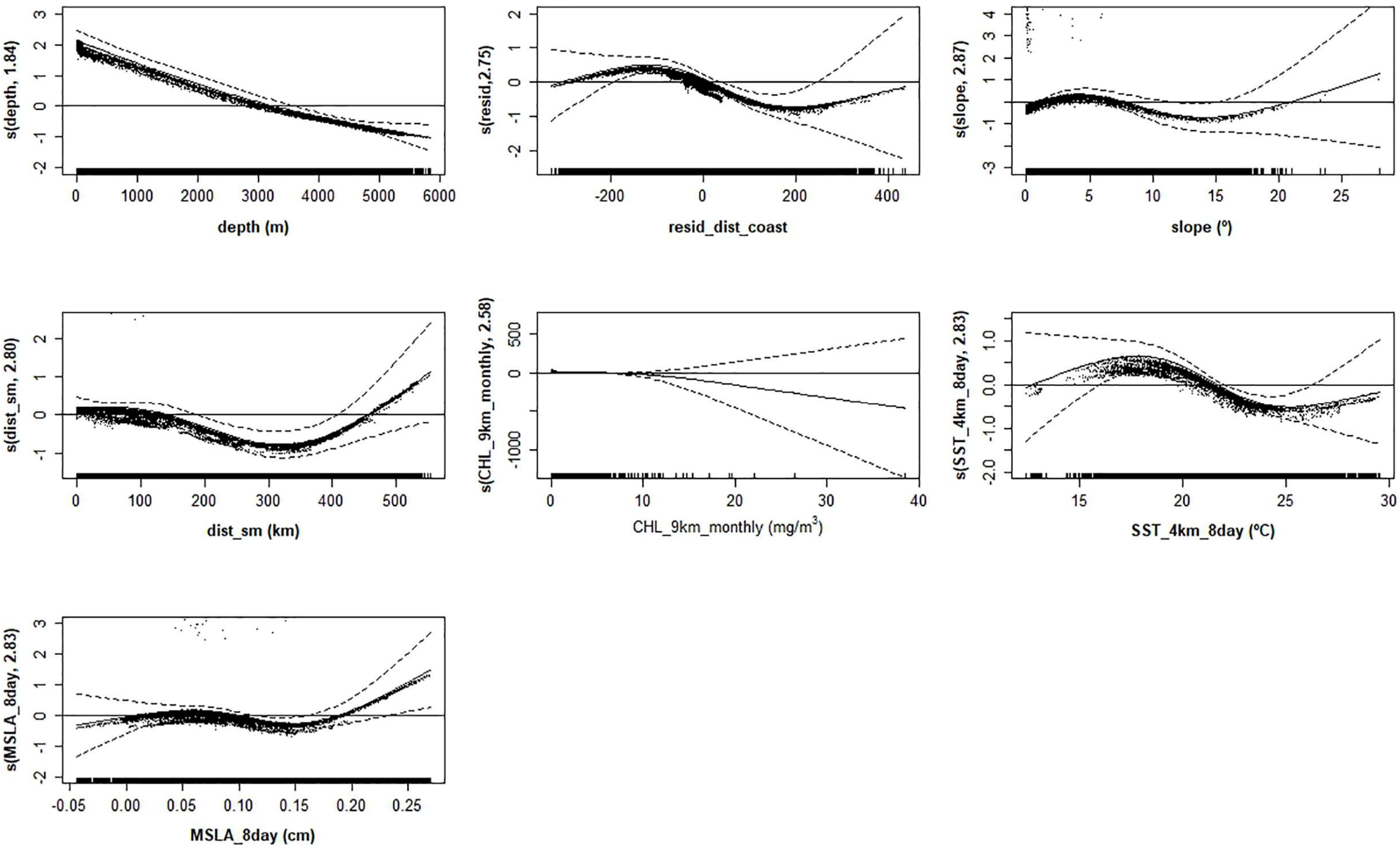
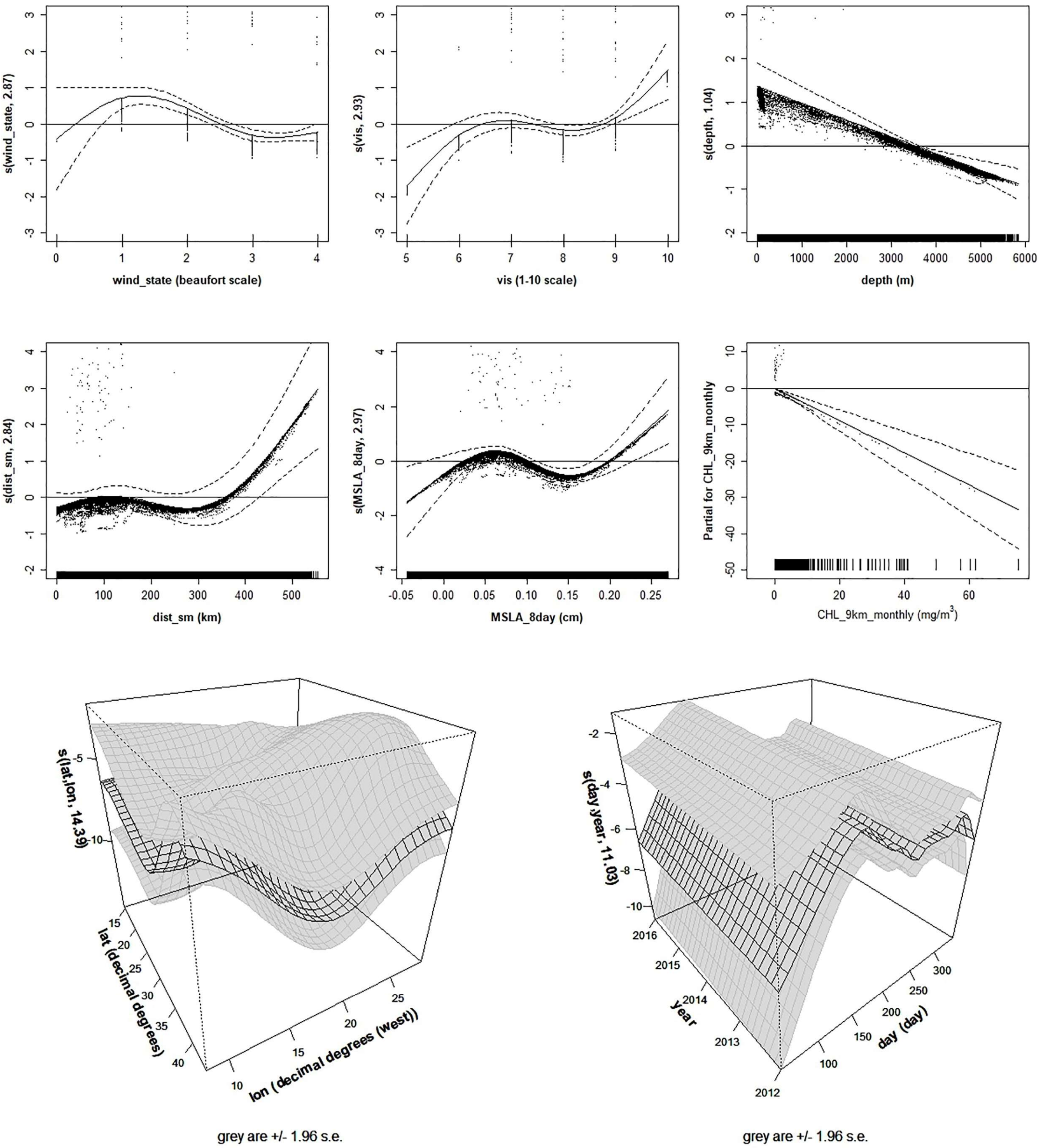
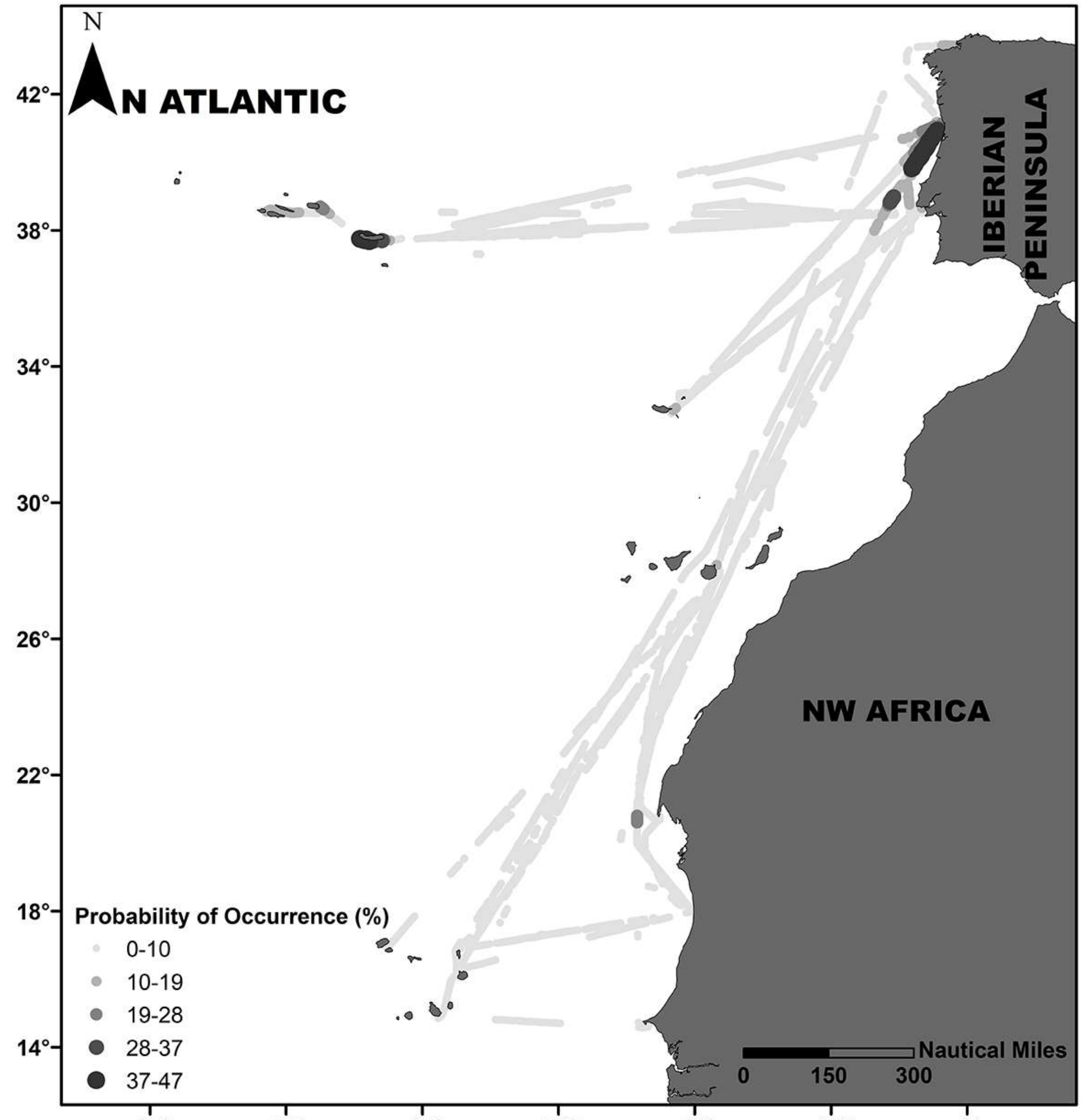

s(depth, 1.84)
depth (m)
s(resid,2.75)
resid_dist_coast
s(slope, 2.87)
slope (º)
s(dist_sm, 2.80)
dist_sm (km)
s(CHL_9km_monthly, 2.58)
CHL_9km_monthly (mg/m³)
s(SST_4km_8day, 2.83)
SST_4km_8day (ºC)
s(MSLA_8day, 2.83)
MSLA_8day (cm)

Figure 6



s(wind_state, 2.87)
wind_state (beaufort scale)
s(vis, 2.93)
vis (1-10 scale)
s(depth, 1.04)
depth (m)
s(dist_sm, 2.84)
dist_sm (km)
s(MSLA_8day, 2.97)
MSLA_8day (cm)
Partial for CHL_9km_monthly
CHL_9km_monthly (mg/m3)
s(lat,lon, 14.39)
lat (decimal degrees)
lon (decimal degrees (west))
grey are +/- 1.96 s.e.
s(day year, 11.03)
year
day (day)
grey are +/- 1.96 s.e.

Figure 7



828

829 Figure 8