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Distribution of cetacean species at a large scale - Connecting continents with the Macaronesian archipelagos in the eastern North Atlantic

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Abstract

Aim: To describe distribution patterns and species richness of cetaceans along a wide geographical range using occurrence data coupled with survey effort, from poorly studied oceanic areas. Specific objectives were to compare species richness and relative abundances among sub-regions and to describe the distribution of each species.

Location: Eastern North Atlantic.

Time period: 2012–2017.

Major taxa studied: Cetacea.

Methods: Cetacean monitoring was performed by dedicated observers from cargo ships, used as platforms of opportunity, along routes between Iberian Peninsula, Macaronesia and north-western Africa. We mapped relative abundance (encounter rates), survey effort and species richness. We examined the dependence of the number of sightings and species richness on survey effort. The area was divided into sub-regions (according to the Exclusive Economic Zones and international waters), and relative abundances of the eight most frequently sighted species, as well as species richness, were compared among them. In addition, we describe the distribution of each species in relation to sea depth, distance to coast, latitude and longitude.

Results: A total of 1,989 sightings were logged, and 26 cetacean species were identified. Species richness and relative abundances of the eight most common species differed substantially between sub-regions. Common and bottlenose dolphins distributed in shallow coastal waters contrasting with the oceanic distribution of *Stenella* dolphins. Cuvier's beaked whale and minke whale had similar distributions. Pilot and sperm whales were distributed in southern waters.

Main conclusions: A considerable amount of survey effort was needed to attain reliable estimates of species richness. In less surveyed areas, species richness and abundance are likely to be underestimated. The offshore waters presented high species richness and several hotspots of cetacean abundance. This work provides new knowledge on cetacean distribution at a large scale in the eastern North Atlantic, relevant to future conservation management.

KEYWORDS
cetaceans, CETUS Project, distribution patterns, distribution range, effort-based data, high seas, relative abundances

1 | INTRODUCTION

Knowledge on distribution patterns of marine species is essential for efficient marine management and biodiversity conservation. While some areas are well-surveyed, the vast majority of the ocean is still lacking baseline data or is insufficiently surveyed to permit a good level of understanding of species diversity and distribution patterns. Hence, identifying priority areas where monitoring efforts are required is essential (Kaschner, Quick, Jewell, Williams, & Harris, 2012; Mannocci et al., 2018).

One of the priorities for research in relation to marine conservation is the assessment of the distribution of pelagic top predators (Boyd, Wanless, & Camphuysen, 2006; Hazen et al., 2019; Heithaus, Frid, Wirsing, & Worm, 2008; Parsons, 2016). These are key species for the maintenance of the structure and functioning of marine ecosystems (Sergio et al., 2008; Sergio, Newton, Marchesi, & Pedrini, 2006). Often, knowledge on their range is lacking or insufficient, as the range is frequently very wide and includes oceanic waters where there are few surveys (Alves, Ferreira, et al., 2018; Correia, Tepsich, Rosso, Caldeira, & Sousa-Pinto, 2015; Kiszka, Macleod, Van Canneyt, Walker, & Ridoux, 2007; Moura, Sillero, & Rodrigues, 2012; Tobeña, Prieto, Machete, & Silva, 2016; Viddi, Hucke-Gaete, Torres-Florez, & Ribeiro, 2010).

Observation platforms of opportunity (OPOs) have been widely used to monitor cetacean presence, allowing the sampling of remote areas, such as the high seas, over long periods of time. This methodology has limitations, for example heterogeneous effort conditioned by the routes, schedules and logistics of the platform of opportunity, usually with a restricted spatial coverage of the study area. However, it is frequently the most cost-effective method to generate baseline data, allowing the collection of valuable data that would otherwise be difficult or impossible to obtain (Aïssi et al., 2015; Alves, Ferreira, et al., 2018; Correia et al., 2015; Evans, Hammond, 2004; Kiszka et al., 2007; Morgado, Martins, Rosso, Moulins, & Tepsich, 2017; Moura et al., 2012; Tobeña et al., 2016; Viddi et al., 2010).

The CETUS Project is a monitoring programme that records cetacean species occurrence in the eastern North Atlantic (ENA). Since 2012, cargo ships from a Portuguese maritime transport company, TRANSINSULAR, have been used as OPOs. On-board observers are trained in cetacean detection and identification, and do not have other duties. Moreover, data collected are effort-based as the survey effort is also recorded, which is fundamental to provide reliable information on distribution and relative abundance, especially when effort is highly heterogeneous and survey activity is conditioned by the weather (Correia et al., 2015; Evans, Hammond, 2004). The project has resulted in a large dataset of cetacean occurrence records across the ENA (Correia, Gandra, et al., 2019).

The ENA is a topographically and oceanographically complex system (Caldeira & Sangrà, 2012; Mason, 2009; Sala, Caldeira, Estrada-Allis, Froufe, & Couvelard, 2013) characterized by high cetacean diversity. In total, 17 species have been recorded along the continental Portuguese coast (Brito & Sousa, 2011; Moura et al., 2017), 17 in north-west Spain (Abollo, López, Gestal, Benavente, & Pascual, 1998; Covelo, Martínez-Cedeira, Llavona, Díaz, & López, 2016; Díaz López, Methion, & Giralt Paradell, 2019; Goetz, Read, Santos, Pita, & Pierce, 2013), 26 in Madeira (Alves, Ferreira, et al., 2018; Freitas, Dinis, Nicolau, Ribeiro, & Alves, 2012), 28 in Azores (Silva et al., 2014; Tobeña et al., 2016), 28 in the Canary Islands (Carrillo, Pérez-Vallazza, & Álvarez-Vázquez, 2010; Pérez-Vallazza, Álvarez-Vázquez, Cardona, Pintado, & Hernández-Brito, 2008), 24 in Cape Verde (Hazevoet et al., 2010; Hazevoet & Wenzel, 2000) and 36 along the north-western African coast (Djiba, Bamy, Bilal, & Van Waerebeek, 2015; Perrin & Waerebeek, 2012; Robineau & Vely, 1998; Weir & Pierce, 2013). The wide latitudinal and longitudinal range as well as the long temporal frame covered by the CETUS surveys, combined with high habitat variability and cetacean diversity in the area, offer the potential to analyse distribution patterns at a large scale.

We provide a descriptive analysis of spatial and temporal patterns in cetacean distribution and species richness, using effort-based data collected within the ENA, from 2012 to 2017, with high survey effort in the open ocean. We identified areas with the highest relative abundance and species richness, which may be priority areas for future research and conservation efforts, and compared species richness and relative abundances among sub-regions (Iberian Peninsula, Azores, Madeira, Canaries, Cape Verde, north-western Africa and international waters).

2 | MATERIAL AND METHODS

2.1 | Study area

The Canary Basin is characterized by a complex geography, including the existence of several archipelagos (Azores, Madeira, Canaries and Cape Verde) that emerge from deep waters, structures such as seamounts and a rugged coastline along the continents of Europe and Africa. It is a very dynamic region, affected by several important oceanographic features, including the North Atlantic subtropical gyre, and is bounded by the Azores Front (separating the anticyclonic eastern subtropical gyre from the northern cyclonic subpolar gyre), and the Cape Verde Frontal Zone (separating the nutrient-rich South Atlantic Central Waters from cooler North Atlantic Central Waters) (Zenk, Klein, & Schroder, 1991). North-easterly trade winds help maintain the strong upwelling system in north-west Africa, one of the major Eastern Boundary Upwelling Systems (EBUS) of the world (Mason, 2009)—biologically productive marine regions covering less than 1% of the world's ocean but supporting up to 20% of the world's capture fisheries (Pauly, Christensen, 1995).

The transects sampled cross a broad range of ocean habitats, including different topographic systems (continental platform, abyssal plains, steep slope, seamounts and canyons) and a diversity of oceanographic features, including four major currents (Portugal, Azores, Canary and Mauritania currents) and several mesoscale eddies (Mason, 2009).

To analyse cetacean occurrence by sub-regions within the area, we defined the spatial limits for each sub-region of analysis based on the Exclusive Economic Zones (EEZs) (Iberian Peninsula, Azores, Madeira, Canaries, Cape Verde, north-western Africa), thus also delimiting international waters (Figure 1).

2.2 | Data collection

Dedicated trained observers followed a standardized protocol for cetacean monitoring along line-transect surveys, aboard cargo ships from TRANSINSULAR (Correia, Gandra, et al., 2019; Correia et al., 2015), which were used as OPOs. The company operates routes for cargo transport between Continental Portugal and Macaronesian archipelagos, with stopovers in the north-west Africa. Between 2012 and 2017, three routes were monitored: Continental Portugal to Madeira (starting in 2012, hereafter Madeira route), Azores (starting in 2014, hereafter Azores route) and Cape Verde (with stopovers in the Canary Islands, Mauritania and Senegal—starting in 2015, hereafter Cape Verde route). On two occasions in 2016, the Cape Verde route included a transect to the north-west Spain, although the track was crossed on-effort only once, due to weather conditions. Each trip followed one of these routes and accommodated two MMOs. Observers stood on the wings of the navigation bridge (at an approximate height of 15 m, measured from sea level, considering maximum draught) looking for cetacean presence, from sunrise to sunset. Normally, the two MMOs each covered 90° (from 0° to ± 90° relative to the heading), from opposite sides of the vessel. When one MMO was resting, as detailed below, the lone MMO covered 180°. MMOs switched side every hour to reduce fatigue. Monitoring was performed mainly by naked eye; binoculars (7 × 50 mm, fitted with a scale and compass) were used for occasional scans (approximately every 5 min) and to support the collection of the data (e.g. to detect vessels and for species identification). Survey effort stopped at sea state or wind state higher than 4 (on the Douglas or Beaufort scales, respectively), when visibility was

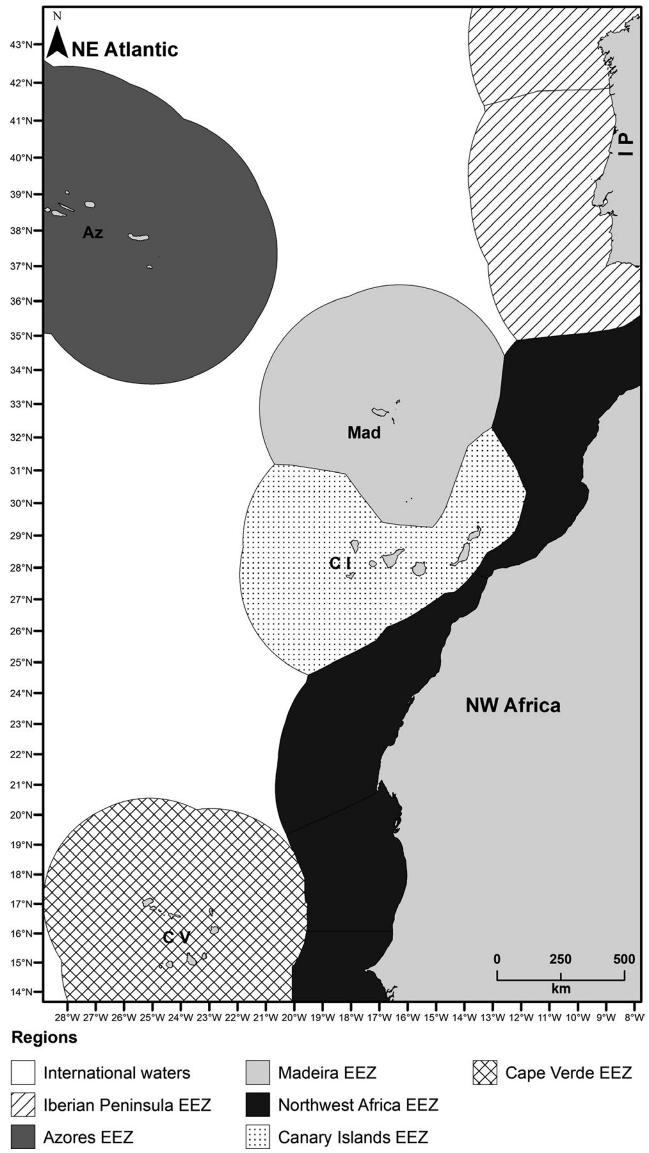


FIGURE 1 Sub-regions for the analysis, considering the limits of the Exclusive Economic Zones in the study area. EEZ, Exclusive Economic Zone; IP, Iberian Peninsula; Az, Azores archipelago; Mad, Madeira archipelago; CI, Canary Islands archipelago; CV, Cape Verde archipelago.

lower than 1 km, during heavy rain, and whenever observers were not allowed in the navigation bridge (e.g. during manoeuvres, safety drills or cleaning of the deck). MMOs rested in turns for an hour each at mealtimes (lunch and dinner), and optionally for additional periods of approximately 40 min (in the morning and in the afternoon). Sightings collected off-effort (i.e. when survey effort had to stop for any of the aforementioned reasons) were considered to be opportunistic and were not included in the present analysis. Weather state was assessed at the beginning and end of each survey leg (defined as a continuous period of sampling, usually a day from sunrise to sunset), or whenever it changed significantly. The number of vessels, by size category (small, medium or large), visible over 360 degrees around the observation stand, was registered at the beginning and end of the survey leg, every hour and following each cetacean sighting. Whenever a cetacean was spotted, if possible, observers recorded species identity, the distance and angle of the position of the animal(s) in relation to the ship (using the scale and compass of the binoculars), the number of animals within the group, their reaction (if any) to the ship and direction of travel. Due to occasional difficulties in determining the exact number of animals present, the minimum and maximum group sizes as well as a best estimate (from the observers' perspective) were recorded. Sightings of other top predators (e.g. turtles, sharks and sunfishes) were also registered. The route was recorded using a tablet with an inbuilt GPS (points along the track were automatically added, every 10 s or every 50 m), and all the waypoints were marked. In the data analysis, the GPS position of the ship at the moment of the sighting was used, as well as the best estimate for the group size.

2.3 | Data analysis

Encounter rates were calculated as the number of cetacean sightings (the all species total and by species) recorded on-effort per 100 km. Yearly and monthly information on total effort, number of sightings, overall encounter rates and number of species, as well as encounter rates for each species by year and by each of the defined subregions, are provided in Table S1 and Figure S1.

For all cells with non-zero effort in a grid of 100 × 100 km, total effort (total distance surveyed within the cells), overall cetacean encounter rate (total sightings of cetaceans on-effort per 100 km) and the total number of species identified (at least to the genus level) were calculated. This was done for the whole study period over the surveyed calendar months (February and March, May to December). The 100 km grid was chosen after testing different spatial resolutions. It provided a suitable sample size for statistical analysis, allowed identification of broad-scale patterns and was suitable for data visualization while also avoiding zero inflation. Distance surveyed on-effort was calculated based on the tracks recorded by the GPS, by transforming the set of on-effort points along the track into lines (the effort tracks) and measuring the distance covered by those lines.

In order to provide an indication of the adequacy of the current level of search effort, we first checked the relationship between encounter rate and survey effort (Figure S2) and then used generalized additive models (GAMs) (Hastie & Tibshirani, 1990) to model number of sightings and number of species in relation to effort. As we expect density and diversity of cetaceans to depend on sea depth and distance to coast (e.g. because shelf species will be replaced by oceanic species as one moves offshore), we also included these variables as covariates. Depth was obtained from bathymetry data in GEBCO (GEBCO, 2017), and distance to coast was calculated using ArcGIS 10.5 (ESRI 2016). These two environmental variables were extracted for the position of the centroid of each cell. They had strong effects on the distribution of the eight most sighted species as revealed by the principal component analysis (PCA) described below. Therefore, the following models were fitted: number of sightings ~ s(effort) + s(distance to coast) + s(depth), and number of species ~ s(effort) + s(distance to coast) + s(depth). Considering that the response variables were counts, we first tested a Poisson distribution (with a log link function). We then checked for overdispersion. Dispersion was adequate for the "number of species model" (0.92) but there was overdispersion for the "number of sightings" model (2.56). As such, for the latter, we fitted a negative binomial distribution (with a log link function). The smoothers obtained essentially depict rarefaction curves.

Before fitting the models, we checked for collinearity between explanatory variables (effort, depth and distance to coast) through Pearson correlation (threshold = 0.75, after Marubini, Gimona, Evans, Wright, & Pierce, 2009) and the variance inflation factor (VIF, threshold = 3) (Zuur, Ieno, & Elphick, 2010). All Pearson correlations and VIF values were lower than the thresholds, so no variables were removed.

Model fitting started by including the three explanatory variables, considering only main effects, followed by backward selection (Quian, 2009). Best models were chosen by using the Akaike information criterion (AIC) as a measure of goodness-of-fit and at each step of model selection, comparing between models that differed in one explanatory variable (i.e. with or without the least significant variable). We retained the model with the lowest AIC value or the simplest model when AIC values differed in less than 2 (following the principle of parsimony, e.g. Burnham & Anderson, 2002).

We verified that there were no influential data points or relationship between model residuals and the explanatory variables in the final best models. Finally, we plotted back-transformed predicted values of number of sightings and number of species for the surveyed cells in the 100 × 100 km grid against the explanatory variables used in the final best models to confirm the relationships.

Models were developed using the "mgcv" package in R 3.4.4. (R Core Team 2018) with RStudio.

Those species (or genera) with more than 30 sightings were selected for further analysis, namely common dolphin (*Delphinus delphis* Linnaeus, 1758), Atlantic spotted dolphin (*Stenella frontalis* Cuvier, 1829), striped dolphin (*Stenella coeruleoalba* Meyen, 1833), sperm whale (*Physeter macrocephalus* Flower, 1864), bottlenose dolphin (*Tursiops truncatus* Montagu, 1821), minke whale (*Balaenoptera acutorostrata* Lacépède, 1804), Cuvier's beaked whale (*Ziphius cavirostris* Cuvier, 1823) and pilot whales (*Globicephala* sp. Lesson, 1828). Considering these taxa, the cetacean community composition (in terms of relative abundances and percentage relative contribution), as well as the monthly presences, was represented for each sub-region. Maps of sightings distribution along tracks were created for these eight taxa and are presented in Figure S3.

To describe and compare species according to their geographical distribution and coastal or oceanic occurrence, we considered four factors (henceforth "species distribution factors" (SDFs)): depth, distance to coast, latitude and longitude. To delimit and characterize the surveyed area, a set of points was created, with a point generated every 5 km within effort tracks (Correia et al., 2015). The SDFs were extracted for this set of points.

TABLE 1 Summary table for the most frequently sighted species

Taxa	No. sightings	ER	Group size	
			Range	Mean ± *SD*
Delphinus delphis	262	0.206	1–2,500	27.44 ± 160.82
Stenella frontalis	167	0.131	1–130	19.31 ± 19.76
Stenella coeruleoalba	119	0.093	1–150	19.60 ± 21.85
Physeter macrocephalus	116	0.092	1–20	2.01 ± 2.17
Tursiops truncatus	92	0.071	1–130	10.44 ± 15.37
Balaenoptera acutorostrata	75	0.059	1–4	1.36 ± 0.65
Ziphius cavirostris	51	0.023	1–7	2.08 ± 1.50
Globicephala sp.	44	0.041	1–100	19.03 ± 21.45

Note: For group size estimates, sightings with associated species are not considered as the number of animals assessed during surveys corresponds to the mixed group, hence was not representative of a single species.

Abbreviations: ER, encounter rate (number of sightings per 100 km surveyed); *SD*, standard deviation.

Summary statistics were calculated for the group size of each species, as well as for the SDFs at the position of the sightings. Values of the quantiles of the distributions for each SDF are presented for each species (see Table S2) and then illustrated with boxplots. To compare the extent and the location of species distributions in the study area (conceptually equivalent to deriving the niche width and niche centre), we applied PCA to the data on the four SDFs (see Fernández et al., 2013). PCA projects data into a lower dimension subspace and is therefore commonly used to search for the linear combination of variables that describe most of the variability on the original data. Moreover, it provides a measure of influence from each of the factors to the principal components (the eigenvalue), which in this case allowed for a better understanding of the most determinant factors in the distribution of cetacean species. Prior to PCA, we first standardized the data by subtracting the mean value of each variable and dividing by the standard deviation for all data points. We ran the Kaiser–Meyer–Olkin (KMO) test and Bartlett's test of sphericity to diagnose for sampling adequacy. Although the overall KMO test result was 0.51, very close to the 0.5 threshold considered for eligible data to run a factor analysis, Bartlett's test result was significant ($p < .001$), indicating that PCA was an adequate and useful test for the dataset. Then, for the most important principal components (PC) (those that together account for more than 75% of the total accumulated variation explained), we used boxplot graphs to represent the quartiles of the PC scores (minimum, 25%, median, 75% and maximum values) for the eight most frequently sighted species. For comparisons of the PC scores among species, we used Kruskal–Wallis and Mann–Whitney tests (test results are given in Table S3). To avoid type I errors on multiple pairwise comparisons, we applied the Bonferroni correction to the Mann–Whitney tests.

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

3 | RESULTS

3.1 | Overall distribution of effort, encounter rates and species richness

Survey effort was concentrated in summer and early autumn (July to October), while other months (February, March, May, June, November and December) were surveyed in only one of the years and there was no survey effort in January or April. Yearly effort increased over time, due to an increase in the number of routes being monitored: one route between 2012 and 2014, two between 2014 and 2015, and three between 2015 and 2017. Effort, number of sightings, encounter rates and number of species all presented a high inter-annual variability (Figure S1).

In total, 124,428 km were surveyed in the study area and 26 cetacean species were identified (at least to the genus level), with 1,989 sightings collected on-effort, resulting in an overall encounter rate of 1.60 sightings per 100 km. The eight most frequently sighted species contributed 45% of the sightings. These were common dolphin, spotted dolphin, striped dolphin, sperm whale, bottlenose dolphin, mink whale, Cuvier's beaked whale and pilot whales. With 262 occurrences, common dolphin was the most frequently sighted species, comprising 12.9% of the sightings. This was also the species with the highest number of individuals recorded during a single sighting, namely approximately 2,500 animals in a group seen off Dakar (Senegal) on the 26th of July 2015 (Table 1 and Table S1).

In general, the areas with the highest survey effort were in offshore waters between Continental Portugal and Madeira and Azores, where a high diversity of species (up to 11 species per 100 km^2) was observed (Figure 2). The highest encounter rates were registered elsewhere: for example, close to Continental Portugal and West Africa, and near the Macaronesian archipelagos (Figure 2). Encounter rate was independent of survey effort, consistent with a sufficient amount of effort for reliable estimates of relative abundance (Figure S2). As for the GAMs, depth was dropped from the final model for

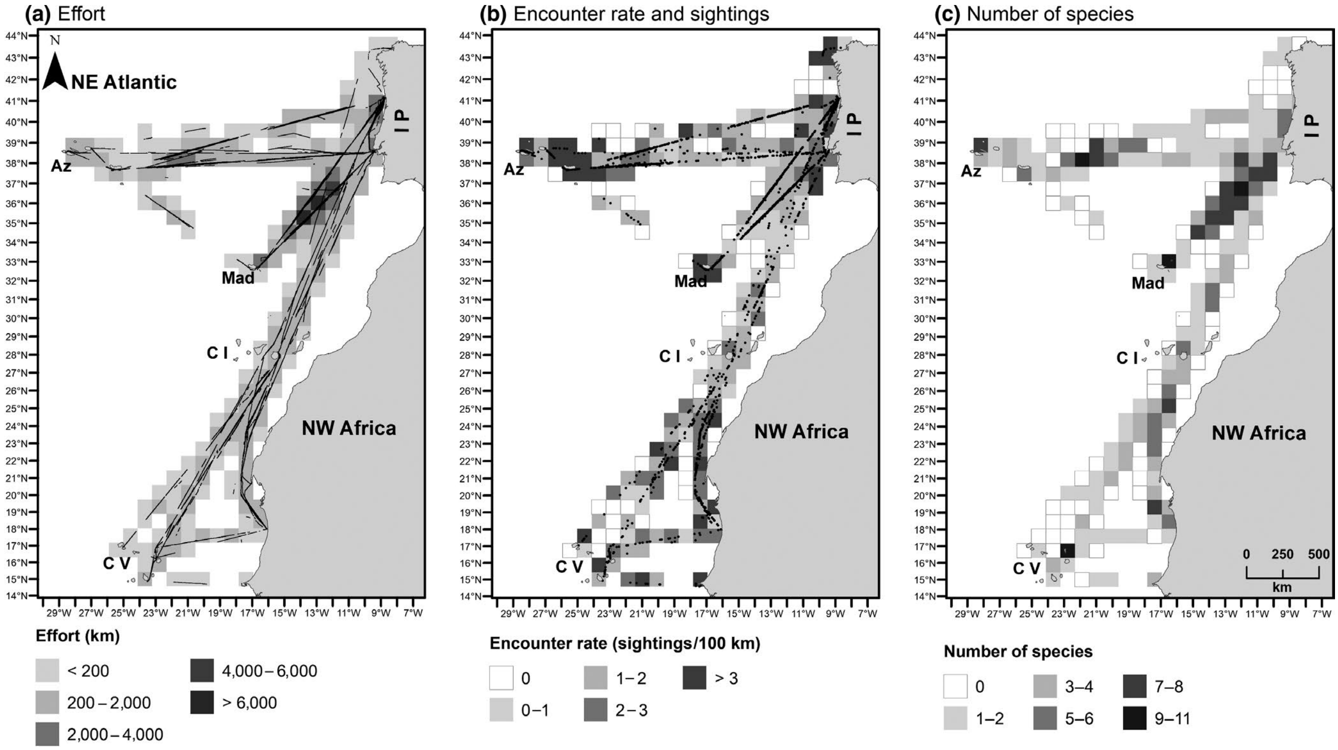


FIGURE 2 Spatial distribution of survey effort, encounter rate and number of species seen. (a) Black lines represent effort tracks. (b) Black dots represent sightings. Grid: 100 × 100 km. IP, Iberian Peninsula; Az, Azores archipelago; Mad, Madeira archipelago; CI, Canary Islands archipelago; CV, Cape Verde archipelago.

"number of sightings," and distance from coast was dropped from the "number of species" model. The number of sightings per grid cell generally increased with survey effort and decreased with distance to coast. Number of species per grid cell increased with effort up to around 3,000 km per 100 km^2, after which it started to stabilize. Species richness peaked at approximately 1,500 m of depth. Confidence intervals for the smoothers were wide at high values of effort and distance to coast due to the low number of sampled grid cells with high survey effort or very distant from the coast (Figure 3).

3.2 | Analysis of the cetacean community composition by sub-region

In all sub-regions, the sightings of the eight most frequently sighted species made up 40% to 50% of total sightings, except in the Cape Verde EEZ, where sightings for other taxa represented about 74% of the total sightings.

In the EEZs of the Iberian Peninsula and Azores, the most frequently encountered species was the common dolphin. The number of common dolphin sightings represented about half of the total for the most frequently sighted species in Iberian waters and about a quarter on the total; in the Azores, Atlantic spotted dolphin was the most frequently sighted species in the Canary Islands and Madeira EEZs and in international waters. Sperm whales were the most frequently sighted species in the EEZs of north-western Africa and the second most frequently encountered in the Canary Islands. The encounter rate for pilot whales was highest in the Cape Verde EEZ, where they were the most frequently sighted species. The second highest encounter rate for this genus was recorded in the EEZs of north-western Africa. They were rarely seen in the remaining sub-regions and never sighted in international waters (Figure 4).

The north-western Africa sub-region had the highest number of species registered (21) and the highest encounter rates for 11 out of the 21 species. The highest overall encounter rate was registered in the Azores EEZ. In international waters, 16 species were recorded, and the overall encounter rate was approximately 1.12 sightings/100 km. Almost 20% of the survey effort was undertaken within these waters (Figure 4 and Table S1).

Regarding temporal patterns, six of the eight most frequently sighted species were seen in international waters every month from July to October but were not seen outside this period. Of the two exceptions, sperm whales were absent in September, while pilot whales were never seen in international waters. In the Canary Islands and Cape Verde, survey effort was low, and the presence of most species was restricted to a few months, although Atlantic spotted dolphin was seen from June to November in the Canary Islands (Figure 5).

3.3 | Distributions of the most frequently sighted species

Surveys covered a wide range of habitats in the study area. The most frequently surveyed areas were in deeper waters, at distances up to

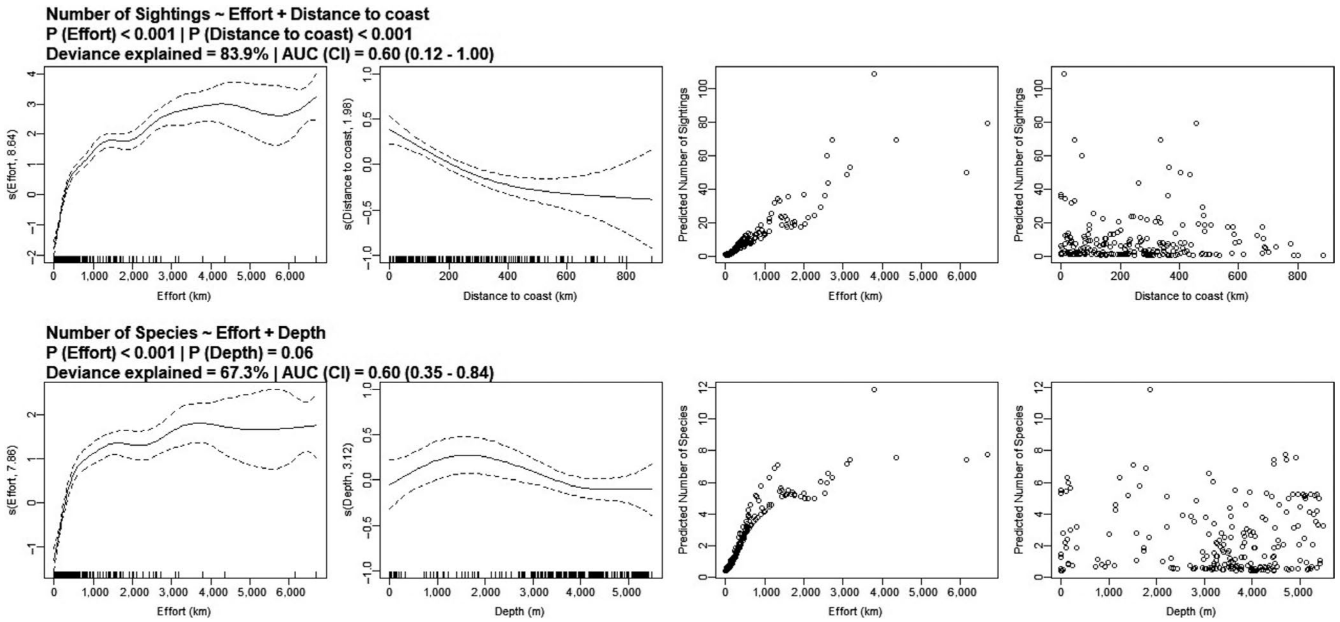


FIGURE 3 GAMs: fitted smoothers and predicted values for (upper panel) number of sightings (per grid cell) versus survey effort and distance to the coast and (lower panel) number of species seen (per grid cell) versus survey effort and water depth. Totals for each variable were calculated over the whole study period for each cell within a grid of 100 × 100 km cells

871 km from the coast, in northern latitudes and at longitudes ranging from 28.62° W to 8.33° W. Common dolphin was the species generally seen furthest to the north and to the east, in the shallowest waters and closest to the coast. Bottlenose dolphins and pilot whales also occurred relatively close to the coast. Common and bottlenose dolphins showed the broadest distribution in terms of sea depth, while pilot whales and sperm whales were associated with more southerly latitudes than the other species. The two *Stenella* species along with Cuvier's beaked whale and minke whale tended to be found in deeper waters (Figure 6 and Table S2).

In the PCA, the first two PCs together explained of 78.3% of variation. The SDFs that contributed the most to PC1 were depth and distance to coast, while PC2 was mainly related to the geographical SDFs (latitude and longitude). Species with higher PC1 scores are found in deeper waters and further from the coast and the species with higher PC2 scores occur more in northern and eastern regions of the study area (Table 2).

Common and bottlenose dolphins had similar PC1 scores but are significantly different according to PC2, essentially confirming the distribution described above and evident in Figure 6. The two species of the genus *Stenella* sp. had similar scores on both PCs, significantly different from those of bottlenose and common dolphins. The PCA results also highlight the similarity of pilot whale and sperm whale distributions (Figures 6 and 7 and Tables S2 and S3).

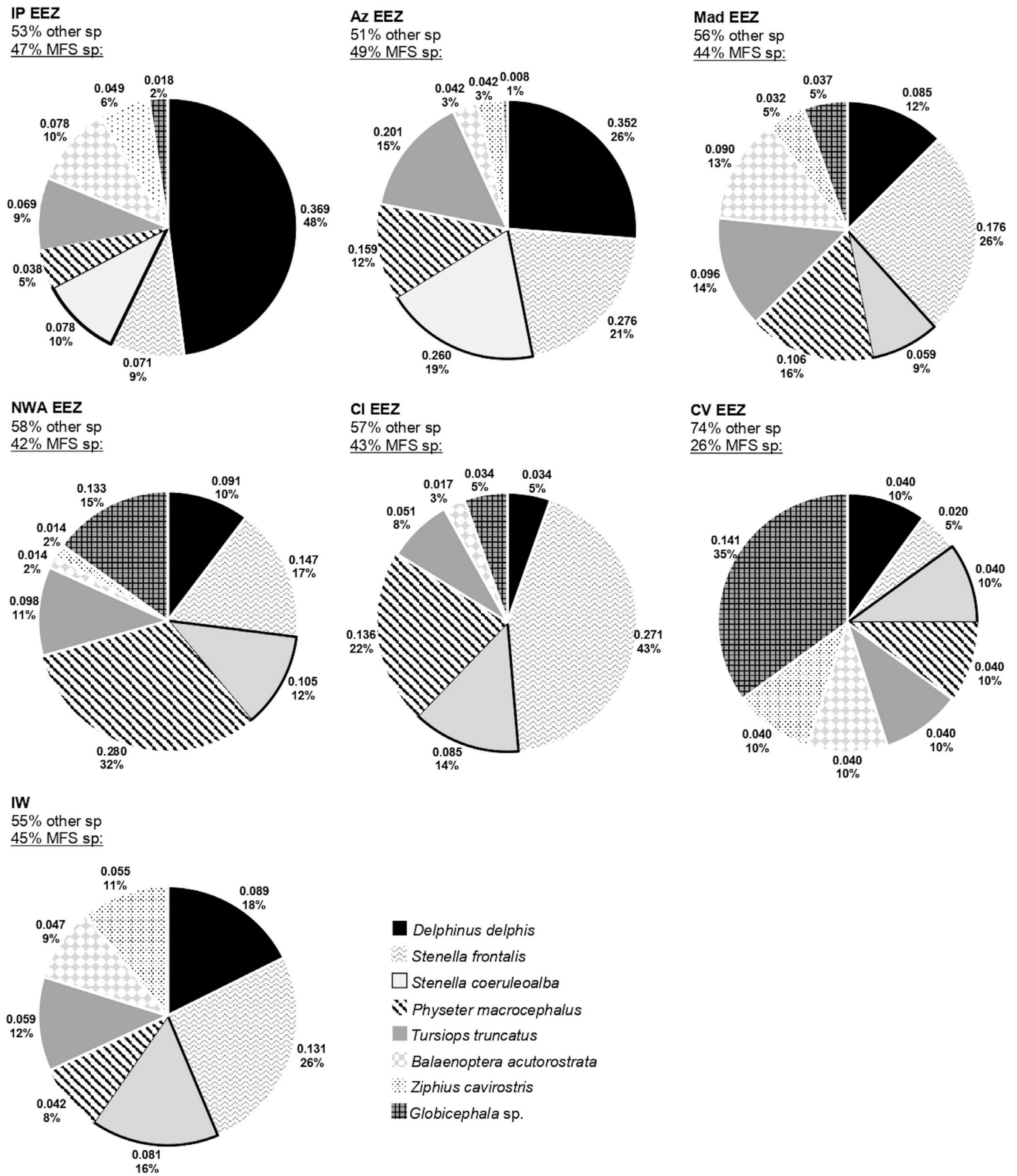
4 | DISCUSSION

The number of species reached a plateau at a high amount of effort (approximately 3,000 km per 100 km^2), while, as expected, number of sightings increased with effort. Even though the overall survey effort in this study was high, it was spatially heterogeneous. Consequently, over much of the study area (i.e. the parts with less surveyed effort), the confidence intervals around estimates of relative local abundance and local cetacean species diversity are wide. In less surveyed areas around the globe, such as offshore waters, cetacean abundance and species richness are likely to be underestimated.

Results confirm the high cetacean diversity previously reported for continental shelf waters within the ENA (e.g. Alves, Ferreira, et al., 2018; Brito & Sousa, 2011; Carrillo et al., 2010; Correia et al., 2015; Djiba et al., 2015; Freitas et al., 2012; Hazevoet et al., 2010; Hazevoet & Wenzel, 2000; Moura et al., 2017; Perrin & Waerebeek, 2012; Robineau & Vely, 1998; Silva et al., 2014; Tobeña et al., 2016; Weir & Pierce, 2013) and show that high species richness extends into the high seas, with peaks of high species diversity in deeper waters, especially along the Madeira and Azores routes. In fact, in international waters, 16 species were identified (at least, to the genus level), making it the sub-region with the second highest cetacean species diversity, after the EEZs of the north-western Africa.

Higher encounter rates were registered in coastal areas, both on the continental shelves and around the islands, with the Azores EEZ being the sub-region with the highest encounter rate. Model results also showed that number of sightings decreased with increasing distance from coast. It is generally recognized that cetacean abundance tends to be higher in inshore waters. This is related, for example, to the influence of strong coastal upwelling phenomena, as in the case of the Iberian and African Atlantic coasts, and to the island mass effect. This phenomenon is, essentially, the topographic disturbance of oceanic flow by an island which leads to increased phytoplankton

Taxa	IP EEZ	AZ EEZ	MAD EEZ	NWA EEZ	CI EEZ	CV EEZ	IW
Total ER	1.622	2.639	1.208	2.045	1.440	1.533	1.123
No. of species	19	14	12	21	12	14	16
Total effort (km)	44955	11938	18794	14282	5901	4957	23600



biomass (Alves, Ferreira, et al., 2018; Correia et al., 2015; Gove et al., 2016; Moura et al., 2012; Tobeña et al., 2016; Viddi et al., 2010). The lower availability of nutrients may limit pelagic community productivity and biodiversity further offshore, while the increasing separation of seabed and photic zone limits the productivity of demersal and benthic communities in deeper waters (Mason, 2009).

FIGURE 4 Cetacean community composition in each sub-region defined, highlighting encounter rates and percentage relative contribution for the eight most frequently sighted species. Pie charts illustrate the encounter rates and percentage of contribution of the most frequently sighted species (identified, at least, to the genus level) for each sub-region (defined in Figure 3). Occurrences with associated species were used to calculate the encounter rate of both taxa only if at least one of the taxa sighted was among the eight most frequently sighted species over the whole study area. ER, encounter rate (sightings per 100 km); sp, species; MFS, most frequently sighted; EEZ, Economic Exclusive Zone; IP, Iberian Peninsula; Az, Azores archipelago; Mad, Madeira archipelago; NWA, north-west Africa; CI, Canary Islands archipelago; CV, Cape Verde archipelago; IW, international waters

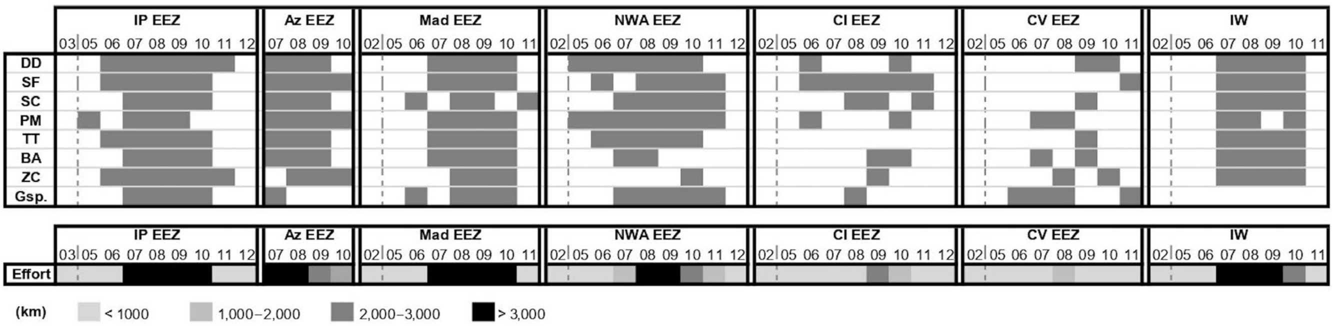


FIGURE 5 Temporal presence of the most frequently sighted species by sub-regions (defined in Figure 3). The occurrences where the species were associated with other taxa were considered. DD, *Delphinus delphis*; SF, *Stenella frontalis*; SC, *Stenella coeruleoalba*; PM, *Physeter macrocephalus*; TT, *Tursiops truncatus*; BA, *Balaenoptera acutorostrata*; ZC, *Ziphius cavirostris*; Gsp., *Globicephala* sp. EEZ, Economic Exclusive Zone; IP, Iberian Peninsula; Az, Azores archipelago; Mad, Madeira archipelago; NWA, north-west Africa; CI, Canary Islands archipelago; CV, Cape Verde archipelago; IW, international waters. For each sub-region, only surveyed months are shown. There were no surveys in January or April in any sub-region

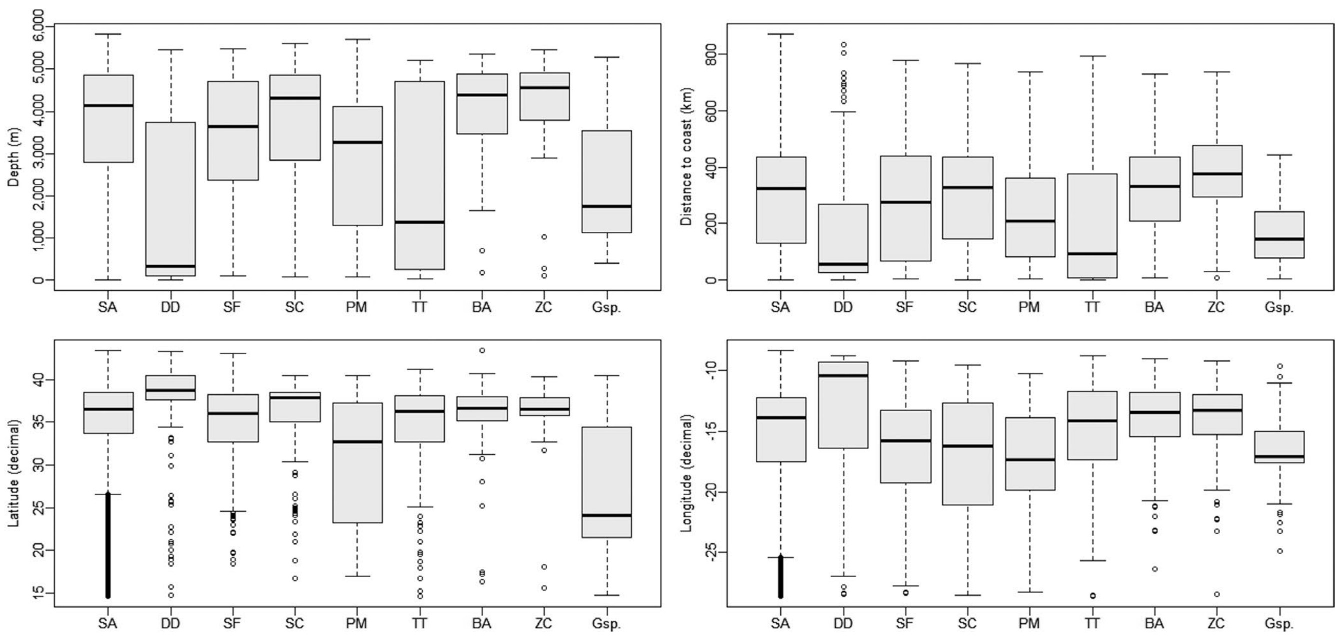


FIGURE 6 Boxplots of species distribution factors (SDFs) for the eight most frequently sighted species. Values of the SDFs were extracted to the position of the occurrence records. The occurrences where the species were associated with other taxa were included in the analysis. The lower 25% and the upper 25% scores are represented by the whiskers, and grey box represent the central 50% of the scores (with median represented by a black line). Outlier scores are illustrated by the circles. SA, surveyed area; DD, *Delphinus delphis*; SF, *Stenella frontalis*; SC, *Stenella coeruleoalba*; PM, *Physeter macrocephalus*; TT, *Tursiops truncatus*; BA, *Balaenoptera acutorostrata*; ZC, *Ziphius cavirostris*; Gsp., *Globicephala* sp

Common dolphin was the most frequently encountered species in this study, as well as the species with the biggest group size. It was also the most frequently sighted species in the EEZs of the Iberian Peninsula and Azores, where it has been often reported as the most abundant cetacean species (Correia et al., 2015; Giralt Paradell, Díaz López, & Methion, 2019; Moura et al., 2012, 2017; Silva et al., 2014). Although most commonly seen close to the coast in relatively shallow waters, common dolphins were also

TABLE 2 PCA results for species distribution factors (SDFs) of the most frequently sighted species

	PC1	PC2	PC3	PC4
Depth	46.193	3.207	1.022	49.578
Distance to coast	46.852	2.498	0.342	50.309
Latitude	5.973	41.835	52.008	0.104
Longitude	0.983	52.460	46.548	0.009
Eigenvalue	1.880	1.250	0.700	0.170
Percentage of variation explained	47.009	31.242	17.504	4.244
Accumulated % variation explained	47.009	78.252	95.756	100.000

Note: Eigen vectors and coefficients of each SDF are indicated for each principal component. Those occurrence records where a species was associated with other taxa were included in the analysis (i.e. as occurrence records for all species in the mixed group).

recorded offshore and in very deep waters. Previous analysis using the CETUS dataset from 2012 to 2016 showed that the species presents clear core areas of occurrence, related to specific environmental conditions (e.g. coastal colder waters related to strong coastal upwelling systems) (Correia, Gil, et al., 2019). Within its range in the ENA, the northern Continental Portugal remains a poorly studied area.

Bottlenose dolphins preferred shallower waters in areas closer to the coast, but also extended over a very wide range of depths, being frequently recorded in the high seas. Genetic studies have shown that resident populations in Galicia and the Sado Estuary are likely to have a strong degree of genetic isolation from the populations in the archipelagos and non-resident individuals. On the other hand, there is high gene flow among the Iberian archipelagos (Fernández, Santos, et al., 2011). Transient individuals have been identified in the archipelagos of Madeira and Azores (Dinis, Alves, et al., 2016; Dinis, Carvalho, et al., 2016; Silva et al., 2014), and some individuals from resident populations in Iberia Peninsula were found to undertake long-distance movements (Fernández, Santos, et al., 2011). Bottlenose dolphins are listed under Annex II of the EU Habitats Directive (Directive 92/43/CEE), so Member States are required to designate Special Areas of Conservation for the protection of the species. In addition, we need to understand the wider movements of bottlenose dolphins and assess their habitat use in high seas to identify important areas beyond the continental platform, and potentially beyond national jurisdiction. Fernández, García-Tiscar, et al. (2011) highlighted that different populations inhabiting different areas (coastal versus oceanic) may present distinct habitat use, which should be considered when designing and implementing conservation measures.

In Madeira, the Canary Islands and international waters, the Atlantic spotted dolphin was the most frequently sighted species, with a similar distribution to that of striped dolphin; both occurred in deeper areas further from the coast. Their occurrence in international waters may indicate a high gene flow among sub-regions. The fact that these species are less frequent during winter in the Portuguese archipelagos (Alves, Ferreira, et al., 2018; Silva et al., 2014) suggests that international waters are even more important during this season.

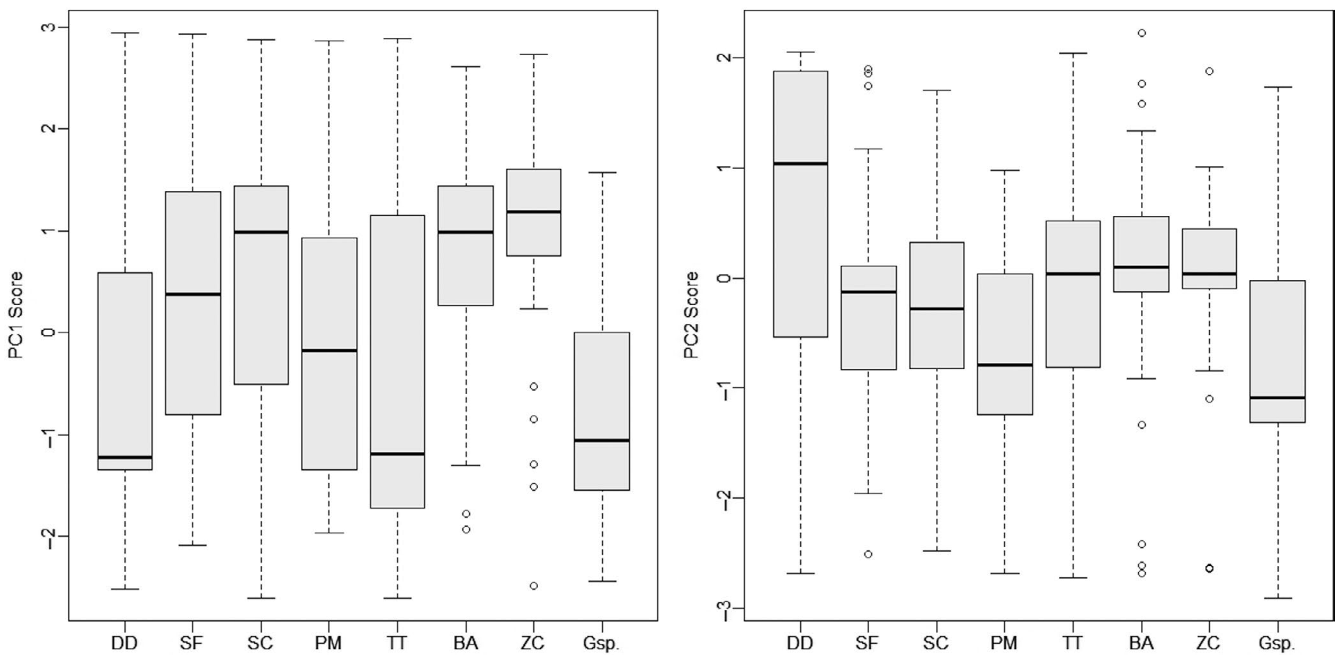


FIGURE 7 Boxplots of PC scores for the eight most frequently sighted species. The occurrences where the species were associated with other taxa were included in the analysis. The lower 25% and the upper 25% scores are represented by the whiskers, and grey box represent the central 50% of the scores (with median represented by a black line). Outlier scores are illustrated by the circles. DD, *Delphinus delphis*; SF, *Stenella frontalis*; SC, *Stenella coeruleoalba*; PM, *Physeter macrocephalus*; TT, *Tursiops truncatus*; BA, *Balaenoptera acutorostrata*; ZC, *Ziphius cavirostris*; Gsp., *Globicephala* sp

Sperm whale was the most abundant cetacean in the EEZs of north-western Africa, which is consistent with previous surveys in Mauritania (Baines & Reichelt, 2014; Camphuysen, van Spanje, & Verdaat, 2012). North-west Africa is a hotspot area for the species, where it has an important role in ecosystem functioning (Morissette, Kaschner, & Gerber, 2010). Several marine management issues, mostly related to inefficient management of fisheries, exist in the EEZs of north-western Africa (Nagel & Gray, 2012). As, according to our results, sperm whales seem to occupy areas closer to the coast, it is likely that their area of occupancy overlaps with areas of intensive fishing, which can have negative consequences for both the animals and the economic activity (Karpouzli & Leaper, 2004; Richard, Guinet, Bonnel, Gasco, & Tixier, 2017; Tixier et al., 2019). The latest IUCN global assessment has determined that sperm whales are vulnerable (www.iucnredlist.org). Thus, there is a need to evaluate anthropogenic impacts on sperm whales in the north-west coast of Africa.

Pilot whales were the most frequently encountered cetacean taxon in the Cape Verde EEZ, where several reports of mass strandings of these animals are reported in the literature (Hazevoet et al., 2010). Alves, Alessandrini, et al. (2018) reported on the ecological connectivity of short-finned pilot whales in Macaronesia (between Azores and Madeira, and between Madeira and Canaries). If the species is capable of moving between Madeira and the Azores, connectivity between Cape Verde and the remaining Macaronesian archipelagos is also plausible and should be investigated. In the present study, no pilot whales were seen in international waters which potentially indicates that their occurrence is mostly restricted to the EEZs (although evidently crossing areas beyond national jurisdiction at least to move between sub-regions, perhaps travelling during the winter).

In general, minke whales showed a preference for very deep waters distant from the coast. The oceanic distribution of this species in the ENA, most likely related to its migratory routes, evidently needs further investigation (Valente, Correia, Gil, Gonzalez-Garcia, & Sousa-Pinto, 2019; Van Waerebeek et al., 1999; Vikingsson & Heide-Jørgensen, 2015). Like the minke whale, Cuvier's beaked whale was also found in areas of deep water distant from the shore. Geographically, both were mostly distributed in western and northern areas, and rarely seen in more tropical waters.

Cuvier's beaked whale was the species of Ziphiidae most frequently sighted during the CETUS campaigns. The status of the species worldwide, and specifically in European waters, is "Data Deficient" (www.iucnredlist.org), revealing the need for further baseline information on occurrence and distribution. The species was encountered most extensively (from June to November) in the Iberian Peninsula EEZ. However, the encounter rate was highest in international waters, highlighting the need to expand sampling efforts into areas beyond national jurisdiction in order to monitor (and ultimately conserve) Cuvier's beaked whale populations in the ENA.

The development of cost-effective monitoring programmes in high seas areas, for example based on the use of OPOs, would help ensure continuity of monitoring to underpin long-term management (Aïssi et al., 2015; Alves, Ferreira, et al., 2018; Correia et al., 2015; Evans, Hammond, 2004; Kiszka et al., 2007; Morgado et al., 2017; Moura et al., 2012; Tobeña et al., 2016; Viddi et al., 2010). Nevertheless, it is important to acknowledge the limitations of non-dedicated surveys. Thus, in the present study, monitoring was limited by the company's schedule and routines. Surveyed routes are thin lines crossing a very wide area, with survey effort covering only a subset of the habitats in the region. Moreover, as in all marine campaigns, survey effort was also conditioned by the weather. The results presented here are mostly representative of cetacean distribution from July to October. Southern areas were less represented and, consequently, the distribution of tropical species was also less represented. The monthly encounter rates and number of species presented a high inter-annual variation, reflecting the heterogeneity of effort, both in space and in time.

Use of OPOs could be complemented by tagging programmes, new technological approaches such as monitoring through automated vehicles and cheap non-invasive techniques such as photo-ID and environmental DNA (Bohorquez, Dvarskas, & Pikitch, 2019).

Worldwide, conservation of cetacean species is mostly focused in areas of national jurisdiction and there is a huge difference in the relative extent of protected areas between waters beyond national jurisdiction and those within the EEZs (1.2% against 16.8%, UNEP-WCMC, IUCN, & NGS, 2018). However, it is evident that international waters play a fundamental role in the cetacean community of the ENA, and further investigation of cetacean use of the entire area is needed. International agreements are essential to ensure cetacean conservation in international waters, obtain baseline data, assess population status and, where necessary, design and implement management measures.

Another challenge is dealing with the dynamism of cetacean distribution related to their life history, migration and movements, which may call for dynamic marine-protected areas. This in turn requires adaptive marine management (Hooker et al., 2011) and is probably not yet feasible in EU waters. Ultimately, to ensure the conservation of species, it would be desirable to define year-round protected areas for all the core habitats of those species (even if they are only used/ preferred during a specific season). Moreover, besides knowledge on occurrence, abundance and habitat use, the assessment of threats (i.e. by-catch, entanglement, collision), at least in core areas of occurrence, is also essential to design specific conservation measures for effective marine management (Díaz López et al., 2019).

We have to recognize the gap between monitoring and mitigation, and specifically that we cannot solve or provide solutions for all the challenges of marine management and conservation in the high seas. Effective measures in offshore waters, and specifically in areas beyond national jurisdiction, are limited by logistic and political factors (Bohorquez et al., 2019). Nevertheless, the present work may be useful for the design of future dedicated campaigns, to efficiently construct a monitoring programme including both areas within the EEZs and in international waters and to support conservation and management efforts in the area. The CETUS Project is ongoing and aims to continue providing updated and reliable data, such as effort-based relative abundances, that could be used as indicators for management purposes (e.g. Marine Strategy Framework Directive), and to construct a long-term dataset. Moreover, this effort-related dataset is key to understanding the distribution of cetaceans in the area and should permit the development of ecological niche models and enable prediction of the consequences of future climate change scenarios for these species, in support of the European agenda for the conservation of marine ecosystems.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in VLIZ, and distributed by OBIS and EMODnet, at https://doi.org/10.14284/350; see also the associated data paper (Correia, Gandra, et al., 2019). Moreover, supplementary material is provided for a complete and detailed description of the dataset.

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BIOSKETCH

Ana Mafalda Tomás Correia has been working with cetacean ecology since 2011, focusing on their biogeography and on ecologic niche modelling. The data here presented were collected within CETUS Project, a monitoring programme led by the research centre, CIIMAR. Among other topics related to cetacean ecology, the authors of this paper study cetacean distribution and habitat within the eastern North Atlantic.

Author contribution: Correia A.M. and Pierce G.J. conceived the ideas and led the writing; Correia A.M., Gil Á. and Valente R. collected the data; Correia A.M., Gil Á., Valente R. and Pierce G.J. analysed the data; Rosso M., Sousa-Pinto I. and Pierce G.J. supervised work from data collection to data publication.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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