Multi-scale analysis reveals changing distribution patterns and the influence of social structure on the habitat use of an endangered marine predator, the sperm whale *Physeter macrocephalus* in the Western Mediterranean Sea.

Enrico Pirotta [a,b*], José María Brotons [c], Margalida Cerdà [c], Sanne Bakkers [d], Luke E. Rendell [d]

[a] Department of Mathematics and Statistics, Washington State University, Vancouver, WA, USA

[b] School of Biological, Earth and Environmental Sciences, University College Cork, Cork, Ireland

[c] Asociación Tursiops, Palma de Mallorca, Balearic Islands, Spain

[d] Sea Mammal Research Unit, School of Biology, University of St Andrews, St Andrews, Scotland, UK

*Corresponding author: Department of Mathematics and Statistics, Washington State University, 14204 NE Salmon Creek Avenue, Vancouver, WA 98686, USA; enrico.pirotta@wsu.edu

Abstract

The habitat use of marine megafauna emerges from the complex interplay between access to patchy and variable food resources and several intrinsic biological factors, such as the interaction with conspecifics and offspring care, resulting in dynamic distribution patterns. Quantifying species' relationships with the underlying environment is further complicated by the scale-dependent nature of these processes. Multi-scale analyses that incorporate aspects of a species' biology and build on large datasets are therefore required to understand long-term distribution and inform appropriate management measures. In this study, we use monitoring data collected over two study periods (2003-2008 and 2012-2018) to assess the habitat use, trend in local occurrence, and change in distribution of sperm whales, *Physeter macrocephalus*, around the Balearic Islands (Spain), one of the few recognised breeding and feeding grounds for the 'Endangered' population in the Mediterranean Sea. Moreover, we investigate the differences in the habitat use of single animals and groups, to explore intra-specific niche partitioning in this highly social but behaviourally dimorphic species. Results suggest that overall the occurrence of sperm whales in the area has been increasing over time. Animals were found to associate with distinct bathymetric features, but the mechanisms generating these relationships, and the underlying oceanographic processes within this habitat, remained uncertain. Sperm whale distribution also underwent a significant shift between the two study periods, with an increased occurrence in the Mallorca channel and north of Menorca, which further points towards a dynamic use of the broader bathymetric range preferred around the archipelago. Finally, our analyses highlighted that single animals and groups used areas with different characteristics, with groups preferring deeper, warmer waters characterised by lower sea level anomaly, which resulted in some fine-scale spatial segregation. The results of this study shed light on the mechanisms underpinning the biogeography and complex social system of the species, and support the design of targeted conservation measures in this important breeding and feeding ground.

Keywords: Habitat modeling, Distribution shift, Long-term monitoring, Sperm whale, Mediterranean Sea, Balearic archipelago.

1. Introduction

Quantifying the relationships between spatio-temporal patterns of animal occurrence and the underlying environment is central to the understanding of a species' ecology (Guisan and Thuiller, 2005). However, habitat modelling generally relies on data that have been collected within a limited time frame and therefore only provides a snapshot of the distribution of a species, unless multiple surveys are combined (Yates et al., 2018). Moreover, both habitats and habitat use can be dynamic, and therefore the importance of different areas can change over time (Roshier and Reid, 2003). This is particularly true for marine megafauna, which can often adjust their habitat use as intrinsic (e.g., population size, habitat knowledge) and extrinsic (e.g., environmental quality) conditions change (Runge et al., 2014). For these species, data collection tends to be constrained to short spatial and temporal windows by logistic and financial limitations (Yates et al., 2018), which restricts our ability to appropriately describe their distribution and complicates the development of effective conservation measures (Lewison et al., 2015; Wilson, 2016). Understanding the dynamic nature of a species' distribution and the degree of plasticity is particularly important as the marine environment is undergoing unprecedented change as a result of climate change (Hazen et al., 2013).

Mechanistically, the availability and abundance of prey resources is one of the major drivers of the movements and distribution of marine predator populations, including marine mammals (Sequeira et al., 2018). Often, prey cannot be sampled at appropriate resolutions (Redfern et al., 2006), but marine mammal occurrence tends to associate with the oceanographic features that affect prey patterns, which can in turn be used in statistical models as proxies of the underlying processes (Elith and Leathwick, 2009). However, identifying the relevant spatio-temporal scale for representing these indirect relationships is challenging (Scales et al., 2017), and the dynamic nature of predator and prey distribution may mean that suitable proxies change over space and time. Intrinsic biological drivers also play a role in determining the observed use of space (Cañadas and Hammond, 2008; Guisan and Thuiller, 2005; Palacios et al., 2014). For example, marine mammals may adjust their distribution to ensure safety for their offspring, interact with members of the same social group, or in response to intra-specific competition for food resources. Intrinsic drivers expressed in behaviour therefore add a layer of complexity that further confounds the relationships with concurrent environmental features. The investigation of intra-specific differences in habitat use could shed light on the forces that regulate interactions with conspecifics and, potentially, the evolution of current biogeographical patterns.

The sperm whale (*Physeter macrocephalus*) is a cosmopolitan cetacean species found across the world in deep waters beyond the shelf edge, where bathymetric and oceanographic features interact to promote upwelling, nutrient mixing and, ultimately, secondary productivity and prey concentrations (Whitehead, 2018). As a result, sperm whales are often encountered in association with steep continental slopes, submarine canyons and seamounts, as well as frontal systems and other mesoscale features such as cyclonic eddies (e.g., O'Hern and Biggs, 2009; Skov et al., 2008; Waring et al., 2001; Wong and Whitehead, 2014), but relationships can be obscured by analyses at inappropriate scales that do not match the spatial and temporal scale at which these oceanographic processes occur (Jaquet, 1996). This species is also characterised by a complex, sexually dimorphic social system, whereby females form strong social units that remain at lower latitudes (< 40°), while males become increasingly solitary as they grow older, migrating to higher latitudes to find food resources that can support their larger size (Whitehead 2003). The evolution of sperm whale social structure may have been promoted by intra-specific competition between males and females, as suggested by observations of lower feeding success of males in areas where they co-occur with females (Whitehead 2003). In turn, strong female social bonds are believed to be the basis for the development of one of the recognized examples of non-human culture (Rendell and Whitehead, 2003; Whitehead and Rendell, 2014), which can also affect patterns of spatial distribution (Eguiguren et al., 2019; Whitehead and Rendell, 2004).

A small, genetically isolated population of sperm whales inhabits the Mediterranean Sea (Rendell and Frantzis, 2016). This population is subject to intense pressure from the extensive human activities in the basin, leading to ship strikes, entanglement in driftnets, and ingestion of plastic, as well as exposure to noise, and chemical pollution. Consideration of both the size of the population and the threats it faces has prompted its classification as 'Endangered' in the International Union for Conservation of Nature (IUCN) Red List (Rendell and Frantzis, 2016). Previous studies have identified a bimodal distribution in the Mediterranean, characterised by the association with topographic singularities close to the coast, and thermal fronts in offshore areas (Azzellino et al., 2012; Frantzis et al., 2014; Gannier and Praca, 2007; Pirotta et al., 2011; Praca et al., 2009; Tepsich et al., 2014). The latitudinal segregation between sexes is much reduced owing to the limited available latitudinal range in the Mediterranean Sea for the more mobile males to explore (Drouot-Dulau and Gannier, 2007). The Balearic archipelago (Spain) is one of the few areas in the Mediterranean Sea where females and calves as well as single males are regularly observed (Rendell and Frantzis, 2016). This led to its recent identification as an Important Marine Mammal Area (IMMA; https://www.marinemammalhabitat.org/portfolio-item/balearic-islands-shelf-slope/ ; Corrigan et al., 2014), which was informed by some of the data presented here. In this area, female groups and single males appear to segregate at a fine spatial scale (Jones et al., 2016).

Pirotta et al. (2011) analysed monitoring and encounter data collected over six consecutive years (2003-2008) around the Balearic archipelago to describe the distribution patterns of the species in this important breeding and feeding ground. In this study, we complement the original dataset with data collected over a subsequent study period of seven years (2012-2018), to evaluate sperm whale medium-term habitat use in the area and assess changes in their occurrence and distribution over time. In addition, we use information on social grouping to investigate the environmental variables associated with the occurrence of groups (mostly females and young individuals) and single animals (likely males), and shed light on the processes that regulate the observed fine-scale segregation. Our results can inform effective management strategies in the region, and support the conservation of the population in the Mediterranean Sea.

2. Material and methods

2.1 Data collection

Data collection methods followed the procedures described in Pirotta et al. (2011). Briefly, dedicated research cruises were carried out in the summer months over two study periods, 2003-2008 and 2012-2018 (Table 1 and Fig. A.1), from 11- to 15-m-long motor-sailing yachts travelling at a speed of approximately 6 knots. Sperm whale presence was monitored acoustically every 30 min using, in 2003, a single dipping hydrophone (Sensor Technology of Canada; frequency response 0.1–22 kHz) and, from 2004 onward, a dual-element towed hydrophone (Benthos AQ4; frequency response 0.1–22 kHz) towed at 100 m. Hydrophones deployed at similar speeds and from similar vessels typically settle at around 10 m depth. Transects were not systematically designed, but extensively covered the shelf-break waters around the archipelago

(Fig. 1). Detection range was unknown, but previous work in the Mediterranean has estimated an effective strip half-width of 10 km (Lewis et al., 2007). Whenever sperm whales were heard, dedicated software (RainbowClick by the International Fund for Animal Welfare (IFAW) before 2012; http://www.marineconservationresearch.co.uk/downloads/logger-2000-rainbowclick-software-downloads/; and PAMGuard https://www.pamguard.org/ from 2012 onward) was used to track and, during daylight hours, approach the animals. An encounter was defined as a period of continuous acoustic contact with the animals, from initial detection to a loss of contact greater than 1 h (either inadvertent or deliberate once all desired data were collected). Searching effort was then generally resumed along the previous route. Encounters with single individuals were distinguished from encounters with groups, defined as individuals (often including young animals) engaging in direct interaction or ‘moving together in a coordinated fashion over periods of at least hours’ (Whitehead, 2003).

Year	**Study period**	**Research period (on-effort)**		**Searching effort (km)**	**Encounters (km)**	**Encounters with groups**	**Encounters with single animals**
2003	1	03-Aug	26-Aug	2467	141	2	1
2004		11-Jul	05-Aug	2070	310	3	6
2005		10-Jul	04-Aug	1992	392	5	7
2006		16-Jul	27-Jul	1702	270	2	7
2007		06-Jul	28-Jul	1835	374	0	11
2008		15-Jul	27-Jul	1033	233	6	6
2012	2	01-Aug	14-Aug	1224	57	1	3
2013		06-Jul	09-Aug	1460	451	7	18
2014		05-Jul	15-Aug	1046	432	16	7
2015		18-Jul	06-Aug	1559	407	3	18
2016		05-Jul	26-Aug	2340	601	7	26
2017		01-Jul	24-Sep	2463	592	5	24
2018		15-May	23-Sep	2379	591	12	11

Table 1. Summary of survey effort and encounters per year.

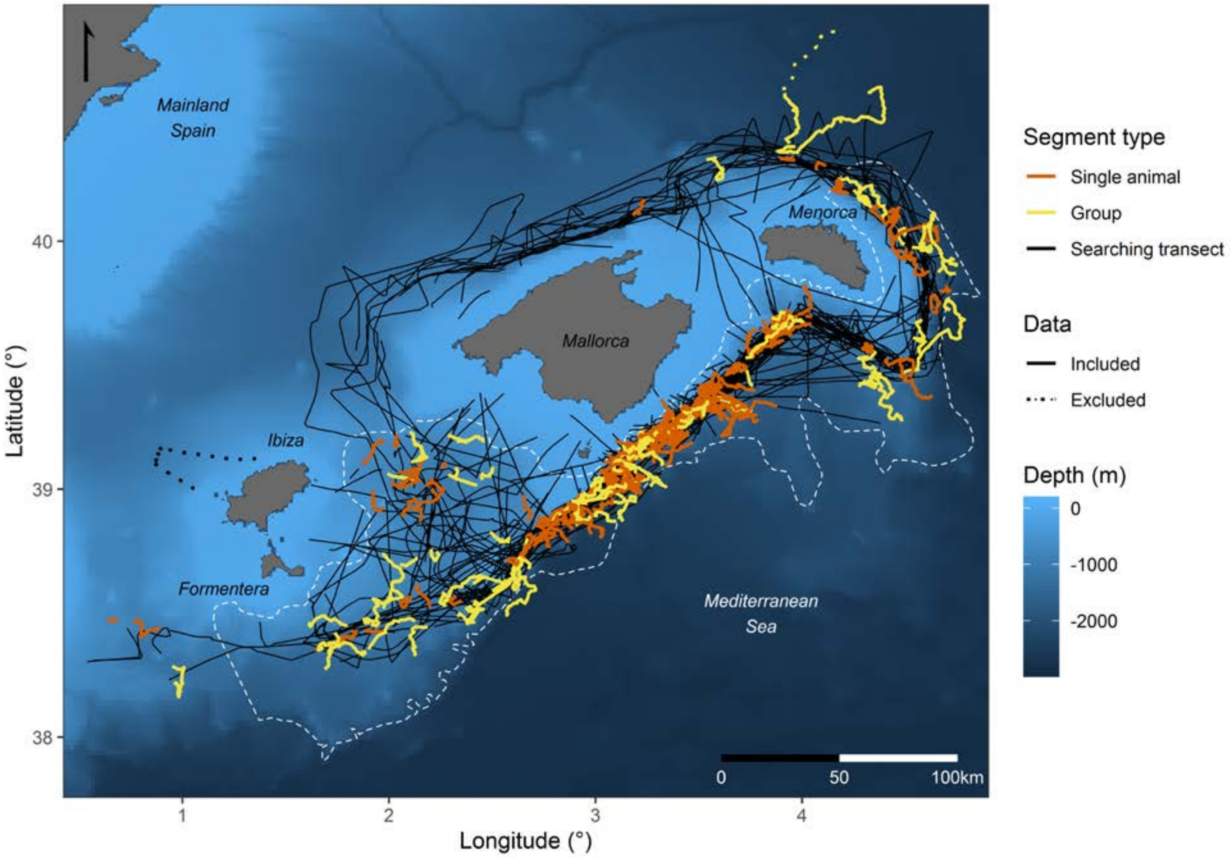

Figure 1. Study area, acoustic searching effort and encounters with group and single sperm whales in the period 2003-2018. Dotted segments indicate data that were excluded from subsequent analyses. The white, dashed line indicates the boundaries of the Important Marine Mammal Area (IUCN-MMPATF, 2017).

2.2 Data processing

For consistency with previous analyses, data were processed following the procedure described in Pirotta et al. (2011). When the hydrophone was not in the water or no systematic acoustic monitoring was conducted, corresponding GPS locations were discarded as off-effort. After preliminary data exploration, we also excluded the limited survey effort north-west of the island of Ibiza and truncated one encounter on 2 August 2004, when whales moved into an area that was never surveyed otherwise, to avoid biasing model results (Fig. 1). On-effort locations were regularised to 20 min intervals using package adehabitatLT (Calenge, 2006) for R (R Core Team, 2019). Points were classified as presences when in acoustic contact with the animals, or absences when no animal was heard, and then grouped into either a follow (that is, a series of consecutive presence points corresponding to an encounter with sperm whales) or a searching transect (that is, a series of consecutive absence points between two follows or off-effort intervals).

Each point was associated with a set of static and dynamic variables, which were chosen to represent the bathymetric and oceanographic processes that characterise sperm whale habitat, and on the basis of their documented relationship with the species' occurrence. These included depth, slope gradient (hereafter slope), slope aspect (hereafter aspect), standard deviation of depth (hereafter rugosity), topographic position index (the difference between depth in a cell and the mean value of the eight surrounding cells; TPI), sea surface temperature (SST), SST deviation from monthly median (to allow whale presence to respond to relative temperatures, because the median SST varied between years, thus better reflecting the choices available to the animals; hereafter SST deviation), SST slope gradient (that is, the steepness of the SST surface, representing potential frontal systems), standard deviation of SST, sea level anomaly (sea surface height above the mean in a twenty-year reference period; SLA), and absolute dynamic topography (instantaneous sea surface height above the geoid; ADT). Depth, slope and aspect were considered at four spatial scales (30 arc-sec, 2.5 arc-min, 5 arc-min, 10 arc-min), while SST was included at two spatial (4 km and 20 km) and two temporal scales (8-day and monthly composites). A description of the available covariates, units, spatio-temporal scales and corresponding datasets is reported in Table 2. Other commonly used environmental variables, such as chlorophyll-a surface concentration, were not included because previous work suggested they were not related to sperm whale occurrence at this scale (Pirotta et al., 2011).

The heterogeneous distribution of searching effort around the archipelago and the variability among years could result in different habitats being surveyed with varying intensity over time, which may confound the relationship between sperm whale occurrence and the underlying environment. To account for this heterogeneity, we developed an effort covariate that summarized the amount of time spent in different sections of the study area in each year. Specifically, we counted the total number of regularised on-effort points that occurred within 0.5° x 0.5° grid cells in each year, and associated each presence and absence point with the effort value for the grid cell it was located in.

Covariate	**Unit**	**Description**	**Origin**	**Spatial scales**	**Temporal scales**
Depth	m	Depth of the seabed	Obtained from the General Bathymetric Chart of the Oceans dataset (GEBCO; http://www.gebco.net), and aggregated at multiple scales (x1, x5, x10, x20) using package raster for R (Hijmans, 2016)	30 arc-sec, 2.5 arc-min, 5 arc-min, 10 arc-min	-
Slope	rise over run	Slope gradient, indicating the maximum rate of change in depth	Calculated from GEBCO dataset using package SDMTools for R (VanDerWal et al., 2014)	30 arc-sec, 2.5 arc-min, 5 arc-min, 10 arc-min	-
Aspect	°	Slope aspect, indicating the	Calculated from GEBCO dataset using package SDMTools for R	30 arc-sec, 2.5 arc-min,	-

		compass orientation of the slope	(VanDerWal et al., 2014)	5 arc-min, 10 arc-min	
Rugosity	m	Standard deviation of depth	Calculated from GEBCO dataset using package raster for R (Hijmans, 2016)	2.5 arc-min	-
TPI	m	Topographic position index, i.e. the difference between the value of depth in a cell and the mean value of the eight surrounding cells	Calculated from GEBCO dataset using package raster for R (Hijmans, 2016)	30 arc-sec	-
SST	°C	Sea surface temperature	Extracted from Moderate Resolution Imaging Spectroradiometer (MODIS) data from NASA's Aqua satellite, processed by the Ocean Biology Processing Group of the Ocean Ecology Laboratory at NASA Goddard Space Flight Center (available at http://oceancolor.gsfc.nasa.gov/)	4 km, 20 km	Monthly and 8-day composites
SST deviation	°C	Deviation of the sea surface temperature in each cell from the monthly median	Calculated from MODIS-Aqua data using package raster for R (Hijmans, 2016)	4 km	Monthly

SST slope gradient	rise over run	Rate of maximum change in sea surface temperature	Calculated from MODIS-Aqua data using package SDMTools for R (VanDerWal et al., 2014)	4 km	Monthly and 8-day composites
Standard deviation of SST	°C	Variation in SST across a window of five cells	Calculated from MODIS-Aqua data using package raster for R (Hijmans, 2016)	20 km	Monthly and 8-day composites
SLA	m	Sea level anomaly, i.e. sea surface height above the mean sea surface in a twenty-year reference period (1993-2012)	Obtained from the Copernicus Climate Data Store (CDS), operated by the European Centre for Medium Range Weather Forecasting on behalf of the European Union (https://cds.climate.copernicus.eu/)	0.125°	Daily
ADT	m	Absolute dynamic topography, i.e. the instantaneous height above the geoid	Obtained from the Copernicus Climate Data Store (CDS), operated by the European Centre for Medium Range Weather Forecasting on behalf of the European Union (https://cds.climate.copernicus.eu/)	0.125°	Daily

Table 2. Description of environmental variables used for the analysis of sperm whale habitat use, including units, origin of the data, and spatio-temporal scales.

2.3 Statistical analysis

We structured the statistical analysis in three parts. First, we investigated the relationships between sperm whale overall distribution and available environmental covariates, modelling sperm whale acoustic presence or absence at each location. Secondly, we assessed whether there was any evidence of a change in distribution between the two study periods using a geographical surface, that is, a two-dimensional smooth of latitude and longitude. While the overall habitat use analysis could also highlight changes in distribution over time, this second model allowed us to explicitly test whether the animals were using different portions of the study area in the two periods. Finally, we evaluated any difference in the habitat used by single animals compared to groups. All analyses were carried out using package MRSea for R (Scott-Hayward et al., 2015), which uses a Spatially Adaptive Local Smoothing Algorithm (SALSA) with cross-validation to fit one-dimensional B-splines and Complex Region Spatial Smoothers (CReSS) (Scott-Hayward et al., 2014; Walker et al., 2011). In all analyses, locations spaced every 20 min were used as the unit of analysis, and the response variable had a binary distribution, which was modelled using a logit link function. Data from 2003-2008, which have already been presented in Pirotta et al. (2011), were reanalysed under the updated modelling framework to ensure that results could be compared between the two study periods.

2.3.1 Overall habitat use

All explanatory variables were standardised to facilitate model convergence. Potential issues of multicollinearity among available covariates were assessed using the variance inflation factor (VIF) and pairwise correlation plots, with values of VIF ≥ 2 and correlation ≥ 0.6 taken to indicate collinearity. Separate models including each of the collinear variables were fitted in MRSea, and the Akaike information criterion (AIC) used to compare model pairs. The same procedure was used for variables available at multiple spatial or temporal scales. The full model then included all non-collinear environmental variables, as well as the effort covariate and year. Aspect was included as a cyclic spline, to reflect the circular nature of this angular measurement.

For each one-dimensional smoother, SALSA uses cross-validation to identify the optimal number and location of knots. The algorithm also evaluates whether the model is improved by alternatively including each variable as a linear term (rather than smooth), or by removing it altogether.

The autocorrelation function (ACF) plot was used to assess the degree of autocorrelation in model residuals, and the final model was refitted as a working independence model in a Generalised Estimating Equations (GEE) framework (Hardin and Hilbe, 2003), where follows and searching transects represented blocks of correlated data points. Under this framework, a sandwich variance estimator provides robust estimates of precision that account for the observed degree of autocorrelation within each block (Hardin and Hilbe, 2003). The significance of retained smooths was evaluated using Wald's tests based on robust standard errors, and the performance of the final model was assessed using a confusion matrix, comparing predicted to observed sperm whale occurrence at each location. The area under the receiver operating characteristic (ROC) curve (AUC), calculated using package ROCR for R (Sing et al., 2005), offered an additional measure of goodness-of-fit.

The estimated relationships between retained explanatory variables and the binary occurrence of sperm whales were visualized using partial residuals plots, where 95% confidence intervals were calculated using a parametric bootstrap of the GEE results (Pirotta et al., 2011; Scott-Hayward et al., 2015); retained covariates were back-transformed to the original scale for ease of interpretation. Model predictions were mapped for each study period using a regular grid of 0.01° x 0.01° cells, cropped to the geographical area covered by survey effort in those years. Values of retained explanatory variables were extracted at the centroid of each cell, and standardised according to the mean and standard deviation in the original data. For dynamic variables, the mean in the month of July (i.e., the median month in each period, and the most consistently data-rich month across the study period) across the years in each of the two study periods was used for predictions. Uncertainty in model predictions was plotted using 95% confidence intervals obtained from a parametric bootstrap of the GEE results.

2.3.2 Change in distribution in the two study periods

The change in distribution of sperm whales between the two periods was investigated using the interaction between a CReSS smooth (that is, a bi-dimensional surface of geographic coordinates) and a categorical variable for study period, effectively fitting two separate spatial surfaces. A range of starting knots for the CReSS surface (4, 8, 12 or 16) was tested, which is advised to avoid the algorithm converging on local minima or maxima (Scott-Hayward et al., 2015). Standardised effort was also included as a one-dimensional smooth term. A similar procedure to the one described for the overall habitat model was followed for model selection, validation and prediction. Due to computing limitations related to the calculation of the distance matrix required by CReSS, spatial predictions were visualised on a coarser grid of 0.1° x 0.1° cells.

2.3.3 Differences between groups and single animals

The third part of the analysis focused on presence points only. Encounter locations with groups were classified as 1s, while encounter locations with single animals were classified as 0s. The binary occurrence of groups (versus single animals) was then modelled as a function of environmental covariates following the same analytical procedure described for the analysis of sperm whale overall habitat use.

We then assessed the extent of the spatial overlap between groups and single animals using Bhattacharyya's affinity (BA), where 0 corresponds to no overlap and 1 to complete overlap (Bhattacharyya, 1943; Grecian et al., 2018). Following Grecian et al. (2018), the bivariate kernel utilization distribution of groups and singletons was calculated (package adehabitatHR for R), with smoothing parameter equal to 10 km and a grid of 1 x 1 km cells. BA for the two utilization distributions was compared to a null distribution obtained by randomly reassigning encounters to the two groupings and recalculating the utilization distributions 1000 times. This procedure generated the expected distribution of BA values in the absence of segregation between groups and singletons.

Finally, for each follow, we calculated the bearing (that is, the angle measured from the north) between the location of first acoustic contact and the last location, which provided a proxy for the direction of the whales' movements during that encounter. The resulting angles were plotted for all encounters, as well as separately for encounters with single animals and groups, using rose diagrams (package circular for R; Agostinelli and Lund, 2017). We used the Rayleigh test to assess whether angles were uniformly distributed (Ruxton, 2017). Analysis code is available via the Open Science Framework (https://osf.io/x5afs/).

3. Results

Over the course of 13 research seasons, 23,570 km were covered looking for sperm whales (11,099 km in the first study period, and 12,471 km in the second; Table 1). Sperm whales were encountered acoustically on 214 occasions (56 in the first study period, 158 in the second), for a total of 4,851 km travelled following animals.

3.1 Overall habitat use

Multicollinearity was identified for slope and rugosity, SLA and ADT, SST slope gradient and the standard deviation of SST, as well as between the same environmental variables at different spatial or temporal scales. Comparison of models including each of the collinear variables in a pair led to an initial full model that included effort, year, depth (30 arc-sec), slope (2.5 arc-min), aspect (5 arc-min), TPI, monthly SST (4 km), SST deviation, SLA, and the standard deviation of monthly SST. The SALSA algorithm retained all variables as smooth terms, with the exception of TPI, which was retained as a linear term. The splines for all other variables were characterised by 4, 2, 2, 2, 6, 2, 6, 5, and 2 internal knots, respectively. The ACF plot suggested that there was large autocorrelation in model residuals, and that the variable identifying searching transects and follows was suitable to separate blocks of correlated residuals. Once accounting for the observed degree of autocorrelation within blocks using a robust sandwich variance estimator, the Wald's tests indicated that only the relationships with effort, depth, aspect and year were significant ($p < 0.05$). The probability of encountering sperm whales initially increased with increasing effort, but then stabilized at larger effort values (Fig. 2a), and there was a general increase in the probability of occurrence over the years (Fig. 2b). Moreover, occurrence increased in deeper waters, with a second peak around 800 m (Fig. 2c). Finally, sperm whales occurred with a lower probability where the slope was directed towards West-Northwest (Fig. 2e). SALSA also estimated that sperm whale probability of occurrence was associated with lower slope gradient, larger TPI, colder (and colder than the median) waters, lower SLA and larger SST variability (Fig. 2), but these relationships were not significant under the Wald's test. The confusion matrix suggested that the final model correctly predicted, on average, 70.8% of presence and absence location. The area under the ROC curve was 0.79, confirming a satisfactory goodness-of-fit.

Model predictions highlighted the areas south, east and north-east of the archipelago as being characterised by a higher probability of encountering the animals in the first period (Fig. 3). In the second period, the probability of sperm whale occurrence was overall greater, illustrated by the effect of year. This intensification also resulted in new areas emerging as relevant for sperm whales, such as the channel between the islands of Mallorca and Ibiza, and areas north of Mallorca and Menorca. For both study periods, the prediction maps showed some edge-effects, predicting high probabilities of sperm whale occurrence in regions of the study area that were poorly surveyed (due to encounters occurring in these low-effort regions, as well as values of the explanatory variables at the extremes of the observed range). Maps of the upper and lower confidence intervals of model predictions derived from the bootstrapping procedure highlighted a moderate degree of uncertainty in the predicted distribution, which reflects the consequences of the large autocorrelation in model residuals (Fig. A.2).

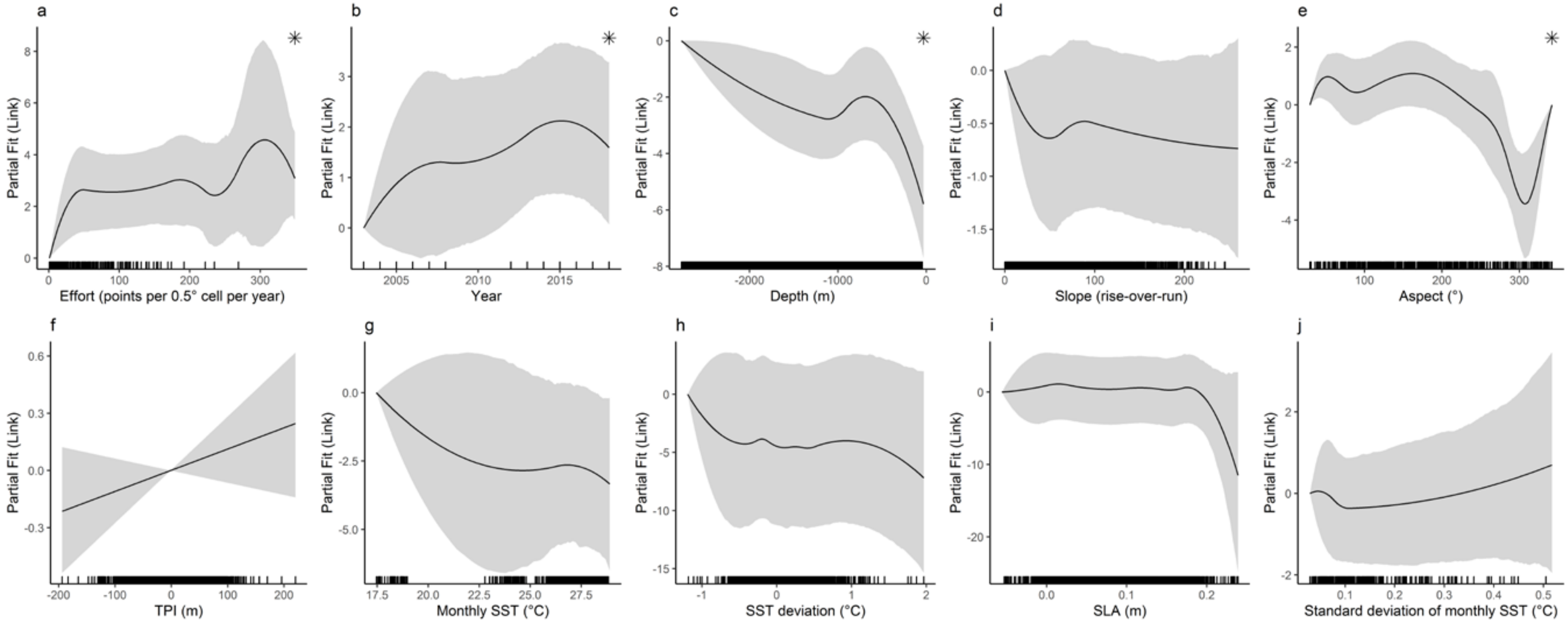

Figure 2. Estimated smooth relationships (on the link scale) between the probability of sperm whale occurrence and survey effort (a), year (b), depth (c), slope (d), aspect (e), topographic position index (TPI; f), monthly sea surface temperature (SST; g), SST deviation from the monthly median (h), sea level anomaly (SLA; i), and the standard deviation of monthly SST (j). Grey shaded areas represent robust, GEE-based 95% confidence intervals. A rug plot of the values of the covariates in the original data is shown at the bottom of each plot. Significant relationships are indicated with the star symbol (*) at the top right of the plot.

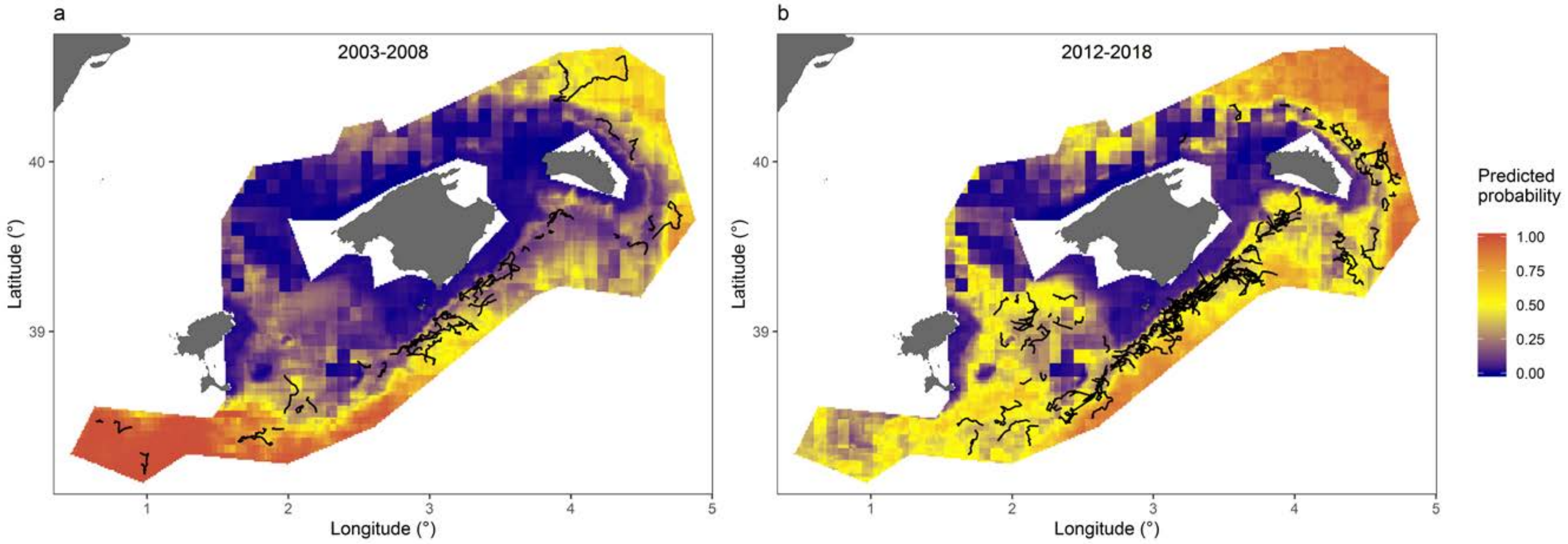

Figure 3. Predicted probability of sperm whale occurrence in the first (2003-2008; a) and second (2012-2018; b) study period, derived from the final model of overall habitat use. In black, the encounters with sperm whales in the corresponding study period.

3.2 Change in distribution in the two study periods

As for the overall habitat use model, the SALSA algorithm retained effort as a smooth term, highlighting an initial increase of the probability of encountering the animals for increasing effort, which stabilised for larger values (Fig. A.4). The CReSS bi-dimensional smooth was estimated to have 20 knots (chosen from a starting value of 12). The ACF plot confirmed the need to correct for autocorrelation within blocks, and the Wald's test suggested that effort, the CReSS surface, and the interaction between the CReSS surface and the study period were all significantly associated with sperm whale occurrence ($p < 0.05$). Therefore, model results suggested a significant change in geographic distribution between the two study periods. Spatial predictions mimicked the results of the overall habitat use model: in the second study period, animals were repeatedly encountered in the channel between Mallorca and Ibiza, and were also found to the north of the island of Menorca, overall occurring across a wider area (Fig. 4). The model correctly classified 68.9% of sperm whale presences and absences on average, a goodness-of-fit that was confirmed by the area under the ROC curve (0.76). As for the overall habitat use model, there was moderate uncertainty in the predicted distribution (Fig. A.3).

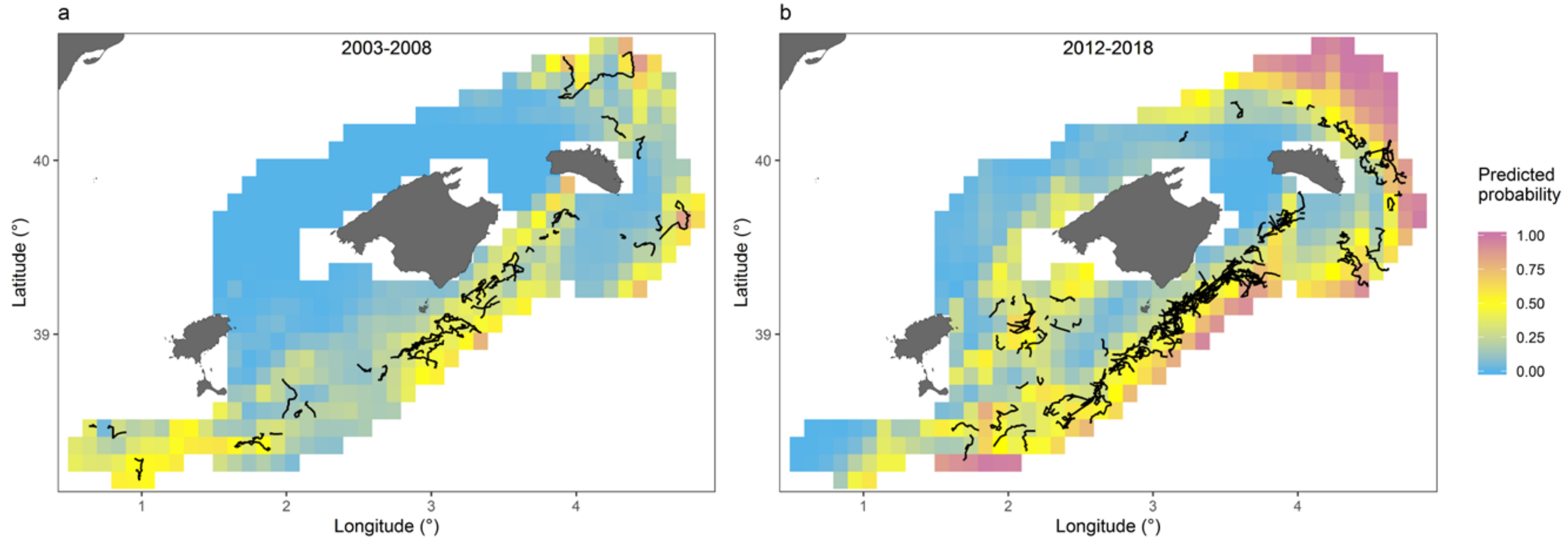

Figure 4. Predicted probability of sperm whale occurrence in the first (2003-2008; a) and second (2012-2018; b) study period, derived from the final model of geographic distribution. In black, the encounters with sperm whales in the corresponding study period.

3.3 Differences between groups and single animals

The patterns of multicollinearity highlighted by the VIF and pairwise correlations were the same as described for the overall habitat use model. The models for each collinear variable in a pair suggested the full initial model should include effort, year, depth (2.5 arc-min), slope (10 arc-min), aspect (5 arc-min), TPI, 8-day SST (20 km), SST deviation, SLA, and the standard deviation of 8-day SST. SALSA retained all covariates as smooth terms, selecting 4, 1, 3, 3, 3, 3, 3, 5, 1, and 3 internal knots, respectively. The relationships of group occurrence (versus single animals) with effort, depth, slope, year, 8-day SST, SST deviation and SLA were found to be significant under the Wald's test using robust standard errors, corrected for the observed degree of correlation within blocks. Specifically, groups were found in deeper, warmer waters (and warmer than the monthly median), with two peaks in slope gradient, and in association with smaller values of SLA (Fig. 5c, d, g-i). There was also a greater probability of occurrence of groups in the first and last years of the survey period, while the relationship with effort showed a peak around high effort values, but was otherwise wiggly (Fig. 5a and b). Some of these relationships had large confidence intervals and should therefore be interpreted with caution. The SALSA algorithm also retained non-significant relationships of group occurrence with greater TPI, slopes oriented towards east and south, and lower variability in SST (Fig. 5). The final model showed high goodness-of-fit (83% of correct grouping classifications, on average, and area under the ROC curve equal to 0.9).

The BA value between group and single animal encounters was 0.835, suggesting a high degree of spatial overlap. However, the distribution of BA values obtained from randomly reassigning encounters to groups or singletons showed that the observed BA value was substantially lower than the null expectation (Fig. A.5), which suggests the existence of some geographic segregation between the two groupings.

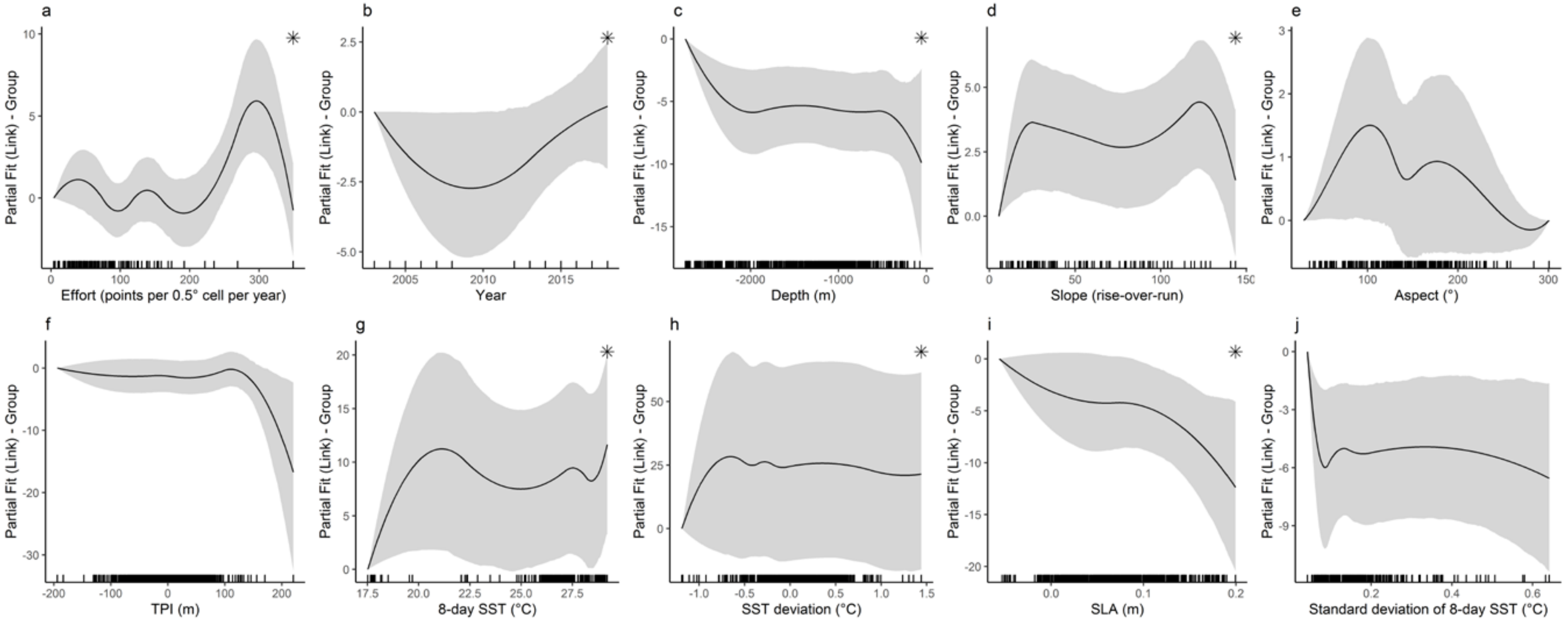

Figure 5. Estimated smooth relationships (on the link scale) between the probability of encountering sperm whale groups (as opposed to single animals) and survey effort (a), year (b), depth (c), slope (d), aspect (e), topographic position index (TPI; f), monthly sea surface temperature (SST; g), SST deviation from the monthly median (h), sea level anomaly (SLA; i), and the standard deviation of monthly SST (j). Grey shaded areas represent robust, GEE-based 95% confidence intervals. A rug plot of the values of the covariates in the original data is shown at the bottom of each plot. Significant relationships are indicated with the star symbol (*) at the top right of the plot.

The rose diagram for the approximate direction of the whales' movements over the course of each encounter showed some tendency to preferentially move towards north-east, south-west and south-east, with a lower occurrence of movements towards north and north-west (Fig. 6). These angles broadly reflect the direction of the continental slope south and east of the islands. The Rayleigh test suggested that observed angles were not uniformly distributed ($p < 0.01$). There were some subtle differences between groups and single animals (Fig. 6), which may reflect the greater occurrence of groups around the island of Menorca, where the continental slope has a different orientation.

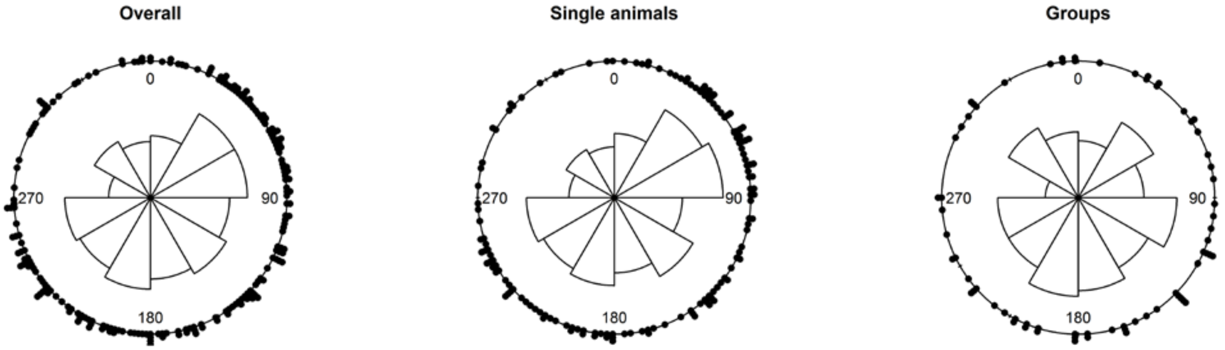

Figure 6. Rose diagrams of the bearing between the first and last location of each follow for all encounters, and separately for encounters with single animals and groups. Black dots on the plot margins represent the actual bearing values.

4. Discussion

We used acoustic monitoring data collected over 13 research seasons to characterise the summer habitat of sperm whales around the Balearic archipelago and its variation over the medium term. Even though estimated relationships with environmental proxy variables showed moderate levels of uncertainty and complexity, they offer the opportunity to generate hypotheses about the potential mechanisms that determine sperm whale distribution. In line with results from previous studies in this area, the Mediterranean Sea and globally, sperm whales were found to associate with bathymetric features, such as depth and continental slopes with specific orientation (Azzellino et al., 2012; Pirotta et al., 2011; Roberts et al., 2016; Rogan et al., 2017; Skov et al., 2008; Tepsich et al., 2014; Virgili et al., 2019; Waring et al., 2001; Whitehead, 2003). The coupling of these features with water circulation is known to promote local upwelling and increased productivity, which ultimately creates predictable feeding opportunities for top predators like sperm whales (Moors-Murphy, 2014). The preference for the habitat associated with the continental slope south and east of the archipelago was also supported by the broad orientation of the encounters highlighted by the rose diagrams, which indicated that whales tended to move along the direction of the slope. In addition, sperm whales were frequently encountered in the channel between Mallorca and Ibiza during the second study period, an area characterised by the presence of three seamounts (Aguilar et al., 2010). The importance of these submarine structures for sperm whales has been previously documented in other regions (Hann et al., 2016; Wong and Whitehead, 2014). In contrast, the characterisation of the dynamic processes that underpin sperm whale distribution in this area remains incomplete, although the final model provided some indication that colder waters, with lower sea level anomaly and larger temperature variability were preferred (Davis et al., 2002; Gannier and Praca, 2007; Virgili et al., 2019). These relationships were highly uncertain (and non-significant once accounting for residual autocorrelation), which could indicate a relative flexibility in habitat use within the broader bathymetric range that the animals appeared to select in this region. Our analyses also confirm the importance of a multi-scale approach for the evaluation of sperm whale habitat

(Jaquet, 1996), with different environmental characteristics being related to animal occurrence at different spatial and temporal scales (e.g., Cotté et al., 2009; Jaquet and Whitehead, 1996; Pirotta et al., 2014). The scale at which oceanographic processes operate and the temporal lags between these processes and the concentration of sperm whale prey thus present an additional complication to the functional description of the habitat of this species (Guisan and Thuiller, 2005), especially when the survey effort concentrates where expected encounter probability is high, like in this case.

Even after accounting for the increasing effort over the research period, sperm whale occurrence in the waters around the Balearic Islands was found to be overall increasing over time. This finding supports the critical role of the area as a breeding and feeding ground for the Endangered Mediterranean population (Rendell and Frantzis, 2016), and reaffirms its identification as an Important Marine Mammal Area under the IUCN IMMA initiative (Corrigan et al., 2014). The abundance and trend of the genetically isolated Mediterranean population is unknown, but numbers are believed to be low (Rendell et al., 2014; Rendell and Frantzis, 2016). A local increase in occurrence does not necessarily imply that the population as a whole is increasing, but reinforces the need to protect sperm whales from recognised threats in this region where they predictably and increasingly occur during the summer months, such as collisions with boats and entanglement in drift nets, and to extend the research and monitoring effort to other periods of the year. The frequent occurrence of calves within groups encountered around the islands (J.M. Brotons, pers. obs.) highlights the importance of these conservation requirements.

Our analyses also highlighted a significant change in the overall geographic distribution of the animals around the islands between the two study periods. Habitat characteristics and increased occurrence over time partly explain this change in spatial distribution, as reflected by the ability of the overall habitat model to capture the emergence of new areas of intense use (e.g. the channel between Mallorca and Ibiza). Further investigation of the oceanography of the area across the study period could elucidate some of these trends. However, this change, together with the lack of clear relationships with dynamic, oceanographic variables, could be an additional indication of the flexible nature of the distribution of the animals within the preferred bathymetric range around the islands, particularly in a phase where local density is increasing. This dynamism may imply that food resources are available across the whole area, and that individuals can plastically adjust their habitat use in response to other intrinsic drivers. Marine mammals have been shown to dynamically alter their habitat use over time, for example in response to changes in density and as a result of social dynamics (Arso Civil et al., 2019; Cantor et al., 2016; Carroll et al., 2014; Mobley et al., 1999).

In highly social species, such as the sperm whale, intrinsic biological factors strongly influence the distribution of individuals in space and time (Cañadas and Hammond, 2008; Guisan and Thuiller, 2005; Palacios et al., 2014). Interactions with members of the same group, sexual segregation and the need to care for the young are expected to contribute to movement decisions. Here, we highlighted that the habitat used by single animals (likely males) and groups (mostly females and young) differed. Encounters with groups occurred in deeper waters, which is consistent with existing evidence from other areas (Gregr and Trites, 2011), characterised by specific slope gradients. Groups were also associated with warmer locations (and warmer than the monthly median), which is in contrast with results of previous analyses on a subset of these data (Pirotta et al., 2011). This contradiction may be partly reconciled by the fact that surface temperature is highly correlated with month (see the corresponding rug plot in Fig. 2g and 5g), and earlier or later months were only surveyed in more recent years; the relationship with temperature (but not with SST deviation) may therefore mask a seasonal trend in the relative occurrence of the two groupings. Finally, group occurrence was related to smaller values of SLA, which could be associated with cyclonic circulation or confluence zones and higher productivity (Davis et al., 2002), supporting the hypothesis that groups exploit better foraging patches (Whitehead, 2003). These differences resulted in some degree of fine-scale spatial segregation, as indicated by Bhattacharyya's affinity, reinforcing the findings of previous work on the differential distribution of single males and social units in this and other areas (Gregr and Trites, 2011; Jones et al., 2016; O'Hern and Biggs, 2009; Whitehead, 2003). Further clarifying patterns of habitat segregation will allow quantifying differences in exposure rate and susceptibility to anthropogenic stressors in the region. Being one of the few recognised breeding ground for the population (Rendell and Frantzis, 2016), the risk of calves being struck by vessels or separated from the females should be minimised, for example by delineating and protecting areas specifically selected by groups (e.g., via restrictions on vessel speeds).

In general, the dynamic nature of sperm whale distribution in the area complicates management efforts, because the whole bathymetric range may require some form of protection, while the exact location of these mobile, social animals may be hard to identify at any moment in time. The increasing use of the Mallorca channel is particularly worrying, as it exposes individuals to the high levels of maritime traffic occurring between the islands (e.g. Fig. A.6). Quantifying the distribution overlap and individual encounter rate with various human activities operating in the region (e.g. via dedicated tagging studies) will therefore also be crucial (e.g., Pirotta et al., 2018).

Passive acoustics is an effective tool for the assessment of sperm whale distribution. While detection range could vary depending on ambient noise levels and environmental conditions, we do not expect systematic biases in certain areas or times. Animals could have also been missed along the line if they were not vocalizing, although sperm whales spend 80% of their time foraging (Watwood et al., 2006), and in a joint visual and acoustic survey sperm whales were always detected acoustically first (Barlow and Taylor, 2005). Future research should continue monitoring the presence and habitat use of sperm whales in this important area. In light of the dynamic distribution highlighted by our results, other areas of the archipelago to which limited effort has been dedicated so far should be targeted by future surveys (e.g., the north of Ibiza and waters further to the north and south of the islands), which would also address some of the edge effects emerging in model predictions. Extending the effort to a wider region will also support additional multi-scale analyses of sperm whale habitat use, which could help clarify the underlying ecological processes. Moreover, given the differences between social groupings, the area offers the unique opportunity to investigate the mechanisms that underpin the social system of the species and how this influences distribution patterns; further studies of sex-specific diet and group-specific habitat use could provide additional evidence towards such understanding. More broadly, the trends in encounter rate and change in distribution in this region should be considered in the context of local variation in other key areas of the basin, to understand the wider dynamics of the population and design effective, integrated measures that can support its conservation.

Acknowledgements

Funding: this work was supported by the National Geographic Society [grant number EC-53116R-18]. One World Wildlife, Whale and Dolphin Conservation, Mallorca Preservation Fund, Marilles Foundation, Obra Social La Caixa, and the Nando Peretti Foundation have also supported the data collection with various grants over the years. We thank all the volunteers that have helped with the data collection, and A. Cañadas (Alnilam, Spain) and C. Mundy (One World Wildlife, UK) for their contribution to the initial design of the monitoring program. We are especially grateful to the Swiss Cetacean Society for their continuous support to the Balearic Sperm Whale Project. We are grateful to L. Scott-Hayward for her advice on the statistical analysis. We thank Emer Rogan and University College Cork for providing desk space to EP. Finally, we thank the Editor-in-Chief Prof. Imants Priede and one anonymous reviewer for their useful comments on the manuscript.

Data availability statement

The dataset and code to run the analysis are available on the Open Science Framework repository (https://osf.io/x5afs/).

Author contributions

L.E.R conceived the original study, which was further developed in collaboration with J.M.B. and E.P.; L.E.R, J.M.B., M.C. and E.P. collected the data; E.P. conceived and carried out the data analysis, with the help of S.B.; E.P. wrote the manuscript, and all authors contributed to revisions.

References

Agostinelli, C., Lund, U., 2017. R package “circular”: Circular Statistics (version 0.4-93). URL https://r-forge.r-project.org/projects/circular/.

Aguilar, R., Pardo, E., Cornax, M.J., García, S., Ubero, J., 2010. Seamounts of the Balearic Islands, 2010: proposal for a marine protected area in the Mallorca Channel (Western Mediterranean). Oceana http://oceana.org/sites/default/files/reports/OCEANA_Seamounts_Balearic_Islands_ENG.pdf.

Arso Civil, M., Quick, N.J., Cheney, B., Pirotta, E., Thompson, P.M., Hammond, P.S., 2019. Changing distribution of the east coast of Scotland bottlenose dolphin population and the challenges of area-based management. Aquat. Conserv. Mar. Freshw. Ecosyst. In press.

Azzellino, A., Panigada, S., Lanfredi, C., Zanardelli, M., Airoldi, S., Notarbartolo di Sciara, G., 2012. Predictive habitat models for managing marine areas: Spatial and temporal distribution of marine mammals within the Pelagos Sanctuary (Northwestern Mediterranean sea). Ocean Coast. Manag. 67, 63–74. https://doi.org/10.1016/j.ocecoaman.2012.05.024

Barlow, J., Taylor, B.L., 2005. Estimates of sperm whale abundance in the northeastern temperate Pacific from a combined acoustic and visual survey. Mar. Mammal Sci. 21, 429–445. https://doi.org/10.1111/j.1748-7692.2005.tb01242.x

Bhattacharyya, A., 1943. On a measure of divergence between two statistical populations defined by their probability distributions. Bull. Calcutta Math. Soc. 35, 99–109.

Calenge, C., 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Modell. 197, 516–519.

Cañadas, A., Hammond, P., 2008. Abundance and habitat preferences of the short-beaked common dolphin Delphinus delphis in the southwestern Mediterranean: implications for conservation. Endanger. Species Res. 4, 309–331. https://doi.org/10.3354/esr00073

Cantor, M., Whitehead, H., Gero, S., Rendell, L., 2016. Cultural turnover among Galápagos sperm whales. R. Soc. Open Sci. 3. https://doi.org/10.1098/rsos.160615

Carroll, E.L., Rayment, W.J., Alexander, A.M., Baker, C.S., Patenaude, N.J., Steel, D., Constantine, R., Cole, R., Boren, L.J., Childerhouse, S., 2014. Reestablishment of former wintering grounds by New Zealand southern right whales. Mar. Mammal Sci. 30, 206–220.

Corrigan, C.M., Ardron, J.A., Comeros-Raynal, M.T., Hoyt, E., Notarbartolo Di Sciara, G., Carpenter, K.E., 2014. Developing important marine mammal area criteria: Learning from ecologically or biologically significant areas and key biodiversity areas. Aquat. Conserv. Mar. Freshw. Ecosyst. 24, 166–183. https://doi.org/10.1002/aqc.2513

Cotté, C., Guinet, C., Taupier-Letage, I., Mate, B., Petiau, E., 2009. Scale-dependent habitat use by a large free-ranging predator, the Mediterranean fin whale. Deep Sea Res. Part I Oceanogr. Res. Pap. 56, 801–811. https://doi.org/10.1016/j.dsr.2008.12.008

Davis, R.W., Ortega-Ortiz, J.G., Ribic, C. a, Evans, W.E., Biggs, D.C., Ressler, P.H., Cady, R.B., Leben, R.R., Mullin, K.D., Würsig, B., 2002. Cetacean habitat in the northern oceanic Gulf of Mexico. Deep Sea Res. Part I Oceanogr. Res. Pap. 49, 121–142. https://doi.org/10.1016/S0967-0637(01)00035-8

Drouot-Dulau, V., Gannier, A., 2007. Movements of sperm whale in the western Mediterranean sea: preliminary photo-identification results. J. Mar. Biol. Assoc. United Kingdom 87, 195–200.

Eguiguren, A., Pirotta, E., Cantor, M., Rendell, L., Whitehead, H., 2019. Habitat use of culturally distinct Galápagos sperm whale Physeter macrocephalus clans. Mar. Ecol. Prog. Ser. 609, 257–270. https://doi.org/10.3354/meps12822

Elith, J., Leathwick, J.R., 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Frantzis, A., Alexiadou, P., Gkikopoulou, K.C., 2014. Sperm whale occurrence, site fidelity and population structure along the Hellenic Trench (Greece, Mediterranean Sea). Aquat. Conserv. Mar. Freshw. Ecosyst. 24, 83–102. https://doi.org/10.1002/aqc.2435

Gannier, A., Praca, E., 2007. SST fronts and the summer sperm whale distribution in the north-west Mediterranean Sea. J. Mar. Biol. Assoc. United Kingdom 87, 187. https://doi.org/10.1017/S0025315407054689

Grecian, W.J., Lane, J., Michelot, T., Wade, H., Hamer, K., 2018. Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. J. R. Soc. Interface 15, 20180084. https://doi.org/10.1098/rsif.2018.0084

Gregr, E.J., Trites, A.W., 2011. Predictions of critical habitat for five whale species in the waters of coastal British Columbia. Can. J. Fish. Aquat. Sci. 58, 1265–1285. https://doi.org/10.1139/f01-078

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Hann, C.H., Smith, T.D., Torres, L.G., 2016. A sperm whale's perspective: The importance of seasonality and seamount depth. Mar. Mammal Sci. 32, 1470–1481. https://doi.org/10.1111/mms.12320

Hardin, J.W., Hilbe, J.M., 2003. Generalized estimating equations, 3rd ed. Chapman & Hall/CRC Press, London.

Hazen, E.L., Jorgensen, S., Rykaczewski, R.R., Bograd, S.J., Foley, D.G., Jonsen, I.D., Shaffer, S.A., Dunne, J.P., Costa, D.P., Crowder, L.B., Block, B.A., 2013. Predicted habitat shifts of Pacific top predators in a changing climate. Nat. Clim. Chang. 3, 234–238. https://doi.org/10.1038/nclimate1686

Hijmans, R.J., 2016. raster: Geographic Data Analysis and Modeling. R package version 2.5-8. https://CRAN.R-project.org/package=raster.

IUCN-MMPATF, 2017. Balearic Islands Shelf and Slope IMMA. The IUCN Global Dataset of Important Marine Mammal Areas (IUCN-IMMA). Downloaded June 2018. Made available under agreement on terms and conditions of use by the IUCN Joint SSC/WCPA Marine Mammal Protected Areas Task .

Jaquet, N., 1996. How spatial and temporal scales influence understanding of Sperm Whale distribution: a review. Mamm. Rev. 26, 51–65.

Jaquet, N., Whitehead, H., 1996. Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. Mar. Ecol. Prog. Ser. 135, 1–9. https://doi.org/10.3354/meps135001

Jones, E.L., Rendell, L., Pirotta, E., Long, J.A., 2016. Novel application of a quantitative spatial comparison tool to species distribution data. Ecol. Indic. 70. https://doi.org/10.1016/j.ecolind.2016.05.051

Lewis, T., Gillespie, D., Lacey, C., Matthews, J., Danbolt, M., Leaper, R., McLanaghan, R., Moscrop, A., 2007. Sperm whale abundance estimates from acoustic surveys of the Ionian Sea and Straits of Sicily in 2003. J. Mar. Biol. Assoc. UK 87, 353. https://doi.org/10.1017/S0025315407054896

Lewison, R., Hobday, A.J., Maxwell, S., Hazen, E., Hartog, J.R., Dunn, D.C., Briscoe, D., Fossette, S., O'Keefe, C.E., Barnes, M., Abecassis, M., Bograd, S., Bethoney, N.D., Bailey, H., Wiley, D., Andrews, S., Hazen, L., Crowder, L.B., 2015. Dynamic ocean management: Identifying the critical ingredients of dynamic approaches to ocean resource management. Bioscience 65, 486–498. https://doi.org/10.1093/biosci/biv018

Mobley, J.R., Bauer, G.B., Hermann, L.M., 1999. Changes over a ten-year interval in the distribution and relative abundance of humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. Aquat. Mamm. 25, 63–72.

Moors-Murphy, H.B., 2014. Submarine canyons as important habitat for cetaceans, with special reference to the Gully: A review. Deep. Res. Part II Top. Stud. Oceanogr. 104, 6–19. https://doi.org/10.1016/j.dsr2.2013.12.016

O'Hern, J.E., Biggs, D.C., 2009. Sperm whale (*Physeter macrocephalus*) habitat in the gulf of Mexico: Satellite observed ocean color and altimetry applied to small-scale variability in distribution. Aquat. Mamm. 35, 358–366. https://doi.org/10.1578/AM.35.3.2009.358

Palacios, D.M., Baumgartner, M.F., Laidre, K.L., Gregr, E.J., 2014. Beyond correlation:

Integrating environmentally and behaviourally mediated processes in models of marine mammal distributions. Endanger. Species Res. 22, 191–203. https://doi.org/10.3354/esr00558

Pirotta, E., Matthiopoulos, J., MacKenzie, M., Scott-Hayward, L., Rendell, L., 2011. Modelling sperm whale habitat preference: A novel approach combining transect and follow data. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps09236

Pirotta, E., New, L., Marcoux, M., 2018. Modelling beluga habitat use and baseline exposure to shipping traffic to design effective protection against prospective industrialization in the Canadian Arctic. Aquat. Conserv. Mar. Freshw. Ecosyst. 28, 713–722.

Pirotta, E., Thompson, P.M., Miller, P.I., Brookes, K.L., Cheney, B., Barton, T.R., Graham, I.M., Lusseau, D., 2014. Scale-dependent foraging ecology of a marine top predator modelled using passive acoustic data. Funct. Ecol. 28, 206–217. https://doi.org/10.1111/1365-2435.12146

Praca, E., Gannier, A., Das, K., Laran, S., 2009. Modelling the habitat suitability of cetaceans: Example of the sperm whale in the northwestern Mediterranean Sea. Deep. Res. Part I Oceanogr. Res. Pap. 56, 648–657. https://doi.org/10.1016/j.dsr.2008.11.001

R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Redfern, J. V, Ferguson, M.C., Becker, E.A., Hyrenbach, K.D., Good, C., Barlow, J., Kaschner, K., Baumgartner, M.F., Forney, K.A., Ballance, L.T., Fauchald, P., Halpin, P., Hamazaki, T., Pershing, A.J., Qian, S.S., Read, A., Reilly, S.B., Torres, L., Werner, F., 2006.

Techniques for cetacean-habitat modeling. Mar. Ecol. Prog. Ser. 310, 271–295. https://doi.org/10.3354/meps310271

Rendell, L., Frantzis, A., 2016. Mediterranean sperm whales, Physeter macrocephalus: The precarious state of a lost tribe. Adv. Mar. Biol. 75, 37–74. https://doi.org/10.1016/bs.amb.2016.08.001

Rendell, L., Simião, S., Brotons, J.M., Airoldi, S., Fasano, D., Gannier, A., 2014. Abundance and movements of sperm whales in the western Mediterranean basin. Aquat. Conserv. Mar. Freshw. Ecosyst. 24, 31–40. https://doi.org/10.1002/aqc.2426

Rendell, L., Whitehead, H., 2003. Vocal clans in sperm whales (Physeter macrocephalus). Proc. R. Soc. London. Ser. B Biol. Sci. 270, 225–231. https://doi.org/10.1098/rspb.2002.2239

Roberts, J.J., Best, B.D., Mannocci, L., Fujioka, E., Halpin, P.N., Palka, D.L., Garrison, L.P., Mullin, K.D., Cole, T.V.N., Khan, C.B., McLellan, W.A., Pabst, D.A., Lockhart, G.G., 2016. Habitat-based cetacean density models for the U.S. Atlantic and Gulf of Mexico. Sci. Rep. 6, 1–12. https://doi.org/10.1038/srep22615

Rogan, E., Canadas, A., Macleod, K., Santos, M.B., Mikkelsen, B., VanCanneyt, O., Vasquez, J.A., Hammond, P.S., 2017. Distribution, abundance and habitat use of deep diving cetaceans in the North East Atlantic. Deep Sea Res. Part II Top. Stud. Oceanogr. 141, 8–19.

Roshier, D.A., Reid, J.R.W., 2003. On animal distributions in dynamic landscapes. Ecography (Cop.). 26, 539–544. https://doi.org/10.1034/j.1600-0587.2003.03473.x

Runge, C.A., Martin, T.G., Possingham, H.P., Willis, S.G., Fuller, R.A., 2014. Conserving mobile species. Front. Ecol. Environ. 12, 395–402. https://doi.org/10.1890/130237

Ruxton, G.D., 2017. Testing for departure from uniformity and estimating mean direction for circular data. Biol. Lett. 13, 20160756. https://doi.org/10.1098/rsbl.2016.0756

Scales, K.L., Hazen, E.L., Jacox, M.G., Edwards, C.A., Boustany, A.M., Oliver, M.J., Bograd, S.J., 2017. Scale of inference: on the sensitivity of habitat models for wide-ranging marine predators to the resolution of environmental data. Ecography (Cop.). 40, 210–220. https://doi.org/10.1111/ecog.02272

Scott-Hayward, L.A.S., Mackenzie, M.L., Donovan, C.R., Walker, C.G., Ashe, E., 2014. Complex Region Spatial Smoother (CReSS). J. Comput. Graph. Stat. 23, 340–360.

Scott-Hayward, L.A.S., Oedekoven, C.S., Mackenzie, M.L., Walker, C.G., Rexstad, E., 2015. MRSea package (version 0.2.2): Statistical Modelling of bird and cetacean distributions in offshore renewables development areas. University of St. Andrews: Contract with Marine Scotland: SB9 (CR/2012/05), <URL: http://creem2.st-and.ac.uk/software.aspx>.

Sequeira, A.M.M., Rodríguez, J.P., Eguíluz, V.M., Harcourt, R., Hindell, M., Sims, D.W., Duarte, C.M., Costa, D.P., Fernández-Gracia, J., Ferreira, L.C., Hays, G.C., Heupel, M.R., Meekan, M.G., Aven, A., Bailleul, F., Baylis, A.M.M., Berumen, M.L., Braun, C.D., Burns, J., Caley, M.J., Campbell, R., Carmichael, R.H., Clua, E., Einoder, L.D., Friedlaender, A., Goebel, M.E., Goldsworthy, S.D., Guinet, C., Gunn, J., Hamer, D., Hammerschlag, N., Hammill, M., Hückstädt, L.A., Humphries, N.E., Lea, M.-A., Lowther, A., Mackay, A., McHuron, E., McKenzie, J., McLeay, L., McMahon, C.R., Mengersen, K., Muelbert, M.M.C., Pagano, A.M., Page, B., Queiroz, N., Robinson, P.W., Shaffer, S.A., Shivji, M., Skomal, G.B., Thorrold, S.R., Villegas-Amtmann, S., Weise, M., Wells, R., Wetherbee, B., Wiebkin, A., Wienecke, B., Thums, M., 2018. Convergence of marine megafauna movement patterns in coastal and open oceans. Proc. Natl. Acad. Sci. 115, 3072–3077. https://doi.org/10.1073/pnas.1716137115

Sing, T., Sander, O., Beerenwinkel, N., Lengauer, T., 2005. ROCR: visualizing classifier performance in R. Bioinformatics 21, 7881.

Skov, H., Gunnlaugsson, T., Budgell, W.P., Horne, J., Nøttestad, L., Olsen, E., Søiland, H., Víkingsson, G., Waring, G., 2008. Small-scale spatial variability of sperm and sei whales in relation to oceanographic and topographic features along the Mid-Atlantic Ridge. Deep. Res. Part II Top. Stud. Oceanogr. 55, 254–268. https://doi.org/10.1016/j.dsr2.2007.09.020

Tepsich, P., Rosso, M., Halpin, P., Moulins, A., 2014. Habitat preferences of two deep-diving cetacean species in the northern Ligurian Sea. Mar. Ecol. Prog. Ser. 508, 247–260. https://doi.org/10.3354/meps10851

VanDerWal, J., Falconi, L., Januchowski, S., Shoo, L., Storlie, C., 2014. SDMTools: Species Distribution Modelling Tools: Tools for processing data associated with species distribution modelling exercises. R package version 1.1-221. https://CRAN.R-project.org/package=SDMTools.

Virgili, A., Authier, M., Boisseau, O., Cañadas, A., Claridge, D., Cole, T., Corkeron, P., Dorémus, G., David, L., Di-Méglio, N., Dunn, C., Dunn, T.E., García-Barón, I., Laran, S., Lauriano, G., Lewis, M., Louzao, M., Mannocci, L., Martínez-Cedeira, J., Palka, D., Panigada, S., Pettex, E., Roberts, J.J., Ruiz, L., Saavedra, C., Santos, M.B., Van Canneyt, O., Vázquez Bonales, J.A., Monestiez, P., Ridoux, V., 2019. Combining multiple visual surveys to model the habitat of deep-diving cetaceans at the basin scale: Large-scale modelling of deep-diving cetacean habitats. Glob. Ecol. Biogeogr. 28, 300–314.

https://doi.org/10.1111/geb.12850

Walker, C.G., Mackenzie, M.L., Donovan, C.R., O'Sullivan, M.J., 2011. SALSA – a spatially adaptive local smoothing algorithm. J. Stat. Comput. Simul. 81, 179–191.

Waring, G.T., Hamazaki, T., Sheehan, D., Wood, G., Baker, S., 2001. Characterization of beaked whale (*Ziphiidae*) and sperm whale (*Physeter macrocephalus*) summer habitat in shelf-edge and deeper waters off the Northeast U.S. Mar. Mammal Sci. 17, 703–717. https://doi.org/10.1111/j.1748-7692.2001.tb01294.x

Watwood, S.L., Miller, P.J.O., Johnson, M., Madsen, P.T., Tyack, P.L., 2006. Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). J. Anim. Ecol. 75, 814–825. https://doi.org/10.1111/j.1365-2656.2006.01101.x

Whitehead, H., 2018. Sperm whale: *Physeter macrocephalus*, in: Encyclopedia of Marine Mammals. Elsevier, pp. 1091–1097. https://doi.org/10.1038/179811c0

Whitehead, H., 2003. Sperm Whales. Social evolution in the ocean. University of Chicago Press, Chicago.

Whitehead, H., Rendell, L., 2014. The cultural lives of whales and dolphins. University of Chicago Press, Chicago.

Whitehead, H., Rendell, L., 2004. Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. J. Anim. Ecol. 73, 190–196. https://doi.org/10.1111/j.1365-2656.2004.00798.x

Wilson, B., 2016. Might marine protected areas for mobile megafauna suit their proponents more than the animals? Aquat. Conserv. Mar. Freshw. Ecosyst. 26, 3–8.

https://doi.org/10.1002/aqc.2619

Wong, S.N.P., Whitehead, H., 2014. Seasonal occurrence of sperm whales (*Physeter macrocephalus*) around Kelvin Seamount in the Sargasso Sea in relation to oceanographic processes. Deep. Res. Part I Oceanogr. Res. Pap. 91, 10–16. https://doi.org/10.1016/j.dsr.2014.05.001

Yates, K.L., Bouchet, P.J., Caley, M.J., Mengersen, K., Randin, C.F., Parnell, S., Fielding, A.H., Bamford, A.J., Ban, S., Barbosa, A.M., Dormann, C.F., Elith, J., Embling, C.B., Ervin, G.N., Fisher, R., Gould, S., Graf, R.F., Gregr, E.J., Halpin, P.N., Heikkinen, R.K., Heinänen, S., Jones, A.R., Krishnakumar, P.K., Lauria, V., Lozano-Montes, H., Mannocci, L., Mellin, C., Mesgaran, M.B., Moreno-Amat, E., Mormede, S., Novaczek, E., Oppel, S., Ortuño Crespo, G., Peterson, A.T., Rapacciuolo, G., Roberts, J.J., Ross, R.E., Scales, K.L., Schoeman, D., Snelgrove, P., Sundblad, G., Thuiller, W., Torres, L.G., Verbruggen, H., Wang, L., Wenger, S., Whittingham, M.J., Zharikov, Y., Zurell, D., Sequeira, A.M.M., 2018. Outstanding Challenges in the Transferability of Ecological Models. Trends Ecol. Evol. 33, 790–802. https://doi.org/10.1016/j.tree.2018.08.001