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Identifying key habitat and seasonal patterns of a critically endangered population of killer whales

RUTH ESTEBAN[1], PHILIPPE VERBORGH[1], PAULINE GAUFFIER[1], JOAN GIMÉNEZ[2], ISABEL AFÁN[3], ANA CAÑADAS[4], PEDRO GARCÍA[5], JOSE LUIS MURCIA[5], SARA MAGALHÃES[6], EZEQUIEL ANDREU[7] AND RENAUD DE STEPHANIS[2]

[1]CIRCE, Conservation Information and Research on Cetaceans, C/Cabeza de Manzaneda 3, Algeciras-Pelayo, 11390 Cadiz, Spain, [2]GEMA, Grupo de Ecología Marina Aplicada, Estación Biológica de Doñana, CSIC; C/Americo Vespucio, s/n, 41092, Isla de la Cartuja, Sevilla, Spain, [3]LAST, Laboratorio de SIG y Teledetección, Estación Biológica de Doñana, CSIC; C/Americo Vespucio, s/n, 41092, Isla de la Cartuja, Sevilla, Spain, [4]Alnilam Research and Conservation, Cándamo 116, 28240 Hoyo de Manzanares, Madrid, Spain, [5]ANSE Asociación de Naturalistas del Sureste Plaza Pintor José María Párraga, 11, Bajo, 30002, Murcia, Spain, [6]MAR ILIMITADO Porto da Baleeira de Sagres, 8650-368 Sagres, Portugal, [7]TURMARES (Turísmo Maritimo del Estrecho), Avd/Alcalde Juan Nuñez 3, 11380 Tarifa, Cadiz, Spain

Killer whales have been described in the Gulf of Cadiz, southern Spain, in spring and in the Strait of Gibraltar in summer. A total of 11,276 cetaceans sightings coming from different sources (dedicated research surveys, whale watching companies and opportunistic observations) were used to create two presence – 'pseudo-absence' predictive generalized additive models (GAM), where presence data were defined as sightings of killer whales and 'pseudo-absence' data as sightings of other cetacean species. One model was created using spring data when killer whales' main prey, Atlantic bluefin tuna, enter the Mediterranean Sea, and the other model used summer data when Atlantic bluefin tuna return to the Atlantic Ocean. Both model predictions show that killer whales are highly associated with a probable distribution of bluefin tuna during their migration throughout the study area, constraining their distribution to the Gulf of Cadiz in spring and the Strait of Gibraltar in spring and summer. Knowledge of the distribution of killer whales in the study area is essential to establish conservation measures for this population.

Keywords: killer whale, *Orcinus orca*, distribution, spatial modelling, generalized additive models (GAM), cetacean, Strait of Gibraltar, southern Iberian Peninsula

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INTRODUCTION

Modelling species distribution is a valuable tool of biological conservation efforts, especially predictive models of marine predators, due to the logistical difficulties of monitoring their distributions at sea. For instance, managers of whale and dolphin populations can benefit from accurate model-derived predictions of cetacean habitat to mitigate anthropogenic effects, such as fisheries by-catch (Torres *et al.*, 2003) and the impacts of habitat alterations on ecosystem function (Baumgartner & Mullin, 2001; D'Amico *et al.*, 2003), in order to protect critical habitat *(*Hooker *et al.*, 1999; Cañadas *et al.*, 2005; Gregr & Trites, 2011) and understand the ecology of these animals (Hamazaki, 2002). By assuming that the distribution of cetaceans is non-random relative to environmental variability, predictive models of cetacean distribution typically identify the ecological relationships between the environment and species habitat selection.

Corresponding author:
R. Esteban
Email: ruth@circe.info

Killer whales, *Orcinus orca* (Linnaeus, 1758) have a widespread distribution throughout the world's oceans and seas, from polar waters to the equator (Leatherwood & Dalheim, 1978; Heyning & Dahlheim, 1988; Forney & Wade, 2007). They are known to be common in many coastal areas, particularly at high latitudes, probably due to higher ocean productivity (Forney & Wade, 2007), but they also occur in offshore and tropical waters (Leatherwood & Dalheim, 1978; Forney & Wade, 2007). Killer whales are known to present seasonal movement patterns, often associated with increased prey availability in the north-east Pacific (Braham & Dahlheim, 1982; Baird & Dill, 1995), North Atlantic (Sigurjónsson & Leatherwood, 1988) and South Atlantic (Iñiguez, 2001). In the Atlantic, they are common around the northern part of the British Isles, along the Norwegian coast and throughout the eastern North Atlantic. They occasionally enter the North Sea and Skagerrak Strait (Reid *et al.*, 2003). Killer whales are regularly seen in the Strait of Gibraltar and adjacent Atlantic waters (Horozco, 1598; Aloncle, 1964a; Casinos & Vericad, 1976; Bayed & Beaubrun, 1987; Guinet *et al.*, 2007; de Stephanis *et al.*, 2008; Esteban, 2008; Foote *et al.*, 2011). Conversely, killer whales are considered as a rare species in the Mediterranean

Sea (Casinos & Vericad, 1976; Raga *et al.*, 1985; Bayed & Beaubrun, 1987; Notarbartolo di Sciara, 1987; Notarbartolo di Sciara & Birkun, 2010).

In southern Spain, killer whales are observed in spring in the Gulf of Cadiz (Guinet *et al.*, 2007; García-Tiscar, 2009), when their main prey, Atlantic bluefin tuna (hereafter ABFT) (*Thunnus thynnus*), enters the Mediterranean Sea (Cetti, 1777; Sella, 1929; Rodríguez-Roda, 1964) and in summer associated with the ABFT long-line fishery of the Strait of Gibraltar (Srour, 1994; de la Serna *et al.*, 2004), when ABFT return from their spawning areas on their way back to the Atlantic Ocean (Lozano, 1958; Aloncle, 1964b; Rodríguez-Roda, 1964; de Stephanis *et al.*, 2008b). These killer whales belong to the same population as killer whales sampled in the Canary Islands, and are significantly different from other populations in the north-east Atlantic (North Sea, Iceland and Norway) (Foote *et al.*, 2011). Additionally, differences in carbon and nitrogen stable isotopes ratios (García-Tiscar, 2009) and parasite load (Mackenzie, 1999; Dwyer & Visser, 2011) among pods from the Strait of Gibraltar–Canary Islands population suggest that it is a non-cohesive population that may not follow the same resource all year round.

Due to their small population size, the killer whales of the Strait of Gibraltar and contiguous waters have been recommended to be included in the 'Critically Endangered' category by ACCOBAMS–IUCN (Cañadas & de Stephanis, 2006). Likewise, the International Whaling Commission has recommended the implementation of a conservation plan for this subpopulation as soon as possible (IWC, 2007), and since 2011 the Spanish Ministry of Environment has considered the killer whales of the Strait of Gibraltar and the Gulf of Cadiz 'Vulnerable' in the Spanish Catalogue of Endangered Species. Both local (Andalusia) and Spanish authorities have recommended studying the spatial distribution of the species in southern Spain, to delineate it and the boundaries to be managed for a correct implementation of the conservation plan.

A great effort has been made to describe the distribution of marine mammals in the Alboran Sea and Strait of Gibraltar (Cañadas *et al.*, 2005; Cañadas & de Stephanis, 2006; Cañadas & Hammond, 2006; Guinet *et al.*, 2007; de Stephanis, *et al.*, 2008a, b; Verborgh *et al.*, 2009; Foote *et al.*, 2011), but little is known about the distribution of killer whales in the whole study area, as only one publication describes the summer distribution in the central area of the Strait of Gibraltar (de Stephanis *et al.*, 2008a), and no information is available for the rest of the Alboran Sea or the Gulf of Cadiz. This study aims to understand the spatial distribution of killer whales in the southern Iberian Peninsula in relation to different environmental variables, both in spring and summer, from data series compiled from research, whale watching vessels and opportunistic data.

MATERIALS AND METHODS

Study area

The present study was carried out in the Gulf of Cadiz, Strait of Gibraltar and the Alboran Sea (Figure 1). It is found between 0°30′E and 9°30′W and between 37°30′ and 35°N, and is bounded to the north by the Iberian Peninsula and to the south by Africa. These areas display different bathymetric features. The Gulf of Cadiz has a wide, smooth shelf and slope. In contrast, the northern shelf of the Alboran Sea is very narrow, but has a very steep shelf and slope gradient. The Gulf of Cadiz, located in the eastern sector of the central North Atlantic, is concave in shape, with a NW–SE orientation (Roberts, 1970; Malod, 1982). The physiographic profile of the margin includes a wide shelf (30–40 km) with a sea-floor slope of 0.2–0.32°, a shelf-break located at a water depth of between 140 and 120 m, and a smooth continental slope, with sea-floor gradients of 1.5° in the upper part and 0.5–1° in the middle and lower parts (Baraza *et al.*, 1999). The Strait of Gibraltar has a length of 60 km (on an E–W axis), and a mean width of 20 km. The shallowest depth, less than 300 m, is found in the main sill of Camarinal and its minimum width of around 14 km coincides with the contraction of Tarifa narrow. The bathymetry of the Strait is characterized by a west to east canyon, with shallower waters (200–300 m) found on the Atlantic side and deeper waters (800–1000 m) on the Mediterranean side. On the eastern side of the Strait of Gibraltar lies the Alboran Sea basin, at the western edge of the Mediterranean Sea. It is arc-shaped, and characterized generally by a complex physiography related to its tectonic history. The Spanish margin has a very narrow, steep shelf (5–10 km) up to the shelf-break at 110–120 m water depth, which establishes the boundary, with a shelf gradient of 0.5–0.7° and a slope of 2.3° (Ercilla *et al.*, 1992; Hernández-Molina, 1993; Hernández-Molina *et al.*, 1994).

Data collection

Sightings from cetaceans collected between 2002 and 2012 in waters of the southern Iberian Peninsula were compiled. The datasets were separated in two datasets as killer whales have been described in different areas during different seasons: shallow waters in the Gulf of Cadiz in spring (April–June) (Guinet *et al.*, 2007), and in the central waters of the Strait of Gibraltar in summer (July–September) (de Stephanis *et al.*, 2008a). We have also based this separation on the migration pattern of their main prey, bluefin tuna (Cetti, 1777; Sella, 1929; Rodríguez-Roda, 1964). Insufficient data were available to make robust spatial models for the rest of the year. A total of 11,276 records of cetaceans were available for this analysis coming from: (1) random transect sightings from a research boat performed by the non-governmental organization (NGO) ANSE (Asociación de Naturalistas del Sureste) in the Murcia region; (2) sightings collected by Alnitak since 2002, a research NGO which performed a random transect throughout the Alboran Sea (Cañadas *et al.*, 2005); (3) sightings collected by Alnilam since 2010, a research company which performed a random transect throughout the Alboran Sea; (4) sightings of CIRCE (Conservation, Information and Research on Cetaceans) since 2002, a research NGO that made random and line transects throughout the Strait of Gibraltar and Gulf of Cadiz (de Stephanis *et al.*, 2008a); (5) sightings of TURMARES (Turismo Marítimo del Estrecho) since 2003, a whale watching company based in the Strait of Gibraltar; (6) sightings from Mar Ilimitado (Tourism and Research) since 2005, a whale watching and research company based in southern Portugal; (7) sightings from Consejería de Medio Ambiente de la Junta de Andalucía, a governmental institution of the local council of Andalucía since

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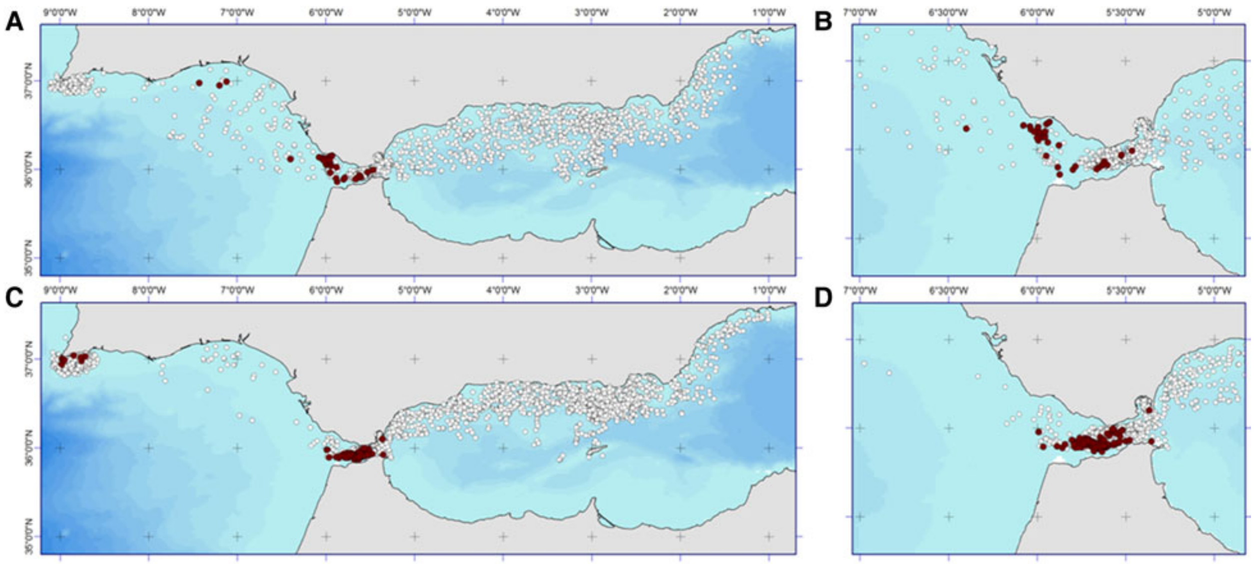

Fig. 1. Cetacean sighting distribution in the study area. In red killer whales sightings and in grey other cetacean sightings: (A) sightings in spring in the southern Iberian Peninsula; (B) sightings in spring in the Strait of Gibraltar; (C) sightings in summer in the southern Iberian Peninsula; (D) sightings in summer in the Strait of Gibraltar.

2005, that performs random and line transects by boat and aeroplane throughout the entire Andalusian region; (8) sightings collected by the EBD-CSIC (Estación Biológica de Doñana – Consejo Superior de Investigaciones Científicas) since 2011, from a small research boat doing line transects in the Gulf of Cádiz; and (9) opportunistic data.

Environmental explicative models

Habitat preferences of killer whales within the study area were investigated. The relationships between the spatial occurrence of the whales, and environmental variables were assessed using generalized additive modelling (GAM) techniques (Hastie & Tibshirani, 1990). The open-source statistical programming language R v. 2.6.2 (http://cran.r-project.org/), and the MGCV library within R were used (Wood, 2001). Given that data were coming from different sources, types of effort are difficult to compare, and therefore a model based on presence and 'pseudo-absence' was used. A GAM with a Tweedie distribution and logit link function was used. The parameter p chosen for the Tweedie distribution, through inspection of the generalized cross validation (GCV) score, an approximation to the Akaike information criterion (AIC) (Wood, 2000), was 1.1, very close to a Poisson distribution but with some over-dispersion. The model used a gamma = 1.4, as recommended by Wood (2006), to prevent overfitting.

All the cetaceans' sightings were used as 'sampling stations'. The presence dataset included sightings of killer whales obtained by the different platforms. We used all the other cetacean species in the study area as 'pseudo-absences'. In these locations, we assumed that an observer was effectively searching whales as other species were sighted, but killer whales were not detected. The general structure of the model was:

$$E(p_i) = \exp\left[\theta_0 + \sum_k f_k(z_{ik})\right].$$

where p_i is the probability to find killer whales, in the ith sampling station, θ_0 is the intercept, f_k are smoothed functions of the explanatory covariates and z_{ik} is the value of the kth explanatory covariate in the ith sampling station. The environmental variables used in this study were depth, obtained from ETOPO2 (Amante & Eakins, 2009), its derivate slope and aspect obtained with the R library SDMtools (VanDerWal *et al.*, 2010), sea surface temperature (SST) and chlorophyll-*a* concentration (Chla) obtained from satellite images of MODIS (Carder *et al.*, 2003). Spatial (geographical) covariates, i.e. latitude and longitude, were also used as potential proxies for other unavailable or unknown features affecting whales' distribution. Model selection was done using three diagnostic indicators: (a) the GCV; (b) the percentage of deviance explained; and (c) the probability that each variable was included in the model by chance. The decision to include/drop a term from the model was adopted following the criteria proposed by Wood (2001).

Environmental predictive models

The best GAM models were used to generate predicted probability values of presence and pseudo-absence on a grid of 2 × 2 km in the study area, which were plotted using ArcMap 10.0. In order to obtain the 95% confidence interval of the predictions, 1000 bootstraps with replacement were run for each model, and a prediction was obtained for each bootstrap iteration. The 95% confidence intervals were obtained from the bootstrap process of the models predictions of killer whales in the study area and were also plotted in to assess the precision of the predictions in every point of the study area.

RESULTS

Between 2002 and 2012, 322 sightings of killer whales and 10,952 sightings of other cetaceans were recorded in the study area. We created two models for the presence of killer

Table 1. Detection-function model fits with the generalized cross validation (GCV) score and ΔGCV between models and Akaike information criterion (AIC) and ΔAIC between models, during the spring period. Only covariates showing significant relationship are shown.

Covariates	GCV	ΔGCV	AIC	ΔAIC	Deviance explained
s(BAT) + s(lon)	0.058853		4102.552		50.40%
s(BAT) + s(lon) + s(ASPECT)	0.061775	0.002922	4100.523	−2.029	47.90%
s(lon) + s(ASPECT)	0.064006	0.005153	4098.398	−4.154	45.90%
s(lon)	0.064558	0.005705	4104.756	2.204	45.30%
s(BAT) + s(ASPECT)	0.093139	0.034286	4117.656	15.104	21.50%
s(BAT)	0.094014	0.035161	4111.666	9.114	20.60%
s(ASPECT)	0.10867	0.049817	4123.602	21.05	8.42%

whales in the area (spring and summer). A total of 44 sightings of killer whales and 3746 of other cetaceans were recorded in spring. During this season the best model included two covariates (see Table 1): depth and longitude, both highly significant, and explaining 50.4% of the deviance. Killer whales presence was expected between 0 and 950 m depth showing a linear increasing pattern towards shallower waters and between 8.5° and 4°W (see Figure 2) with an equally higher presence for this longitude range and a decrease for the rest of the area, with a higher coefficient of variation (see Figure 4).

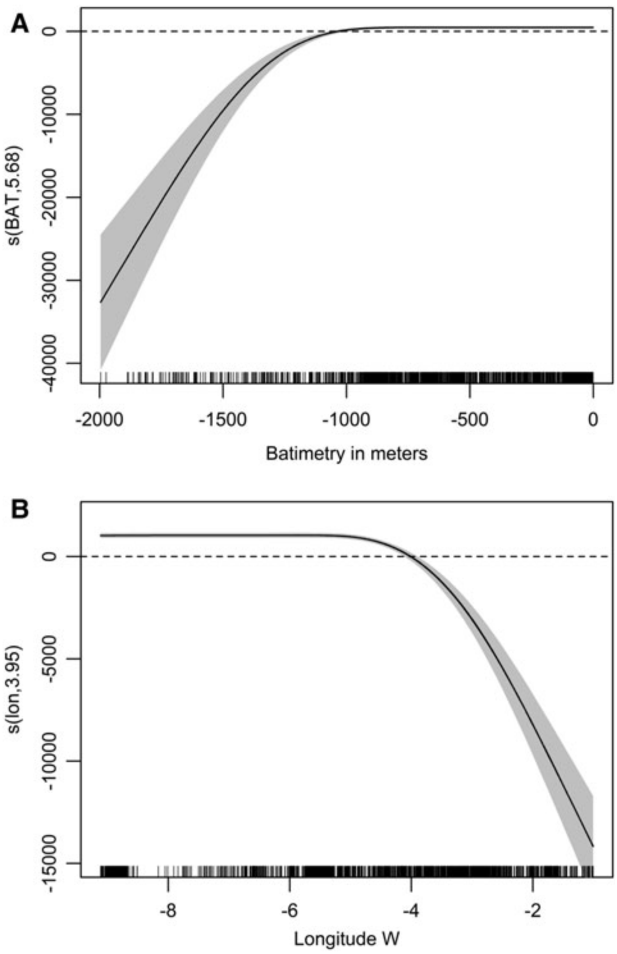

Fig. 2. Smoothed functions for the selected predictive covariates in the model of probability of presence of killer whales in the study area in spring. Continuous line represents the point estimate and grey areas represent ±ISE. The small ticks on the X axis represent the samples. (A) Bathymetry; (B) longitude.

In summer 278 sightings of killer whales and 7206 of other cetaceans were recorded. The best model included three covariates (Table 2): depth, longitude and sea surface temperature, all of them significant and explaining in total 49.60% of the deviance. Presence probability was higher at 0–950 m depth, between 8.5° and 4°W and at 19–24°C SST (see Figure 3).

The spring model prediction map shows two important areas for the presence of killer whales, one in the eastern part of the Gulf of Cadiz in shallow Spanish and Moroccan waters and another one in the south of Portugal (Figure 4). While the variance is very low for the Gulf of Cadiz, it is high in the south of Portugal (Figure 4).

The summer model prediction map shows a high presence only in the western-central part of the Strait of Gibraltar (Figure 5), with little variance in the prediction (Figure 5).

DISCUSSION

This study highlights the importance of collaborative datasets to understand the distribution of animals with low encounter rates. The kind of datasets we have used are statistically difficult to deal with, due to the differences in surveying conditions, but these data are of great importance in understanding which environmental variables are responsible for the spatial distribution of this species. Here we have solved the heterogeneity of effort from different datasets by using other cetacean species' presence as a proxy for killer whale absence. Recent studies have highlighted several methods for selection of pseudo-absence, including: random (Stockwell, 1999); random with geographical-weighted exclusion (Hirzel *et al.*, 2001), random with environmentally-weighted exclusion (Zaniewski *et al.*, 2002) and locations that have been visited (i.e. occurrences for other species, as in our case) but where the target species was not recorded (Elith & Leathwick, 2007). The benefits of each technique have been discussed previously (Lütolf *et al.*, 2006; Phillips & Dudík, 2008), and are outside the scope of this study. Although the chosen approach is not ideal, in our opinion it is suitable due to the high amount of sightings of other cetacean species in the study area, and the non-availability of homogeneous effort.

We have demonstrated clear and predictable influences of environmental and geographical factors on the distribution of killer whales in this region. The results support previous studies showing that killer whales are encountered in shallow waters of the south-western part of the Strait of Gibraltar in summer (de Stephanis *et al.*, 2008a). The distribution pattern of the species seems to be closely linked to the bathymetric structure within the area. Previous studies

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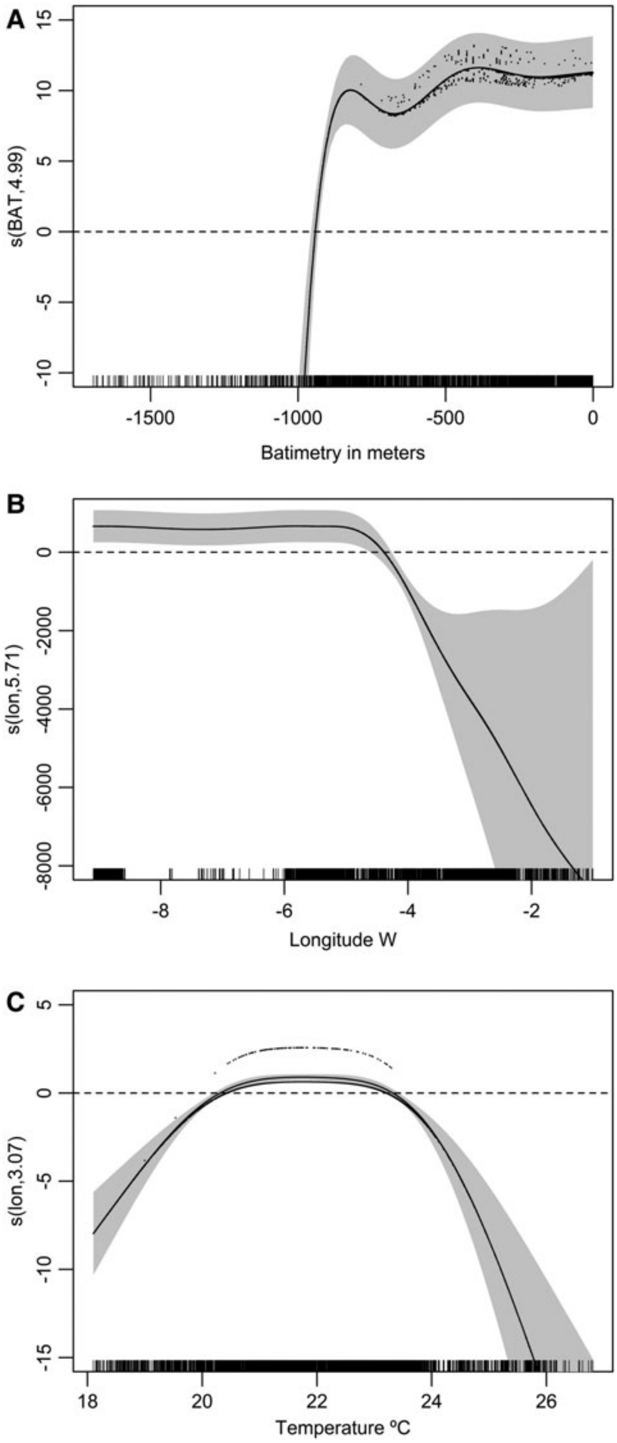

Fig. 3. Smoothed functions for the selected predictive covariates in the model of probability of presence of killer whales in the study area in summer. Continuous line represents the point estimate and grey areas represent ±ISE. The small ticks on the X axis represent the samples. (A) Bathymetry; (B) Longitude; (C) sea surface temperature.

have shown that water depth can be a significant factor in determining the distribution of marine top predators, (e.g. Selzer & Payne (1988), de Stephanis *et al.* (2008a) and Schneider (2008) have suggested that the importance of water depth is related to prey availability.

Atlantic bluefin tuna (ABFT) live in pelagic ecosystems of the entire North Atlantic and its adjacent seas, primarily the Mediterranean Sea (Fromentin & Powers, 2005). Some tuna born in the Mediterranean Sea, leave and undertake trophic migrations within the eastern Atlantic Ocean up to age 4 or 5 years, at which point they reach sexual maturity and return to the Mediterranean Sea to spawn in spring (Aloncle, 1964b; Dicenta & Piccinetti, 1978; Cort, 1990; Mather et al., 1995). Then, ABFT return to the Atlantic Ocean in summer crossing the Strait of Gibraltar in a trophic migration (Sella, 1929; Rodríguez-Roda, 1964). The different predicted spatial distributions of killer whales in spring and summer match the spawning and trophic migrations of ABFT through the study area.

The spring model predicts killer whales presence in shallow waters close to the west coast of the study area, where they would be capable of hunting schools of ABFT entering the Mediterranean, using the endurance–exhaustion hunting technique described in the Gulf of Cadiz (<100 m depth) by Guinet *et al.* (2007). Killer whales are known to dive to depths no more than 300 m (Bowers & Henderson, 1972). Hunting in shallow waters can prevent ABFT from taking refuge at depths (Guinet *et al.*, 2007).

In addition to depth and longitude, temperature had a significant influence on the presence probability of killer whales during summer, restricting their distribution area to the Strait of Gibraltar. Quílez-Badia *et al.* (2012) showed that ABFT were crossing the Strait in water temperatures between 19 and 24°C while swimming to the Atlantic Ocean, which matches the temperature range predicting the presence of killer whales in the Strait of Gibraltar in summer in this study. Deep dives have been reported through the use of tags on ABFT while they are crossing the Strait of Gibraltar (Wilson & Block, 2009), suggesting: (a) that they may forage on squid and fish inhabiting deep Mediterranean outflow waters; (b) that maybe these dives were related to predator avoidance by the killer whales; or (c) that the dives were related to thermoregulation and energetic saving associated with avoiding ocean currents. Since 1995, Spanish and Moroccan fisheries have been established and developed near sea mounts in the Strait of Gibraltar during the western tuna migration (Srour, 1994; de la Serna *et al.*, 2004). Killer whales have been observed among fishing boats at least since 1999 in the central part of the Strait (de Stephanis *et al.*, 2008a) either (a) depredating tuna from the long-lines or (b) actively chasing tuna in the area, in these shallower waters where ABFT are not able to avoid them by performing deep dives. The presence of ABFT long-line fisheries, the shallow waters of the Strait, as well as the bottleneck that represents the Strait of Gibraltar for the migration of the ABFT would explain the high predictability of the species in the area both in summer and spring.

In the Alboran Sea a large effort has been made for the study of cetaceans, but only four sightings of killer whales have been recorded in the area in 10 years (Figure 1), and none of the selected models have identified any important area for killer whales in that area in this study (Figures 4 & 5). The Alboran Sea is characterized by a narrow, steep shelf (5–10 km) (Ercilla *et al.*, 1992; Hernández-Molina, 1993; Hernández-Molina *et al.*, 1994) compared to the wide shelf (30–40 km) of the Gulf of Cadiz (Baraza *et al.*, 1999). This difference could be crucial for the presence of killer whales in the area, as they seem to prefer hunting in shallow areas (Guinet *et al.*, 2007). Therefore, it seems better for the killer whales to wait for ABFT near the shallow sea mounts of the

Table 2. Detection-function model fits with generalized cross validation (GCV) score and ΔGCV between models and Akaike information criterion (AIC) and ΔAIC between models and the deviation explained for each model, during the summer period. Only covariates showing significant relationship are shown.

Covariates	GCV	ΔGCV	AIC	ΔAIC	Deviance Explained
s(BAT) + s(lon) + s(SST)	0.14259		9384.136		49.60%
s(BAT) + s(lon)	0.14326	0.00067	9389.616	5.48	49.30%
s(lon)	0.17302	0.03043	9451.718	67.582	38.70%
s(BAT) + s(SST)	0.18114	0.03855	9444.685	60.549	35.90%
s(BAT)	0.18902	0.04643	9459.7	75.564	33%
s(SST)	0.26926	0.12667	9567.393	183.257	4.69%

Strait of Gibraltar and adjacent waters. In southern Portugal (Algarve), there are few sightings of killer whales (Figure 1), but the spring model predicts an important area near Faro (Figure 4). This area used to be one of the main places for Portuguese tuna trap nets (Ravier & Fromentin, 2001), therefore it could be a suitable area for killer whale endurance–exhaustion hunting (Guinet *et al.*, 2007). Little effort was available in the Algarve, and the model prediction shows a great variance in the area (Figure 4), that could be due to the low availability to 'pseudo-absences' in the models (Figure 1). Therefore, this area should be further surveyed to improve the spring model prediction. No cetacean survey has been made in Moroccan waters; however, the spring model has identified the North Atlantic coast of Morocco as an important area. Further studies should focus on refining habitat predictions and examining relationships between killer whale distributions and environmental correlations over the years and in areas not so well studied as Moroccan and Portuguese coasts and offshore waters of the southern Iberian Peninsula. Scarce sightings (both of killer whales and other species) were recorded in autumn and winter, which did not allow modelling of their presence during these periods of the year.

Conservation of the eastern Atlantic stock of killer whale prey is essential for the future of both endangered predator and prey in the area, as ABFT has been overfished (Collette *et al.*, 2012) and Iberian killer whales have a highly specialized diet (García-Tiscar, 2009). The fecundity of another population of killer whales in the eastern Pacific Ocean has been strongly related to the abundance of their prey,

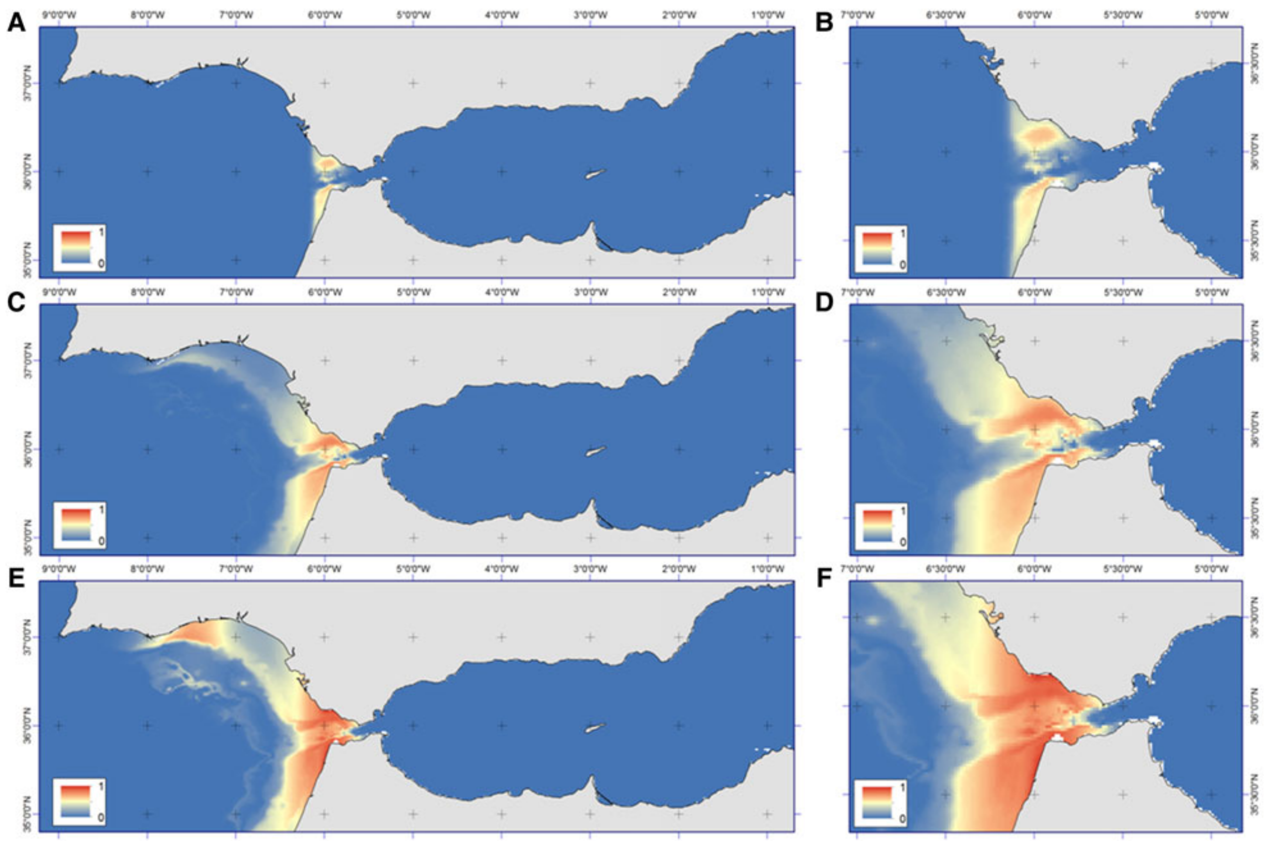

Fig. 4. Predicted density surface map of killer whales in the area from spatial modelling in spring by bootstraps: (A) the inferior 95% CI of the predicted model at southern Iberian Peninsula; (B) the inferior 95% CI of the predicted model in the Strait of Gibraltar; (C) best predicted model at southern Iberian Peninsula; (D) best predicted model in the Strait of Gibraltar; (E) the superior 95% CI of the predicted model at southern Iberian Peninsula; (F) the superior 95% CI of the predicted model in the Strait of Gibraltar.

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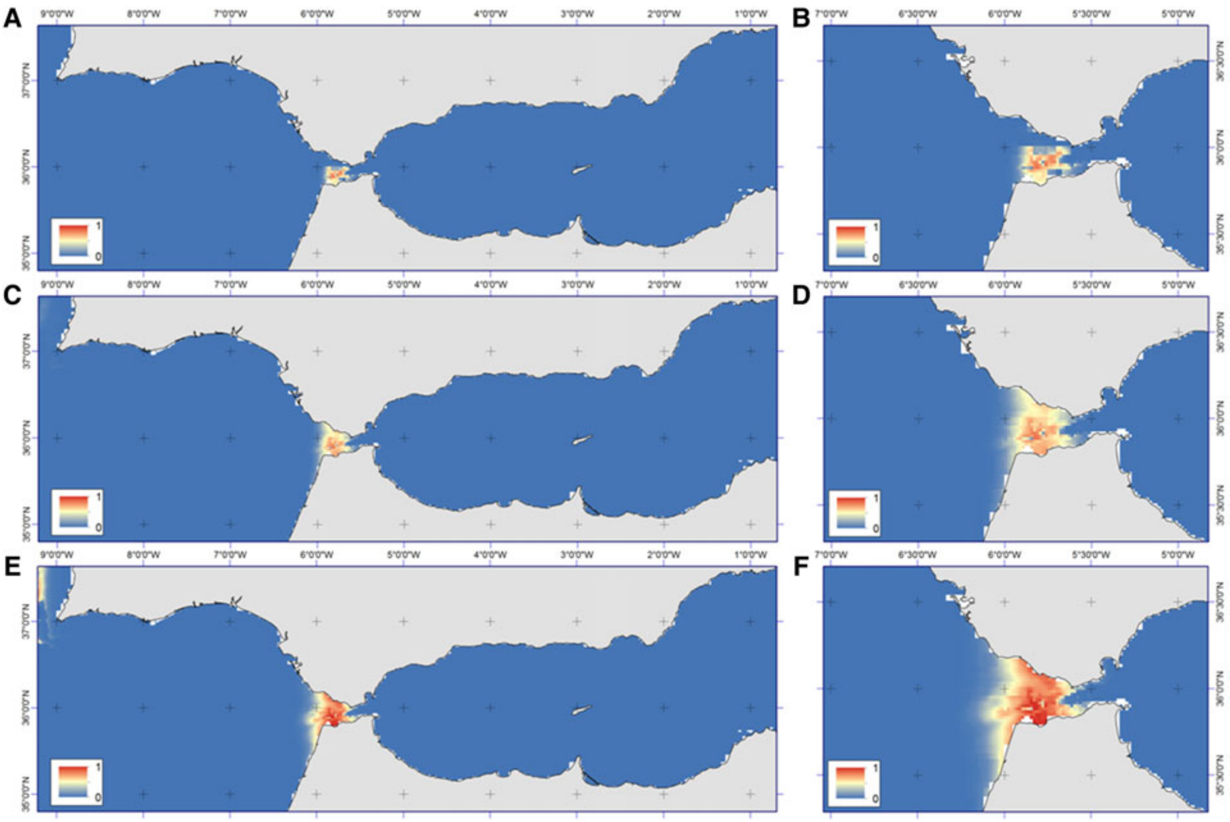

Fig. 5. Predicted density surface map of killer whales in the area from spatial modelling in summer by bootstraps: (A) the inferior 95% CI of the predicted model at southern Iberian Peninsula; (B) the inferior 95% CI of the predicted model in the Strait of Gibraltar; (C) best predicted model at southern Iberian Peninsula; (D) best predicted model in the Strait of Gibraltar; (E) the superior 95% CI of the predicted model at southern Iberian Peninsula; (F) the superior 95% CI of the predicted model in the Strait of Gibraltar.

the Chinook salmon, where a decrease in salmon populations caused senescence in the whales and affected their fecundity rates (Ward *et al.*, 2009). For that reason, any decrease in the abundance of ABFT could set the Iberian population of killer whales at greater risk. Therefore, important areas for southern Iberian killer whales require adequate protection, such as the creation of an exclusion zone where activities that may disrupt their hunting technique, such as whale watching, military exercises or sport fishing, are prohibited in spring in the eastern areas of the Gulf of Cadiz (both in Spain and Morocco). The conservation of this killer whale population distributed across national borders will only be achieved through collaboration and coordination between the neighbouring countries Spain, Portugal and Morocco, and the implementation of a joint action plan to protect the habitat.

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REFERENCES

Aloncle H. (1964a) Premières observations sur les petits cétacés des côtes marocaines. *Bulletin d l'Institut des Pêches Maritimes du Maroc* 12, 21–42.

Aloncle H. (1964b) Note sur le thon rouge de la Baie Ibéro-Marocaine. *Bulletin de l'Institut des Pêches Maritimes du Maroc* 12, 43–59.

Amante C. and Eakins B. (2009) *ETOPO1 1 Arc-minute global relief model: procedures, data sources and analysis*. NOAA Technical Memorandum NESDIS NGDC-24, 19 pp. March 2009.

https://doi.org/10.1017/S002531541300091X Published online by Cambridge University Press

Baird R.W. and Dill L.M. (1995) Occurrence and behaviour of transient killer whales: seasonal and pod-specific variability, foraging behaviour, and prey handling. *Canadian Journal of Zoology, Fisheries and Aquatic Sciences* 73, 1300–1311.

Baraza J., Ercilla G. and Nelson C. H. (1999) Potential geologic hazards on the eastern Gulf of Cadiz slope (SW Spain). *Marine Geology* 155, 191–215.

Baumgartner M. and Mullin K. (2001) Cetacean habitats in the northern Gulf of Mexico. *Fisheries Bulletin* 99, 219–239.

Bayed A. and Beaubrun P. (1987) Les mammifères marins du Maroc: inventaire préliminaire. *Mammalia* 51, 437–446.

Bowers C.A. and Henderson R.S. (1972) *Project Deep Ops: deep object recovery with pilot and killer whales.* San Diego, CA: Naval Undersea Center.

Braham H.W. and Dahlheim M.E. (1982) *Killer whales in Alaska documented in the Platforms of Opportunity Program. Report of the International Whaling Commission.* Cambridge: IWC.

Carder K., Chen F., Lee Z., Hawes S. and Cannizzaro J. (2003) *MODIS Ocean Science Team Algorithm Theoretical Basis Document, ATBD-MOD-19, Ver. 7.* Available at: http://modis.gsfc.nasa.gov/data/atbd/atbd_mod19.pdf (accessed 17 July 2013).

Cañadas A. and de Stephanis R. (2006) Killer whale, or Orca *Orcinus orca* (Strait of Gibraltar subpopulation). In Reeves R.R. and Notarbartolo di Sciara G. (eds) *The status and distribution of cetaceans in the Black Sea and Mediterranean Sea.* Malaga: IUCN, Centre for Mediterranean Cooperation, pp. 34–38.

Cañadas A. and Hammond P. (2006) Model-based abundance estimates for bottlenose dolphins off southern Spain: implications for conservation and management. *Journal of Cetacean Research and Management* 8, 13–27.

Cañadas A., Sagarminaga R., de Stephanis R., Urquiola E. and Hammond P.S. (2005) Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. *Aquatic Conservation: Marine and Freshwater Ecosystems* 15, 495–521.

Casinos A. and Vericad J.R. (1976) The cetaceans of the Spanish coasts: a survey. *Mammalia* 40, 267–290.

Cetti F. (1777) *Storia naturale di Sardegna. III. Anfibi e Pesci.* Cagliari, Italy: Tip. Giuseppe Piattoli, 208 pp.

Collette B., Amotin A.F., Boustanu A., Carpenter K.E., De Oliveira Leite N. Jr, Di Natale A., Die D., Fox W., Fredou F.L., Graves J., Viera Hazin F.H., Hinton M., Juan Jorda M., Schratwieser J., Texeira Lessa R.P., Pires Ferreira Travassos P.E. and Uozumi Y. (2012) *Thunnus thynnus.* In *IUCN Red List of Threatened Species. Version 2012.2.* Gland: IUCN.

Cort J. (1990) Biología y pesca del atún rojo, 'Thunnus thynnus'(L.), del mar Cantábrico. *Publicaciones Especiales. Instituto Español de Ocenografia* 4, 272.

D'Amico A., Bergamasco A., Zanasca P., Carniel S., Nacini E., Portunato N., Teloni V., Mori C. and Barbanti R. (2003) Qualitative correlation of marine mammals with physical and biological parameters in the Ligurian Sea. *IEEE Journal of Oceanic Engineering* 28, 29–43.

de la Serna J.D., Alot E., Majuelos E. and Rioja P. (2004) La migración trófica post reproductiva del atún rojo (*Thunnus thynnus*) a través del estrecho de Gibraltar. *Collective Volume of Scientific Papers ICCAT* 56, 1196–1209.

de Stephanis R., Cornulier T., Verborgh P., Salazar Sierra J., Pérez Gimeno N. and Guinet C. (2008a) Summer spatial distribution of cetaceans in the Strait of Gibraltar in relation to the oceanographic context. *Marine Ecology Progress Series* 353, 275–288.

de Stephanis R., García-Tiscar S., Verborgh P., Esteban Pavo R., Pérez S., Minvielle-Sebastia L. and Guinet C. (2008b) Diet of the social groups of long-finned pilot whales (*Globicephala melas*) in the Strait of Gibraltar. *Marine Biology* 154, 603–612.

Dicenta A. and Piccinetti C. (1978) Desove del atun (*Thunnus thynnus*) en el Mediterráneo occidental y evaluacion directa del stock de reproductores, basado en la abundancia de sus larvas. *Collective Volume of Scientific Papers ICCAT* 7, 389–395.

Dwyer S. and Visser I. (2011) Cookie cutter shark (*Isistius* sp.) bites on cetaceans, with particular reference to killer whales (orca) (*Orcinus orca*). *Aquatic Mammals* 37(2), 11–138.

Elith J. and Leathwick J. (2007) Predicting species distributions from museum and herbarium records using multiresponse models fitted with multivariate adaptive regression splines. *Diversity and Distributions* 13, 265–275.

Ercilla G., Alonso B. and Baraza J. (1992) Sedimentary evolution of the northwestern Alboran Sea during the Quaternary. *Geo-Marine Letters* 12, 144–149.

Esteban R. (2008) *Abundancia, Estructura social y Parámetros demográficos de la orca* (Orcinus orca*) en el Estrecho de Gibraltar.* Master's thesis. Universidad de Cádiz, Spain.

Foote A., Vilstrup J., de Stephanis R., Verborgh P., Nielsen S.C.A., Deaville R., Kleivane L., Martín V., Miller P.J.O., Øien N., Pérez-Gil M., Rasmussen M., Reid R.J., Robertson K.M., Rogan E., Similä T., Tejedor M.L., Vester H., Víkingsson G.A., Willerslev E., Gilbert M.T.P. and Piertney S.B. (2011) Genetic differentiation among North Atlantic killer whale populations. *Molecular Ecology* 20, 629–641.

Forney K.A. and Wade P. (2007) Worldwide distribution and abundance of killer whales. In Estes J. (ed.) *Whales, whaling and ocean ecosystems.* Berkeley, CA: University of California Press, pp. 145–162.

Fromentin J.M. and Powers J.E. (2005) Atlantic bluefin tuna: population dynamics, ecology, fisheries and management. *Fish and Fisheries* 6, 281–306.

García-Tiscar S. (2009) *Interacciones entre delfines mulares y orcas con pesqueerías en el Mar de Alborán y Estrecho de Gibraltar.* PhD thesis. Universidad Autónoma de Madrid, Spain.

Guinet C., Domenici P., de Stephanis R., Barrett-Lennard L., Ford J.K.B. and Verborgh P. (2007) Killer whale predation on bluefin tuna: exploring the hypothesis of the endurance–exhaustion. *Marine Ecology Progress Series* 347, 111–119.

Hamazaki T. (2002) Spatiotemporal prediction models of cetacean habitats in the mid-western North Atlantic ocean (from Cape Hatteras, North Carolina, USA to Nova Scotia, Canada). *Marine Mammal Science* 18, 920–939.

Hastie T. and Tibshirani R. (1990) *Generalized additive models. Monographs on statistics and applied probability, 43.* Boca Raton, FL: Chapman & Hall/CRC Press.

Hernández-Molina F.J. (1993) *Dinámica sedimentaria y evolución durante el Pleistoceno Terminal–Holoceno del margen noroccidental del Mar de Alboran. Modelo de estratigrafia secuencial de muy alta resolución en plataformas continentales.* Master's thesis. Universidad de Granada, Spain.

Hernández-Molina F., Somoza L., Rey J. and Pomar L. (1994) Late Pleistocene–Holocene sediments on the Spanish continental shelves: Model for very high resolution sequence stratigraphy. *Marine Geology* 120, 129–174.

Heyning J.E. and Dahlheim M.E. (1988) *Orcinus orca. Mammalian Species* 304, 1–9.

Hirzel A.H., Helfer V. and Metral F. (2001) Assessing habitat-suitability models with a virtual species. *Ecological Modelling* 145, 111–121.

Hooker S.K., Whitehead H. and Gowans S. (1999) Marine Protected Area design and the spatial and temporal distribution of cetaceans in a submarine canyon. *Conservation Biology* 13, 592–602.

Horozco A. (1598) *Historia de la ciudad de Cádiz.* 2nd edition. Cadiz, Spain: El Excmo. Ayuntamiento de esta M.N.. M. L. y M. H. Ciudad.

Iñiguez M.A. (2001) Seasonal distribution of killer whales (*Orcinus orca*) in Northern Patagonia, Argentina. *Aquatic Mammals* 27, 154–161.

Leatherwood J.S. and Dalheim M.E. (1978) Worldwide distribution of pilot whales and killer whales. *Naval Ocean Systems Center Technical Report 443*, pp. 1–39.

Lozano F. (1958) Los escómbridos de las aguas españolas y marroquíes y su pesca. *Trabajos Instituto Español de Oceanografia* 25, 254.

Lütolf M., Kienast F. and Guisan A. (2006) The ghost of past species occurrence: improving species distribution models for presence-only data. *Journal of Applied Ecology* 43, 802–815.

Mackenzie K. (1999) Parasites as biological tags in population studies of marine organisms. *Parasitology* 124, S153–S163.

Malod J.A. (1982) *Comparaison de l'évolution des marges continentales au Nord et au Sud de la Péninsule Ibérique*. PhD thesis. Université Curie, Paris, France.

Mather F., Mason J. and Jones A. (1995) *Historical document: life history and fisheries of Atlantic bluefin tuna*. NOAA Technical Memorandum NMFS-SEFSC-370, 163 pp.

Notarbartolo di Sciara G. (1987) Killer whale, *Orcinus orca*, in the Mediterranean Sea. *Marine Mammal Science* 3, 356–360.

Notarbartolo di Sciara G. and Birkun A.J. (2010) *Conserving whales, dolphins and porpoises in the Mediterranean and Black Seas. ACCOBAMS status report*. Monaco: ACCOBAMS, 212 pp.

Phillips S.J. and Dudík M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31, 161–175.

Quílez-Badia G., Cermeño P. and Tudela S. (2012) *Movements of bluefin tuna revealed by electronic tagging in the Mediterranean sea and in Atlantic waters of Morocco in 2011*. ICCAT SCRS/2012/123.

Raga J.A., Raduán A. and Blanco C. (1985) Contribución al estudio de la distribución de cetàceos en el Mediterráneo y Atlantico Ibérico. *Miscelánia Zoológica* 9, 361–366.

Ravier C. and Fromentin J.-M. (2001) Long-term fluctuations in the eastern Atlantic and Mediterranean bluefin tuna population. *ICES Journal of Marine Science* 58, 1299–1317.

Reid J., Evans P.G.H. and Northridge S.P. (2003) *Atlas of cetacean distribution in north-west European waters*. Peterborough: Joint Nature Conservation Committee (JNCC), 82 pp.

Roberts D.G. (1970) The Rif–Betic orogen in the Gulf of Cadiz. *Marine Geology* 9(5), M31–M37.

Rodríguez-Roda J. (1964) Talla, peso y edad de los atunes, *Thunnus thynnus* (L.), capturados por la almadraba de Barbate (costa sudatlántica de España) en 1963 y comparación. *Investigación Pesquera* 26, 3–48.

Schneider D.C. (2008) Habitat selection by marine birds in relation to water depth. *Ibis* 139, 175–178.

Sella M. (1929) *Migrazioni e habitat del tonno (*Thunnus thynnus L*) studiati col metodo degli ami, con osservazioni su l'accrescimento, sul regime delle tonnare ecc.* Venice: Univ.-Bibliothek Frankfurt an Main.

Selzer L.A. and Payne P.M. (1988) The dsitribution of white-sided (*Lagenorhynchus acutus*) and common dolphins (*Delphinus delphis*) VS. environmental features of the continental shelf of the Northeastern United States. *Marine Mammal Science* 4, 141–153.

Sigurjónsson J. and Leatherwood S. (1988) The Icelandic live-capture fishery for killer whales, 1976–1988. *Rit Fiskideildar* 11, 307–316.

Srour A. (1994) Développment de la nouvelle pêcherie artisanale au thon rouge dans la région de Ksar sghir. *Note d'Information ISPM* 26, 10–11.

Stockwell D. (1999) The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographical Information Science* 13, 143–158.

Torres L.G., Rosel P.E., D'Agrosa C. and Read A.J. (2003) Improving management of overlapping bottlenose dolphin ecotypes through spatial analysis and genetics. *Marine Mammal Science* 19, 502–514.

VanDerWal J., Shoo L. and Januchowski S. (2010) *SDM Tools. Species Distribution Modelling Tools: tools for processing data associated with species distribution modelling exercises. R package version 1*. Available at: https://www.rforge.net/SDMTools/ (accessed 17 July 2013).

Verborgh P., de Stephanis R., Pérez S., Yaget Y., Barbraud C. and Guinet C. (2009) Survival rate, abundance, and residency of long-finned pilot whales in the Strait of Gibraltar. *Marine Mammal Science* 25, 523–536.

Ward E.J., Holmes E.E. and Balcomb K.C. (2009) Quantifying the effects of prey abundance on killer whale reproduction. *Journal of Applied Ecology* 46, 632–640.

Wilson S. and Block B. (2009) Habitat use in Atlantic bluefin tuna *Thunnus thynnus* inferred from diving behavior. *Endangered Species Research* 10, 355–367.

Wood S. (2000) Modelling and smoothing parameter estimation with multiple quadratic penalties. *Statistical Society: Series B* 62, 413–428.

Wood S. (2001) mgcv: GAMs and generalized ridge regression for R. *R News* 1(2), 20–25.

Wood S. (2006) On confidence intervals for generalized additive models based on penalized regression splines. *Australian and New Zealand Journal of Statistics* 48, 445–464.

and

Zaniewski A.E., Lehmann A. and Overton J.M. (2002) Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecological Modelling* 157, 261–280.

Correspondence should be addressed to:
R. Esteban
CIRCE, Conservation Information and Research on Cetaceans, C/Cabeza de Manzaneda 3,
Algeciras-Pelayo, 11390 Cadiz, Spain
email: ruth@circe.info

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