Journal of the
MARINE BIOLOGICAL ASSOCIATION
of the United Kingdom

CAMBRIDGE
UNIVERSITY PRESS

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

Journal:	*Journal of the Marine Biological Association of the United Kingdom*
Manuscript ID:	JMBA-12-12-SI-0444.R1
Manuscript Type:	Special Issue Article
Date Submitted by the Author:	13-Jun-2013
Complete List of Authors:	Esteban, Ruth; CIRCE, Conservation Information and Research on Cetaceans Verborgh, Philippe; CIRCE, Conservation Information and Research on Cetaceans Gauffier, Pauline; CIRCE, Conservation Information and Research on Cetaceans Giménez, Joan; GEMA, Grupo de Ecología Marina Aplicada, Estación Biológica de Doñana, CSIC Afan, Isabel; LAR, Laboratorio de SIG y Teledetección, Estación Biológica de Doñana, CSIC García, Pedro; ANSE, Asociación de Naturalistas del Sureste Murcia, Jose Luis; ANSE, Asociación de Naturalistas del Sureste Magalhães, Sara; Mar Ilimitado, Andreu, Ezequiel; TURMARES, Turísmo Maritimo del Estrecho de Stephanis, Renaud; GEMA, Grupo de Ecología Marina Aplicada, Estación Biológica de Doñana, CSIC
Keywords:	Killer whale, Orcinus orca, distribution, spatial modelling, GAM, cetacean, Strait of Gibraltar, Southern Iberian Peninsula
Abstract:	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 generalised 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, enters the Mediterranean Sea and the other model used summer data when Atlantic bluefin tuna returns 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. Abstract.doc

Running Head: Habitat of killer whales in the southern Iberian Peninsula

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], 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.
[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

Corresponding author: R. Esteban
E-mail: ruth@circe.info

ABSTRACT

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 generalised 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, enters the Mediterranean Sea and the other model used summer data when Atlantic bluefin tuna returns 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, GAM, cetacean, Strait of Gibraltar, Southern Iberian Peninsula

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) 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.

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 Northeast 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; Rodríguez-Roda, 1964; Aloncle, 1964b; de Stephan *et al.*, 2008). 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 northeast 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 Island population" suggest that it is a non-cohesive population that may not follows 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 to implement a conservation plan for this subpopulation as soon as possible (IWC 2007) and since 2011, the Spanish Ministry of Environment considers the killer whales of the Strait of Gibraltar and the Gulf of Cadiz as "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 done 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 comprised between 0º30' East and 9º30' West and between 37º30' and 35º North, 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 (Malod, 1982; Roberts, 1970). 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 east-west 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 characterised by a west to east canyon, with shallower waters (200 to 300 m) found on the Atlantic side and deeper waters (800 to 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 characterised 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 data sets 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 NGO ANSE (Asociación de Naturalistas del Sureste) in the Murcia region; (2) sightings collected by Alnitak since 2002, a research NGO which performed random transect throughout the Alboran Sea (Cañadas et al., 2005); (3) sightings collected by Alnilam since 2010, a research company which performed 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 transect throughout the Strait of Gibraltar and Gulf of Cadiz (de Stephanis *et al.*, 2008); (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 and 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 2005, that performs random and line transect by boat and airplane 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 generalised additive modelling (GAM) techniques (Hastie & Tibshirani, 1990). The open-source statistical programming language R version 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 GCV (Generalised Cross Validation score, an approximation to 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, however 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 i^{th} sampling station, θ_0 is the intercept, f_k are smoothed functions of the explanatory covariates, and z_{ik} is the value of the k^{th} explanatory covariate in the i^{th} 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 (geographic) 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 (Generalised Cross Validation score, an approximation to AIC); (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 2x2km 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 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 meters depth showing a linear increasing pattern towards shallower waters and between 8.5º and 4º longitude West (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).

In summer 278 sightings of killer whales and 7206 of other cetaceans were recorded. The best model included three covariates: 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 meters depth, between 8.5º and 4º longitude West and at 19-24ºC sea surface temperature (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 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 to understand 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 whales absence. Recent studies have highlighted several methods for selection of pseudo-absence including: random (Stockwell, 1999); random with geographic-weighted exclusion (Hirzel, Helfer, & Metral, 2001), random with environmentally weighted exclusion (Zaniewski *et al.*, 2002) and locations that have been visited (i.e., occurrences for other species, like 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 out of 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 homogenous 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.*, 2008). The distribution pattern of the species seems to be closely linked to the bathymetric structure within the area. Previous studies 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.*, 2008; Schneider, 2008). These authors suggested that the importance of water depth was related to prey availability.

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, at which point they reach sexual maturity and return to the Mediterranean Sea to spawn in spring (Aloncle, 1964b; Cort, 1990; Dicenta & Piccinetti, 1978; Mather, Mason, & Jones, 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 between 19 and 24ºC 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 that

(a) they may forage on squid and fish inhabiting deep Mediterranean outflow waters, or (b) maybe these dives were related to predator avoidance by the killer whales, or (c) 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.*, 2008), (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 and 5). The Alboran Sea is characterised 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 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 whales endurance-exhaustion hunting (Guinet *et al.*, 2007). Little effort was available in 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 correlates 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 their presence during these periods of the year.

Conservation of the eastern Atlantic stock of killer whales' 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 specialised 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, 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 would be prohibited in spring in the eastern areas of the Gulf of Cadiz (both in Spain and Morocco), such as whale watching, military exercises or sport fishing. 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 their habitat.

ACKNOWLEDGEMENTS

We would like to specially thank Alnitak for supplying their sighting data-base. Thanks are due to the Consejería de Agricultura, Pesca y Medio Ambiente of the Junta de Andalucía and the Agencia de Medio Ambiente y Agua of the Junta de Andalucía, especially to Manuel Fernández Casado, Diego Moreno, Agustin Barrajón, Maria del Carmen Arroyo, Julio de la Rosa y Jose Miguel Remón, Eduardo Fernández Tabales and María Soledad Vivas. Thanks to Rebecca Bringley, Teo Todorov, Javier Elorriaga, Rafael García, José María Carceles and Clive Finlayson for supplying killer whale sightings. João Nuno Gonçalves, Bruno Claro, CIRCE volunteers and research assistants helped in the field work of CIRCE and the EBD-CSIC. This work was funded by the Loro Parque Foundation, CEPSA, Ministerio de Medio Ambiente, Fundación Biodiversidad, Life Indemares (LIFE 07 NAT.E.000732) and LIFE "Conservación de Cetáceos y tortugas de Murcia y Andalucía" (LIFE02NAT/E/8610), the "Plan Nacional I+D+I" of the Spanish "Ministerio de Economía y Competitividad". De Stephanis was supported by the "Ministerio de Economía y Competitividad" through the "Subprograma Juan de la Cierva". Thanks are also due to the IFAW for providing the software Logger 2000.

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*, Data Sources and Analysis. NOAA Technical Memorandum NESDIS NGDC-24, 19 pp, March 2009.*

Báez J., Camiñas J. and Torreblanca D. (2007) Análisis de la distribución espacial de aves y mamíferos marinos en el Golfo de Cádiz (Sudoeste de la Península Ibérica) durante el periodo de primavera. *Boletín de la Real Sociedad Española de Historia Natural. Seccion Biológica*, 102, (1-4) 93–97.

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, (7) 1300–1311.

Baraza J., Ercilla G. and H. Nelson C. (1999) Potential geologic hazards on the eastern Gulf of Cadiz slope (SW Spain). *Marine Geology*, 155, (1-2) 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, (3) 437–446.

Bowers C. A. and Henderson R. S. (1972) *Project Deep Ops: Deep Object Recovery with Pilot and Killer Whales.* San Diego, CA.

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*.

Carder K., Chen F., Lee Z., Hawes S. and Cannizzaro J. (2003) MODIS Ocean Science Team Algorithm Theoretical Basis Document, *ATBD-MOD-19, Ver. 5.0*.

Casinos A. and Vericad J. R. (1976) The cetaceans of the Spanish coasts: a survey. *Mammalia*, 40, (2) 267–290.

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

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, (1) 13–27.

Cañadas A. and Hammond P. (2008) Abundance and habitat preferences of the short-beaked common dolphin Delphinus delphis in the southwestern Mediterranean: implications for conservation. *Endangered Species Research*, 4, 309–331.

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, (5) 495–521.

Cetti F. (1777) *Storia naturale della Sardegna.* Sassari, Piattoli.

Collette B., Amotin A. F., Boustanu A., Carpenter K. E., De Oliveira Leite Jr. N., 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 Theatened Species. Version 2012.2*,

Cort J. (1990) Biología y pesca del atún rojo,“ Thunnus thynnus”(L.), del mar Cantábrico (Tesis doctoral). *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, (1) 29–43.

de la Serna J. D. la, Alot E., Majuelos E. and Rioja P. (2004) La migración trófica post reproductiva del atún rojo (*Thunnus thynnus*) a través del estrecho de Gibraltar. *Collect. Vol. Sci. Pap. ICCAT*, 56, (3) 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.

de Stephanis R., Verborgh P., Pérez S., Esteban R., Minvielle-Sebastia L. and Guinet C. (2008c) Long-term social structure of long-finned pilot whales (*Globicephala melas*) in the Strait of Gibraltar. *Acta ethologica*, 11, 81–94.

De Stephanis R., Giménez J., Carpinelli E., Guitierrez-Expósito C. and Cañadas A. (in press). As main meal for Sperm whales: plastic deris.Marine Pollution Bulletin. *Marine Pollution Bulletin*,

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. *Col. Vol. Sci. Pap. ICCAT*, 7, (2) 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, (3) 265–275.

Ercilla G., Alonso B. and Baraza J. (1992) Sedimentary evolution of the northwestern Alboran Sea during the Quaternary. *Geo-Marine Letters*, 12, (2-3) 144–149.

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

Foote A. D., Newton J., Piertney S. B., Willerslev E. and Gilbert M. T. P. (2009) Ecological, morphological and genetic divergence of sympatric North Atlantic killer whale populations. *Molecular Ecology*, 18, 5207–5217.

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., Pasmussen 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: *Whales, whaling and ocean ecosystems*, pp. 145–162.

Fromentin J.M. and Powers J. E. (2005) Atlantic bluefin tuna: population dynamics, ecology, fisheries and management. *Fish and Fisheries*, 6, (4) 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,

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 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, (3-4) 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, (2-3) 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, (3) 592–602.

Horozco A. (1598) *Historia de la ciudad de Cádiz.* 2nd edition. 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, (2) 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*, 1–39.

Lozano F. (1958) Los escómbridos de las aguas españolas y marroquíes y su pesca. *Trab. Inst. Esp. Ocean*, 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, (4) 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, 163pp.

Notarbartolo di Sciara G. (1987) Killer whale, *Orcinus orca*, in the Mediterranean Sea. *Marine Mammal Science*, 3, (4) 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*

Phillips S. J. and Dudík M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, 31, (2) 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, (6) 1299–1317.

Reid J., Evans P. G. H. and Northridge S. P. (2003) Atlas of cetacean distribution in north-west European waters. *Joint Nature Conservation Committee (JNCC),* Peterborough, 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. *Inv. Pesq*, 26, 3–48.

Schneider D. C. (2008) Habitat selection by marine birds in relation to water depth. *Ibis*, 139, (1) 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.

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 Norheastern United States. *Marine Mammal Science*, 4, (2) 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, (2) 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, (3) 502–514.

VanDerWal J., Shoo L. and Januchowski S. (2010) SDMTools: Species Distribution Modelling Tools: tools for processing data associated with species distribution modelling exercises. *R package version 1*,

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, (3) 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, (3) 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 (2): 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 & New Zealand Journal of Statistics*, 48(4):445-464.

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, (2-3) 261–280.

FIGURES LEGENDS

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) sighting in spring in the Strait of Gibraltar; (C) sightings in summer in the southern Iberian Peninsula and (D) sightings in summer in the Strait of Gibraltar.

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 ±1 se. The small ticks on the X axis represent the samples. (A) Bathymetry and (B) Longitude.

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 ±1 se. The small ticks on the X axis represent the samples. (A) Bathymetry; (B) Longitude and (C) Sea Surface Temperature.

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

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

TABLE LEGENDS

Table 1: Detection-function model fits with GCV(Generalised Cross Validation score) ΔGCV between models, AIC (Akaike Information Criterion) and ΔAIC between models, during the spring period. Only covariates showing significant relationship are shown

Table 2: Detection-function model fits with GCV(Generalised Cross Validation score) ΔGCV between models, AIC (Akaike Information Criterion) and ΔAIC between models and the deviation explained for each model, during the summer period. Only covariates showing significant relationship are shown

FIGURES and TABLES

FIGURES:

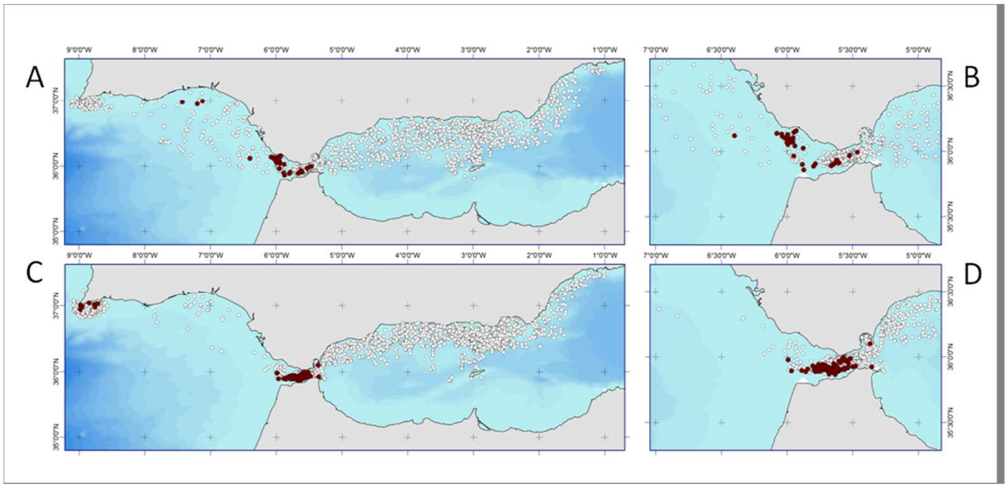

Fig. 1. Cetacean sighting distribution in the study area. In red killer whales sightings and in grey other cetacean sightings. (A) sightings in spring in the southern Iberian Peninsula; (B) sighting in spring in the Strait of Gibraltar; (C) sightings in summer in the southern Iberian Peninsula and (D)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

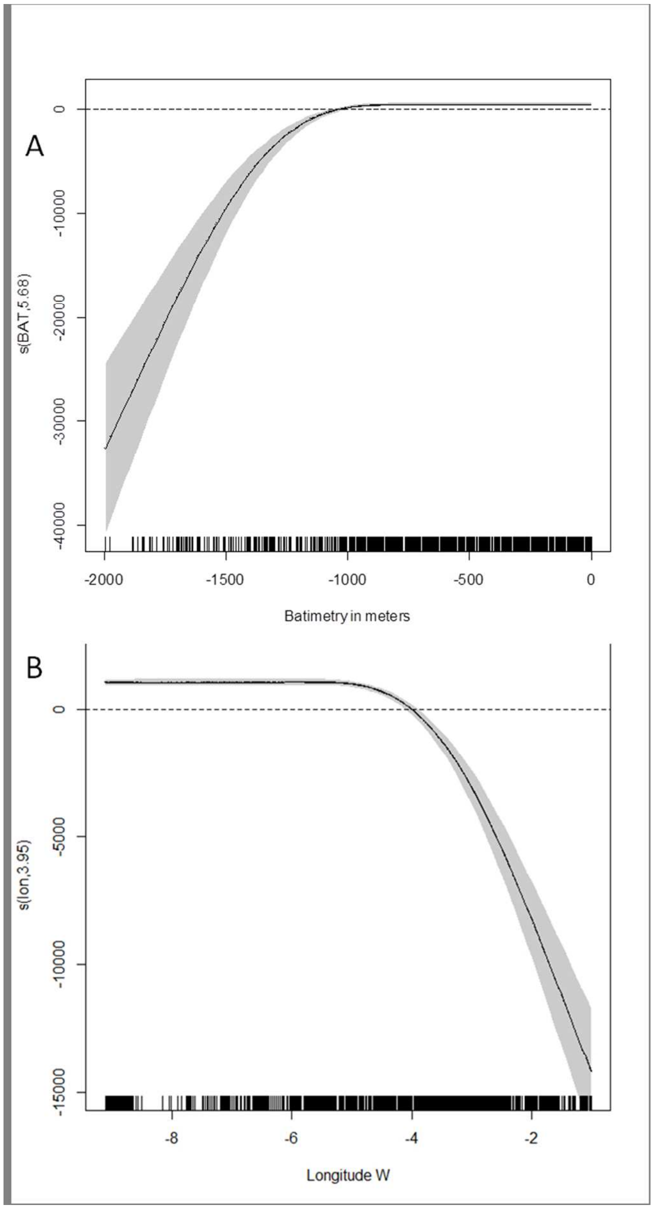

Fig.2. Smoothed functions for the selected predictive covariates in the model of probability of presence of killer whales in the study area in spring. Continuous line represents the point estimate and grey areas represent ±1 se. The small ticks on the X axis represent the samples. (A) Bathymetry and (B) Longitude.

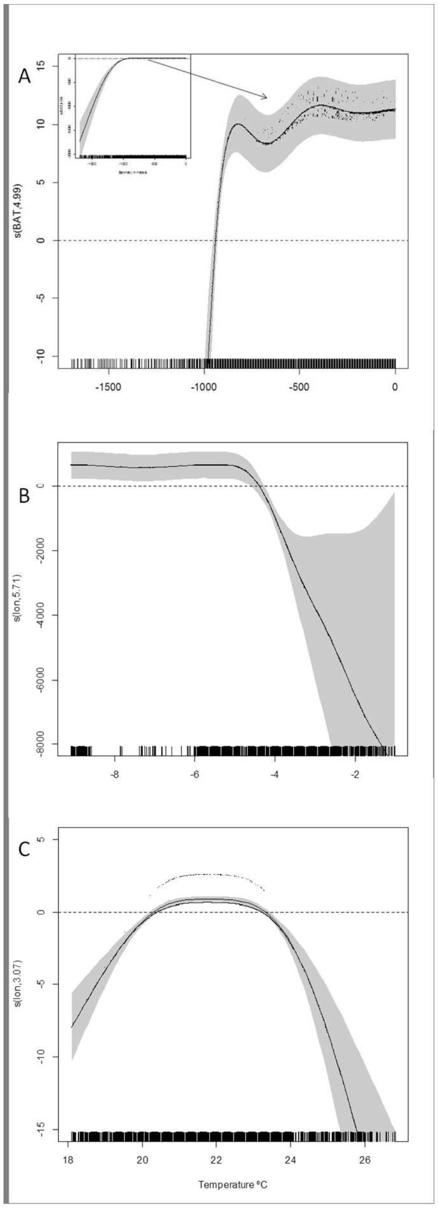

Fig. 3. Smoothed functions for the selected predictive covariates in the model of probability of presence of killer whales in the study area in summer. Continuous line represents the point estimate and grey areas represent ±1 se. The small ticks on the X axis represent the samples. (A) Bathymetry; (B) Longitude and (C) Sea Surface Temperature.

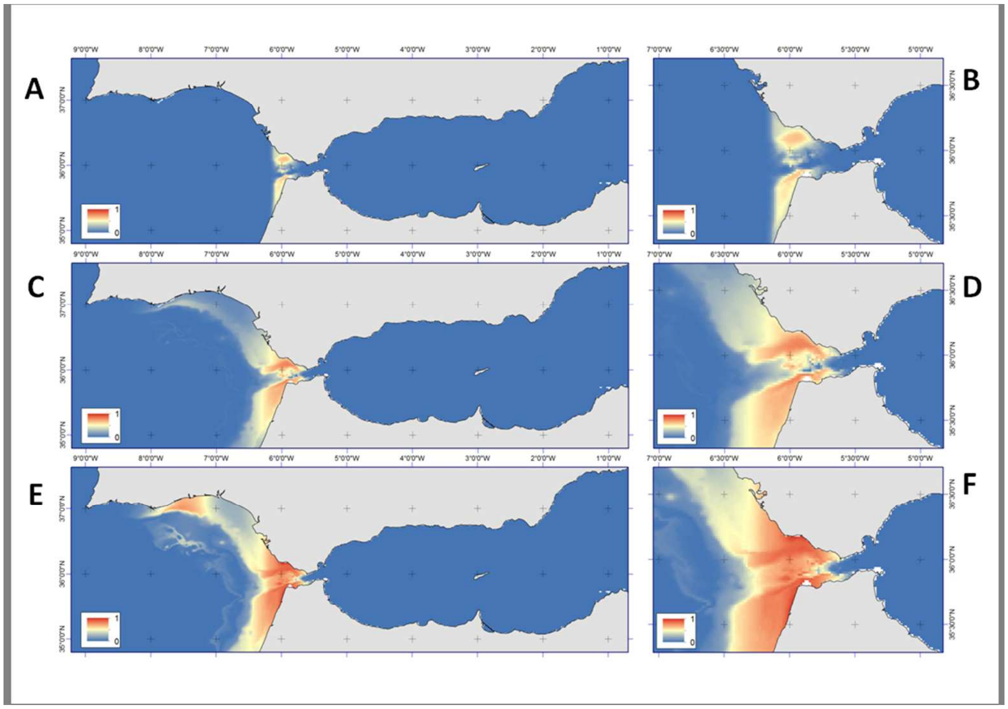

Fig. 4. Predicted density surface map of killer whales in the area from spatial modelling in spring by bootstraps. (A) the inferior 95% C.I. of the predicted model at southern Iberian Peninsula; (B) the inferior 95% C.I. of the predicted model in the Strait of Gibraltar; (C) best predicted model at southern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

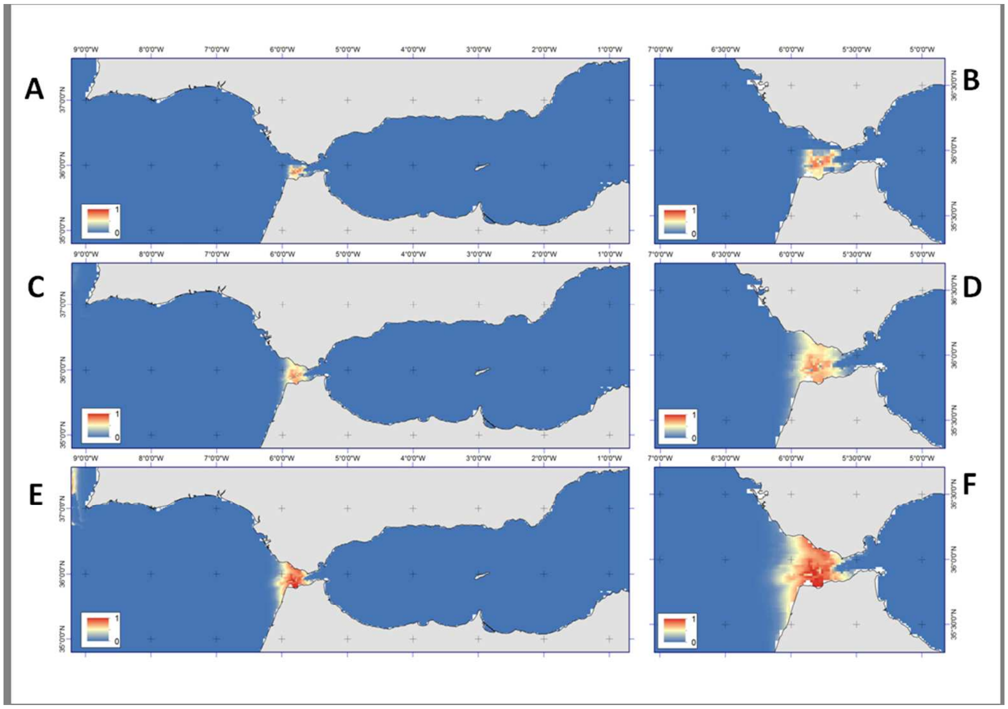

Fig. 5. Predicted density surface map of killer whales in the area from spatial modelling in summer by bootstraps. (A) the inferior 95% C.I. of the predicted model at southern Iberian Peninsula; (B) the inferior 95% C.I. of the predicted model in the Strait of Gibraltar; (C) best predicted model at southern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

Covariates	GCV	ΔGCV	AIC	ΔAIC	Dev 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%

Covariates	**GCV**	**ΔGCV**	**AIC**	**ΔAIC**	**Dev 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%