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

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	<p>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.</p> <p>Abstract.doc</p>

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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

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26 ABSTRACT

27 *Killer whales have been described in the Gulf of Cadiz, southern Spain, in spring and in*
28 *the Strait of Gibraltar in summer. A total of 11,276 cetaceans sightings coming from*
29 *different sources (dedicated research surveys, whale watching companies and*
30 *opportunistic observations) were used to create two presence-“pseudo-absence”*
31 *predictive generalised additive models (GAM), where presence data were defined as*
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33 *species. One model was created using spring data when killer whales’ main prey,*
34 *Atlantic bluefin tuna, enters the Mediterranean Sea and the other model used summer*
35 *data when Atlantic bluefin tuna returns to the Atlantic Ocean. Both model predictions*
36 *show that killer whales are highly associated with a probable distribution of bluefin*
37 *tuna during their migration throughout the study area, constraining their distribution to*
38 *the Gulf of Cadiz in spring and the Strait of Gibraltar in spring and summer.*
39 *Knowledge of the distribution of killer whales in the study area is essential to establish*
40 *conservation measures for this population.*

41

42 Keywords: killer whale, *Orcinus orca*, distribution, spatial modelling, GAM, cetacean, Strait of
43 Gibraltar, Southern Iberian Peninsula

44

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

70 North Sea and Skagerrak Strait (Reid *et al.*, 2003). Killer whales are regularly seen in
71 the Strait of Gibraltar and adjacent Atlantic waters (Horozco, 1598; Aloncle, 1964a;
72 Casinos & Vericad, 1976; Bayed & Beaubrun, 1987; Guinet *et al.*, 2007; de Stephanis
73 *et al.*, 2008; Esteban, 2008; Foote *et al.*, 2011). Conversely, killer whales are considered
74 as a rare species in the Mediterranean Sea (Casinos & Vericad, 1976; Raga *et al.*, 1985;
75 Bayed & Beaubrun, 1987; Notarbartolo di Sciara, 1987; Notarbartolo di Sciara &
76 Birkun, 2010).

77 In Southern Spain, killer whales are observed in spring in the Gulf of Cadiz (Guinet et
78 al., 2007; García-Tiscar, 2009), when their main prey, Atlantic bluefin tuna (hereafter
79 ABFT) (*Thunnus thynnus*), enters the Mediterranean Sea (Cetti, 1777; Sella, 1929;
80 Rodríguez-Roda, 1964) and in summer associated with the ABFT long-line fishery of
81 the Strait of Gibraltar, (Srour, 1994; de la Serna *et al.*, 2004) when ABFT return from
82 their spawning areas on their way back to the Atlantic Ocean (Lozano, 1958;
83 Rodríguez-Roda, 1964; Aloncle, 1964b; de Stephan *et al.*, 2008). These killer whales
84 belong to the same population as killer whales sampled in the Canary islands, and are
85 significantly different from other populations in the northeast Atlantic (North Sea,
86 Iceland and Norway) (Foote *et al.*, 2011). Additionally, differences in carbon and
87 nitrogen stable isotopes ratios (García-Tiscar, 2009) and parasite load (Mackenzie,
88 1999; Dwyer & Visser, 2011) among pods from the “Strait of Gibraltar-Canary Island
89 population” suggest that it is a non-cohesive population that may not follows the same
90 resource all year round.

91 Due to their small population size, the killer whales of the Strait of Gibraltar and
92 contiguous waters have been recommended to be included in the “Critically
93 Endangered” category by ACCOBAMS-IUCN (Cañadas & de Stephanis, 2006).
94 Likewise, the International Whaling Commission has recommended to implement a

95 conservation plan for this subpopulation as soon as possible (IWC 2007) and since
96 2011, the Spanish Ministry of Environment considers the killer whales of the Strait of
97 Gibraltar and the Gulf of Cadiz as “Vulnerable” in the Spanish Catalogue of
98 Endangered Species. Both local (Andalusia) and Spanish authorities have recommended
99 studying the spatial distribution of the species in southern Spain, to delineate it, and the
100 boundaries to be managed for a correct implementation of the conservation plan.

101 A great effort has been done to describe the distribution of marine mammals in the
102 Alboran Sea and Strait of Gibraltar (Cañadas *et al.*, 2005; Cañadas & de Stephanis,
103 2006; Cañadas & Hammond, 2006; Guinet *et al.*, 2007; de Stephanis, *et al.*, 2008a, b;
104 Verborgh *et al.*, 2009; Foote *et al.*, 2011), but little is known about the distribution of
105 killer whales in the whole study area, as only one publication describes the summer
106 distribution in the central area of the Strait of Gibraltar (de Stephanis *et al.* 2008a), and
107 no information is available for the rest of the Alboran Sea or the Gulf of Cadiz. This
108 study aims to understand the spatial distribution of killer whales in the southern Iberian
109 Peninsula in relation to different environmental variables, both in spring and summer,
110 from data series compiled from research, whale watching vessels and opportunistic data.
111

112 MATERIALS AND METHODS

113

114 *Study Area*

115

116 The present study was carried out in the Gulf of Cadiz, Strait of Gibraltar and the
 117 Alboran Sea (Figure 1). It is comprised between 0°30' East and 9°30' West and between
 118 37°30' and 35° North, and is bounded to the North by the Iberian Peninsula and to the
 119 south by Africa. These areas display different bathymetric features. The Gulf of Cadiz
 120 has a wide, smooth shelf and slope. In contrast, the northern shelf of the Alboran Sea is
 121 very narrow, but has a very steep shelf and slope gradient. The Gulf of Cadiz, located in
 122 the eastern sector of the central North Atlantic, is concave in shape, with a NW–SE
 123 orientation (Malod, 1982; Roberts, 1970). The physiographic profile of the margin
 124 includes a wide shelf (30–40 km) with a sea-floor slope of 0.2–0.32°, a shelf-break
 125 located at a water depth of between 140 and 120 m, and a smooth continental slope,
 126 with sea-floor gradients of 1.5° in the upper part and 0.5–1° in the middle and lower
 127 parts (Baraza *et al.*, 1999). The Strait of Gibraltar has a length of 60 km (on an east-west
 128 axis), and a mean width of 20 km. The shallowest depth, less than 300 m, is found in the
 129 main sill of Camarinal and its minimum width of around 14 km coincides with the
 130 contraction of Tarifa narrow. The bathymetry of the Strait is characterised by a west to
 131 east canyon, with shallower waters (200 to 300 m) found on the Atlantic side and
 132 deeper waters (800 to 1000 m) on the Mediterranean side. On the eastern side of the
 133 Strait of Gibraltar lies the Alboran Sea basin, at the western edge of the Mediterranean
 134 Sea. It is arc-shaped, and characterised generally by a complex physiography related to
 135 its tectonic history. The Spanish margin has a very narrow, steep shelf (5–10 km) up to
 136 the shelf-break at 110–120 m water depth, which establishes the boundary, with a shelf

137 gradient of 0.5–0.7° and a slope of 2.3° (Ercilla *et al.*, 1992; Hernández-Molina, 1993;
138 Hernández-Molina *et al.*, 1994).

139

140 ***Data Collection***

141

142 Sightings from cetaceans collected between 2002 and 2012 in waters of the southern
143 Iberian Peninsula were compiled. The datasets were separated in two data sets as killer
144 whales have been described in different areas during different seasons: shallow waters
145 in the Gulf of Cadiz in spring (April-June) (Guinet *et al.*, 2007), and in the central
146 waters of the Strait of Gibraltar in summer (July-September) (de Stephanis *et al.*,
147 2008a). We have also based this separation on the migration pattern of their main prey,
148 bluefin tuna (Cetti, 1777; Sella, 1929; Rodríguez-Roda, 1964). Insufficient data were
149 available to make robust spatial models for the rest of the year. A total of 11,276
150 records of cetaceans were available for this analysis coming from: (1) random transect
151 sightings from a research boat performed by the NGO ANSE (Asociación de
152 Naturalistas del Sureste) in the Murcia region; (2) sightings collected by Alnitak since
153 2002, a research NGO which performed random transect throughout the Alboran Sea
154 (Cañadas *et al.*, 2005); (3) sightings collected by Alnilam since 2010, a research
155 company which performed random transect throughout the Alboran Sea; (4) sightings of
156 CIRCE (Conservation, Information and Research on Cetaceans) since 2002, a research
157 NGO that made random and line transect throughout the Strait of Gibraltar and Gulf of
158 Cadiz (de Stephanis *et al.*, 2008); (5) sightings of TURMARES (Turismo Marítimo del
159 Estrecho) since 2003, a whale watching company based in the Strait of Gibraltar; (6)
160 sightings from Mar Ilimitado (Tourism and Research) since 2005, a whale watching and
161 research company and based in southern Portugal; (7) sightings from Consejería de
162 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:

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

190 Where p_i is the probability to find killer whales, in the i^{th} sampling station, θ_0 is the
191 intercept, f_k are smoothed functions of the explanatory covariates, and z_{ik} is the value of
192 the k^{th} explanatory covariate in the i^{th} sampling station. The environmental variables
193 used in this study were depth, obtained from ETOPO2 (Amante & Eakins, 2009), its
194 derivative slope and aspect (obtained with the R library SDMtools (VanDerWal *et al.*,
195 2010), sea surface temperature (SST) and chlorophyll a concentration (Chla) obtained
196 from satellite images of MODIS (Carder *et al.*, 2003). Spatial (geographic) covariates,
197 i.e. latitude and longitude, were also used as potential proxies for other unavailable or
198 unknown features affecting whales' distribution. Model selection was done using three
199 diagnostic indicators: (a) the GCV (Generalised Cross Validation score, an
200 approximation to AIC); (b) the percentage of deviance explained; and (c) the probability
201 that each variable was included in the model by chance. The decision to include/drop a
202 term from the model was adopted following the criteria proposed by Wood (2001).

203

204 *Environmental predictive models*

205

206 The best GAM models were used to generate predicted probability values of presence
207 and pseudo-absence on a grid of 2x2km in the study area, which were plotted using
208 ArcMap 10.0. In order to obtain the 95% confidence interval of the predictions, 1000
209 bootstraps with replacement were run for each model, and a prediction was obtained for
210 each bootstrap iteration. The 95% confidence intervals were obtained from the bootstrap
211 process of the models predictions of killer whales in the study area and were also
212 plotted in to assess the precision of the predictions in every point of the study area.

213

214 RESULTS

215

216 Between 2002 and 2012, 322 sightings of killer whales and 10,952 sightings of other
217 cetaceans were recorded in the study area. We created two models for the presence of
218 killer whales in the area (spring and summer). A total of 44 sightings of killer whales
219 and 3746 of other cetaceans were recorded in spring. During this season the best model
220 included two covariates (see Table 1): depth and longitude, both highly significant, and
221 explaining 50.4% of the deviance. Killer whales presence was expected between 0 and
222 950 meters depth showing a linear increasing pattern towards shallower waters and
223 between 8.5° and 4° longitude West (see Figure 2) with an equally higher presence for
224 this longitude range and a decrease for the rest of the area, with a higher coefficient of
225 variation (see Figure 4).

226 In summer 278 sightings of killer whales and 7206 of other cetaceans were recorded.
227 The best model included three covariates: depth, longitude and sea surface temperature,
228 all of them significant and explaining in total 49.60% of the deviance. Presence
229 probability was higher at 0-950 meters depth, between 8.5° and 4° longitude West and at
230 19-24°C sea surface temperature (see Figure 3).

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

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

237

238 DISCUSSION

239

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

256 We have demonstrated clear and predictable influences of environmental and
257 geographical factors on the distribution of killer whales in this region. The results
258 support previous studies showing that killer whales are encountered in shallow waters
259 of the south-western part of the Strait of Gibraltar in summer (de Stephanis *et al.*, 2008).
260 The distribution pattern of the species seems to be closely linked to the bathymetric
261 structure within the area. Previous studies have shown that water depth can be a
262 significant factor in determining the distribution of marine top predators e.g. (Selzer &

263 Payne, 1988; de Stephanis *et al.*, 2008; Schneider, 2008). These authors suggested that
264 the importance of water depth was related to prey availability.

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

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

281 In addition to depth and longitude, temperature had a significant influence on the
282 presence probability of killer whales during summer, restricting their distribution area to
283 the Strait of Gibraltar. Quílez-Badia *et al.* (2012) showed that ABFT were crossing the
284 Strait between 19 and 24°C while swimming to the Atlantic Ocean, which matches the
285 temperature range predicting the presence of killer whales in the Strait of Gibraltar in
286 summer in this study. Deep dives have been reported through the use of tags on ABFT
287 while they are crossing the Strait of Gibraltar (Wilson & Block, 2009), suggesting that

288 (a) they may forage on squid and fish inhabiting deep Mediterranean outflow waters, or
289 (b) maybe these dives were related to predator avoidance by the killer whales, or (c)
290 thermoregulation and energetic saving associated with avoiding ocean currents. Since
291 1995, Spanish and Moroccan fisheries have been established and developed near sea
292 mounts in the Strait of Gibraltar during the western tuna migration (Srouf, 1994; de la
293 Serna *et al.*, 2004). Killer whales have been observed among fishing boats at least since
294 1999 in the central part of the Strait (de Stephanis *et al.*, 2008), (a) depredating tuna
295 from the long-lines or (b) actively chasing tuna in the area, in these shallower waters
296 where ABFT are not able to avoid them by performing deep dives. The presence of
297 ABFT long-line fisheries, the shallow waters of the Strait, as well as the bottleneck that
298 represents the Strait of Gibraltar for the migration of the ABFT would explain the high
299 predictability of the species in the area both in summer and spring.

300 In the Alboran Sea a large effort has been made for the study of cetaceans, but only four
301 sightings of killer whales have been recorded in the area in 10 years (Figure 1), and
302 none of the selected models have identified any important area for killer whales in that
303 area in this study (Figures 4 and 5). The Alboran Sea is characterised by a narrow, steep
304 shelf (5–10 km) (Ercilla *et al.*, 1992; Hernández-Molina, 1993; Hernández-Molina *et*
305 *al.*, 1994) compared to the wide shelf (30–40 km) of the Gulf of Cadiz (Baraza *et al.*,
306 1999). This difference could be crucial for the presence of killer whales in the area, as
307 they seem to prefer hunting in shallow areas (Guinet *et al.*, 2007). Therefore, it seems
308 better for the killer whales to wait for ABFT near the shallow sea mounts of the Strait of
309 Gibraltar and adjacent waters. In southern Portugal (Algarve), there are few sightings of
310 killer whales (Figure 1), but the spring model predicts an important area near Faro
311 (Figure 4). This area used to be one of the main places for Portuguese tuna trap nets
312 (Ravier & Fromentin, 2001), therefore it could be a suitable area for killer whales

313 endurance-exhaustion hunting (Guinet *et al.*, 2007). Little effort was available in
314 Algarve, and the model prediction shows a great variance in the area (Figure 4), that
315 could be due to the low availability to “pseudo-absences” in the models (Figure 1).
316 Therefore, this area should be further surveyed to improve the spring model prediction.
317 No cetacean survey has been made in Moroccan waters; however the spring model has
318 identified the north Atlantic coast of Morocco as an important area. Further studies
319 should focus on refining habitat predictions and examining relationships between killer
320 whale distributions and environmental correlates over the years and in areas not so well
321 studied as Moroccan and Portuguese coasts and offshore waters of the Southern Iberian
322 Peninsula. Scarce sightings (both of killer whales and other species) were recorded in
323 autumn and winter, which did not allow modelling their presence during these periods
324 of the year.

325 Conservation of the eastern Atlantic stock of killer whales’ prey is essential for the
326 future of both endangered predator and prey in the area, as ABFT has been overfished
327 (Collette *et al.*, 2012) and Iberian killer whales have a highly specialised diet (García-
328 Tiscar, 2009). The fecundity of another population of killer whales in the eastern Pacific
329 Ocean has been strongly related to the abundance of their prey, the Chinook salmon,
330 where a decrease in salmon populations caused senescence in the whales and affected
331 their fecundity rates (Ward *et al.*, 2009). For that reason, any decrease in the abundance
332 of ABFT could set the Iberian population of killer whales at greater risk. Therefore,
333 important areas for southern Iberian killer whales require adequate protection, such as
334 the creation of an exclusion zone where activities that may disrupt their hunting
335 technique would be prohibited in spring in the eastern areas of the Gulf of Cadiz (both
336 in Spain and Morocco), such as whale watching, military exercises or sport fishing. The
337 conservation of this killer whale population distributed across national borders will only

338 be achieved through collaboration and coordination between the neighbouring countries
339 Spain, Portugal and Morocco and the implementation of a joint action plan to protect
340 their habitat.

341

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360

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549 FIGURES LEGENDS

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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) 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) Δ GCV between models, AIC (Akaike Information Criterion) and Δ AIC 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) Δ GCV between models, AIC (Akaike Information Criterion) and Δ AIC between models and the deviation explained for each model, during the summer period. Only covariates showing significant relationship are shown

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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%

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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%

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