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Influence of environmental factors on small cetacean distribution in the Spanish Mediterranean

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Habitat distribution models are one of the most up to date methods to study the habitat usage of wildlife populations. They allow animal distribution to be related to environmental features and also the prediction of the distribution of animals based on this relationship. Seasonal aerial surveys were conducted in central Spanish Mediterranean waters from June 2000 to March 2003 to obtain information on the distribution of cetacean species. Data from the three most common cetacean species (striped dolphin, Stenella coeruleoalba*, bottlenose dolphin,* Tursiops truncatus*, and Risso's dolphin,* Grampus griseus*) were related, using generalized linear models, to local environmental features: depth, slope, sea surface temperature and chlorophyll concentration. For bottlenose dolphins, no significant relationship was found with any covariate and no dolphins were observed in waters greater than 1000 m. The distribution of both striped and Risso's dolphin was significantly related to depth. The striped dolphin showed a preference for waters between 900 and 1500 m deep and Risso's dolphin for waters more than 1500 m deep. In addition, for the latest two species, maps of distribution were predicted by means of the spatial models. The areas of higher probabilities of occurrence coincide to a large extent with the marine protected areas previously proposed for the conservation of oceanic cetacean species.*

Keywords: striped dolphin; bottlenose dolphin; Risso's dolphin; distribution; environmental factors; generalized linear models; MPAs.

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INTRODUCTION

One of the fundamental problems in ecology is to accurately understand and describe the processes that determine the distribution of animals. In the case of cetaceans this problem is accentuated because of, on the one hand, the biological characteristics of this group (complex social behaviour and high mobility) and, on the other hand, the fluidity of the ecosystem where they live (Redfern *et al.*, 2006). The marine environment is highly variable, both spatially and temporally, in most of its physical processes, e.g. the upwelling or the transport of planktonic organisms in surface currents. This makes it difficult to distinguish relationships between animal distribution and the habitat predictor variables. Thus, careful selection of the variables and their scale is required (Redfern *et al.*, 2006). Additionally, as this habitat is so inaccessible and costly to study, data on many of the predictor variables are typically difficult to obtain. For example, as predator, foraging is an important factor influencing cetacean distribution, but spatial information on prey species is not usually available. However, some physiographic and hydrographic features play an important role in the distribution of prey species, and may thus provide an indirect explanation of cetacean distribution (Davis *et al.*, 1998; Cañadas *et al.*, 2002).

Recently, the development of habitat distribution models allows animal distribution to be related to environmental features and also the prediction of the distribution of animals based on this relationship. This application has been used as a tool for conservation and management purposes, such as, studies of population trends (Forney, 2000) or delimitation of marine protected areas (MPAs) (Hooker *et al.*, 1999; Cañadas *et al.*, 2005).

In 2000, the Spanish Ministry of Environment initiated a three-year project to provide ecological information of cetaceans in Spanish Mediterranean waters and define MPAs for their conservation (Raga & Pantoja, 2004). In the central Spanish waters MPAs were selected based on areas of high density and/or biodiversity of cetacean species (Gómez de Segura *et al.*, 2004). However, the distribution of cetaceans may vary in the future because of changes in their habitat (prey, environmental conditions, etc.), and in this case MPAs based on just distribution patterns may not be very useful. Understanding cetacean–habitat relationships can lead to a better delimitation of MPAs both at present and in the future.

The present study aims to understand better the ecological processes determining the distribution of the three most common cetacean species in the central Spanish Mediterranean (striped dolphin, *Stenella coeruleoalba*, bottlenose dolphin, *Tursiops truncatus* and Risso's dolphin, *Grampus griseus*). Using spatial habitat models, distribution data of each species obtained from aerial surveys were related to local environmental features: depth, slope, sea surface temperature (SST) and chlorophyll concentration. Additionally, these relationships were used to predict areas that were important for each cetacean species. These areas were compared with the MPAs proposed previously to the Ministry in the area (Gómez de Segura *et al.*, 2004) to

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determine whether the current proposals are supported and whether they will be effective in the future.

MATERIALS AND METHODS

Data collection

The study area comprised the waters of the Valencia and Murcia Regions (central Spanish Mediterranean), from the coastline to between 30 to 80 km offshore, with depths ranging from 10 m to 2800 m (Figure 1). The field methods used in this study to collect cetacean data were the same as those used to estimate absolute cetacean abundance; these methods are described in detail in Gómez de Segura *et al.* (2006).

Seasonal line transect surveys were conducted from spring 2000 to winter 2003 although in some seasons the area could not be surveyed completely due to poor weather conditions. Transects followed a systematic saw-tooth pattern that covered the area representatively (Buckland *et al.*, 2001) (Figure 1). The fieldwork platform was a high-wing aeroplane ('push–pull' Cessna 337) flying at an altitude of 152 m (500 ft) and at a groundspeed of approximately 166 km/h (90 knots). Two observers, positioned on each side of the aircraft, scanned the sea surface and a recorder took note of data reported: species, number of animals, location (obtained from a global positioning system (GPS)), time, and environmental conditions, including Beaufort sea state. Environmental conditions were updated whenever changes occurred and GPS provided a continuous record of position (updated every few seconds). Surveys were conducted only in good sighting conditions of Beaufort sea state ≤ 3. No effect of environmental conditions on the detectability of striped dolphin schools was observed during the surveys (Gómez de Segura *et al.*, 2006).

Environmental features

Based on the available data in the area and previous studies of odontocetes, five oceanographic features were included as potential covariates in the analysis: (i) water depth, derived from the General Bathymetric Chart of the Oceans (GEBCO); (ii) seabed slope, calculated as maximum depth–minimum depth/distance between them; (iii) chlorophyll-*a* concentration (monthly and annual average); (iv) SST (monthly and annual average); and (v) temporal variability of SST (standard deviation of the monthly average SST over the year). Data on SST and chlorophyll were extracted from satellite images obtained from the CREPAD service of the INTA (National Institute for Aerospace Technology) with a pixel resolution of 2 km^2. The SST images came from the NOAA sensor AVHRR and chlorophyll images came from the NASA sensor SeaWiFS.

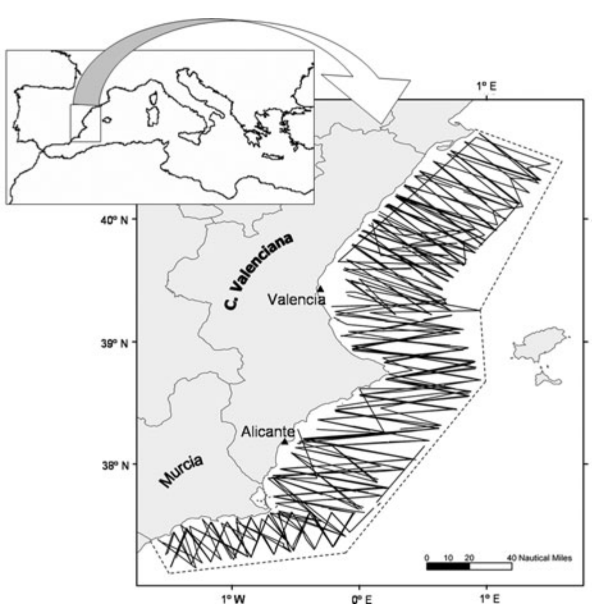

Fig. 1. Study area showing all transects searched on effort during the seasonal aerial surveys from 2000 to 2003.

Data analysis

Using a geographical information system (GIS, ArcMap 8.2.), effort legs were divided into five nautical mile (9.26 km) segments and each segment characterized by the presence or absence of each cetacean species and by the mean of the environmental parameters. This length was chosen to balance the number of segments without sightings (too many makes model fitting problematic) with not losing too much resolution in the environmental covariates, which can reduce explanatory power. The data for the three most common cetacean species (striped dolphin, bottlenose dolphin and Risso's dolphin) were analysed using generalized linear models (GLMs) (McCullagh & Nelder, 1989). The presence/absence of each species were used as the response variable and the environmental features as covariates.

The availability of the different habitats present in the study area could influence the relationships observed. For example, if there were a high proportion of shallow zones in the study area and a low proportion of deep zones, animals may have been found more often in shallow waters because they were more available, not because they were preferred. To account for this, we defined a series of 'habitat types' combining the values of environmental variables (e.g. shallow with moderate slope and high productivity) and grouping the segments according to these 'habitat types'.

First, each variable was divided into a series of equally sized 'bins' using visual inspection of the data to indicate the minimum number of bins needed to describe the variation observed in (e.g. low, moderate and high slope). Data were then organized as a contingency table in which each row constituted a 'habitat type', defined by the combination of the explanatory variables, and the response variable was the proportion of positive observations, i.e. number of segments with positive cetacean observation divided by the total number of segments of this habitat type.

The GLMs were used to model the proportion of positive observations in the different habitat types available, following the method described by Boyce & McDonald (1999) and weighted by the amount of effort (number of segments) in each habitat type. A binomial distribution was used with the logit link function. The general structure of the model was:

$$E(p_i) = \frac{\exp\,[ß_o + \Sigma f_i(z_{ij})]}{1 + \exp\,[ß_o + \Sigma f_i(z_{ij})]}$$

where: p_i is the proportion of positive observations in the i^{th} habitat type, $ß_o$ is a parameter to be estimated and z_{ij} represents the value of the j^{th} explanatory variable in the

i^{th} habitat type fitted as some unknown function f_i to be estimated. Interaction terms were also included in the models to account for relationships between variables (particularly depth with slope) but no significant relationships were found.

A stepwise procedure was applied to select the models that were best supported by the data, using Aikake's information criterion (AIC), in which the measure of model fit is penalized by the number of environmental parameters. The model with the minimum AIC was selected, but when two models had a difference in AIC (delta–AIC) smaller than two they were considered to have equivalent support from the data (Burnham & Anderson, 1998). In all models, the significance of the deviance was tested with a χ^2-test and a visual inspection of the residuals was made, especially to look for trends.

The study area was divided into 631 grid cells, each with a resolution of 5 minutes latitude (5 n.m.) by 5 minutes longitude (3.8 n.m.). Each cell was characterized by the mean of each environmental parameter and this grid was used to predict the distribution of each cetacean species based on the model selected. The results were displayed on a map using GIS. This map was compared visually with the distribution of sightings to confirm that the model was a realistic representation of the data. In cases where there was no clear best model, a comparison of the predicted distributions from the top models (delta–AIC$<$ 2) was made. If only small differences were observed, the most parsimonious model (with fewest parameters) was selected and considered robust.

RESULTS

We conducted 11 surveys in the study area with a total of 20,200 km searched on effort (Figure 1) during which 182 striped dolphin groups, 29 bottlenose dolphin groups and 17 Risso's dolphin groups were observed (Table 1). The distribution of the different species observed is shown in Figure 2.

Depth was divided into five bins and the other parameters were divided into three bins giving 405 possible habitat types, of which only 64 were found in the study area.

Striped dolphin

The GLM with the minimum AIC retained linear, quadratic and cubic functions of depth and the mean annual SST (Table 2). However, the distribution of the striped dolphin was significantly related only to depth at the 5% level. The same model but without annual SST had a delta–AIC less than two from the top model (Table 2). Striped dolphins were observed in waters between 70 and 2600 m; the models showed that they preferred areas between 900 and 1900 m deep (Figure 3A). The predicted distribution of this species based on the relationship with depth and SST is shown in Figure 4A, and is based on the relationships with only depth in Figure 4B. Both predictions are quite similar, supporting the result that, of those environmental features included, depth is the principal one influencing the distribution of striped dolphins.

Bottlenose dolphin

This species was the most coastal-based species encountered; no observations were detected in waters greater than 1000 m depth. No significant relationship was found with any of the ocean parameters studied, including depth. Within 1000 m, bottlenose dolphins did not show a preference for any depth range (Figure 3B).

Risso's dolphin

The distribution of Risso's dolphin was also significantly related only to depth. The terms included in the best model were linear and quadratic functions of depth (Table 2). The next best model incorporating the temporal variability of SST had a delta–AIC of 58.03. Risso's dolphins were sighted in depths between 500 and 2600 m, preferring waters between 1500 and 2500 m deep (Figure 3C). Figure 5 shows the model prediction of the distribution of this species.

DISCUSSION

Based on the results of this study, water depth is the principal factor that defines the distribution of the three most common cetacean species in central Spanish Mediterranean waters. Depth was the principal variable selected by the model in the case of striped and Risso's dolphin and, although there was no significant relationship for bottlenose dolphin, the distribution of this species was limited to waters less than 1000 m deep. Furthermore, the preferred habitat according to depth is different for each species: bottlenose dolphin 0–1000 m;

Table 1. A summary of the aerial surveys carried out in the study area showing effort (km) and the number of schools and animals of the different species of cetaceans observed.

Survey	Date	Effort	Sc schools	Sc animals	Tt schools	Tt animals	Gg schools	Gg animals
Spring 2000	June 2000	675.9	0	0	1	3	0	0
Summer 2000	July 2000	2092.0	13	819	1	3	2	5
Winter 2001	February 2001	370.4	2	402	3	73	0	0
Spring 2001	May 2001	2170.0	7	208	1	20	1	7
Summer 2001	July 2001	2021.1	6	304	2	17	0	0
Autumn 2001	October 2001	2116.4	24	659	3	43	3	15
Winter 2002	March 2002	2102.8	18	435	5	46	3	4
Spring 2002	June 2002	2205.4	19	526	3	21	1	80
Summer 2002	August 2003	1957.7	26	741	1	24	2	25
Autumn 2002	December 2002	2286.8	29	237	5	52	2	4
Winter 2003	March 2003	2200.1	38	332	4	38	3	12
Total		20198.7	182	4663	29	340	17	152

Sc, *Stenella coeruleoalba*; Tt, *Tursiops truncatus*; Gg, *Grampus griseus*.

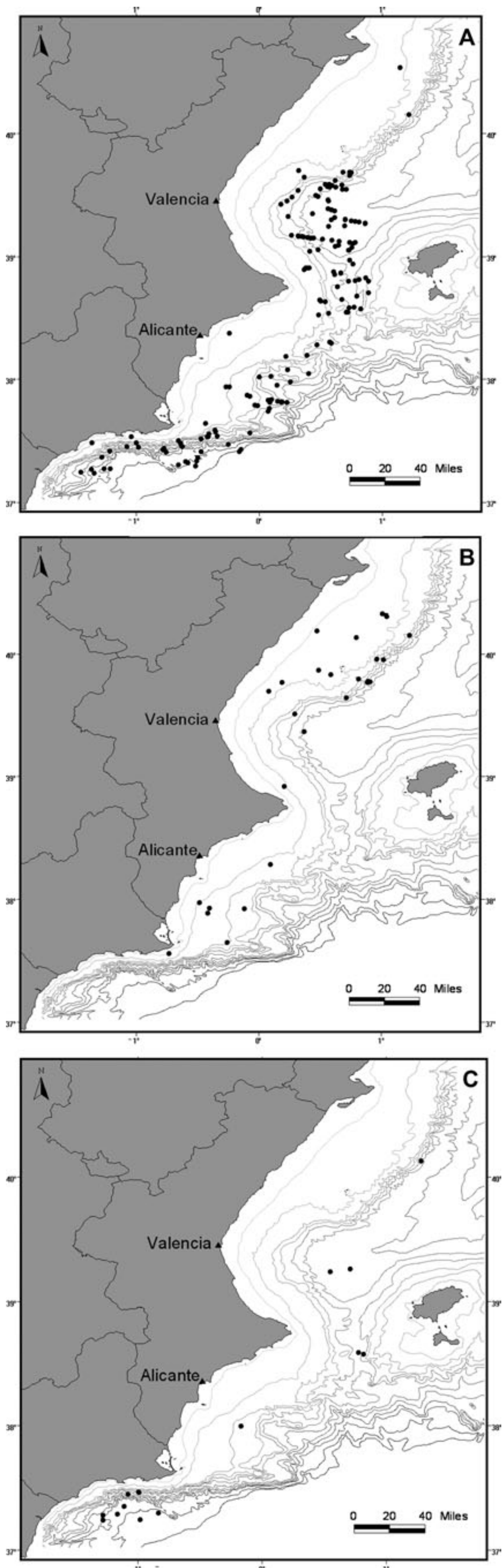

Fig. 2. Distribution of observed sightings of: (A) striped dolphin; (B) bottlenose dolphin; and (C) Risso's dolphin. The 50, 100, 200, 400, 600, 800, 1000, 1400, 1800, 2000, 2200 and 2600 m isobaths are shown.

striped dolphin 900–1900 m; and Risso's dolphin 1500–2500 m. On the basis these results, these three most abundant species appear to occupy almost separate ecological niches categorized by depth in the study area.

Striped dolphin

Striped dolphin distribution was significantly related only to depth and was weakly influenced by annual water temperature. The model with depth alone largely explained the distribution observed in the area (compare Figure 2A with Figure 4B). In the south-western Mediterranean (Cañadas *et al.*, 2002) and the western North Atlantic Ocean (Hooker *et al.*, 1999; Hamazaki, 2002) the distribution of this species was also related to depth. Furthermore, Cañadas *et al.* (2002) found that striped dolphin distribution was related to temperature (mean annual values of SST) in the Alboran Sea (western Mediterranean) but not in the Gulf of Vera (between the Alboran Sea and our study area). The distribution of striped dolphin, at a large scale, is limited by water temperature and in many areas its distribution is correlated with warm currents (Perrin *et al.*, 1994 and references therein). However, at a small scale (e.g. 100s of kilometres), it seems that temperature does not play an important role, unless there is high spatial contrast in SST within the area. The Alboran Sea is characterized by the flow of cold superficial water that comes from the Atlantic through the Gilbraltar Strait. The convergence of this water with the warm Mediterranean waters produces high differences in SST within this sea. However, in our study area (4° latitude x 3° longitude), spatial variation in temperature is very low; no more than 4 degrees in mean monthly SST and no more than 2 degrees in mean annual temperature. Hamazaki (2002) also found a relationship between striped dolphin distribution and SST using mean weekly values in the mid-western North Atlantic. This quite large study area (13° latitude x 18° longitude) is characterized by a high variation in the SST (more than 15°C). Nevertheless, it is also possible that we failed to relate dolphin distribution to temperature because of inadequate temporal resolution in the SST data. Mean weekly values of SST could not be used in our analyses because they were unavailable in some weeks due to cloud cover.

Striped dolphins in this study showed a preference for waters between 900 and 1900 m deep. A recent study of delphinids in the whole Mediterranean indicated a preference of striped dolphin for open waters (>2000 m deep) although a high percentage of sightings also occurred in waters between 1000 and 2000 m (Gannier, 2005). A smaller scale study in the Ligurian Sea showed similar habitat use results (Gannier, 1998). However, in other Mediterranean areas (Italian waters, Notarbartolo di Sciara *et al.*, 1993 and the Alboran Sea, Cañadas *et al.*, 2002) dolphins did not prefer such deep waters, as also seen in our study area. In the Ligurian Sea a diurnal offshore–inshore movement was observed indicating that dolphin depth preferences changed depending on the hour of the day (Gannier, 1999). A visual inspection of sightings obtained in our study area showed no difference in distribution during the day.

Cephalopods dominate the stomach contents of stranded striped dolphins in the study area; 88% of the prey ingested (60% of the species) were pelagic or bathypelagic and 99% were either partially or completely oceanic during the life

Table 2. Results for the best models selected for striped dolphin (Sc) and Risso's dolphin (Gg). The estimate values and the significance value (P) derived from the z-test are shown.

	Variable	Estimate	SE	*P*
Sc model 1 (AIC = 151.71)	Intercept	23.24	9.084	0.01050*
	Depth	0.008	0.002	1.26E−06***
	Depth^2	−4.98E−06	1.61E−06	0.00200M**
	Depth^3	8.83E−10	4.25E−10	0.03765*
	Annual SST	9.41E−01	4.99E−01	0.05965
Sc model 2 (AIC = 153.27)	Intercept	−6.197	0.513	<2E−16***
	Depth	0.009	0.002	3.16E−07***
	Depth^2	−5.12E−06	1.59E−06	0.00130**
	Depth^3	8.87E−10	4.21E−10	0.03534*
Gg (AIC = 55.74)	Intercept	−8.19	1.12	2.65E−13***
	Depth	0.005	0.002	0.00841**
	Depth^2	−1.13E−06	6.08E−07	0.06369

AIC, Aikake's information criterion; SE, standard error; SST, sea surface temperature. Significance levels of the *P* value: ***, 0.001; **, 0.01; *, 0.05.

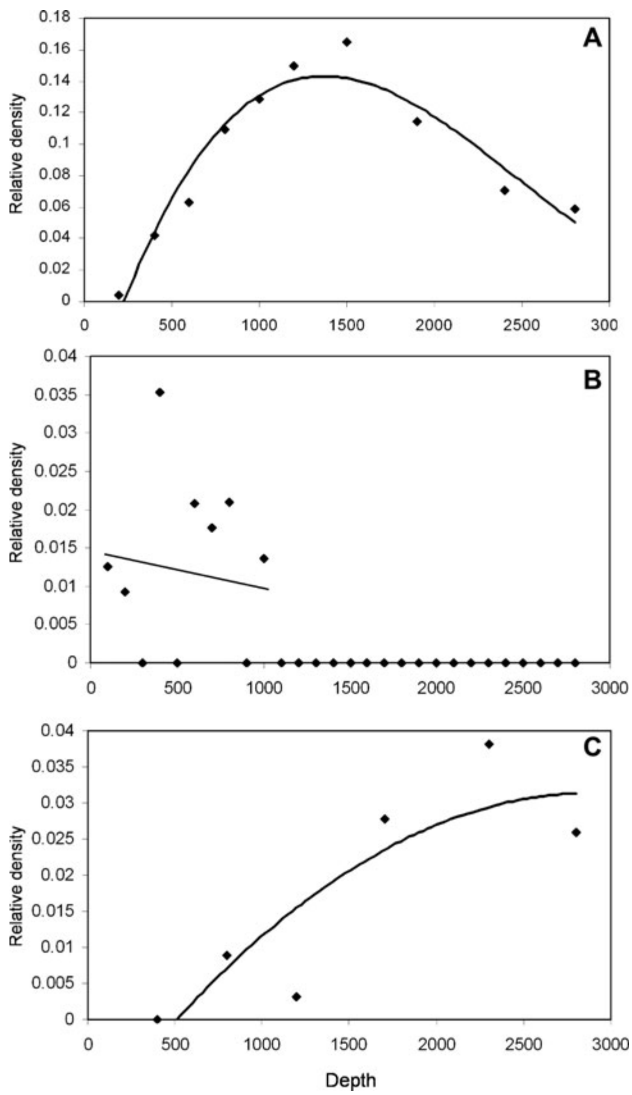

Fig. 3. Relative density (animal per nautical mile searched) vs depth for the three species: (A) striped dolphin; (B) bottlenose dolphin; and (C) Risso's dolphin. Quadratic or cubic functions fitted by the generalized linear model analysis are shown.

cycle (73% of the species) (Blanco *et al.*, 1995). This diet, composed principally of oceanic species, agrees with the results obtained in this study.

Bottlenose dolphin

Bottlenose dolphin distribution was not related to any of the modelled covariates. In the Alboran Sea, however, bottlenose dolphin distribution was related with depth and seabed slope (Cañadas *et al.*, 2002) being associated with submarine mountains. In United States waters of the Gulf of Mexico the distribution of this species was also related to variability in water temperature suggesting an association with ocean fronts (Baumgartner *et al.*, 2001). In our study area, neither important ocean fronts nor submarine mountains occur. It is likely that there are other factors, that have not been investigated here, which are determining the distribution of this species in the study area.

Bottlenose dolphins were only found in waters less than 1000 m deep but within this range groups were distributed uniformly with respect to depth (Figure 3B). Previous information on this species in the Mediterranean shows a coastal distribution with very scarce sightings outside the continental shelf (0–200 m) (Notarbartolo di Sciara *et al.*, 1993; Marini *et al.*, 1997). However, Gannier (2005) in his study of the whole Mediterranean showed that although most bottlenose dolphins were detected on the continental shelf (78% of sightings), bottlenose dolphins were also observed in the upper continental slope (200–1000 m). Cañadas *et al.* (2002) also observed in the Alboran Sea that dolphins sometimes prefer deeper waters than the continental shelf such as the continental slope (200–400 m).

Elsewhere, two forms of bottlenose dolphin exist in many regions, the coastal and the offshore form, with different depth preferences, genetic profiles, parasite load, stomach content and morphology (Leatherwood & Reeves, 1990). In the United States, the coastal form occurs on the continental shelf and the offshore form ranges primarily in waters between the 200 and 2000 m isobaths (Leatherwood & Reeves, 1990; Waring *et al.*, 1997) and out to the 6000 m isobath based on satellite tracking studies (Wells *et al.*, 1999).

A diet study of bottlenose dolphins stranded in the area showed that most prey species were of demersal and/or benthic origin from the continental shelf (0–200 m),

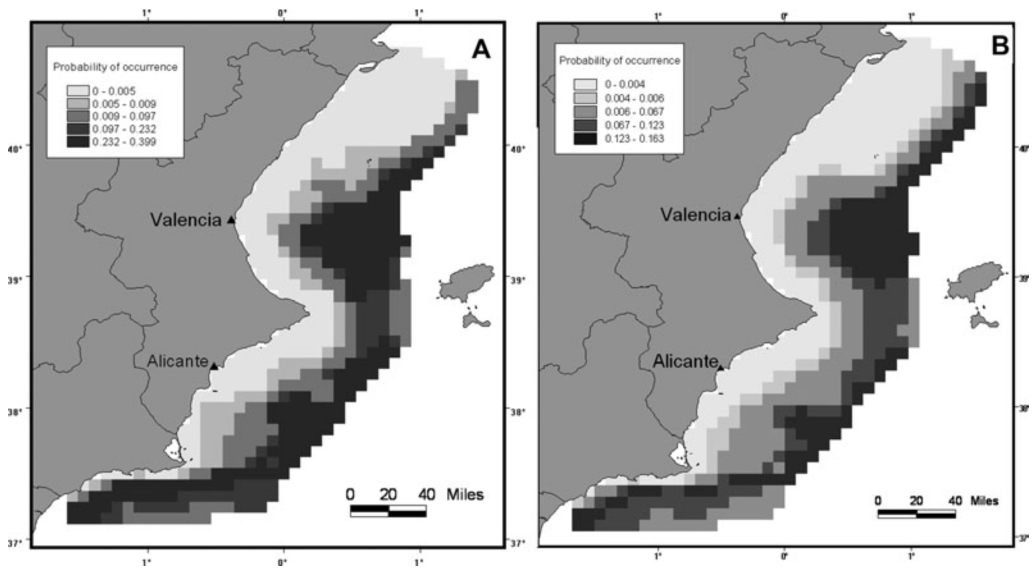

Fig. 4. Predicted distribution of striped dolphin based on the generalized linear models: (A) model 1, depth and annual sea surface temperature; and (B) model 2, depth only.

suggesting that this habitat is most frequently used by bottlenose dolphins. However, oceanic prey species were also found, and the length of hake (*Merluccius merluccius*) ingested suggested two different feeding behaviours (Blanco *et al.*, 2001). Adult females associated with calves and juveniles were found to consume smaller hake that use more near-shore regions. Other adult females and adult males consumed larger hake that live in deeper waters along the continental slope. During aerial surveys no schools with calves were observed in waters deeper than 200 m although many schools comprising only large animals were also observed in the continental self.

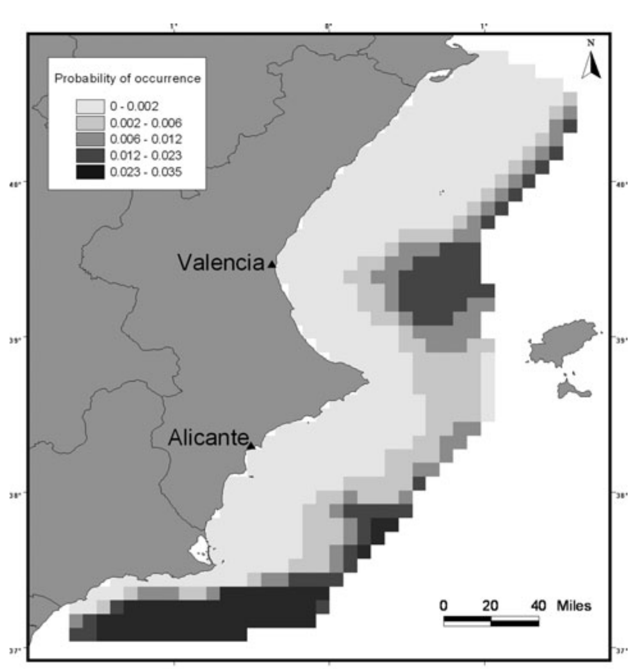

Fig. 5. Predicted distribution of Risso's dolphin based on the generalized linear model—depth only.

The results on habitat use from the present study together with results on feeding behaviour, suggest that the bottlenose dolphin observed in our study area is, at present, a coastal form; one that is not restricted to the continental shelf but also uses deeper waters of the continental slope. This agrees with the hypothesis suggested by Natoli & Hoelzel (2000) based on genetic studies that the western Mediterranean population of bottlenose dolphins originated from the offshore Atlantic ecotype, but later adopted mostly coastal habits.

Risso's dolphin

Risso's dolphin distribution was also related only to depth but the distribution predicted by the model did not fit as well to the distribution of the sightings obtained during the aerial surveys, compared to the striped dolphin. This is probably because of the low density of Risso's dolphin in the study area (Gómez de Segura *et al.*, 2006). The distribution of this species was found to be related to depth and slope in the Alboran Sea (Cañadas *et al.*, 2002) and in the Gulf of Mexico (Baumgartner, 1997; Baumgartner *et al.*, 2001).

Our results show a preference of Risso's dolphin for waters greater than 1500 m deep but as most of our study area consists of waters less than 1500 m deep, this result should be interpreted with care. An extension of the study area in future studies should lead to a better understanding of Risso's dolphin depth preferences. Our results do not agree with the previous information on Risso's dolphin in the Mediterranean (France, Gannier, 1998; Italy, Notarbartolo di Sciara *et al.*, 1993; Alboran Sea, Cañadas *et al.*, 2002), which showed a preference for the continental slope with depths ranging between 500 and 1500 m. Indeed, Blanco *et al.* (2006) in a study of Risso's dolphin diet in the study area showed that this species feeds preferentially on the middle slope (600–800 m depth). However, Gannier (2005) in his recent study of the whole Mediterranean showed that Risso's dolphin was more frequent over the upper continental slope (200–1000 m, 37% of sightings) and deep slope (1000–2000 m, 37% of sightings) but it was also frequent in open waters (>2000 m, 25% of sightings). Nevertheless, in all the studies Risso's dolphin preferred waters shallower than striped dolphin, in contrast to the results in our study area.

Conservation applications

Gómez de Segura *et al.* (2004) proposed to the Spanish Ministry of Environment two areas of special interest (MPAs) for the conservation of oceanic cetacean species (including striped and Risso's dolphin) in central Spanish Mediterranean waters. Figure 6 (from Gómez de Segura *et al.*, 2004) shows the two MPAs proposed. These areas were proposed based on their high diversity and density of cetacean species. The limits of the two areas proposed coincide with the zones of highest probability of occurrence areas predicted by the GLMs for both striped and Risso's dolphin. The MPAs proposed comprise 37% of the study area but cover together 60% and 62% of the probability of occurrence for striped and Risso's dolphin in the study area, respectively. These results are in accordance with the guidance that at least 60% of the principal habitats should be included for a good conservation plan (CTE/CN, 1996).

The areas predicted by the spatial models, which coincide with the MPAs proposed, have been delimited based on the relationship of cetaceans with depth, an environmental feature that does not change over time. Therefore, it seems that, at least for these two oceanic species, the MPAs proposed should be effective in the future. However, if relationships between the animals and their environment change, model predictions may not hold over time. It will therefore be important in the future to check this by collecting new data and conducting updated analyses.

Due to the limited number of sightings obtained during the surveys, we did not attempt cross-validation by fitting to a subset of the data and comparing the model predictions to the remaining data. Nevertheless, our results are an important addition to the small number of studies demonstrating that this method is valuable for approaching similar questions for other cetacean species in other areas (Hooker *et al.*, 1999; Cañadas *et al.*, 2005). If dynamic covariates are included in the models, any predictions of temporal, especially seasonal, changes in distribution could potentially be used to maximize the effectiveness of MPAs.

Finally, in this study spatial models were not useful for bottlenose dolphins because no relationship was found with any of the environmental features for which data were available. Whether this was because bottlenose dolphins are actually evenly distributed in this area or because of data limitations is unknown. Regardless, the results cannot inform the delineation of MPA boundaries in this case.

Fig. 6. Marine protected areas proposed to the Spanish Environment Ministry for the conservation of oceanic cetacean species (from Gómez de Segura *et al.*, 2004).

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