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Spatial and temporal partitioning of the Western Mediterranean Sea by resident dolphin species

Estefanía TORREBLANCA[1], Raimundo REAL[1], Juan Antonio CAMIÑAS[2,3], David MACÍAS[4], Salvador GARCÍA-BARCELONA[4] and José CARLOS BÁEZ [4,5]

[1] Department of Animal Biology, University of Malaga, Malaga, Spain
[2] Spanish Herpetological Association, Madrid, Spain
[3] Malaga Academy of Sciences, Malaga, Spain
[4] Oceanographic Center of Malaga, Spanish Institute of Oceanography (CSIC), Spain
[5] Ibero-American Institute for Sustainable Development, Universidad Autónoma de Chile, Temuco, Chile

Corresponding author: José CARLOS BÁEZ; josecarlos.baez@ieo.es

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Abstract

A classic issue in ecology is to understand how similar species coexist in a given area (i.e., sympatry). The situation of dolphins in the Western Mediterranean Sea may represent a special case of sympatry in that three similar species (the short-beaked common dolphin [*Delphinus delphis*], the striped dolphin [*Stenella coeruleoalba*], and the bottlenose dolphin [*Tursiops truncatus*) are under strong human impacts in the same area. From the viewpoint of ecology and conservation biology, it is challenging to determine how these three dolphin species live together and avoid competitive exclusion in the setting of such impacts. The Spanish Institute of Oceanography has a dataset of dolphin species opportunistic sightings. Using these data, we constructed three binary variables, comprising the sighting of one species *versus* the sighting of either of the other two species. We obtained three significant probability models after performing logistic regression of these binary variables on a set of spatio-temporal explanatory variables. We analysed these models from the perspective of fuzzy set theory by applying the favourability function to the probability models, fuzzy operations overlap, and entropy. The results show that common dolphins are differentially favoured in the eastern part of the study area and far away from main shipping routes. The striped dolphin was differentially favoured in the western part of the study area, above deep waters, near main shipping routes, and in summer and spring. Finally, bottlenose dolphins were differentially favoured in the mid-western part of the study area, in winter, and over shallow waters.

Keywords: *Delphinus delphis*; distribution; favourability; fuzzy set theory; modelling; niche; *Stenella coeruleoalba*; *Tursiops truncatus*.

Introduction

A classic issue in ecology is to understand how similar species coexist in a given area (i.e., sympatry) (e.g., Hutchinson, 1961). The situation of dolphins in the Western Mediterranean Sea may represent a special case of sympatry in that three similar species (the short-beaked common dolphin [*Delphinus delphis*], the striped dolphin [*Stenella coeruleoalba*], and the bottlenose dolphin [*Tursiops truncatus*] are under strong human impacts in the same area (e.g., Notarbartolo di Sciara *et al.*, 2002; Bearzi, 2003; Bearzi *et al.*, 2008; Gambaiani *et al.*, 2009; Aguilar & Gaspari, 2012; Bearzi *et al.*, 2012; Mira *et al.*, 2019). It is striking that these dolphin species have a worse conservation status in the Mediterranean Sea than they have worldwide. From the viewpoint of ecology and conservation biology, it is challenging to determine how these three dolphin species live together and avoid competitive exclusion in the setting of such impacts.

Previous studies have found trophic segregation between the small dolphins (striped and short-beaked common dolphins) and bottlenose dolphins, and a greater degree of spatial segregation between cetacean species by depth with some overlap among offshore species (i.e., short-beaked common and bottlenose dolphins) (Giménez *et al.*, 2017a; 2018a). Mixed groups of dolphins are frequent in the Mediterranean, where they can also coexist or at least exist in spatial sympatry (Bearzi, 2005; Bearzi *et al.*, 2016). These sympatric species may mix in shared groups, engage in interspecific associative behaviour, and even give rise to hybrids (Herzing & Elliser, 2013; Bearzi *et al.*, 2016; Espada *et al.*, 2019).

It is far from easy to assess the effects of one species on the distribution of another. When a database of presences of a species is available, it has been customary to compare these presences in relation to the background area purportedly to model the realized niche (i.e., the environmental space from which the species has not been excluded by biotic competition) (Hutchinson, 1957; Elith & Leathwick, 2009). However, this approach does not guarantee that specific competition is taken into account, such as that between one dolphin species and another. Nevertheless, some databases provide records of several species in the same area, which can be compared to assess the differential use of the territory. This modelling approach explicitly includes the presence of potential competitor species in the models and is better suited to model Hutchinson's concept of realized niches and to assess the effects of competition on species distribution. Realized niches cannot be interpreted as the fundamental niches of species, because the territories and environments analysed are much smaller than the global distribution and environmental space of species. However, this approach can be used to assess the differential spatio-temporal responses of species to the characteristics of the area analysed. Such data are of crucial importance in understanding key local interactions between species, which are useful for local conservation planning.

The main aim of this study was to perform a macroscale biogeographical analysis of the differential distribution of sightings of three dolphin species in the Western Mediterranean Sea in order to understand the complex system of partly shared and partly unshared use of these waters by these species in the area. We also discuss the implications of the results in relation to conserving these species.

We applied a fuzzy approach to this issue. Fuzzy set theory is being increasingly used in biogeography (Robertson *et al.*, 2004; Real *et al.*, 2009; 2017;2022 Olivero *et al.*, 2011; 2017). A fuzzy set is a class of objects with a continuum of degrees of membership in the set ranging from zero to one. Thus, fuzzy sets do not have sharply defined boundaries and may better reflect the continuous character of nature (Salski, 2006). Fuzzy set theory may be more successful than crisp approaches when dealing with typical fuzzy notions such as differential favourability for the occurrence of a species in a particular region or similarity between the responses of different species to the environmental conditions (Zadeh, 1965; Acevedo & Real, 2012; Real *et al.*, 2017). Hutchinson (1957) applied classic set theory to define fundamental and realized niches, while drawing attention to the limitations of this approach. Such limitations included the assumption that all points within each fundamental niche implied the equal probability of species persistence and all points outside such niches implied zero probability of survival. We suggest that the application of fuzzy set theory (Zadeh, 1965) may surmount this limitation. Furthermore, the complexity of the shared and unshared use of waters typical of dolphin species means that fuzzy set theory provides a more suitable basis on which to investigate this issue (Zadeh, 1965).

Material and Methods

Study area

The study area comprised the Western Mediterranean Sea from the Strait of Gibraltar to Sardinia (35.9º N, 43.1º N; 5.5º W, 9.4º E) (Fig. 1). This area includes two subregions, the Alboran Sea/Strait of Gibraltar and the Algero-Provençal Basin (UNEP-MAP-RAC/SPA, 2010), and is characterized by a narrow continental shelf. The north coast is highly urbanized and the Alboran Sea and the Strait of Gibraltar have one of the highest vessel densities in the world. Primary production is spatially heterogeneous and is influenced by the effect of currents, submarine canyons, runoff of fresh water from rivers, and the mix of water layers generated by local winds (Goffredo & Dubinsky, 2014).

Many dolphin studies conducted in the Mediterranean

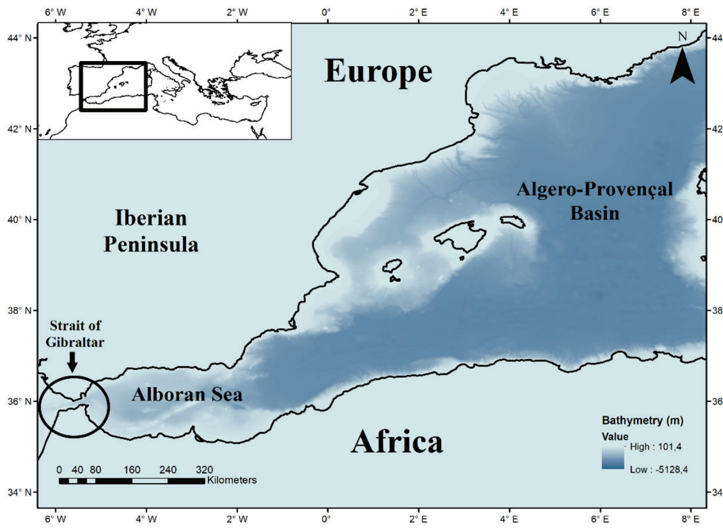


Fig 1: Study area.

have typically focused on the International Sanctuary for the Protection of Mediterranean Marine Mammals. This area is generally known as the called "Pelagos Sanctuary" (Notarbartolo di Sciara *et al.*, 2008), and is a large protected area for cetaceans situated in the north-east of the Western Mediterranean Sea (Laran & Drouot-Dulau, 2007; Gnone *et al.*, 2011; Azzellino *et al.*, 2012). However, this focus has led to a scarcity of knowledge on other areas of the Mediterranean Sea, especially in its southern parts (UNEP-MAP-RAC/SPA, 2010).

Data collection

Since 1995, the Spanish Institute of Oceanography (IEO) has been collecting opportunistic sightings (OS) of dolphins in the Western Mediterranean Sea. These data have been provided by scientific observers aboard fishing boats operating in the area, those working in the IEO fishery-program, and volunteer experts in marine mammal observations previously trained in cetacean identification and data collection. The OS dataset up to 2014 contained 482 records of dolphin species (Fig. 2, Table S1) comprising 120 sightings of short-beaked common dolphins, 322 sightings of striped dolphins, and 40 sightings of bottlenose dolphins. Each sighting represents individuals or groups and includes data on position, time, date, kind of vessel, and observer. When mixed groups were seen, the sighting of each species was recorded in the same position. In this way, the bias due to uneven sampling effort, which is typical of OS data, is consistent over all the observations and cannot be the cause of differential patterns between the three species in the dataset.

Explanatory variables

Spatio-temporal variables were chosen according to their availability and theoretical potential for describing, explaining, and predicting the spatio-temporal use of the Western Mediterranean waters by these species (Hooker *et al.*, 1999; Barbosa *et al.*, 2001; Real *et al.*, 2003; Carlucci *et al.*, 2016; Arcangeli *et al.*, 2017; Torreblanca *et al.*, 2019; Dwyer *et al.,* 2020). These variables were assumed to be at least correlated with the main drivers of the broad-scale spatio-temporal patterns (Torreblanca *et al.*, 2019). We divided the variables into four explanatory factors:

1. Physiographical variables: These are used to measure the effect of the environment and oceanography on dolphin distribution:
   - Bathymetry (BA): This is a continuous spatial variable that is used to measure the depth of the water column at a chosen point. This variable is known to influence the presence of cetaceans (Hooker *et al.*, 1999). The bathymetry layer was obtained from the European Marine Observation and Data Network "EMODnet" (http://www.emodnet.eu/bathymetry, version released 2018).
   - Distance to the coast (DC): This is a continuous spatial variable that is used to measure the effect of emerged areas. When the DC is long, species distribution is more affected by the pelagic ecosystem than by the continent. The DC was calculated using the shapefile "coastline" from the following webpage: http://www.naturalearthdata.com/downloads/10m-physical-vectors/10m-coastline/. We expected that the probability of dolphin observations would increase according to their known neritic/pelagic habitat preferences. For example, there would be a higher probability of observing bottlenose dolphins near the coast (*e.g.,* Arcangeli *et al.*, 2017).

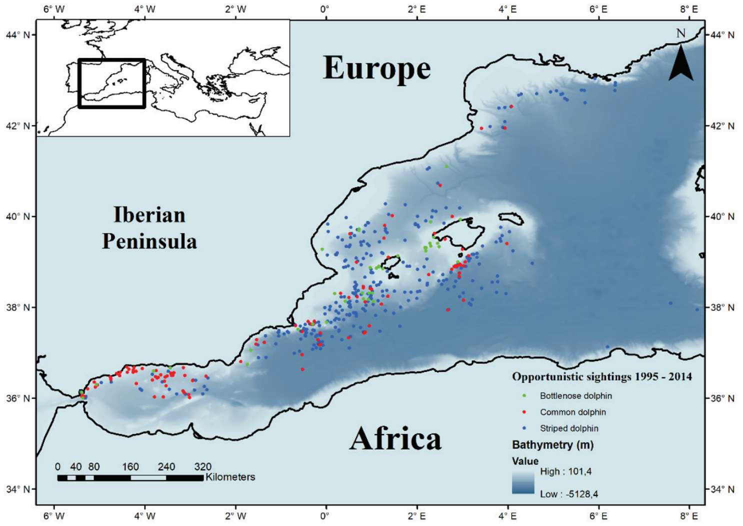


Fig. 2: Geographical distribution of the opportunistic sightings (1995-2014) analysed. Green dots indicate bottlenose dolphins, red dots indicate short-beaked common dolphins, and blue dots indicate striped dolphins.

2. Temporal factor. Season is a categorical variable that is used to measure changes in the probability of observation of these species over a year, which could be due to their feeding, reproductive, or migratory behaviour (Dwyer *et al.*, 2020). The categories used were spring (Spr; 21 March–20 June), summer (Sum; 21 June–22 September), autumn (Aut; 23 September–21 December), and winter (Win; 22 December–20 March).
3. Pure spatial factor: Degrees latitude (Lat) and longitude (Lon) are continuous coordinates obtained during sightings. These variables were included to take into account the spatial structure of the observed data. The spatial structure of species distribution could be due to interactions between environmental factors and space (Legendre & Fortin 1989; Borcard *et al.*, 1992) or by contagious biotic processes in space that are inherent to the population dynamics of the species (Legendre, 1993; Barbosa *et al.*, 2001; Real *et al.*, 2003).
4. Anthropogenic spatial factors: These are associated variables that are used to indirectly measure disturbances generated by human activities (Carlucci *et al.*, 2016;):
   - Distance to main shipping routes (MSR): This is a continuous variable used to measure whether large commercial ships affect dolphin distributions. A shapefile that included the main maritime routes in the study area was created using the information that appears in *Google* maps. We digitized the lines representing the commercial vessel routes into a shapefile (Torreblanca *et al.*, 2019). The distance in kilometres from each sighting to the nearest route was calculated using ArcGis 10.1.
   - Distance to coastal cities with more than 100 000 inhabitants (DCi): This is a continuous variable used to assess whether proximity to large coastal cities affects the probability of sightings (Torreblanca *et al.*, 2019). A shapefile was created that included coastal cities with more than 100 000 inhabitants in the study area. The distance in kilometres from each sighting to the nearest city was calculated using ArcGIS 10.1.

Building the differential distribution models

Species distribution models are useful (e.g. Cañadas *et al.*, 2002; Cañadas & Hammond 2006; McClellan *et al.*, 2014) for disentangling complex distribution patterns. Generalized Linear Models are a powerful modelling technique for dichotomous variables (Peng *et al.*, 2002) that do not require normal distributions or homogeneous variance in the dataset (Hosmer & Lemeshow, 2000; Guisan & Zimmermann, 2000). In particular, binary logistic regression has been frequently used to compare a dependent binary variable to predictors of the two states of the variable. This approach makes it possible to test whether the probability of occurrence of an event can be predicted from a set of quantitative and qualitative predictor variables (Hosmer & Lemeshow, 2000). Binary logistic regression has already been used to investigate cetacean distribution (Gordon *et al.*, 2000; Azzellino *et al.*, 2012; Torreblanca *et al.*, 2019). However, OS provide information about occurrences. For this reason, a binary variable for the occurrence of a species was built by using the occurrence of any of the other two species as a contrasting state. This implies that the probability values derived from these models represent the differential response of each species compared to that of the two others (Torreblanca *et al.*, 2019).

In a first step, we obtained a multivariate probability model for each species by performing a forward-backward stepwise logistic regression of the occurrence of each species against the occurrence of any of the other two on the explanatory variables. This procedure started with a null model (i.e., a model with no predictor variable), which yields a constant probability of the sighting of the target species being equal to the prevalence of the species in the OS dataset. Next, a significant combination of predictor variables (y or logit) was built by adding the variables that provided the most significant contribution—and only if the contribution was statistically significant—to the model obtained in the previous step (Hosmer & Lemeshow, 2000). Variables entered in the first steps were those with overall broad-scale predictive power, while those entered in subsequent steps added significant nuances to the previous predictive model. The definitive model was obtained when no more variables significantly added to the predictive power of the model. The effect of the excluded variables, if any, was effectively included in the model via correlated variables, such that their exclusion avoided redundancy. We checked that the model obtained in the final step had a better AIC value than those in the previous steps (Akaike, 1973). This model provided the probability of sighting a species instead of any of the other species according to the explanatory conditions.

However, sightings of the more common species is always more likely irrespective of environmental conditions (Acevedo & Real, 2012). Therefore, in a second step, we calculated the favourability function (Real *et al.*, 2006a) according to each multivariate probability model. This function was calculated using the probability obtained in the logistic regression using the following function:

$$F = \frac{\frac{P}{(1-P)}}{\frac{n_1}{n_0} + \frac{P}{(1-P)}}$$

where n_1 is the number of sightings of the target species, n_0 is the number of sightings of either of the other two species, and P is the probability value obtained in the logistic regression. This function describes the degree to which the environmental conditions are differentially favourable for each species compared to those of the other two species.

Favourability values range from 0 to 1 and are not affected by an unequal proportion of occurrences of the different species in the dataset (Real *et al.*, 2006a). When the probability of occurrence of a species is the same as its prevalence in the dataset, the favourability value is 0.5. Thus, the use of favourability allows for comparisons between models that differ in relation to prevalence (Real *et al.*, 2009; Acevedo *et al.*, 2010). For this reason, the favourability function has been widely used to identify interspecific relations (Real *et al.*, 2006b; 2009; Acevedo *et al.*, 2010; Reino *et al.*, 2017).

Fuzzy differential relationships

Favourability values can be used with fuzzy logic operators to compare different species models, whereas probability values cannot be used in this way (Zadeh, 1965; Real *et al.*, 2009; Acevedo *et al.*, 2010). This is the case because the favourability value for the occurrence of a dolphin species in a locality compared to that of any of the other species in the same locality can be regarded as the membership value of the locality in the fuzzy set of localities that are differentially favourable for this species (Real *et al.*, 2006a). The size of this fuzzy set is called the cardinal of the fuzzy set and is the sum of the membership values of all the localities (Zadeh, 1965): that is, the sum of all the favourability values

$$Ci = \Sigma(Fi)$$

where Fi is the favourability value calculated at each location for each species i. The higher the cardinal of a favourability model the more favourable are the overall conditions for the species when compared with those of the other species.

The minimum favourability value for two or three species at a given location can be regarded as the membership value in the fuzzy intersection between the two or three fuzzy sets (Zadeh, 1965). In this way, it is possible to identify the degree to which the locations are simultaneously favourable for the species compared:

$$F_a \cap F_b = Min\left[F_A(x), Ff_B(x)\right], \qquad x \in X$$

where F_a and F_b are the favourability values of each species at each location.

If the cardinal of the intersection between the favourability models for several species is high, then the response of the species to the predictor variables is very similar.

The maximum favourability value at a given location among those of two or more species can be regarded as the fuzzy union between the fuzzy sets (Zadeh, 1965):

$$F_a \cup F_b = Max\left[F_A(x),\ F_B(x)\right], \qquad x \in X$$

which identifies the degree to which the locations are differentially favourable for either of several species. If the cardinal of the union between several fuzzy sets is high, then the differential response of the species to the predictor variables is also high.

We also calculated the fuzzy overlap index for each pair of species and for the triplet. The overlap between two fuzzy sets is defined as the cardinal of their intersection divided by the cardinal of their union:

$$FOI = \frac{C(F_a \cap F_b)}{C(F_a \cup F_b)}$$

where values range from 0 (no favourability overlap) to 1 (complete favourability overlap) (Dubois & Prade, 1980; Kunchenva, 2001; Acevedo *et al.*, 2010).

The complementary of a fuzzy set (*A*) is another fuzzy set (*A'*) in which the membership value of each location is 1 minus the favourability value in the original fuzzy set (Zadeh, 1965). Fuzzy entropy is the cardinal of the fuzzy intersection of a fuzzy set with its complementary fuzzy set divided by the cardinal of the fuzzy union of the fuzzy set with its complementary (Kosko, 1986):

$$FE = \frac{A \cap A'}{A \cup A'}$$

The species with the highest entropy value would be the most generalist of the three species.

Overall information on the differential biogeography of the species is provided by all these values, which were obtained in the framework of fuzzy set theory (favourability at a location, the cardinal of favourability, the cardinal of the intersection, the cardinal of the union, the fuzzy overlap index, and fuzzy entropy). For a more detailed analysis of the results, we divided the differential favourability for each species into 10 intervals of equal range and computed the mean favourability of all the species at every interval (Acevedo *et al.*, 2010).

Evaluation of the models

The statistical significance of the models was tested using the Omnibus test. The statistical significance of the parameters and that of the variables introduced in the model were determined using the Wald test (Peng *et al.*, 2002; Azzellino *et al.*, 2012). The goodness of fit, or calibration, of the models was evaluated using the Hosmer-Lemeshow test, which compares the observed and expected frequencies of each value of the binary variable according to its probability (Hosmer & Lemeshow, 2000). For correctly adjusted models, no significant differences are expected between the observed and expected distributions (Peng *et al.*, 2002).

A confusion matrix (Fielding & Bell, 1997) was built using the favourability value F= 0.5 as a threshold to classify sighting locations as corresponding to the target species (positive event) or to any of the two others (negative event). The classification power of this matrix was evaluated by calculating its sensitivity (right classification rate of observed positive events), specificity (right classification rate of observed negative events), correct classification rate (CCR; right classification rate of observed positive and negative events), overprediction rate (proportion of predicted positive events not matched by the observations), underprediction rate (proportion of predicted negative events not matched by the observations), and Cohen's kappa (Fielding & Bell, 1997; Anderson *et al.*, 2003; Barbosa *et al.*, 2013).

The discrimination capacity of the model was also evaluated with the area under the receiver operating characteristic curve (AUC). The AUC of a model is a value between 0 and 1, with 0.5 denoting no discrimination (Lobo *et al.*, 2008). Hosmer and Lemeshow (2000) considered that AUC values higher than 0.9 indicate outstanding discrimination, values higher than 0.8 mean excellent discrimination, and those higher than 0.7 are indicative of acceptable discrimination. In our case, AUC values above 0.7 indicate a marked differential response, values above 0.8 indicate a high differential response, and values above 0.9 indicate an extremely differential response.

Results

The results of the Omnibus test showed that there were three significant models, one for each target species. Table 1 shows the variables that explained the differential distribution of the three species. The AUC values indicate that the differential response of short-beaked common and striped dolphins has good discrimination capacity, whereas the differential response of bottlenose dolphins has high discrimination capacity (Table 1). The results of the Hosmer-Lemeshow test showed that all the models had good calibration, because no significant differences were found between the observed and expected values.

Favourability as a function of explanatory variables

The logit functions presented in Table 1 show that favourability for striped dolphins and bottlenose dolphins increases and decreases with depth, respectively. The mean depth was 1450.44 ± 805.82 m for striped dolphins, 540.9 ± 510.39 m for bottlenose dolphins, and 991.43 ± 809.67 m short-beaked common dolphins. This suggests that bottlenose dolphins are differentially favoured by shallow waters, whereas striped dolphins are differentially favoured by deeper waters. This pattern is can be clearly seen in Fig. 3, which shows favourability for the three species by depth.

The coefficients of the logits presented in Table 1 show that favourability for striped dolphins and, to a lesser extent, for bottlenose dolphins, increases in the eastern part of the study area, whereas favourability for short-beaked common dolphins increases in the western part. Figure 4 presents the differential favourability of each species by geographic longitude, showing that short-beaked common dolphins and striped dolphins present opposite patterns. However, no clear pattern appears for bottlenose dolphins, even though longitude is a significant variable in the favourability function (Table 1). Longitude was only entered in the model after bathymetry, which suggests that bottlenose dolphins, at the same depth, are favoured in the eastern part of the study area, although this effect is obscured by these parts being quite deep.

The coefficients of the logit functions shown in Table 1 suggest that distance to the MSRs segregate striped dolphins from short-beaked common dolphins, which are differentially favoured by short distances and long distances to these routes, respectively. Figure 5 shows the distance to MSRs by differential favourability for each species. Due to its topography, the Alboran Sea funnels marine traffic and so shipping density is very high. Thus, we constructed two figures comprising the whole study area (Fig. 5A) and the Alboran Sea (Fig. 5B), and compared them to determine any local differences in the Alboran Sea. Although no clear trend is observable in Fig. 5A, Fig. 5B shows that favourability for short-beaked common dolphins and bottlenose dolphins increases by distance from the MSRs, whereas it decreases for striped dolphins.

Table 1. Significant differential distribution models for the three dolphin species and results of the evaluation measures applied to the different models. Variables in the logits are ordered according to the order of entrance in the stepwise modelling procedure. Lon: Geographic Longitude. MSR: Distance to main shipping routes. BA: Bathymetry. AUC: Area Under the receiver-operating-characteristic Curve. Kappa: Cohen's Kappa. CCR: Correct classification rate.

	Short-beaked common dolphin	Striped dolphin	Bottlenose dolphin
Logit function			
Omnibus test	χ2=89.690; g.l.=2; P<0.001	χ2= 110.811; g.l.=6; P<0.001	χ2=55.758; g.l.=5; P<0.001
AUC	0.744	0.766	0.807
Hosmer-Lemeshow test	χ2=11.045; g.l.=8; P=0.199	χ2= 12.048; g.l.=8; P=0.149	χ2=8.305; df = 8; P= 0.404
Kappa	0.35594781	0.43374483	0.20684026
Sensitivity	0.54166667	0.76397516	0.700
Specificity	0.82320442	0.6875	0.74434389
CCR	0.75311203	0.73858921	0.7406639
Underprediction	0.15580737	0.40860215	0.03519062
Overprediction	0.49612403	0.16891892	0.80141844

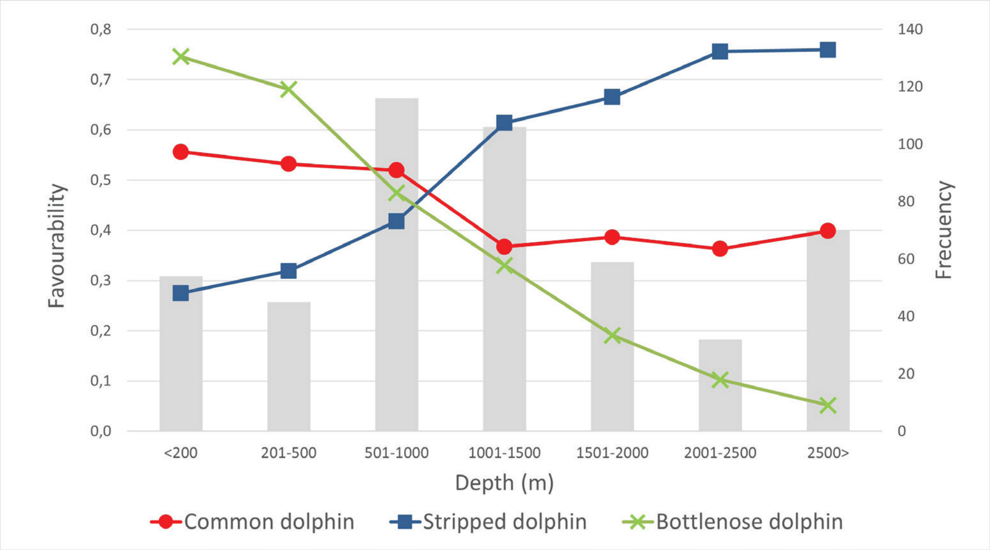


Fig. 3: Favourability for the three dolphin species by depth. Lines connect the mean favourability values of each species in every depth bin. The frequency of opportunistic sightings in each bin is represented by histograms (shown in grey).

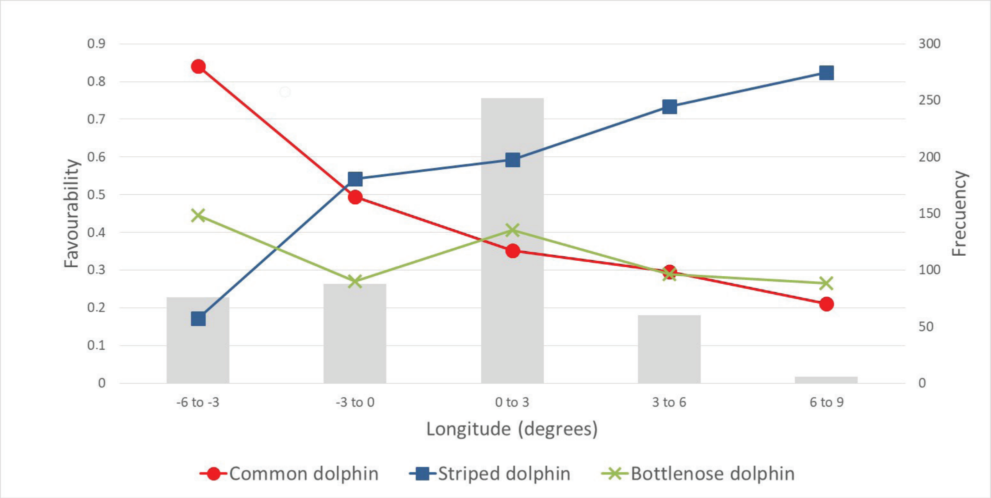


Fig. 4: Favourability according to longitude. Lines connect the mean favourability values of each species in every longitude bin. The frequency of opportunistic sightings in each bin is represented by histograms (shown in grey).

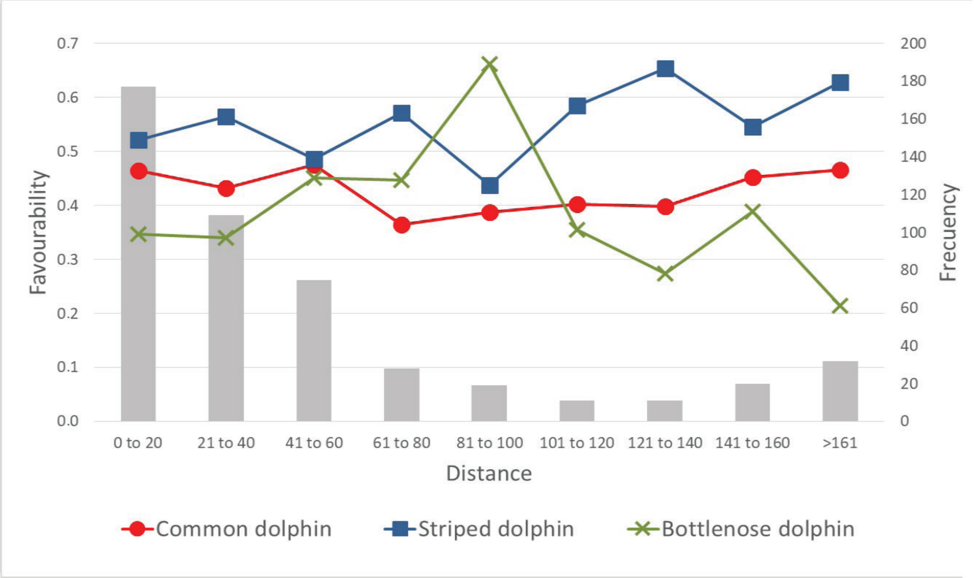


***Fig. 5**:* Favourability according to the distance from the main shipping routes. A: favourability values in the whole study area. B: favourability values in the Alborán Sea. Lines connect the mean favourability values of each species at every distance to main shipping routes bin. The frequency of opportunistic sightings in each bin is represented by histograms (shown in grey).

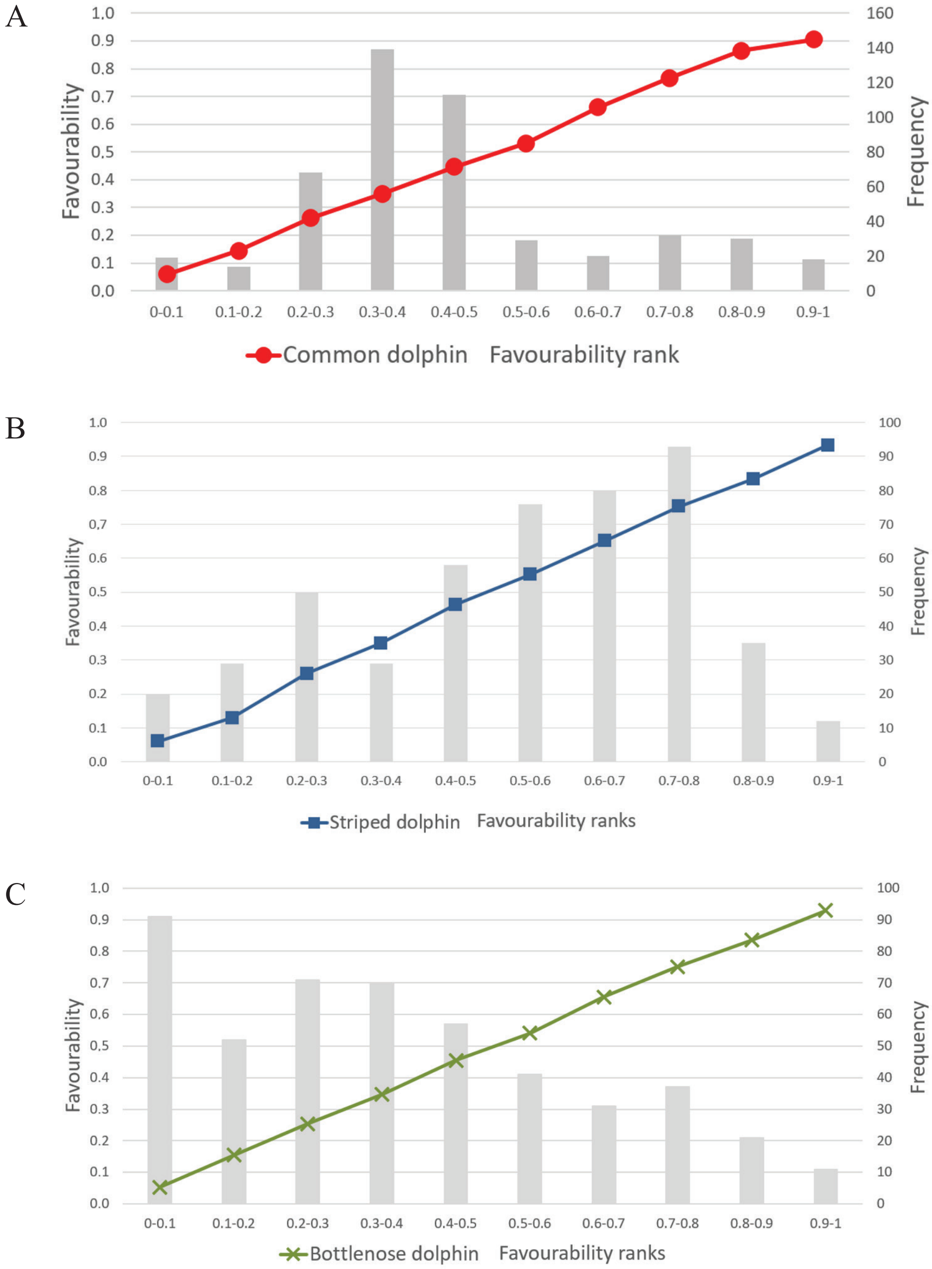
Figure 6 shows variations in differential favourability for the three species as well as the frequency of the different favourability intervals for each species in the Western Mediterranean Sea.

Figure 7 shows the location of the most differentially favourable OS for each species (F>0.8) and the species that were actually sighted at each location.

The following fuzzy overlap indexes were obtained: short-beaked common dolphins and striped dolphins (0.473), short-beaked common dolphins and bottlenose dolphins (0.497), and striped dolphins and bottlenose dolphins (0.397). The fuzzy overlap index for the three species was 0.293. The values of the cardinals presented in Table 2 show that the largest fuzzy set of locations fa-

Table 2. Cardinal and entropy values of each fuzzy set of locations differentially favourable for each species.

	Cardinal	Entropy
Short-beaked common dolphin	218.85	0.4680
Striped dolphin	251.41	0.4374
Bottlenose dolphin	218.03	0.3463



ig. 6: Variation in mean differential favourability for the three dolphin species (shown in 0.1intervals). The frequency of opportunistic sightings in each interval is represented by histograms (shown in grey). A: short-beaked common dolphin, B: striped dolphin, and C: bottlenose dolphin.

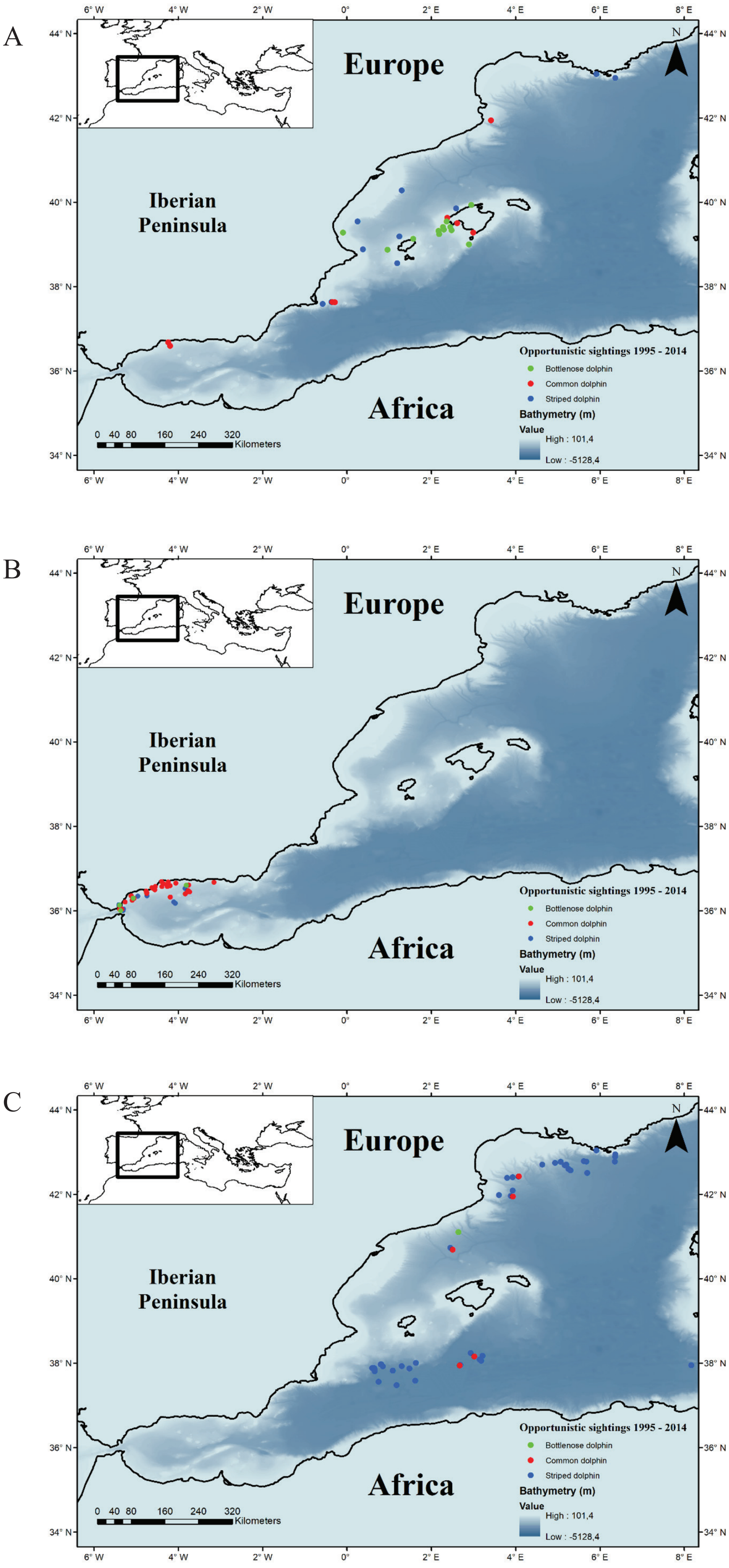


Fig. 7: Locations in which differential favourability was more than 0.8 for each species. Colours represent the different species that were actually sighted. A: locations highly favourable for bottlenose dolphins. B: locations highly favourable for short-beaked common dolphins. C: locations highly favourable for striped dolphins.

vourable for any species was that of striped dolphins. The lowest entropy value was that of the bottlenose dolphin (Table 2), suggesting that this species had a stronger differential response than the other species.

Discussion

The meaning of a differential favourability pattern

The models obtained can be referred to as multispecific models given that sightings of two species were used to contrast sightings of each target species. Thus, all the results should be interpreted in terms of the differential distribution of one species compared to that of the other species (MacLeod *et al.*, 2008; Torreblanca *et al.*, 2019). Nevertheless, these models had a discriminatory power that was similar to or higher than (see AUC values in Table 1) that obtained in previous cetacean studies that contrasted presences with absences. For example, Praca *et al.* (2009) obtained discrimination values of AUC=0.70 and AUC=0.79 for sperm whale distribution. This result suggests that adjusting the differential distribution models of some species versus others could yield models with better discrimination than models that compare the presence of a species in relation to unsuitable locations.

This result may have implications regarding the application of the ecological niche concept to our models. Distribution models built from presence/absence data usually apply the Hutchinsonian niche concept (Hutchinson, 1957), which includes the notion of fundamental niche as an n-dimensional volume comprising the physical and biological environmental space where a species can maintain a viable population and persist over time without migration. Most authors rarely include biological variables in their distribution models, thus restricting their niche to the abiotic conditions, typically arguing that they are modelling the realized niche, which is defined as the portion of the fundamental niche from which a species is not excluded due to biotic competition. However, the direct comparison of the actual distribution with the environmental space better fits the notion of occupied niche (Pearson, 2007), which includes constraints other than competition, such as historical and geographical limitations to the species' ability to reach suitable areas, and other biotic interactions such as predation, symbiosis, and parasitism. Given that we included the presence of potential competitor species in the models, we explicitly assessed the effects of competition on dolphin species distributions, thus modelling Hutchinson's realized niche. The application of fuzzy set theory (Zadeh, 1965) allowed us to describe an internal structure of Hutchinson's realized niche. This description is closer to the niche concept proposed by Maguire (1973), who suggested that niches are the responses of species as a function of the habitat conditions. As Maguire (1973) suggested, favourability models are functions that represent niches as interactions between species and environments (Gouveia *et al.*, 2020). The differential favourability models we obtained are restricted to interactions between the species analysed in the spatio-temporal setting of the Western Mediterranean Sea. Similar to the way in which Maguire's niche is a property of the complex comprising the species and environment, the differential distribution models we obtained are properties of the complex comprising the three dolphin species and the spatio-temporal characteristics of the Western Mediterranean Sea. This approach to the concept of niche differs from other approaches, which are more universal. However, our approach is of more practical usefulness in understanding the spatio-temporal distribution of dolphin species.

Factors associated with the differential spatio-temporal use of Western Mediterranean waters by dolphins

Significant relationships were found between the differential use of the Western Mediterranean Sea by the three dolphin species and four variables: bathymetry, longitude, MSR, and season (Table 1).

Bathymetry had opposite effects on striped dolphins and bottlenose dolphins (Fig. 3, Table 1). Bottlenose dolphins were differentially favoured by shallow waters and striped dolphins were differentially favoured by pelagic waters (Notarbartolo di Sciara *et al.*, 1993; Kiszka *et al.*, 2007; Anderwald *et al.*, 2012; Pikesley *et al.*, 2012; Azzellino *et al.*, 2014). This result is suggestive of niche differentiation between these dolphin species. Short-beaked common dolphins occupied an intermediate position between these two patterns (Fig. 3). Bottlenose dolphins and short-beaked common dolphins are often seen near coasts and over the continental shelf (Anderwald *et al.*, 2012; Arcangeli *et al.*, 2017). However, short-beaked common dolphins have also been described as following a bimodal pattern, with higher densities on edges of the continental shelf and another maximum in deep waters (Cañadas & Hammond, 2008). Analysis of the dataset shows that only bottlenose dolphins were differentially sighted over shallower waters. This result may be due to the fact that short-beaked common dolphins and bottlenose dolphins are trophically segregated (Giménez *et al.*, 2018a) in the sense that short-beaked common dolphins tend to prey on mesopelagic species (Giménez *et al.*, 2018b), whereas bottlenose dolphins predominantly prey on benthic species, such as *Merluccius merlucius* and *Conger conger* (Giménez *et al.*, 2017b).

Longitude had opposite effects on short-beaked common dolphins and striped dolphins (Fig. 4, Table 1). At coordinates close to zero, all species overlapped, whereas the three species were segregated at values of more than 4°W (Fig. 4). Other longitudinal biodiversity patterns have been reported in the Mediterranean Sea. Examples include the higher Chondrichthyes species richness near the Strait of Gibraltar (Meléndez *et al.*, 2017) and also in relation to dolphin species, which corroborates our results for short-beaked common dolphins (Karamitros *et al.*, 2020). This result suggests that these types of longitudinal pattern are relevant in the Mediterranean Sea and that the populations of many species could be structured by this purely spatial factor.

Main shipping routes also had opposite effects on short-beaked common dolphins and striped dolphins (Fig. 5, Table 1). A detailed analysis of their response as a function of MSR (see Fig. 5) shows that the three species are segregated at an average of more than 60 km. Changes in traffic between seasons could also influence changes in species range (Coomber *et al.*, 2016).

Finally, season also had opposite effects on striped dolphins and bottlenose dolphins. The results suggest that there are seasonal changes in striped dolphin abundance, with higher abundance in spring and summer and a dispersed distribution in autumn and winter. Such changes have been identified in previous studies (Gomez de Segura *et al.*, 2006; Arcangeli *et al.*, 2017) and are probably driven by prey availability. In contrast, although Arcangeli *et al.* (2017) did not detect bottlenose dolphins in winter, our results suggest that the most favourable season is winter. This result has also been described by Lambert *et al.* (2017), and could be due to competition with striped dolphin; favourability for bottlenose dolphins is higher in autumn and winter, when the distribution of the striped dolphin is more dispersed. However, as suggested by Lambert *et al.* (2017), it could also be due to phenological constraints, given that bottlenose dolphins migrate to neritic waters in summer for calving. Further research is needed to understand their annual movements, especially on the high seas (Arcangeli *et al.*, 2017), but it seems clear that they use different parts of the Western Mediterranean for summering, wintering, or year-round (Cotté *et al.*, 2010). Thus, these findings suggest that there is a differential spatio-temporal distribution of the three dolphin species in the Western Mediterranean Sea.

Differential distribution of short-beaked common dolphins

Short-beaked common dolphins are known to be present in both neritic and pelagic waters (Notarbartolo di Sciara *et al.*, 1993; Cañadas *et al.*, 2002): however, in the Western Mediterranean Sea, they are mainly present in coastal areas (Forcada & Hammond, 1998) and particularly in waters that are shallower than those inhabited by striped dolphins (Notarbartolo di Sciara *et al.*, 1993). The analyses confirm that bathymetry has a differential effect on short-beaked common dolphins and striped dolphins, but suggest that this effect is because striped dolphins prefer pelagic waters rather than because short-beaked common dolphins prefer neritic areas. Although this factor has little differential effect on short-beaked common dolphins, it would appear that it has the opposite effect on striped dolphins and bottlenose dolphins. This hypothesis is based on the fact that bathymetry was not included in the short-beaked common dolphin model, whereas the differential favourability model for striped dolphins included deeper waters and the model for bottlenose dolphins included shallower waters. This hypothesis should be tested with further studies.

The differential favourability model for short-beaked common dolphins included the effect of geographical longitude showing that differential favourability increases to the west. In fact, in recent decades, the short-beaked common dolphin population has decreased in the Western Mediterranean Sea, but maintains the highest abundance in the Alboran Sea in the westernmost part of the Mediterranean Sea (Forcada & Hammond, 1998; Karamitros *et al.*, 2020; Notarbartolo di Sciara, 2002; Bearzi *et al.*, 2003; Cañadas & Hammond, 2008). It has been reported that the Alboran Sea supports a large population of short-beaked common dolphins (Forcada & Hammond 1998; Notarbartolo di Sciara, 2002; Bearzi *et al.*, 2003; Cañadas & Hammond, 2008). Moreover, within the Alboran Sea, the abundance of short-beaked common dolphins increases from east to west (Bellido *et al.*, 2012). The western part of the Alboran Sea has cooler waters and so this geographical pattern could be related to this species' preference for cool waters (Reilly & Fiedler, 1994). Previous studies have shown that cool waters in this area are related to the distribution of its prey (Cañadas & Vázquez, 2017). The results show that the Alboran Sea is the area with the highest differential favourability for short-beaked common dolphins (Fig. 6A).

Such differential favourability for this species decreases near to main shipping routes. This effect is more evident in the Alboran Sea (see Fig. 5B) and is of particular concern because this area is the most favourable area for this species and has a high density of shipping routes. In summary, shipping routes have a differential negative anthropogenic effect on short-beaked common dolphins -which is the most threatened dolphin species in the Mediterranean- and an even more pronounced effect in this most critical of areas.

Differential distribution of striped dolphins

Striped dolphins are the most abundant dolphin species in the Mediterranean Sea (Gómez de Segura *et al.*, 2006; Notarbartolo di Sciara & Birkun, 2010) and their population is increasing (Cotté *et al.*, 2010; Panigada *et al.*, 2011; Azzellino *et al.*, 2012). This species is the most sighted dolphin in our dataset and in other studies (e.g. see Gannier, 2005). Moreover, this species has the broadest and most ubiquitous distribution, which has led several authors to suggest that striped dolphins have weak habitat preferences (Gordon *et al.*, 2000; Panigada *et al.*, 2008; Cotté *et al.*, 2010; Azzellino *et al.*, 2012). Our results also suggest that this species has the broadest distribution, given that the largest fuzzy set of differentially favourable locations was obtained for striped dolphins (Table 2). However, the results contradict the suggestion that this species has weak habitat preferences, because striped dolphins had a differential response to MSR (favourability increases near shipping routes), bathymetry (a preference for locations above deeper waters), season (the highest favourability is in summer), and longitude (favourability increases in the east).

The differential response of striped dolphins to bathymetry underlines its pelagic habitat preference, as reported in other studies conducted in different areas of the Western Mediterranean Sea, such as the Northwestern Mediterranean sea (Gordon *et al.*, 2000; Panigada *et al.*, 2008; Azzelino *et al.*, 2012), the Alboran Sea (Cañadas *et al.*, 2002; Giménez *et al.*, 2017a), the Northern Ionian Sea (Carlucci *et al.*, 2016), the Spanish Levantine coast (Gómez de Segura *et al.*, 2008), and in other areas in the Mediterranean basins such as the Gulf of Corinth (Bearzi *et al.*, 2016). According to the dataset analysed, this species was sighted in waters with an average depth of 1450.44 ± 805.82 m. Kiszka *et al.* (2007) also found that there were more short-beaked common dolphins in the oceanic waters of the Bay of Biscay. These results are also in agreement with those of Gordon *et al.* (2000), who observed that striped dolphins are more abundant in offshore waters, with a peak between 2000 m and 2500 m in the Ligurian Sea. In general, striped dolphins are more frequent in open sea, whereas short-beaked common dolphins and bottlenose dolphins are more frequent closer to the coast and on the shelf, respectively (Ganier, 2005). Azzellino *et al.* (2012) found a direct correlation between the presence of striped dolphins in the Pelagos Sanctuary and maximum depth and minimum slope, thus showing the preference of these animals for pelagic waters, although they were also found in the area of the continental slope and shelf (Azzellino *et al.*, 2012; Arcangeli *et al.*, 2017).

Carlucci *et al.* (2016) found no significant association between commercial vessels and this species. This result could be due to the small size of their study area, although they did find significant associations between other anthropogenic variables and striped dolphins. We found that differential favourability for striped dolphins was higher closer to shipping routes, although this result does not imply that shipping routes favour the presence of this species. Rather, shipping routes have less differential effect on striped dolphins than on the other two dolphin species.

Favourability for striped dolphins was higher in summer, followed by spring, which is line with observations in the Ligurian Sea by Laran *et al.* (2010) and Panigada *et al.* (2011). Further research is needed on the relationship between this temporal pattern and the phenology and migration patterns of this species.

Differential distribution of bottlenose dolphins

The variables in the bottlenose dolphin model were bathymetry, season, and longitude. Higher differential favourability was obtained in shallower waters, showing that this species is neritic in the Western Mediterranean Sea, where it has been mainly recorded on the continental shelf (Gannier, 2005; Gómez de Segura *et al.*, 2008; Arcangeli *et al.*, 2017). The strong influence of depth on this species is well established, given that this species is known to prefer shallow waters (Forcada *et al.*, 2004: Cañadas & Hammond 2006; Alessi & Fiori 2014; Carlucci *et al.*, 2016). According to Azzellino *et al.* (2012), as maximum depth increases, the probability of bottlenose presence decreases. The habitat preferences of bottlenose dolphins are associated with coastal areas and depths of less than 400 m in the Pelagos Sanctuary and in the North Tyrrhenian Sea area (Azzellino *et al.*, 2012). In the OS dataset analysed, the mean depth under the locations of bottlenose dolphin sightings was 540 m. However, distance to the coast was not a significant variable in any of the models, which suggests that the differential presence of bottlenose dolphins in coastal areas was not due to the effect of emerged areas, but to the effect of bathymetry.

This model also showed a higher differential favourability for bottlenose dolphins in the east. However, its highest differential favourability was around the Balearic Islands, where 65% of the OS of this species occurred (Fig. 2 and Fig. 7C).

Bottlenose dolphin sightings were differentially favoured in winter and autumn. Similar seasonal changes have been previously observed for this species in Mediterranean areas (Forcada *et al.*, 2004). Further research is needed on this seasonality pattern to assess if summer tourism activities may negatively impact bottlenose dolphin habitats and trigger a differential temporal response in this species.

Analysis of the fuzzy set of differential favourability

The fuzzy overlap index shows that the greatest overlap in differential spatio-temporal distributions was between short-beaked common dolphins and the other two species. In addition to the fact that short-beaked common dolphins also had the highest entropy (Table 2), this result suggests that they may be more easily sighted in areas that are favourable for other dolphin species. In fact, this outcome can be observed in Fig. 7. Although the distribution range of short-beaked common dolphins could be influenced by the habitat preferences of striped dolphins—as has been suggested to occur in other areas (Bearzi *et al.*, 2016) —short-beaked common dolphins have a broad variety of feeding behaviour according to habitat. This aspect has been proposed as evidence of their generalist behaviour (Santos *et al.*, 2013) and is supported by the high entropy value obtained for this species.

Bearzi (2005) found that striped dolphins display opportunistic behaviour as well as the weakest response to environmental variables compared to that of other dolphin species (Reilly & Fiedler, 1994). According to these results, striped dolphins would be less affected by habitat changes and would have higher entropy values. In fact, we found that the entropy value for striped dolphins was close to that of short-beaked common dolphins and much higher than that of bottlenose dolphins (Table 2). The fuzzy set of differentially favourable locations was largest for striped dolphins, with the highest cardinal (Table 2) for the three species, which indicates that overall conditions are more differentially favourable for striped dolphins in the Western Mediterranean Sea.

Finally, bottlenose dolphins in the Western Mediterranean Sea had the lowest entropy value. This result suggests that the differential biogeographical response was more pronounced in bottlenose dolphins (which have more specialist behaviour) than in the other two species.

Azzellino *et al.* (2014) found the highest correlation between this species and the dynamics of the fishery sector in the Pelagos Sanctuary, which they associated with the species opportunistically taking advantage of fisheries discard. However, this behaviour may result in a more constrained distribution pattern and, thus, a lower entropy value in the differential distribution pattern.

Further research and monitoring are needed, especially in the southern part of the study area, which has been generally overlooked. However, in the current context of climate change (Gambaiani *et al.*, 2009) and the under-resourcing of marine research (Richardson & Poloczanska, 2008), any kind of distribution data, such as opportunistic sightings, is of great value. Our approach shows that valuable information may be extracted from these data, if they are correctly analysed.

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Supplementary Data

The following supplementary information is available online for the article:
Table S1. Dataset.