AQUATIC CONSERVATION: MARINE AND FRESHWATER ECOSYSTEMS

Aquatic Conserv: Mar. Freshw. Ecosyst. **27**: 436–451 (2017)

DOI: 10.1002/aqc.2669

Linking small pelagic fish and cetacean distribution to model suitable habitat for coastal dolphin species, Delphinus delphis *and Tursiops truncatus, in the Greek Seas (Eastern Mediterranean)*

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ABSTRACT

1. A large-scale assessment of the summertime suitable habitat for *Delphinus delphis* (short-beaked common dolphin) and *Tursiops truncatus* (common bottlenose dolphin) in Greek Seas (Eastern Mediterranean) was conducted using data from dedicated and opportunistic cetacean surveys and published data records.

2. Using a presence/absence approach, generalized additive models were applied to define a suite of environmental, bathymetric and biotic factors that best describe common and bottlenose dolphin spatial distribution, during early (May, June, July) and late (August, September) summer.

3. A geographic information system (GIS) was used to integrate sightings data with environmental characteristics, distance from the coast and sardine probability of presence. These variables were considered as good proxies for defining species-suitable habitat within the study area's coastal environment.

4. The final selected models were used to produce annual probability maps of the presence of the species in the entire Greek Seas, as a measure of habitat suitability. Based on the mean probability and standard deviation maps for the study period GIS techniques were subsequently used to determine the persistent (areas with high mean and low variation) and occasional (high mean and high variation) habitat of each species.

5. Results showed that there was a high probability of common dolphin presence in areas with a high probability of sardine presence. For bottlenose dolphin, higher probability of the presence of species occurred in areas closer to the shore, with a high probability of sardine presence and with high concentrations of chlorophyll-*a*.

6. In both seasons, the North Aegean Sea and the Inner Ionian Sea Archipelago were indicated as the most suitable areas for common dolphin distribution. Persistent habitat areas of the bottlenose dolphin included enclosed seas, continental shelf waters, and waters surrounding islands. The indicated suitable areas are discussed along with deficiencies of the models and future implications for conservation.

Received 09 October 2015; Revised 26 February 2016; Accepted 25 March 2016

KEY WORDS: Habitat suitability modelling; marine mammals; small pelagics; *Delphinus delphis*; *Tursiops truncatus*; generalized additive models; Eastern Mediterranean

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INTRODUCTION

Habitat suitability modelling (HSM, or species distribution modelling, SDM) enables species distributions to be predicted over large areas from habitat-descriptor data (e.g. environmental and prey data) and species occurrence records. These techniques represent a promising tool for predicting cetacean distributions and understanding the ecological processes that determine these distributions (Redfern *et al*., 2006). The application of such statistical models to understand and predict relationships between species and environmental variables has become frequent for many marine species in the last two decades (Guisan and Zimmermann, 2000; Redfern *et al*., 2006; Giannoulaki *et al*., 2011, 2013), while habitat modelling for marine mammals has made considerable advances in the last decade (Redfern *et al*., 2006; De Segura *et al*., 2007; Azzellino *et al*., 2008; Best *et al*., 2012; Blasi and Boitani 2012; Druon *et al*., 2012; Keller *et al*., 2012; Thorne *et al*., 2012; Marini *et al*., 2015).

The aim of the present study was to assess and map the summertime suitable habitat for two cetacean species: the short-beaked common dolphin (*Delphinus delphis*, Linnaeus, 1758; hereafter referred to as 'common dolphin') and the common bottlenose dolphin (*Tursiops truncatus*, Gervais, 1855; hereafter referred as 'bottlenose dolphin') focusing on the Ionian, Aegean and Cretan Seas within the Eastern Mediterranean basin. Both marine mammal species are under strict protection according to the Habitats Directive (Annex IV), the Protocol for Specially Protected Areas, the Biological Diversity in the Mediterranean of the Barcelona Convention (Annex II), the ACCOBAMS agreement and within national laws of most Mediterranean countries.

The common dolphin is a cosmopolitan species, which is found mainly in temperate and tropical waters and habitats. In the Mediterranean, it usually occurs over the continental shelf, in coastal waters with a preference for surface water temperatures greater than 10 °C throughout the year, and often following the aggregations of small pelagic fish populations, such as sardine and anchovy (Bearzi *et al*., 2003; Frantzis, 2009). Moreover, the foraging ecology of common dolphin in the Mediterranean indicates relatively flexible feeding habits, with a preference for small pelagic and mesopelagic fish, as well as eurybathic cephalopod and crustacean species (Bearzi *et al*., 2003 and references therein). Anchovies and sardines are known to be key prey for common dolphin in the coastal waters of the Inner Ionian Sea Archipelago (Bearzi *et al*., 2003). The Mediterranean sub-population of short-beaked common dolphin has severely declined in recent years and is listed as an endangered species in the IUCN Red List of Threatened Species (Notarbartolo di Sciara and Birkun, 2010). A significant proportion of the Mediterranean common dolphin population is assumed to exist in Greece (Frantzis *et al*., 2003). This population has been assessed as endangered (EN) according to the National IUCN criteria (Paximadis and Frantzis, 2009).

The bottlenose dolphin is one of the most common cetaceans in the Mediterranean Sea where the species is characterized as predominantly 'coastal' (Bearzi *et al*., 2008a). It is generally an opportunistic species that feeds on a wide range of prey, mostly consisting of demersal fish species (e.g. European hake, red mullet, European conger) (Bearzi *et al*., 2008a; Frantzis, 2009), as well as small pelagic fish species depending on their availability and abundance (Bearzi *et al*., 2006; Piroddi *et al*., 2011; Holcer, 2012). For example, in certain areas such as the central Adriatic (Holcer, 2012), the Inner Ionian Sea Archipelago (Bearzi *et al*., 2006; Piroddi *et al*., 2011) and Amvrakikos Gulf (Bearzi *et al*., 2008a), certain small pelagic fish (European anchovy and European sardine) are known to be an important part of bottlenose dolphin's diet. In the Mediterranean Sea, owing to a population decline of at least 30% over the last 60 years, the International Union for the Conservation of Nature (IUCN) has listed, as a precautionary measure, bottlenose dolphin as a vulnerable species under the Red List of Threatened Species (Bearzi and Fortuna, 2006; Paximadis and Frantzis 2009). The need for identification and protection of special conservation areas are required by the EU Habitats Directive, thus the identification of suitable areas for the species can be an important tool for conservation purposes.

Environmental (e.g. climatological, oceanographic, geomorphological characteristics) along with biotic (e.g. prey availability and distribution, behavioural changes) and anthropogenic variables (e.g. fishery, fish cages, marine traffic, pollution) have been shown to affect the spatial distribution of cetaceans (Azzellino *et al*., 2008; Bearzi *et al*., 2008b; Bonizzoni *et al*. 2014; Gonzalvo *et al*., 2015). One of the main drawbacks in assessing the contribution of each of these factors to the spatial distribution of cetaceans is the difficulty of determining the factors over an appropriate and consistent spatio-temporal scale covering extended areas of several nautical miles. In addition, the collection of marine mammals' occurrence data is hampered by the elusiveness and mobility of these animals (Kaschner *et al*., 2006). As a result, dolphins' habitat modelling studies in the Mediterranean Sea have been concentrated in Italian (Northern Adriatic: Bearzi *et al*., 2008b; Simeoni, 2014; Tyrrhenian Sea: Blasi and Boitani 2012; Ligurian Sea: Azzellino *et al*., 2008; Marini *et al*., 2015) and Spanish (Cañadas *et al*., 2005; Cañadas and Hammond, 2008; Druon *et al*., 2012) waters using environmental related variables only. Relating cetaceans' distribution to their prey can significantly improve modelling (Hastie *et al*., 2004; Pendleton *et al*., 2012; Lambert *et al*., 2014; Hazen *et al*., 2015; Scales *et al*., 2015) but it demands the availability of prey information at a suitable spatial scale which is generally scarce or not always available (Torres *et al*., 2008).

Knowledge of the habitat of the common and bottlenose dolphins in the Eastern Mediterranean is limited to certain areas, such as in the Inner Ionian Sea Archipelago (Bearzi *et al*., 2006), Amvrakikos Gulf (Bearzi *et al*., 2008c) and North Evoikos Gulf (Bonizzoni *et al*., 2014). The present study is the first large-scale approach to habitat modelling covering the entire Greek Seas, as well as the first one to apply habitat modelling for a cetacean species in the Mediterranean Sea using the probability of presence of a potential prey species as a covariate. Habitat suitability modelling, although new as a tool, can have important conservation and management implications especially for cetacean species (Redfern *et al*., 2006). The present work aims to examine the potential of biotic factors (i.e. sardine probability of presence), environmental variables (i.e. ecosystem productivity, temperature) and invariant topographic elements (i.e. distance from the coast) to describe the habitat preferences of the two species and subsequently assess and map their summertime habitat over the entire Greek Seas. The combination of variables used in the analysis are not considered as the only factors affecting cetaceans' spatial distribution but rather as predictor variables, that can explain cetaceans' suitable habitat either directly (e.g. bottom depth, slope) (Azzellino *et al*., 2008, 2012) or as proxies for other causal factors. Although sardines are not the only prey species for bottlenose dolphins, when analysed along with a productivity index they can provide a robust proxy of the suitable prey availability for the species within the coastal environment studied here. The fact that sardine probability of presence was available at an adequate spatial and temporal resolution for the entire Greek Seas (Tugores *et al*., 2011), enabled the modelling approach to be undertaken at an appropriate spatio-temporal scale. Indicated suitable areas are discussed along with the deficiencies of models and future improvements.

METHODS

Cetaceans data availability

Sightings of common and bottlenose dolphin (Table 1, Figure 1(a), (b)), were obtained from three different sources: (a) dedicated cetacean surveys from the Pelagos Cetacean Research Institute in the period 1994–2014 (Frantzis, 2009; unpublished data) and IFAW/MCR Song of the Whale Research Team in 2013 (Ryan *et al*., 2014); (b) opportunistic data during the MEDIAS surveys carried out on board R/V Philia (HCMR unpublished data); and (c) published data (common dolphin: Angelici and Marini, 1992; Frantzis, 2009; bottlenose dolphin: Zafiropoulos and Merlini, 2001; Dede and Öztürk, 2007; Bearzi *et al*., 2008c; Frantzis, 2009). In all surveys, cetaceans were identified by experienced observers on board.

Table 1. Sources and period covered of cetacean sightings used for analysis

Species	Source	Period covered	Month	Sightings
Common dolphin	Sightings from cetacean surveys	1990–1999	05–09	41
		2000–2014	05–09	61
	Sightings from the MEDIAS fisheries monitoring surveys	2006–2013	05–09	10
Bottlenose dolphin	Sightings from cetacean surveys	1990–1999	05–09	82
		2000–2014	05–09	144
	Sightings from the MEDIAS fisheries monitoring surveys	2006–2013	05–09	31
	Published references	2000–2005	05–09	19

Questionable observations were classified as unidentified delphinids and were discarded from the dataset. Most cetaceans are highly mobile and spend a substantial amount of time below the surface, making detection and group size estimation inherently difficult and often unreliable. In addition, bad weather and rough sea state condition can increase the uncertainty in group size estimation. Hence, the geographic location of each sighting was used without taking into consideration estimation of the group size. Data covered the summertime period 1990–2014 and they were stratified into early summer (May, June, July) and late summer (August, September) observations. This allowed any potential seasonal effect to be taken into account, supported by a substantial number of observations. Moreover, available data were split into a training dataset (i.e. used for model selection) and a validation dataset (i.e. records not included in model selection to evaluate model predictive performance). Common dolphin sightings from the Gulf of Corinth were eliminated from the analysis, since the respective local population forms mixed-species groups with striped dolphin and presents very different behaviour and ecological habits, showing a preference for pelagic habitats and deep waters (Frantzis and Herzing, 2002; Bearzi *et al*., 2011).

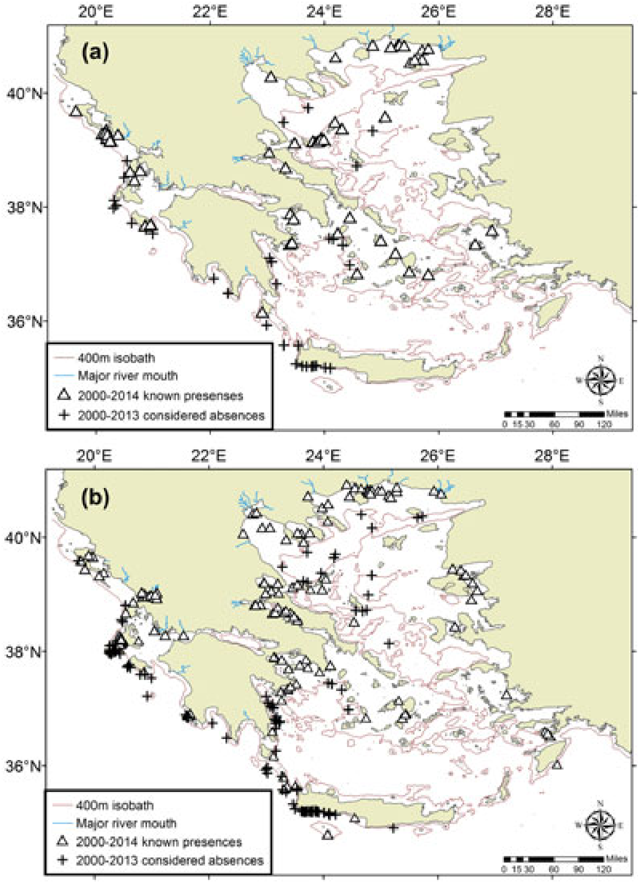

Figure 1. Survey area with the records used for modelling of (a) common dolphin and (b) bottlenose dolphin. The 400 m isobath is shown along with the main river mouths over Greece.

Modelling

Generalized additive models (GAMs) (Hastie and Tibshirani, 1990) were applied to define a suite of environmental and biotic factors that best describe bottlenose and common dolphin spatial distribution in the study area, during early and late summer for the period 2000–2013. This methodology required the dependent variable (y variable) in the form of presence/absence data. According to surveys of marine mammals in deep waters, bottlenose dolphin and common dolphin distribution in the Greek Seas is known to rarely exceed the 250 m isobaths (Frantzis, 2009). Thus, for modelling purposes survey locations where available sightings referred only to the striped dolphin (*Stenella coeruleoalba*; Meyen 1833), generally found at depths >400 m, were considered as absence locations for both species. A number of explanatory variables were used to construct the habitat models, including a combination of static, dynamic and biotic (i.e. SARD: sardine probability of presence) features.

Monthly averaged environmental imagery from daily measurements were downloaded for the study area and processed in a GIS (Geographic Information System) environment. At the location of each marine mammal's record, the following environmental variables were retrieved as time-resolved estimates for early (May–June–July) and late summer (August–September), depending on the month and year sampled: sea surface chlorophyll concentration (Chl-a in mg m^{-3}, log transformed to achieve a uniform distribution), sea surface temperature (SST in °C), photosynthetically active radiation (PAR in Einstein m^{-2} day^{-1}), sea level anomaly (MSLA in cm), salinity (SAL in psu) and sea surface current speed (in cm s^{-1}) (for details see Table 2).

Similarly, at the same coordinates, a set of time invariant variables (static) were retrieved including depth (cube root transformed to achieve a uniform distribution of bottom depth), slope (SL in degrees from north), distance from the coastline (DCOAST in km) and distance from main river mouths (DRIVER in km). The latter variables were estimated using ESRI's high resolution shoreline shapefile and the ArcGIS Spatial Analyst extension and proximity tools (see details in Table 2).

Finally, the probability of presence of sardine, was retrieved for each of the marine mammal records based on the available annual habitat suitability maps of the entire Greek Seas for June (early summer) and September (late summer) of each year and the period 2004–2008 (Tugores *et al.*, 2011). Based on the same GAM model as described in Tugores *et al.* (2011) and the satellite environmental variables for the period 2000–2003 and 2009–2013, probability of the presence of sardine was estimated at the location of each of the marine mammal records per year and season.

The selection of the GAM smoothing predictors was done using the MGCV library in R statistical software (R Development Core Team, 2012). The degree of smoothing was chosen based on the observed data and the restricted maximum likelihood estimation (REML) that outperforms the generalized cross-validation (GCV) smoothing parameter selection, as suggested by Marra and Wood (2011). To avoid over-fitting the maximum degrees of freedom (measured as number of knots k) allowed the smoothing functions were limited to the main effects at $k = 5$. The binomial error distribution with the logit link function was used and the natural cubic spline smoother (Hastie and Tibshirani, 1990) was applied for smoothing the independent variables and GAM fitting.

All available predictor variables were iteratively tested for multicollinearity based on Spearman's rank correlation (rs, 0.5). This resulted in a subset of eight uncorrelated predictor variables (i.e. Chl-a,

Table 2. Variables used as covariates for modelling along with information on the available resolutions and their source

Variables	Units	Sensor/model	Resolution	Source
Bathymetry (DEP)	m	GEBCO08	800 m	http://www.gebco.net
Sea surface temperature (SST)	°C	MODISA, SeaWiFS	4 km	http://oceancolor.gsfc.nasa.gov
Near surface chlorophyll (CHL)	Mg m^{-3}	MODISA, SeaWiFS	4 km	http://oceancolor.gsfc.nasa.gov
Photosynthe-tically active radiation (PAR)	einstein m^{-2} day^{-1}	MODISA, SeaWiFS	4 km	http://oceancolor.gsfc.nasa.gov
Sea surface salinity (SAL)	psu	NOAA NCEP EMC CMB GODAS models	0.333o	http://iridl.ldeo.columbia.edu
Sea surface current speed	cm s^{-1}	Merged Satellites	0.125o	http://www.aviso.altimetry.fr
Mean sea level anomaly (MSLA)	cm	Merged Satellites	0.125o	http://www.aviso.altimetry.fr
Bottom slope	Degrees from north	GIS calculation by the present study	800 m	Based on bathymetry layer of GEBCO08 Hydrography Portal
Distance from coast (DCOAST)	km	Euclidian distance (GIS calculation by the present study)	400 m	Coast location from ESRI Data and Maps (2012)
Distance from river (DRIVER)	km	Least-cost path (GIS calculation by the present study)	400 m	River mouth location from ESRI Data and Maps (2012)

DCOAST, PAR, MSLA, SAL, DRIVER, SST, SARD). For each species, a final model was built by testing all variables that were considered biologically meaningful, starting from a simple initial model with one explanatory variable. Season (i.e. early and late summer) was also tested as a factorial variable. The best model was selected based on minimization of Akaike's information criterion (AIC) and the level of deviance explained (0–100%; the higher the percentage, the more deviance explained), also taking into account the model's predictive ability.

Validation graphs (e.g. residuals versus fitted values, QQ-plots and residuals versus the original explanatory variables) were plotted to detect the existence of any pattern and possible model mis-specification. Residuals were also checked for autocorrelation. The output is presented as a simple plot of the best-fitted GAM.

Model validation

The final model was evaluated for its predictive performance, using the initial data (training dataset) and a validation dataset including: (a) the first decade 1990–1999 (~37% of the total records for common dolphin and ~33% for the bottlenose); and (b) the records of the most recent year, 2014. The estimation of the probability of presence of sardine for the period 1990–1999 was based on the respective statistical model (Tugores *et al*., 2011) and climatology data (available from NASA Oceancolor website: http://oceancolor.gsfc.nasa.gov/cms/), as satellite SeaWiFS Chl-a values were available only for September 1997 onwards. Assuming that the GAM model described in Tugores *et al.* (2011) also represents a good indicator of the recent presence of sardine, satellite environmental variables for 2014 were used to estimate the probability of presence of sardine at the location of each of the marine mammal records.

The receiver operating characteristic curve (ROC) and the area under the curve (AUC; a threshold-independent metric) were estimated. The latter measures the ability of a model to discriminate habitats where a species is present, versus those where it is absent, ranging from 0 to 1, where 0.5 indicates that performance is poor and close to random, while 1 indicates perfect discrimination (Elith *et al*., 2006; Franklin, 2009).

Sensitivity (i.e. proportion of observed positives that are correctly predicted) and specificity (i.e. proportion of observed negatives that are correctly predicted) indices were also calculated for the training and test dataset, according to the threshold criterion that maximizes the specificity–sensitivity sum (Jiménez-Valverde *et al*., 2008; Lobo *et al*., 2008).

All metric estimation was performed using the 'Presence/Absence' library of R statistical language.

Mapping

The final model was applied in a predictive mode to obtain annual habitat suitability maps over a grid at a GIS resolution of 4 km for the period 2004–2008 (period that coincides with the best available sardine data), on an annual and seasonal basis covering the entire Greek Seas. Thus areas with suitable conditions to support common dolphin and bottlenose dolphin presence were mapped. Subsequently, the mean average probability estimates and the respective standard deviation were estimated by means of GIS techniques (Geographic Information Systems; ArcMap, version 10.0) at each grid point, and were the basis for defining preferential and occasional common dolphin habitat (limits used for occasional: mean > 0.25, standard deviation > 0.05 and for preferential: mean > 0.75, standard deviation < 0.05) (*sensu* Giannoulaki *et al*., 2013).

RESULTS

Common dolphin

The final GAM included the effect of the probability of the presence of sardine along with the season effect (early and late summer). Environmental variables, as well as DCOAST and DRIVER did not show any significant correlation with common dolphin occurrences for the given dataset. Modelling results indicated high probability of common dolphin presence in areas with high probability of sardine presence (Figure 2). The final model explained

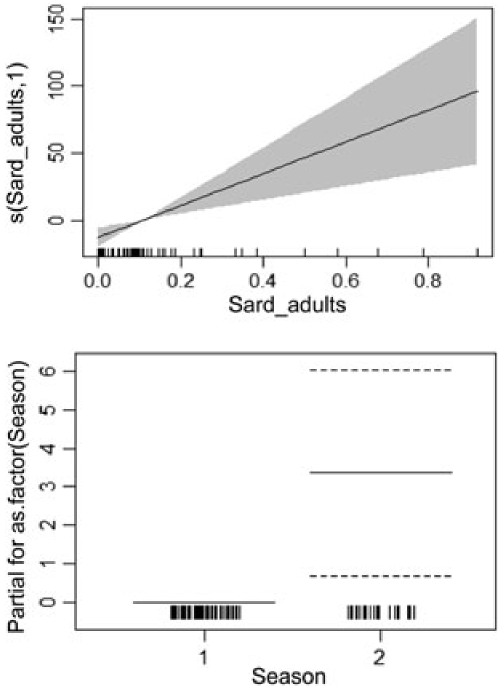

Figure 2. Common dolphin (*Delphinus delphis*): plots of the coefficients included in the final GAM model. Sard_adults: probability of sardine presence. Shaded regions and dashed lines delimit the 95% confidence regions for the function. The dashes on the x axis show the density distribution of x values.

67.5% of the deviance (Table 3) whereas sardine alone explained 58.2%, while the model validation generally showed good model fit (Table 4). Higher probability of common dolphin occurrence appears in areas with probability of the presence of sardine higher than 0.1, while the pattern of common dolphin presence is affected by the seasonal effect.

Model validation generally showed good model fit. AUC was 0.99 for the training dataset and 0.89 for the validation dataset (Table 4). The estimated sensitivity and specificity values (based on the threshold criterion that maximized their sum), also indicated good discrimination ability (>0.83) and equally good discrimination ability for both true absence and true presence records.

Habitat allocation maps of common dolphin habitat showed summertime favourable areas that largely coincide with the areas of known records for the period 2000–2014, as well as past records for the period 1990–2000 (Figure 3). In both seasons, the Northern Aegean and Ionian seas appear to be the most suitable areas to support common dolphin presence. Cyclades plateau and Dodecanese Islands also present extended persistent coastal areas. Preferential and occasional habitats of common dolphin tend to change in size between early summer (expanding) and late summer (reducing in size).

Bottlenose dolphin

The final GAM included the effect of the probability of presence of sardine, log-transformed chlorophyll-a concentration, distance from the coast and the seasonal effect on bottlenose dolphin presence (Figure 4). The effect of MSLA, SAL, PAR, DRIVER and SST were not found to be significant. Higher bottlenose dolphin presence occurred closer to the shore (<7 km), with sardine probability of presence >0.2 and high concentration of chlorophyll-a (> 0.135 mg m^{-3}), explaining 72.6% of the deviance (Table 3). Sardine probability of presence alone explained ~61% of the deviance verifying that it operates as a good proxy for the habitat preferences of the species.

Area under the curve showed high discrimination ability, as it reached 0.98 for the training dataset and 0.82 for the validation dataset that was not included in the model selection (Table 4). Estimated sensitivity and specificity values (based on the threshold criterion that maximized their sum) also indicated high discrimination ability. However, sensitivity and specificity values for the test dataset indicated better discrimination of the model for the true presence records (~0.84) than the true absence ones (~0.64).

Table 3. Final fitted GAM models of the target cetacean species. Sard_pres: sardine probability of presence; CHLlog: log-transformed near surface chlorophyll concentration (mg m^{-3}); DCOAST: distance from coast (km); Residual d.f.: residual degrees of freedom; *P*-value: statistical significance; AIC: Akaike Information Criterion

Species	Parameters	Residual d.f.	Deviance explained	*P*-value	AIC
Common dolphin	s(Sard_pres) + as.factor (Season)	88.99	67.5%	<0.001	45.76
Bottlenose dolphin	s(Sard_pres) + s(CHLlog) + s(DCOAST) + as.factor (Season)	285.41	72.6%	<0.001	119.16

Table 4. Mean values of area under curve (AUC), sensitivity and specificity accuracy measures ± standard error for the threshold criterion that maximizes the specificity–sensitivity sum

Species	Model	AUC	Sensitivity	Specificity
Common dolphin	Training dataset	0.987 ± 0.011	0.947 ± 0.030	0.943 ± 0.040
	Validation dataset	0.889 ± 0.034	0.830 ± 0.055	0.877 ± 0.037
Bottlenose dolphin	Training data	0.981 ± 0.007	0.929 ± 0.019	0.982 ± 0.013
	Validation dataset	0.820 ± 0.034	0.840 ± 0.038	0.642 ± 0.054

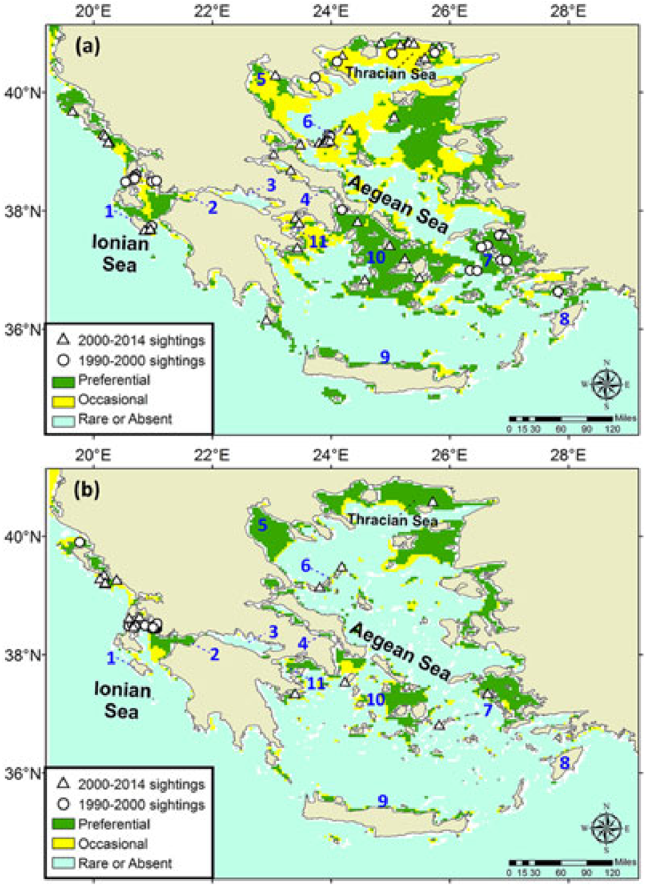

Figure 3. Common dolphin (*Delphinus delphis*): habitat allocation maps for (a) early and (b) late summer in the period 2004–2008. Sightings for the periods 1990–2000 and 2000–2014 are also shown. 1: Zakynthos Island, 2: Patraikos Gulf, 3: Gulf of Corinth, 4: South Evoikos Gulf, 5: Thermaikos Gulf, 6: Sporades, 7: Dodekanese Islands, 8: Rhodos Island, 9: Cretan Sea, 10: Cyclades, 11: Saronikos Gulf.

Habitat allocation maps of bottlenose dolphin habitat indicated preferential, occasional and rare areas for the species. Summertime favourable areas largely coincide with the areas of known records for the period 2000–2014, as well as past records for the period 1990–2000 (Figure 5). Areas suggested as preferential habitat for the bottlenose dolphin are dominated by enclosed seas, continental shelf waters, and waters surrounding islands like the Cyclades and Dodecanese complexes.

The Northern Aegean and Ionian seas appear as the most suitable areas to support bottlenose dolphin presence during early summer. Cyclades plateau and Dodecanese Islands also present extended persistent coastal areas, along with Amvrakikos Gulf that also presents high probability of bottlenose dolphin presence during early and late summer 2004–2008. Generally, enclosed areas such as Thermaikos Gulf, North Evoikos Gulf and Strymonikos Gulf are suitable environments for the species. Similarly for late summer, favourable areas that presented the highest probability of finding bottlenose dolphin include the Northern Aegean and Ionian seas, as well as around islands in the Cyclades plateau and more enclosed areas i.e. gulfs like Amvrakikos Gulf and North Evoikos Gulf. Mean average probability for late summer 2004–2008, along with the respective standard deviation were also estimated at each grid point (Figure 5). Similar areas to those during early summer appear suitable to support bottlenose dolphin presence during late summer, including enclosed areas like Amvrakikos Gulf, Thermaikos Gulf and Strymonikos Gulf. Preferential and occasional habitats of bottlenose dolphin tend to change in size between early summer (expanding) and late summer (reducing in size). Areas with the highest probability of bottlenose dolphin presence were the Northern Aegean Sea, Cyclades plateau and Ionian Sea during the early summer, exceeding 0.75 probability of presence in both seasons.

DISCUSSION

A large-scale cetacean habitat suitability modelling approach, covering the entire Greek Seas in the Eastern Mediterranean basin, is presented. For the

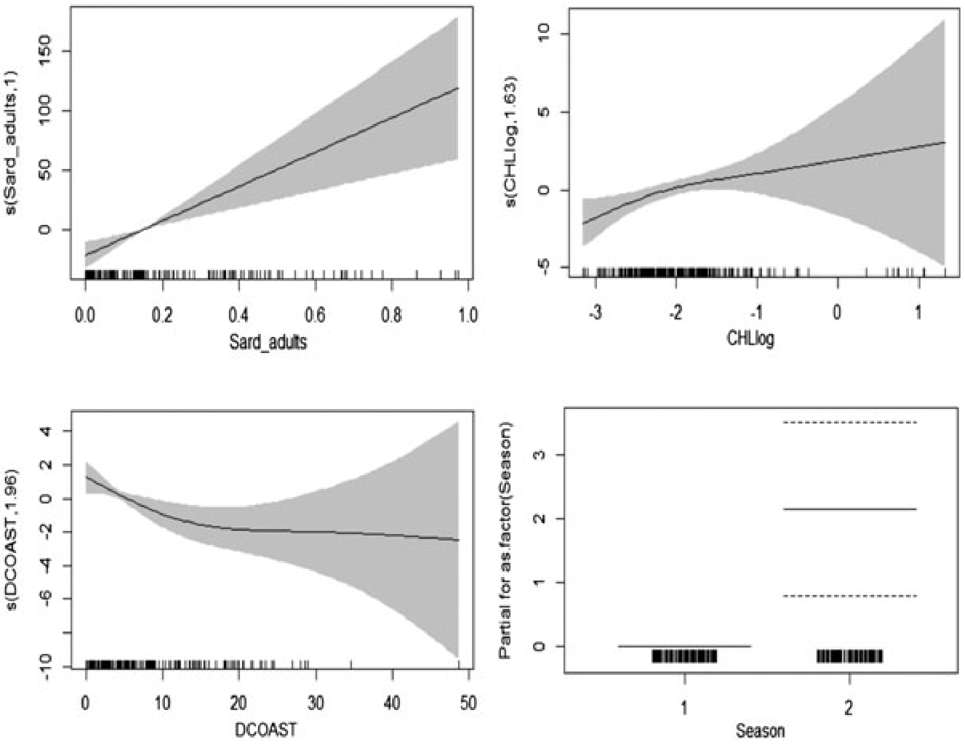

Figure 4. Bottlenose dolphin (*Tursiops truncatus*): plots of the coefficients included in the final GAM model. Sard_adults: probability of sardine presence; CHLlog: log-transformed near surface chlorophyll-a concentration; DCOAST: distance from the coast. Shaded regions and dashed lines delimit the 95% confidence regions for the function. The dashes on the x axis show the density distribution of x values.

first time the local potential habitats of common and bottlenose dolphins are described based on a modelling approach that incorporates the probability of sardine presence as an additional covariate in the respective models. Results showed that GAMs performed quite well (with deviance explained exceeding 60%) in assessing the suitable habitat of both species during summertime. The development of cetacean-habitat models is challenging, as they should be flexible enough to accommodate various sources of information and different types of habitat variables if they are to explain or predict species distributions (Redfern *et al.*, 2006). An additional challenge in the approach was to combine existing species occurrence datasets from different sources (i.e. dedicated targeted cetacean surveys along with opportunistic data collected during fisheries monitoring surveys) into a common meta-analysis within the entire Greek Seas, expanding the bounds (e.g. season, year, geographic extent) of the individual data sources. The latter has a very important benefit as it allows an understanding of the target species habitat over a wider area and temporal scale with reduced cost.

Probability of the presence of sardine, along with the seasonal effect largely explain common dolphin potential habitat. Bearzi *et al.* (2006) also mention prey availability and season as primary factors correlated with common dolphins' potential habitat. In both seasons, the coastal waters of the Thracian Sea, Thermaikos Gulf and Inner Ionian Sea Archipelago were indicated as the most suitable environments for common dolphin in the Greek Seas. It appears that the preferential and occasional habitats of common dolphin tend to change in size (i.e. occupied area) between early summer (expanding) and late summer (reducing in size). The current findings are largely in agreement with the known distribution of the species within the Ionian Sea, where common dolphins are found in the shallow waters between Lefkada, Kefallonia and Zakynthos Islands and the mainland (Frantzis *et al.*, 2003). In the latter area, Bearzi *et al.* (2006)

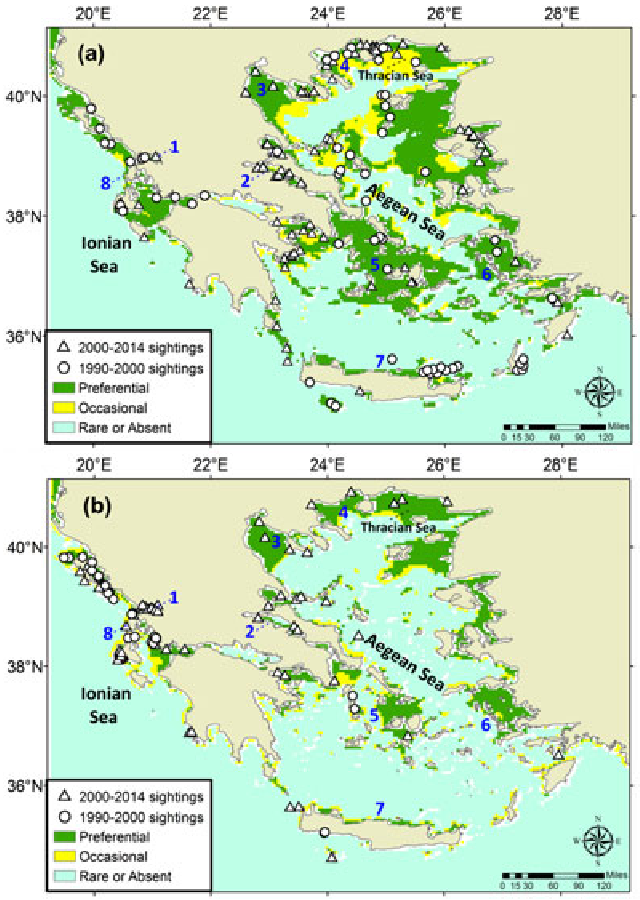

Figure 5. Bottlenose dolphin (*Tursiops truncatus*): habitat allocation maps for (a) early and (b) late summer in the period 2004–2008. Sightings for the periods 1990–2000 and 2000–2014 are also shown. 1: Amvrakikos Gulf, 2: North Evoikos Gulf, 3: Thermaikos Gulf, 4: Strymonikos Gulf, 5: Cyclades, 6: Dodekanese Islands, 7: Cretan Sea, 8: Lefkada Island.

found that sardines constituted 62.8% of common dolphin prey in the coastal waters of the eastern Ionian Sea and considered prey depletion as one of the key factors responsible for the decline of common dolphin local population. Another study from the inner part of the eastern Ionian Sea based on ecosystem modelling (Piroddi *et al.*, 2011) has shown that intensive fishing pressure on small pelagic stocks reduced prey availability for common dolphin and possibly induced the sharp decline of their population in the coastal waters of the Inner Ionian Sea Archipelago. Available habitat studies in Spanish Mediterranean waters (i.e. the Gulf of Vera) for common dolphin report a clear preference for cooler waters (around 18–20 °C), a peak in abundance around the shelf break (150–200 m depth), as well as a large increase in abundance towards areas of higher chlorophyll-a concentrations (Cañadas and Hammond, 2008). This observed pattern is similar to the Greek Seas where no sightings were recorded at water depths exceeding 400 m.

Persistent habitat for common dolphin was also shown in the coastal areas of Cyclades plateau and Dodecanese Islands. As common dolphin is known to be widely but discontinuously distributed in the Aegean Sea, certain deficiencies of common dolphin model output were detected. During both seasons, areas in the northern part of Crete were predicted as suitable for the species. However, common dolphin's known range in the Aegean Sea is considered to be delimited by an imaginary line that crosses Greece from south of Peloponnese to south of Cyclades and to north of Rodos Island (Frantzis *et al.*, 2003; Frantzis, 2009). A possible explanation for the absence of the species in north Crete (and some other locations) could be the fact that the suitable habitat appears as a limited and very narrow coastal zone that cannot sustain the survival of a resident dolphin community. As Bearzi *et al.* (2003) report, common dolphins were widespread in much of the Mediterranean Sea until the late 1960s, but as their population declined they are now missing from large areas of their former range (e.g. the northern Adriatic Sea, the Balearic Sea, Provençal Basin, and Ligurian Sea). Currently, they are abundant only in the Alboran Sea and with small concentrations in Algeria, Tunisia, northern Sardinia, south-eastern Tyrrhenian, around the Maltese islands, in parts of the Aegean Sea and the eastern Ionian Sea. Since there is no well-documented knowledge of the past distribution of the species, the absence of common dolphin from some areas could be for reasons other than habitat suitability, such as biogeography and/or the oligotrophic nature of the offshore waters. For example, the oligotrophic nature of the offshore waters in the North Cretan Sea (Stergiou *et al.*, 1997) could have impaired the longevity of a sustainable resident population for common dolphin.

Another misleading prediction is the case of Patraikos Gulf, which is foreseen as suitable habitat (due to high probability of sardine presence), although common dolphins are reportedly absent from this area (Frantzis, 2009; unpublished data). Patraikos Gulf supports a mosaic of human activities including fisheries, urbanization, heavy industry, tourism, aquaculture, pile driving activities, as well as high shipping traffic. Moreover, the area is subject to high and frequent seismic activity. Sound levels over certain thresholds are known to cause behavioural responses such as displacement in marine mammals (Southall *et al.*, 2007). So, although there is no obvious explanation for this confirmed absence, increased noise pollution in the area might be the reason for the absence of common dolphins (Gordon *et al.*, 2003; Southall *et al.*, 2007) instead of the lack of suitable habitat.

Moreover, the absence of the Gulf of Corinth from the indicated suitable habitat areas for the species, although a permanent small population of common dolphin is known to inhabit the area (Frantzis and Herzing, 2002), is attributed to the special bathymetry and oceanographic characteristics of this area. The Gulf of Corinth although a closed basin, has very steep slopes particularly along the south coasts with bottom depth exceeding 500 m within a short distance from shore, while shallow areas <100 m depth represent less than 23% of the sea surface area (Frantzis and Herzing, 2002). In this special area the respective local population of common dolphin forms mixed-species groups with striped dolphin and presents very peculiar behaviour, as well as ecological habits showing a preference for pelagic habitats and deep water (Frantzis and Herzing, 2002; Bearzi *et al.*, 2011) instead of a typical coastal behaviour. As the current analysis modelled the suitable habitat of the coastal population of common dolphin, it did not identify this area as suitable habitat for the species. In a further step, the knowledge of preferred habitats for common dolphin with respect to their different needs such as feeding, reproduction, females with calves is absolutely essential for effective conservation and specific management measures.

Most studies in the Mediterranean on bottlenose dolphin habitat modelling focus on the determination of factors related to species habitat instead of mapping. For example, Bearzi *et al.* (2008c) in the northern Adriatic Sea relate environmental variables and bottom depth to bottlenose dolphin habitat use, while Bonizzoni *et al.* (2014) in North Evoikos Gulf relate the species habitat use mainly with distance from fish farms and bottom depth. Recently, Marini *et al.* (2015) related the occurrence of bottlenose dolphin to short distance from the coast (~3 km) in the Ligurian Sea. They note that bottlenose dolphin concentrate near the 100 m isobath and they do not distribute over 200 m depth. Their finding is also in accordance with current findings, as well as Cañadas *et al.* (2002) and Azzellino *et al.* (2012), who demonstrated that the species prefers coastal areas within the 400 m isobath. The current study in the Greek Seas showed that the probability of sardine presence, chlorophyll-a concentration > 0.135 mg m^{-3}, coastal waters (distance from the coast <7 km) along with a seasonal effect largely explain bottlenose dolphin potential habitat. This confirms that probability of sardine presence along with productivity, distance from the coast and season act as proxies for other biological factors. For example, anthropogenic factors often related to the presence of bottlenose dolphins such as small-scale fishing activity (Bearzi *et al.*, 2008a; Gonzalvo *et al.*, 2011, 2015) or the presence of fish farms (Bearzi *et al.*, 2008a; Bonizzoni *et al.*, 2014) are carried out within the continental shelf and largely overlap with sardine main distribution grounds as shown by Giannoulaki *et al.* (2011) and Tugores *et al.* (2011).

A significant seasonal effect indicating shrinkage of the preferential and occasional habitat from early to late summer towards more coastal areas is also observed. Bottlenose dolphin calving season (peak in July and August, Bearzi *et al.*, 1997) is known to coincide with increased abundance in coastal waters (Evans *et al.*, 2003) that may assure food availability or the protection of the young ones. This could explain the seasonal shift in species habitat.

The maps suggest preferential habitat for bottlenose dolphin in the Greek Seas include the continental shelf waters of the Thracian Sea, Thermaikos Gulf and the inner part of the Ionian Sea, semi-closed seas like Amvrakikos Gulf and

North Evoikos Gulf as well as the waters surrounding islands, e.g. the Cyclades plateau or the Cretan shelf in accordance with Frantzis *et al.* (2003) and Bearzi *et al.* (2005, 2008c). Amvrakikos Gulf is a well-known area that hosts a resident population of bottlenose dolphin (Zafiropoulos *et al.*, 1999; Bearzi *et al.*, 2008c; Gonzalvo *et al.*, 2015).

An abundant community is also known to occur in the inner part of the Ionian Sea between Lefkada Island and the mainland (Politi *et al.*, 1992; Zafiropoulos *et al.*, 1999; Bearzi *et al.*, 2006). The species was also often reported in the North and South Evoikos gulfs (Zafiropoulos *et al.*, 1999; Zafiropoulos and Merlini, 2003; Bonizzoni *et al.*, 2014). In North Evoikos Gulf, Bonizzoni *et al.* (2014) recently associated the species presence with fish farms. The habitat of bottlenose dolphin is known to overlap with aquaculture in several coastal areas around the world (Würsig and Gailey, 2002; Watson-Capps and Mann, 2005). Greece is one of the largest producers of commercial aquaculture finfish species (i.e. more than 60% for seabass and seabream) and 28% of total finfish (Hofherr *et al.*, 2015) of all European Union and Mediterranean countries (Trujillo *et al.*, 2012; FAO FishStatJ, 2015). In Europe, fish farm cages are in general positioned very close to the coastline with median values of less than 1000 m in all countries (Hofherr *et al.*, 2015). Fish farms operating in Greek waters are coastal finfish farms, placed on average very close to the coastline (68 m, Hofherr *et al.*, 2015) with a maximum distance of 300 m from shore (Trujillo *et al.*, 2012). Thus the bottlenose dolphin's potential habitat described as within 7 km distance from the shore, high concentration of chlorophyll-a and increased probability of sardine presence largely overlaps with the existing 'fish farm locations' in the Greek Seas.

The findings concerning both target species are also in accordance with the theory that cetaceans with a high energy requirement, like the common dolphin (Spitz *et al.*, 2010) and bottlenose dolphin (Bearzi *et al.*, 2008a), preferentially exploit habitats of high primary production (Mannocci *et al.*, 2014a, b). In Greece and the Mediterranean, the most important threats to these two cetacean species are considered to be prey depletion caused by overfishing and fishery-related mortality (Bearzi *et al.*, 2008d). Their diet includes mainly fish and they may be competing with fisheries and/or impeding recovery of depleted fish stocks. In addition, there is fishery-related mortality such as from by-catch (Bearzi *et al.*, 2008d; Gonzalvo *et al.*, 2011) or even direct, intentional killing (Bearzi *et al.*, 2008d, Gonzalvo *et al.*, 2015). The positive association of both species presence with an increase in the probability of sardine presence, especially in the case of common dolphin, underlines the importance of fish populations decline as a threat for both cetacean species. Examining the overlap of persistent habitat areas with important fishing grounds for specific gears such as long liners can help to further understand cetacean–fisheries interactions (Kaschner, 2004) and potentially ensure more effective protection and management measures such as defining fishing restricted areas for certain gears based on the identification of 'hot spot areas', e.g. areas presenting high probabilities for both species.

Additional data, with emphasis on the true absences of the species, as well as more records from late summer are expected to improve the model accuracy. Caution is required when extrapolating the results to unsurveyed areas because the models are 'predictive' rather than 'explanatory', and different environmental characteristics and processes may occur elsewhere. No discrimination in behaviour was taken into account such as travelling, feeding, socializing, milling or resting. However, the type of behaviour in which a group was engaged when encountered can influence the selection of the habitats. Cañadas and Hammond (2008) note that the largest difference was observed between groups feeding and groups socializing. Thus modelling based on data addressing a specific type of behaviour like feeding, the presence of calves and lactating females, or group size can provide further and more detailed insights into the importance of certain areas as suitable habitats. For example, 64% of bottlenose data from the North Aegean Sea in the period 2006–2014 referred to groups of over three individuals and 47% to groups exceeding five individuals. In the case of common dolphin 50% of the records in the period 2006–2014 involved groups exceeding four individuals. This confirms the tendency for larger group sizes to occur in shallow waters around the shelf edge as Cañadas and Hammond (2008) observed in Southern Almería. Knowledge on preferred habitats, especially with respect to their different needs such as feeding or reproduction, is absolutely essential for effective conservation. Knowing the areas mostly used by mothers with calves, or for feeding could lead to specific management measures for those areas, which may need special or different treatment from other areas.

Although further research is needed, knowledge on the suitable habitat of the species over extended areas can improve our ability to monitor, detect, and respond to shifts in species distribution and trends as well as our understanding of climate change impacts on marine mammals' distribution. Climate change, both natural and human-induced, has the potential to affect the distribution of marine mammals (Leaper *et al.*, 2006). The nature of such effects is likely to be variable and habitat suitability modelling has the potential to help visualize possible habitat alterations and how resilient habitat can be over time (Salvadeo *et al.*, 2010; Heide-Jørgensen, 2011). Most important, habitat suitability modelling can assist with the establishment of marine protected areas for any of the endangered populations of the cetacean species present in the Greek Seas. The latter is essential for the development and management of conservation plans or to define Special Areas of Conservation under the EU Habitats Directive and the EU Marine Spatial Planning Framework Directive to focus conservation measures in relation to human activity (e.g. by-catch reduction measures; disturbance by shipping, tourism, etc.). In addition, the ecosystem in which marine mammals live often encompasses the waters of more than one country. This is the case in the Aegean Sea but also a common situation in the Mediterranean Sea, where 21 countries share the coastline. Habitat suitability modelling allows the identification of the suitable habitat for the species over wider areas, providing the means to strengthen protection for the species beyond individual country's territorial waters. Currently, this knowledge on the suitable habitat of bottlenose and common dolphins might be the only basic tool under the current Annex II of the EU 92/43 Habitat Directive and Natura 2000 framework to help identify Special Areas of Conservation.

Existing marine protected areas (MPAs) in the Eastern Mediterranean and especially in the coastal waters of the Greek Seas are underrepresented (Micheli *et al.*, 2013). This is more pronounced for the offshore waters (Micheli *et al.*, 2013). The ACCOBAMS (Agreement on the Conservation of Cetaceans in the Black Sea Mediterranean Sea and Contiguous Atlantic Area) has proposed six areas of special importance for the common dolphin in Greek waters, i.e. the area of Kalamos Island (located between Lefkada Island and the mainland, in the Ionian Sea), the Gulf of Saronikos and adjacent waters of southern Evoikos Gulf, the northern Sporades, the northern Aegean Sea and waters surrounding the Dodecanese (http://www.accobams.org). For the bottlenose dolphin the only area of special importance suggested by the ACCOBAMS is the Amvrakikos Gulf in the Ionian Sea. All these areas are identified in the results of the current study.

Persistent 'hot spot areas' for both cetacean species indicated here, include the northern Sporades, the coastal waters of the Thracian Sea, waters surrounding the central part of Cyclades plateau, waters surrounding the northern Dodecanese and the coastal waters of the eastern part of the Aegean Sea. Besides the wider area of Northern Sporades Islands which was established as a National Marine Park in 1992 and where various activities are prohibited, existing management measures, if any, in the majority of these 'hot spot areas' are limited to fishing restrictions for bottom trawlers and purse seines according to national law (e.g. a large part of North Evoikos Gulf, Amvrakikos Gulf). Food web ecosystem models with a spatial component like Ecopath with Ecosim/Ecospace (Piroddi *et al.*, 2011) that are available for the Aegean (Tsagarakis *et al.*, 2010) and Ionian Seas (Moutopoulos *et al.*, 2009), can integrate the indicated 'hot spot areas' for the two cetacean species and subsequently simulate the effect of these areas as MPAs or fishing protected areas with respect to the population status of the two dolphins species.

However, proposing management measures such as MPAs or MPA networks cannot be based on the protection of one or two marine mammal species. Recently, Micheli *et al.* (2013) proposed an exhaustive framework for Conservation Planning in the Mediterranean and highlighted the need to evaluate all uses including the spatial variability of anthropogenic uses and the associated cost of excluding uses for conservation needs. In each case, identifying the conservation goals and assessing the ecological coherence of suggested MPA networks is essential.

ACKNOWLEDGEMENTS

We wish to thank Dr. Konstantinos Tsagarakis as an on board observer during the MEDIAS surveys and Mrs. Maria Myrto Pyrounaki for her assistance on the estimates of sardine probability data, as well as those who have contributed with visually documented opportunistic observations included in the national database of Pelagos Cetacean Research Institute. Finally, we wish to thank the Song of the Whale Research Team of Marine Conservation Research International and the International Fund for Animal Welfare (IFAW) for providing sighting data from a dedicated survey in the Aegean Sea in 2013.

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