



Predicting common bottlenose dolphin habitat preference to dynamically adapt management measures from a Marine Spatial Planning perspective



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ABSTRACT

At the European Level, SACs (Special Areas of Conservation) are considered among the most reliable tools for increasing the efficiency of protective actions and to identify species vulnerability hotspots across spatial scales. Nevertheless, SACs may fail in their scope when design and management are not dynamically adapted to meet ecological principles. Knowledge of the spatial distribution of relevant key species, such as common bottlenose dolphin (*Tursiops truncatus*), is crucial in order to achieve the objective of the Habitat Directive (92/43/EEC), and is a fundamental step in the process of Marine Spatial Planning. From this perspective, new data and analysis are required to produce forecasts at spatio-temporal scales relevant to individual organisms. Here, we propose a study based on a MaxEnt modelling exercise to define the spatial distributional patterns of bottlenose dolphin at different temporal scales (over periods of multiple months and years) to increase the ecological understanding of how the species use the eco-space, and to delimit boundaries of a SAC in the waters surrounding Lampedusa Island, a hotspot for cetaceans in the Southern Mediterranean Sea. We show that bottlenose dolphin prefer shallower feeding grounds that often host complex and rich food webs, but also that this preference is constrained by disturbance factors such as boat traffic. As sea-related tourism, including dolphin-watching, is one of the most important economic activities of the island, the study results can be used from a management perspective, in order to reach a solution regarding two apparently conflicting needs - species protection and economic development.

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1. Introduction

Global environmental change is forcing organisms to acclimate, adapt and/or migrate to track alterations in their environment across space and time, and there is a need to improve projections of the future status of marine biodiversity under rapidly changing conditions (Pacifi et al., 2015). Large ecosystem shifts are, however, ultimately driven by cumulative impacts of small-scale processes acting at organismal and population levels. In order to predict future changes in species distributions, new data are required to produce forecasts at spatio-temporal scales relevant to

individual organisms (Halpern et al., 2015).

Cetaceans are among the most threatened marine species. These threats have become such a concern as to warrant a specific regulatory action at the European Community level, as dictated by the Habitats Directive (Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora). This Directive aims to establish a network of SACs (Special Areas of Conservation) that are known collectively as “Natura 2000”. The Natura network comprises sites identified by the Member States as hosting particular habitat types (listed in Annex I of the Directive), or the habitats of particular species (listed in Annex II). To date, two species of cetaceans have been listed on Annex II, namely the harbour porpoise (*Phocoena phocoena*) and the common bottlenose dolphin (*Tursiops truncatus*, Montagu, 1821). SACs, and other Marine Protected Area in general, are considered among the most reliable tools for increasing the efficiency of conservation actions and for

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defining species vulnerability hotspots across spatial scales (Canada et al., 2005; Agardy et al., 2011).

Knowing the distribution and ranging patterns of cetaceans is important for adapting effective boundaries for SACs and MPAs and is a fundamental requirement for all species listed in the Habitats Directive. Moreover, knowing the spatial distribution of ecologically relevant species is also one of the fundamental steps in achieving the goals of most Marine Spatial Planning Directives worldwide (e.g., the European Directive 2014/89 “Establishing a framework for maritime spatial planning”, or the “Interim Framework for Effective Coastal and Marine Spatial Planning” in the USA). In fact, among basic principles proposed to address Ecosystem-based Marine Spatial Planning, those dealing with key species, such as *Tursiops truncatus*, are essential in increasing the reliability of management measures (*sensu* Stamoulis and Delevaux, 2015). Dolphins are at the top of trophic chains worldwide and they share the role of ecosystem functioning drivers with a few other top level species. An anomalous fluctuation in their distributional range due to the pervasive effects of human actions can alter community structure and depress ecosystem functioning.

However, for most marine species (such as cetaceans and fish), identifying marine areas useful to their life and reproduction may be difficult. The high mobility of many marine species and the difficulty in observing them may complicate the investigation of their distribution considerably, increasing research costs and experimentation time. An effective ecosystem-level management depends acutely upon the quality of information available, not only for defining boundaries but also for understanding how these areas are used by animals, and which components (biotic, abiotic and factors of anthropogenic origin) influence their distribution and abundance (Wilson et al., 1997). Marine mammals are recognized as not permanently resident species (Wilson et al., 1997), and this makes the design of SACs/MPAs and the related management actions highly challenging. Even if many cetaceans have been shown to display relatively consistent preferences in terms of environmental variables and bottom topography (Hastie et al., 2005), few studies have predicted the habitat use of bottlenose dolphins in relation to environmental variables through the application of species distribution modelling (SDMs) in the Mediterranean Sea (Canadas et al., 2002, 2005; Azzellino et al., 2008, 2012; Gomez et al., 2008; Marini et al., 2014). SDMs have a long tradition in ecology to help both researchers and managers to increase their understanding of current species distribution patterns, and to predict future distributions in the face of climate change, human-assisted invasions, and many other ongoing environmental changes (Yackulic et al., 2013). One of the most recently used SDMs is that based on the Maximum Entropy (MaxEnt) method. MaxEnt is a presence-only statistical model, and it is highly reliable in producing useful predictions when absence data are not available or not sufficiently reliable. In the case of cetacean sampling, many locations cannot be surveyed systematically or may receive little survey effort, leading to a lack of definitive absence data. MaxEnt represents the most effective correlative modelling approach in context of SDM (Guisan and Thuiller, 2005), providing an important ecological tool for the prediction of species geographical distribution within the context of environmental change from local to global. MaxEnt attempts to minimize the relative entropy between two probability densities, one estimated from occurrence data and the other from the background environment defined in covariate space (Elith et al., 2011). The maximum entropy distribution is built only from what is known about the occurrence of the species and its associated variables, while avoiding making assumptions about anything unknown (Jaynes, 1989). This method is especially useful for modelling species distributions with incomplete information on sampling effort and not independent data, and is becoming an

increasingly important tool in the field of marine conservation and management (Edren et al., 2010; Thorne et al., 2012). Moreover, MaxEnt has a predictive power that is consistently competitive with the highest performing methods (Elith et al., 2006, 2011). Here, we used MaxEnt to define the spatial distribution pattern of *T. truncatus*, at different temporal scales (years and months) in order to increase the ecological knowledge about the species, and to define boundaries of a SAC in the waters surrounding the Archipelago of Pelagie (Southern Mediterranean Sea). Such an area is a key habitat for cetaceans (Ben Naceur et al., 2004; Canese et al., 2006) and meets all the criteria required for the localization of SACs: i) the continuous or regular presence of the species, as demonstrated in the past and in the present study on the basis of MaxEnt predictions; ii) good population density, in relation to neighbouring areas (Pulcini et al., 2010); iii) high ratio of juveniles to adults all year round (Pace et al., 2003).

2. Methods

2.1. Study area

Lampedusa is the biggest island in the Archipelago of Pelagie (Southern Mediterranean Sea), with an extension of 20 km² and a length of 10.5 km. It is located on the northern African continental shelf, about 130 km from the Tunisian coast and 205 km from the Sicilian coast. This region is an exchange area for the water masses of the eastern and western Mediterranean basins, with a complex bathymetry that strongly influences water currents (Pernice, 2002). A coastal portion of this zone was declared a Marine Protected Area by the Italian Ministry of the Environment in 2002. The protected area covers an area of 4136 ha and encompasses three zones with different protection regimes (integral, general and partial). In 2005, the local Sicilian Government established a Site of Community Importance (SIC –ITA040002) whose marine area corresponded to the boundaries of the MPA. The study area extended approximately 7 nautical miles offshore covering an area of 992 km² (Fig. 1). Lampedusa is inhabited by about 6100 persons and tourism represents the most important source of economic income. This is showed by the increase of the touristic presence during summer (from a few thousands in winter to almost 30,000 in summer; LEGAMBIENTE, 2009). Despite the fact that the Archipelago is characterized by relatively low human impact for the majority of the year, the waters surrounding Lampedusa are characterized by highly concentrated heavy boat traffic, from July to September, when tourism is at its highest. In this period, recreational motorboats (small motorized and/or inflatable rental boats and watercraft) making excursions around the island and dolphin-watching trips (both organized and accidental) represent the largest component of boat traffic in these waters (approximately 90% of the total; La Manna et al., 2010). Other than tourism, fishery is the other important economic activity for the island inhabitants. The local fishery fleet consists of 95 operating boats with fishing licences; the most common systems are bottom trawls, hand lines, trolling lines and, after these, gill nets, long lines, pots and purse seines (Celoni et al., 2007). The main fishing area is localized in the southern part of the island, down to 50 m depth (La Manna pers. obs.). Furthermore, owing to the great abundance of fish (among the highest in the Mediterranean Sea - Cristina et al., 2006), Lampedusa's waters are used by several trawlers from the mainland of cross-border Mediterranean countries.

2.2. Data collection

Sightings of *T. truncatus* were collected during the dedicated boat survey, following a standard research protocol, on board 5 m

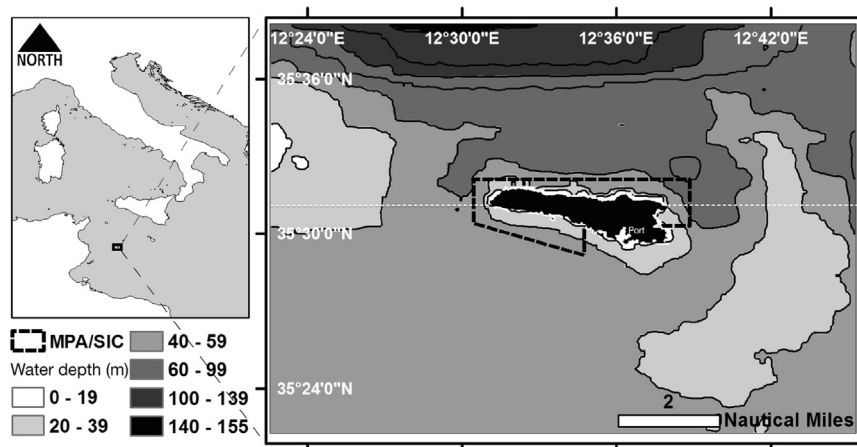


Fig. 1. Lampedusa island. The solid line delimited the study area and the dotted lines the boundaries of the MPA and the SIC. The white line delimited the northern and southern sectors of the study area.

and 7 m length inflatable boats. From May to October, between 2005 and 2009 and during 236 surveys, 6169 km were surveyed, and a total of 243 sightings were recorded. (Table 1). Surveys followed a random sampling design and routes were planned to homogeneously cover the study area, with a generally perpendicular direction with respect to the coast and depth contours. At least two experienced observers scanned the sea surface at an average boat speed between 10 and 16 km per hour, during daylight and with a visibility of over 3 miles. Navigation routes were interrupted in case of sighting or when sea conditions deteriorated (sea state > 2 Douglas; wind force > 2 Beaufort). A dolphin sighting was defined as an observation of one or a group of dolphins. A group was defined as dolphins observed in apparent association, moving in the same direction and often, but not always, engaged in the same activity (Shane, 1990). The position of the boat (automatically recorded every minute) and the location of each sighting were recorded using a Garmin handheld GPS. During each dolphin sighting data about group size and estimated sex and age classes were recorded together with photo-identification data and behavioral states of the group (by focal group sampling). For the elaboration of the spatial model each dolphin sighting was treated as one presence record regardless of group size.

Occurrence data and environmental variables were elaborated with ESRI ArcMap 9.3. Cetaceans may differentially select habitats in relation to environmental conditions, topographic features, and prey availability (Canadas et al., 2002; Davis et al., 2002; Gomez et al., 2008; Azzellino et al., 2008, 2012; Thorne et al., 2012;

Marini et al., 2014; Bohrer do Amaral et al., 2015). Thus, the selection of environmental variables that are functionally relevant to species is an important phase of any species modelling process, as they represent good proxies for prey availability, good calving area or protection from risks. Based on previous cetacean habitat studies (Canadas et al., 2002; Davis et al., 2002; Gomez et al., 2008; Azzellino et al., 2008, 2012; Thorne et al., 2012; Marini et al., 2014; Bohrer do Amaral et al., 2015) the following environmental variables were selected: sea surface temperature (SST - degree Celsius), Chlorophyll-a concentration (Chl-a - mg/m^3), water depth (m), slope (degree), distance to the coast (m) and aspect. Water depth was mapped using LANDSAT TM satellite images acquired with high resolution (30 m). Raster bathymetry data were obtained with a resolution of 0.002 decimal degrees (250×250 m approximately). This spatial resolution was maintained for the calculation of the variables SST, Chl-a, slope and aspect. Monthly 4 km MODIS SST and Chl-a data from NOAA (National Ocean and Atmospheric Administration) satellite imagery were downloaded and clipped to the study area using Marine Geospatial Ecology Tools (Roberts et al., 2010). The point data were interpolated using an inverse distance weighted (IDW) technique using “Interpolation” function in Spatial Analyst Tools in ArcGIS 9.3, and averaged to create predictor layers for the models. Slope defined the bathymetric gradient along the study area and was measured in degrees. A continuous raster surface of seabed gradient was derived using “Slope” function in Spatial Analyst Tools in ArcGIS 9.3. Aspect measures the heterogeneity of the downslope direction and was calculated by deriving

Table 1

Number of dolphin sightings and kilometers of effort between 2005 and 2009, as a function of months and geographical sectors of the study area. In parentheses is shown the percentage contribution of effort for each sector (North and South) of the study area.

		May	Jun	Jul	Aug	Sept	October	North	South	Total
2005	Sightings	10	11	14	10	6	4	10	45	55
	Km	383.0	205.2	381.53	296.10	198.66	128.9	497.67 (31%)	1092.67 (69%)	1590.3
2006	Sightings	10	8	15	8	8	3	18	34	52
	Km	251.4	397.11	594.90	357.97	298.41	246.0	924.89 (43%)	1220.89 (57%)	2145.8
2007	Sightings	–	0	12	13	3	–	4	24	28
	Km	–	71.69	135.23	184.42	168.01	–	244.32 (43%)	315.03 (57%)	559.35
2008	Sightings	–	14	14	20	9	–	12	45	57
	Km	–	180.61	283.66	287.50	277.19	–	358.19 (35%)	670.77 (65%)	1028.96
2009	Sightings	–	11	23	10	7	–	11	40	51
	Km	–	128.62	373.75	192.44	150.04	–	358.86 (42%)	485.99 (58%)	844.85
Total	Sightings	20	44	78	61	33	7	55	188	243
	Km	634.4	983.20	1769.07	1318.43	1092.31	371.9	2383.93 (38%)	3785.35 (62%)	6169.28

the maximum rate of change in value from each cell to its neighbours, using “Aspect” function in Spatial Analyst Tools in ArcGIS 9.3. Aspect was a categorical variable, with 8 classes, coded as follow: N (1); NW (2); NE (3); S (4); SW (5); SE (6); W (7); E (8). Distance was calculated for each cell centroid from shoreline shapefile using “Near” function in Spatial Analysis Tools in ArcGIS 9.3. Thus the environmental predictors included in the analysis were 5 continuous variables (SST, Chl-*a*, depth, slope, distance to the coast) and 1 categorical variable (aspect). Statistics of each environmental predictor as a function of years and months are shown in Table 2.

2.3. Data analysis

MaxEnt software (version 3.3.3 k) was used to elaborate probabilistic predictions of *T. truncatus* spatial distribution at different temporal scales. MaxEnt uses environmental data at locations of species sightings in comparison with environmental variability in the background data to describe the distribution of a species, thus predicting the relative occurrence rate (ROR) as a function of the environmental predictors at that location. The background data were a large number of points randomly selected from within the study region during the modelling procedure, and provided a sample of available habitat of a species within a specific region (Phillips et al., 2006). The probability of occurrence can be interpreted as an estimate of the probability of presence under a similar level of sampling effort as that used to obtain the known occurrence data (Phillips and Dudík, 2008). From the collection of biologically plausible predictors, the removal of highly correlated predictors using correlation analysis is recommended (Merow et al., 2013). To test correlation between the six environmental predictors, the Pearson's correlation coefficient was applied to each pair of variables. Statistical significance was tested at the $P < 0.05$ level. None of the variables were highly correlated, thus all of them were included in the models (Table 3). In order to evaluate monthly and yearly change patterns in habitat suitability, models were performed for the five years of sampling (2005–2009), for each single year and for each single month, from May to October. The winter months were not included in the analysis due to limited sampling efforts. MaxEnt settings were chosen in relation to the specific questions of the study and data limitations (Merow et al., 2013): i) logistic output to easily understand where the model predicts the occurrence of dolphins, and to use the maps as a tool for planning conservation measures; ii) hinge features to improve the performance of the models without increasing the complexity

Table 3

Average test AUC and standard deviation (in parentheses).

Months	AUC (SD)	Years	AUC (SD)
May	0.792 (0.201)	2005	0.829 (0.094)
Jun	0.756 (0.129)	2006	0.801 (0.100)
Jul	0.849 (0.035)	2007	0.861 (0.096)
Aug	0.908 (0.043)	2008	0.841 (0.076)
Sept	0.832 (0.080)	2009	0.863 (0.057)
Oct	0.965 (0.030)	2005–2009	0.847 (0.019)

(Phillips and Dudík, 2008); iii) default regularization parameters; iv) 10-fold cross-validation, a process that allows model results to be based on ten randomly selected portions of the data and model performance to be assessed by withheld portions of the data (Phillips et al., 2006); v) the maximum number of background points was 10,000 (over 25,988 available) as number of background points greater than 10,000 does not improve the predictive ability of the model (Phillips and Dudík, 2008). The performance of each MaxEnt model was assessed using the AUC (area under the receiver operating characteristic curve) threshold-independent metric, which assesses model discriminatory power by comparing model sensitivity (i.e., true positives) against model 1-specificity (false positives) from a set of test data (Phillips et al., 2006). The AUC value provides a threshold-independent metric of overall accuracy, and ranges between 0 and 1. According to the classification proposed by Swets (1998) for the interpretation of AUC value, models with values from 0.7 higher are considered those with good discrimination ability (0.7–0.8: moderate discrimination; 0.8–0.9 good discrimination; 0.9–1: excellent discrimination). To illustrate how much each variable contributed to the MaxEnt run, we obtained alternative estimates of variable importance for our models by conducting a Jackknife analysis. This technique was realized in two stages: 1) considering only one variable at a time and generating the corresponding model, it was possible to evaluate the contribution (gain) of each variable with respect to the whole ensemble of variables; 2) excluding one variable at a time and generating the corresponding model with the remaining variables, it was possible to evaluate the effects of the lack of the selected variable on the model based on the set of overall variables. To evaluate dolphin habitat suitability based on model results, we created maps from the logistic output for each monthly, yearly and total averaged distribution predicted by MaxEnt. The likelihood of dolphin occurrence was represented in five classes of equal size (very low, low, moderate, high and very high) for a more immediate

Table 2

Descriptive statistic of the environmental predictors as a function of month and year.

Seasonal variables	SST (°C)				CHL- <i>a</i> (mg/m ³)			
	Min	Max	Mean	SD	Min	Max	Mean	SD
2005	24.816	25.156	25.024	0.060	0.074	0.091	0.083	0.004
2006	25.410	25.880	25.726	0.075	0.073	0.087	0.079	0.003
2007	25.664	26.016	25.834	0.089	0.072	0.084	0.078	0.002
2008	25.301	25.617	25.468	0.049	0.066	0.078	0.072	0.002
2009	25.796	26.110	25.950	0.074	0.070	0.087	0.076	0.003
May	19.232	19.985	19.508	0.105	0.118	0.139	0.128	0.004
Jun	22.059	22.709	22.463	0.125	0.094	0.108	0.101	0.002
Jul	25.856	26.148	26.005	0.063	0.066	0.083	0.073	0.004
Aug	26.785	27.049	26.925	0.055	0.062	0.071	0.065	0.001
Sept	26.183	26.462	26.338	0.057	0.068	0.087	0.077	0.004
Oct	23.972	24.332	24.133	0.076	0.070	0.102	0.083	0.007
Fix variables	Depth (m)				Slope			
	Min	Max	Mean	SD	Min	Max	Mean	SD
	–154.5	–0.1	–55.6	24.5	0.0	12.6	0.8	1.05

Table 4

Percent contribution and permutation importance of relative contributions of the environmental variables to the MaxEnt model on a yearly base. Permutation importance is obtained through random permutation of the values of that variable on training presence and background data.

Variable	Percent contribution %						Permutation importance					
	May	Jun	Jul	Aug	Sept	Oct	May	Jun	Jul	Aug	Sept	Oct
Depth	0	0.4	8	2.7	0.3	0	0	0.5	20	3.9	1.4	0
Distance to coast	33.5	82.8	65.9	6.6	77.5	67.7	69.7	88.7	70.2	3.9	83	86.6
Slope	11.2	3.9	4.6	5.1	2.2	0.2	18	3.7	2.9	0.9	2.5	0.1
Aspect	16	7.3	4.6	2	12.2	9.7	5.4	1.9	2.9	1	9.8	3.8
Stt	7.2	3.5	0.4	6.2	7	20.2	3.1	3.8	0.2	6.1	1.9	8.1
Chl	32.2	2.1	16.5	77.4	0.8	2.1	3.8	1.3	4.9	84.2	1.4	1.5

interpretation of the maps. For the localization of the SAC, the recommendations for selection criteria for SAC (European Commission, 2011) was followed. The boundaries of the SAC were designed in order to include all the cells that had a value of likelihood of dolphin occurrence equal to or higher than 0.2 in at least one of the time periods analyzed.

3. Results

Despite the attempt to cover the area homogeneously, the southern sector accounted for 62% of the total sampling effort compared to 38% of the northern sector. This is mainly due to the position of the harbour, in the southern part of the island, and to the strongest wind from the northwest which reduced the possibility of navigating more frequently in the northern sector of the island. MaxEnt models obtained AUC values larger than 0.8 indicating that they were accurate in the prediction of dolphin occurrence and habitat suitability (Table 3), with only two partial exceptions (May and June; AUC > 0.75). The most important contributing variable (Tables 4 and 5, Fig. 3) to the models was the distance to the coast throughout all study periods, with only one exception (August). The highest logistic probability for finding dolphins was between 700 and 1370 m from the coast; later, the probability decreased rapidly up to 0.5 at 4500 m, 0.2 at 8300 m, reaching approximately 0 going over 11,000 m up to 23,000 m (Fig. 2a). While these extension ranges were constant year to year, they seemed to change at smaller temporal scales (months): the dolphin occurrence probability at shorter distances from the coast decreased from June to September (Fig. 5). Slope, aspect and depth were relatively weak predictors (Fig. 3). Apart from few exceptions (September, 2007 and 2008), ROC showed that the logistic probability of finding dolphins was larger at a depth between 20 and 60 m and rapidly decreased at lower or higher depth (Fig. 2b). The probability of occurrence for the whole period (2005–2009) increased with a slope higher than 4° (Fig. 2c), even though this pattern was not constant and changed in different years and months. While SST was a weak predictor (Tables 4 and 5; Fig. 3), overall Chl-a efficiently collected a large quota of percentage contribution in explaining dolphin occurrence above all during high primary productivity periods (Tables 4 and 5).

Within the study area (992 km²), the area where dolphin occurrence was higher than 0.2 was about 350 km² (35.6%), throughout the study period with small annual changes (Fig. 4). The area where it was possible to find dolphins with the highest probability (from 0.6 to 1.0) was small, and ranged from about 40 to 70 km² (on average 58.2 km²). The area associated with the highest probability was always smaller than 10 km². The boundaries of the SAC were designed to comprise all the cells with a likelihood of dolphin occurrence >0.2 for a total area of 710 km², corresponding to 71% of the whole study area (Fig. 6) (see Table 6).

4. Discussion

4.1. Model considerations

There has been a great debate regarding the performance of statistical-correlative SDMs in terms of model predictive power (i.e., the so called model skill, the degree of correspondence between model predictions and field observations) and stationarity (i.e., the ability of a model generated from data collected at one place/time to predict processes at another place/time). Nevertheless, this class of SDMs is considered important in designing future management strategies. We are aware that our modelling exercise is indeed not lacking in limitations. Some common issues derive from sample size, spatial scale and nature of environmental datasets, which are all capable of influencing the accuracy of the MaxEnt algorithms (Elith et al., 2006). For instance, an insufficient occurrence of sampling localities in the model building process and biased sampling effort can reduce the model skill (Phillips et al., 2006, 2009). To reduce the effect of such issues, in the present study, the winter months were excluded from the analysis due to the small number of sightings and the reduced sampling effort. The non-homogeneous distribution of the sampling effort around the island (less intense in the farther northern part) may increase the risk of bias. To have a greater control over this sample selection bias (Phillips et al., 2009), some authors have suggested gaining information to discriminate among environmentally unsuitable and under-sampled areas (Clements et al., 2012). Here, we did not apply the methods suggested to reduce sample selection bias (Phillips

Table 5

Percent contribution and permutation importance of relative contributions of the environmental variables to the MaxEnt model on a monthly base. Permutation importance is obtained through random permutation of the values of that variable on training presence and background data.

Variable	Percent contribution %						Permutation importance					
	2005	2006	2007	2008	2009	2005–09	2005	2006	2007	2008	2009	2005–09
Depth	10.3	1.5	1.2	4.8	0.5	5.9	22.1	1.9	6.4	10.9	1.1	8.6
Distance to coast	68.3	84.4	67.6	54.6	71.3	76.1	64.3	87.8	80.2	75.7	80.9	85.5
Slope	3.1	5.5	4.5	1.3	10.8	5.6	2.2	4.7	0.8	1.6	1.5	1.1
Aspect	14.2	4.6	11.8	1	4.3	1.5	7.3	3.1	7.4	1	3.7	0.3
Stt	1.2	1.5	14.5	1.6	13	8.3	3.3	1.1	5.1	0.3	13.1	3.9
Chl	2.9	2.5	0.5	36.7	0.1	2.6	0.8	1.9	0	10.6	0.3	0.3

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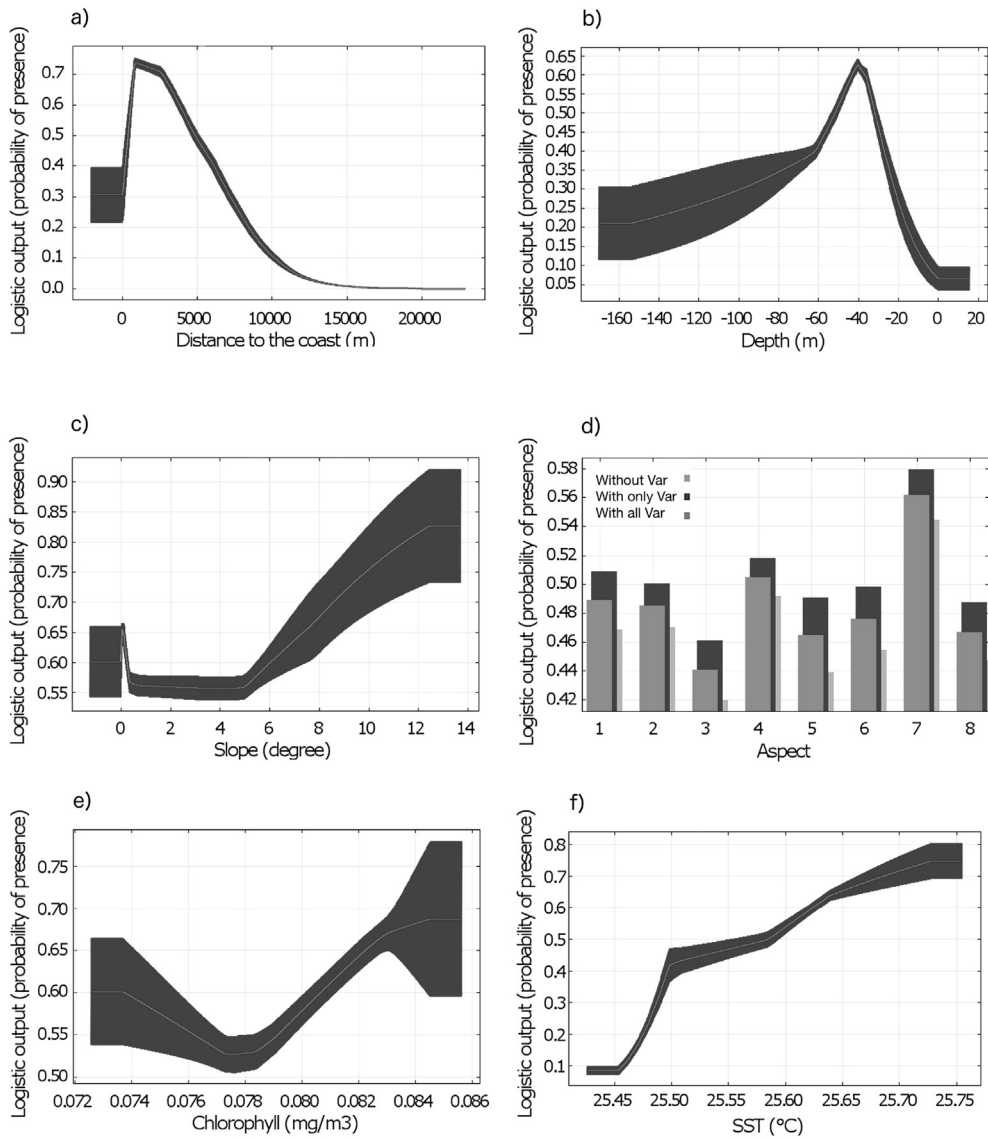


Fig. 2. Logistic output (probability of presence) as a function of the environmental predictors for the entire period (2005–2009).

et al., 2009; Fourcade et al., 2014) for two reasons: i) a lower probability of occurrence of animals in the northern part of the island was evident in all the investigated periods, even those in which the sampling effort in both sectors, North and South, were similar; ii) a greater likelihood of occurrence of animals in the southern part of the island was not considered as generating an

implicit modelling artefact, and the same result was found in many other studies performed with different methods (Azzolin et al., 2007; Pulcini et al., 2010). SDMs may be influenced by geographical bias in the sampling points used to train models (Costa et al., 2009). In the case of dolphins, sightings associated with trawlers or other fishing activities can generate geographically biased

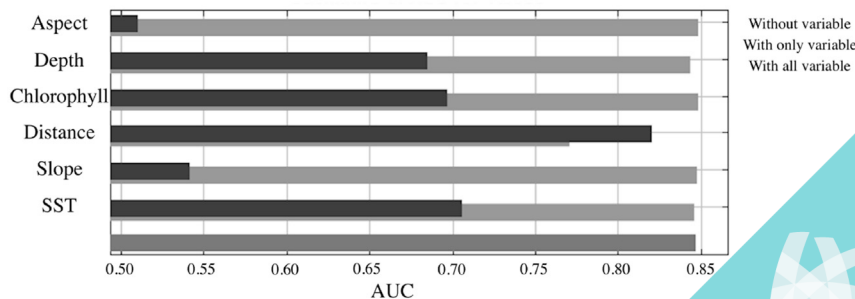


Fig. 3. Outputs of the Jackknife analysis for the entire period (2005–2009).



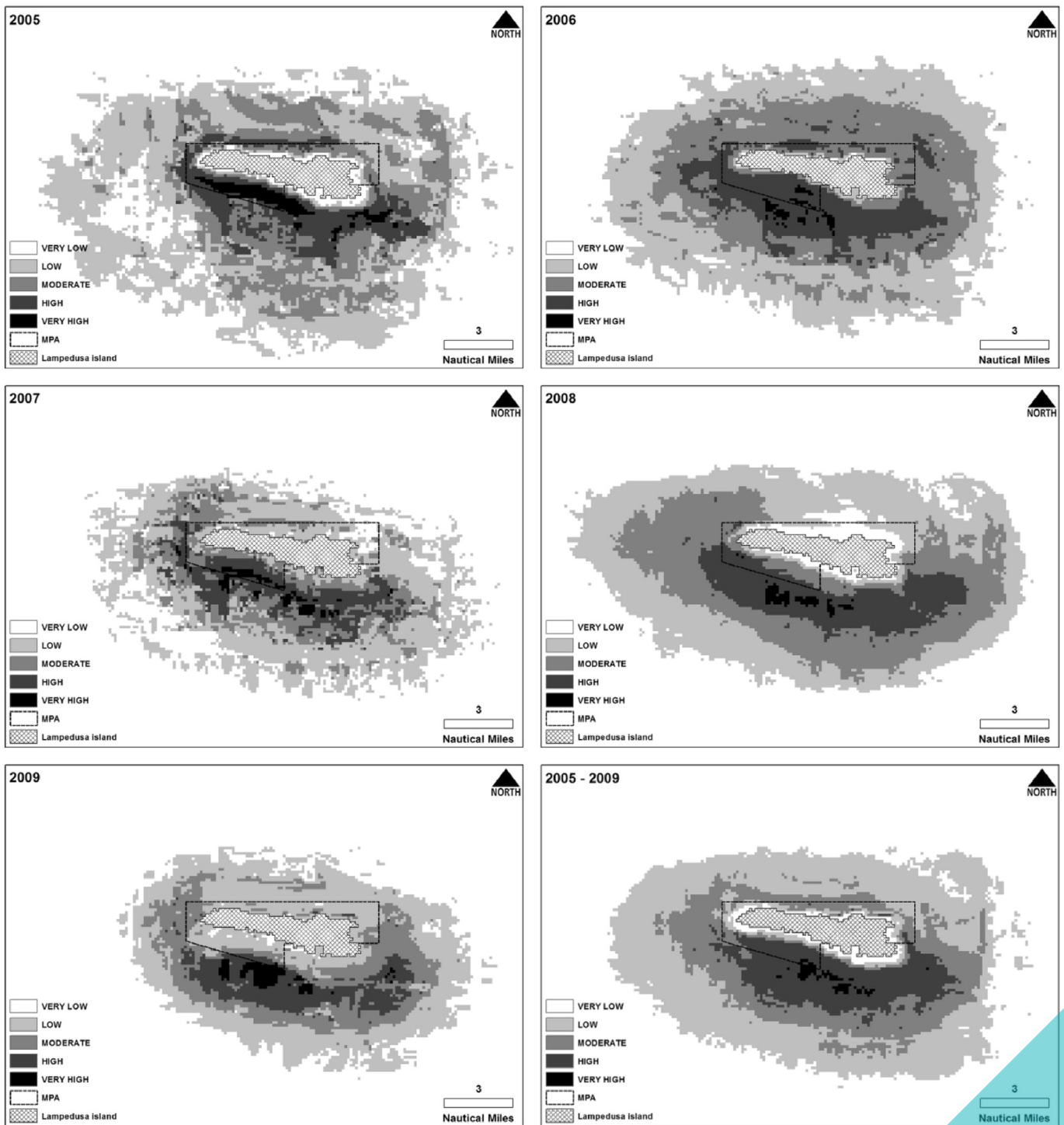


Fig. 4. Likelihood of occurrence of *T. truncatus* as a function of year.

distributional data with respect to that gained through a truly random distribution. This may generate a less accurate prediction of dolphin occurrence. However, here, we adopted a random sampling design which was not specifically constrained by the presence of trawlers or fishing nets. Finally, we were aware that during the phase of the creation of predictor layers, the modelling exercise required a process of averaging and interpolation of the environmental data and that this may influence the actual spatial and temporal variation in the environmental conditions. The

limited set of predictors chosen for this type of study certainly cannot encapsulate all potential factors that could influence the spatial distribution of dolphins (Pitchford et al., 2014). As a consequence, we tried to soften this possible interference by proposing an interpretation of our data in terms of the likelihood of occurrence within the range of the mean environmental conditions. In our study, as an example, information about the local sedimentary characteristics or human pressure, in terms of fishing and sea-related tourism, may increase the accuracy by identifying

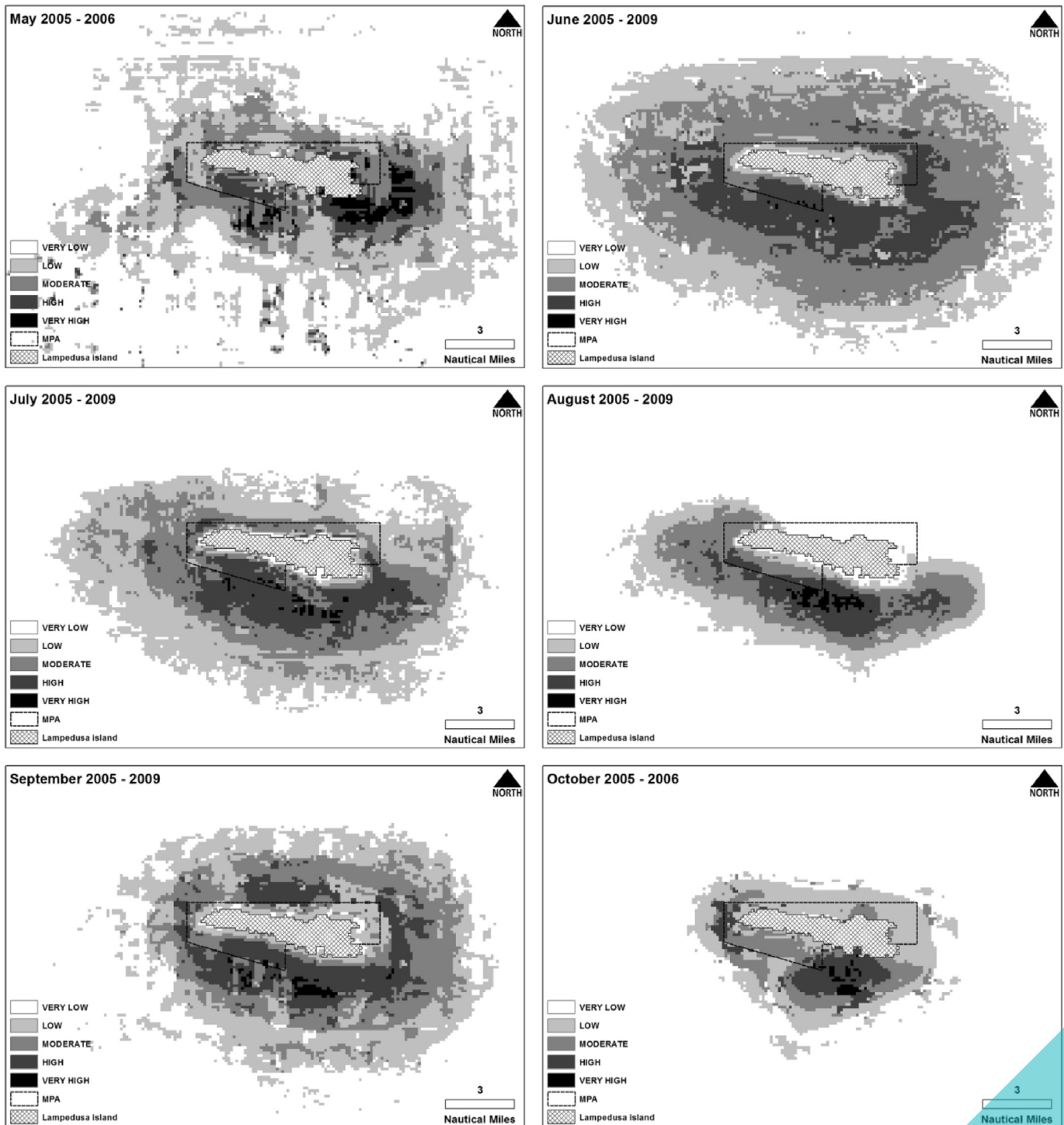


Fig. 5. Likelihood of occurrence of *T. truncatus* as a function of month.

associational causes between dolphin occurrence and sites.

4.2. Dolphin habitat preference

The distribution of a species can be explained in terms of a trade-off between benefits met in a certain habitat and costs deriving from the exposure to risks. Dolphins, like all other animals, increase their benefits by addressing behavioral strategies for staying where the likelihood of prey detection may be higher and

the risk of exposure may be lower. Human activities may increase risks as already highlighted in other studies (Allen and Read, 2000; Davis et al., 2002; La Manna et al., 2013; Marini et al., 2014) showing that dolphin habitat preferences tend to optimize the compromise between hydrological and morphological factors interacting with the disturbance effect of human presence.

In this study, MaxEnt offered a great opportunity to weigh the contribution of morphological and oceanographic factors when studying *T. truncatus* habitat preference within a geographic area

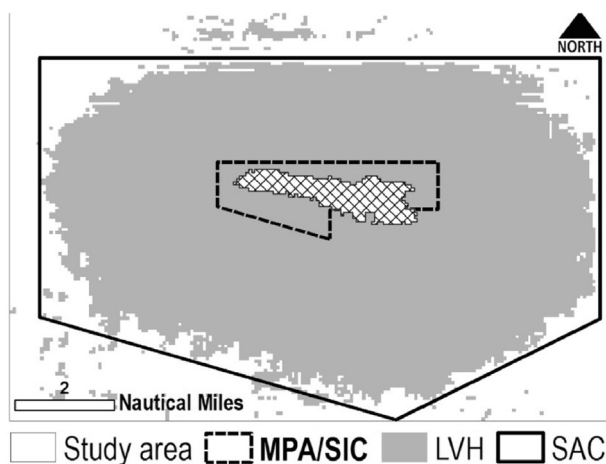


Fig. 6. Proposed SAC for *T. truncatus*. LVH = likelihood of dolphin occurrence from low to very high (0.2–1).

considered a biodiversity hot spot in the Southern Mediterranean Sea (Goffredo and Dubinsky, 2013). Lampedusa dolphins were tightly associated to the most coastal part of the island, which is also the most congested one in terms of boat traffic and related boat noise (La Manna et al., 2010, 2014). The factor first selected by our Jackknife analysis was the distance to the coast, which seems to be a very good predictor for dolphin occurrence. The area with the highest likelihood of dolphin occurrence was between 700 m and 1370 m from the coastline, in those sites where water column depth did not exceed 60 m. In Lampedusa, what seems more important for *T. truncatus* is the shallowness of its feeding grounds, as they often host complex and rich food webs such as those associated with rocky reef and seagrass beds (Lloret et al., 2002). Dolphins seem to spend as much time as possible close to those areas, as it increases their likelihood of finding preferential (demersal) prey (Demestre et al., 2000; Bearzi et al., 2008). This result partially contrasts with other data reporting that this species may also exploit deeper sea sites, between 100 m and 400 m (Canadas et al., 2002; Azzellino et al., 2008, 2012; Marini et al., 2014). The reason for this discrepancy should be further investigated, although site-specific geo-morphological factors combined with the geographical segregation of Lampedusa from the rest of the continental shelf waters may provide a plausible explanation.

The preference of *T. truncatus* for the shallower portion of the continental shelf showed a monthly pattern. The reduced likelihood of dolphin occurrence in area nearest to the coast during summer, when the boat traffic usually reaches the highest level (La Manna et al., 2010), could demonstrate that the presence of

dolphins is constrained also by disturbance factors such as boat traffic and the consequent effect of displacement (La Manna et al., 2013). Boat traffic is recognized as one of the major sources of disturbance in marine ecosystems (Abdulla and Linden, 2008) and the characteristics of disturbance (in terms of intensity, frequency and duration, sensu Miller et al., 2011) deeply affect the amount of time dolphins spend in a certain area (La Manna et al., 2013, 2014). Nevertheless, failing to include specific data on boat traffic may be a source of modelling bias that needs to be further clarified.

Slope and aspect, usually used to describe local factors such as hydrodynamics and light irradiance affecting primary producers, were poor predictors. This is consistent with other studies (Gomez et al., 2008; Marini et al., 2014). In contrast, Chl-*a*, the most used proxy for local primary production in open-sea waters and close to coastal areas (e.g. Sarà et al., 2011), was the second most important predictor of likelihood of dolphin occurrence, especially in certain periods. Chl-*a* is not able *per se* to drive dolphin distribution, but it works as a good proxy for other bio-ecological factors (Moure et al., 2012) involved in their feeding preference, such as the distribution of zooplankton and indirectly of zooplankton fish. While no extensive data exists to demonstrate broadness of the trophic spectrum available to *T. truncatus* in the waters surrounding Lampedusa, overall Mediterranean bottlenose dolphins seem to optimize where they mainly rely on demersal prey (Bearzi et al., 2008). Thus, even though there is an indirect link between primary biomass (as expressed by Chl-*a*) and dolphin occurrence (mediated by at least two or three steps of their food web), satellite Chl-*a* seems useful in seeking and identifying hot spots where dolphins may concentrate their presence. This could be strategic in Marine Spatial Planning actions when designing monitoring plans in order to predict the distribution of marine mammals. The same was not true for SST, which, in the present study, weakly predicted the probability of dolphin occurrence with the exception of one of the coldest months (October) and the hottest years (2007 and 2009). The weak correlation between SST and dolphin occurrence should not be surprising, as marine mammals are homeotherms. However, some stronger correlations (as in October and in 2007 and 2009) can sometimes emerge as SST is the most important effector of trophic dynamics of oceanic marine food webs, which are essentially based on ectotherms (from phytoplankton to fish). Thus, MaxEnt was able to capture the effect of SST only in some periods, when the link between dolphin occurrence and SST was most likely stronger.

5. Conclusion

Our modelling effort indirectly increased our understanding of how natural and human factors may interact in determining the habitat preference of *T. truncatus*. This aspect is crucial (Ingram and

Table 6

Area (in km) associated with classes of probability of dolphin occurrence as a function of year and month.

Period	Very high (%)		High (%)		Moderate (%)		Low (%)		Very low (%)	
2005	9.81	1.0%	46.09	4.6%	111.97	11.3%	222.81	22.5%	601.71	60.6%
2006	3.62	0.4%	65.41	6.6%	148.34	14.9%	191.98	19.3%	583.04	58.8%
2007	5.84	0.6%	38.50	3.9%	63.51	6.4%	153.84	15.5%	730.70	73.6%
2008	3.93	0.4%	56.83	5.7%	129.08	13.0%	183.51	18.5%	619.04	62.4%
2009	6.22	0.6%	35.18	3.5%	71.34	7.2%	150.07	15.1%	729.58	73.5%
2005–2009	3.55	0.4%	54.62	5.5%	91.05	9.2%	203.73	20.5%	639.44	64.4%
May 2005–2006	11.00	1.1%	34.25	3.5%	83.63	8.4%	206.03	20.8%	657.48	66.3%
Jun 2005–2009	0.50	0.1%	85.62	8.6%	213.57	21.5%	220.32	22.2%	472.38	47.6%
Jul 2005–2009	2.71	0.3%	53.47	5.4%	103.27	10.4%	182.13	18.4%	650.81	65.6%
Ago 2005–2009	4.16	0.4%	30.14	3.0%	62.98	6.3%	62.98	6.7%	829.00	83.5%
Sept 2005–2009	3.93	0.4%	63.92	6.4%	111.92	11.3%	158.82	16.0%	653.80	65.9%
Oct 2005–2006	2.52	0.3%	20.50	2.1%	32.50	3.3%	72.40	7.3%	864.47	87.1%

Rogan, 2002) to the planning and management of the conservation of the species under the Environmental Directives worldwide.

Present results may be well suited in the context of Marine Spatial Planning (MSP). MSP is rapidly gaining momentum (Stamoulis and Delevaux, 2015) and represents a powerful tool for detecting when and where to initiate and undertake human activities at sea in order to ensure sustainability and economic efficiency. MPAs and SACs can play an important role, as they are arguably the most powerful tools available to date for containing the ever-increasing over-exploitation of marine resources, the degradation of marine habitats (Agardy et al., 2011), and for the maintenance and restoration of key species populations. Nevertheless, MPAs/SACs may fail in their scope when the initial size and design are not dynamically adapted to meet ecological principles and when consequent management measures are not properly planned (Mangano et al., 2015). In the waters around Lampedusa, the boundaries of the MPA and the SCI were initially designed (some decades ago) without calibrating their size and position in the light of *T. truncatus* distributional range around the island. The semi-quantitative only-presence information provided here by MaxEnt seems sufficiently reliable in predicting the distribution of *T. truncatus* around Lampedusa. Thus, our findings allow us to suggest a SAC for bottlenose dolphins of about 710 km² around Lampedusa. SAC proposal was not only based on dolphin encounter rate data (Azzolin et al., 2007), but exploited valuable information based on the link between relative abundance and environmental covariates. This well responds to the request of high quality spatial data and analysis as first step in making the practice of MSP possible (Collie et al., 2013).

Datasets such as those found in this study may help in the accomplishment of the second MSP step which relies on the assessment of human activities in the marine eco-space. Lampedusa local population, like those living on many geographically segregated islands worldwide, bases its local economy on both fishing and tourism, with dolphin-watching often representing one among the most important components of the annual economic income. Thus, since the modern concept of sustainability is grounded on the assumption that ecological, economic and social needs (United Nations General Assembly, 1987) should all be satisfied simultaneously, a proper management plan at these latitudes should consider the SAC for dolphins in order to design and periodically adjust (dynamically) the local exploitation level. This would permit to reach a solution regarding two apparently contrasting needs - biodiversity protection and economic development. Nevertheless, a coordination at the regional level among many institutions belonging to cross-border countries is necessary for increasing the efficiency of management measures. In the end, an integrated action over larger spatial scales (a portion of the Basin rather than only one island) represents the fundamental step for the correct use of Marine Spatial Planning. In fact, tailoring MPAs and SACs to local conditions may individually solve localized, species-specific, or habitat-specific conservation problems, but the total sum of MPAs/SACs at the regional level within the context of a wider strategic marine plan is the only path to increasing the effectiveness of the ecosystem-based management practices (Agardy et al., 2011) at larger spatial scale. Thus this results should be interpreted in the perspective of best practices, practices that, once verified their applicability at local scale, can be exported on a broader geographical scale.

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