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Seamounts as hot-spots of large pelagic aggregations

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Abstract

The distribution of four top predators in the Tyrrhenian Sea, a sub-basin of the Mediterranean Sea, was investigated by means of random forest regression considering depth, distance from the coast, seafloor slope, and distance from seamounts as habitat descriptors on a 2x2–nautical mile regular grid. RF results are processed to estimate variable importance and model performance. Random forest architecture reached optimal sensitivity and specificity, thus providing a consistent support tool for identifying suitable habitats. The considered species are characterized as having patched suitable habitats with a number of hot-spot areas where the different species' habitats overlap. These hot-spot areas' locations correspond to those of specific seamounts identifying the attraction effect of these topographic structures. The mean features typifying the most attractive seamounts are investigated and found to be shallow peak and base depths but wide base area and high relative elevation.

Keywords: Stenella coeruleoalba; Thunnus thynnus; Puffinus yelkouan; Caretta caretta; Random forest.

Introduction

Seamounts (SMs) are ecologically important seafloor structures that may have different origins and are features of all the world's high seas (Würtz & Rovere, 2015). They may be distinguished as hot-spots of biodiversity, greatly affecting the productivity of offshore ecosystems and the distribution of pelagic top predators (Morato *et al.,* 2010). SMs are generally not ecologically isolated or island-like systems, and they can have species assemblages similar to those found in adjacent deep-sea habitats but have a different structure in terms of the abundance or frequency of species (McClain, 2007; Clark *et al.,* 2010; Würtz & Rovere, 2015). In the last several years, increasing human pressures on SMs (in particular, fishing pressure) have made clear the conservation needs for seamounts (e.g., Probert *et al.,* 2007), including the need for a protected area system to protect seamount biodiversity and ecosystem structure and function (e.g., Johnston & Santillo, 2004; George *et al.,* 2007). In this framework, seamounts have been recently proposed as possible Ecologically or Biologically Significant Marine Areas (EBSAs) since many of the proposed indicators for the identification of EBSAs are extremely relevant for SMs (Dunstan *et al.,* 2011; Clark *et al.,* 2014).

In an open ocean context, seamounts and their effect on the pelagic domain have already been described (e.g., Kaschner, 2008; Morato *et al.,* 2008, 2010; Kvile *et al.,* 2014). It was demonstrated that seamounts may attract pelagic visitors, which aggregate within a variable distance (5–15 nautical miles) from the summit depending on the seamount's characteristics (peak depth, elevation, circulation, etc.) and on the species. While one recent study found a high concentration of seamounts (227 structures) in the Mediterranean Sea basin (Würtz & Rovere, 2015), the potential attracting effect of seamounts on pelagic fauna in this region is poorly investigated. In particular, Fiori *et al.* (2015) detected an attraction effect of seamounts on the distribution of top pelagic predators, identifying a role played by seamounts in pooling a number of different species in a narrow range surrounding Mediterranean seamounts. Still, nothing is known about the seamount characteristics that may influence the attraction effect and that can make a specific seamount more important for the pelagic domain than others. With the aim to fill this gap, the distribution of four pelagic top predators –*Stenella coeruleoalba* (Meyen, 1833), *Thunnus thynnus* (Linnaeus, 1758), *Puffinus yelkouan* (Acerbi, 1827), and *Caretta caretta* (Linnaeus, 1758)– was investigated.

The striped dolphin (*Stenella coeruleoalba*) is a small dolphin with a Mediterranean subpopulation. This subpopulation has been subject to a number of threats that, cumulatively, have reduced its size (Bortolotto *et al.,* 1992; Aguilar & Raga, 1993). It is listed as vulnerable on the

IUCN Mediterranean red list (IUCN, 2016). This Mediterranean dolphin prefers open sea from the continental slope to offshore, highly productive waters (Notarbartolo di Sciara *et al.,* 1993; Forcada *et al.,* 1994; Frantzis *et al.,* 2003; Gannier, 2005; Panigada *et al.,* 2008). The striped dolphin's distribution is related to the areas typified by a permanent system of upwelling currents, which support particularly high levels of primary productivity. These zones represent the feeding areas for this species, which feeds on a range of mesopelagic fish, cephalopods, and, to a lesser extent, planktonic crustaceans (Würtz & Marrale, 1993; Blanco *et al.,* 1995; Meotti & Podestà, 1997; Panigada *et al.,* 2008).

Thunnus thynnus's (bluefin tuna) population has been reported to be declining since the 1960s. In fact, bluefin tuna have been overfished by the industrial fisheries of North America, Europe, and Japan (Block *et al.,* 2001; Chase, 2002). Because of this continuous decline in population and the presence of a number of pressures (mainly fishing activity), *T. thynnus* is listed as endangered on the IUCN Red List (IUCN, 2016). Bluefin tuna are present in the Mediterranean basin and the Black Sea. Their reproduction areas are various throughout the basin (Oray & Karakulak, 2005). The Mediterranean stock lays eggs in the Mediterranean basin between May and August. The tuna's diet consists of fish, especially sardines, but it also feeds on pelagic cephalopods (Battaglia *et al.,* 2013).

Puffinus yelkouan (Mediterranean shearwater) is on the IUCN Red List as vulnerable (IUCN, 2016). This is because of a rapid population decline caused by extremely low breeding success due to predation by other species and adult survival owing to fisheries' bycatch. This species is endemic of the Mediterranean basin, but an accurate distribution assessment is still lacking (Bourgeois and Vidal, 2008). The main reproductive sites are concentrated in the east and central sectors of the Mediterranean basin, mainly on rocky islands and coastal cliffs. Foraging sites are mainly concentrated over muddy substrates in waters 100–150 meters deep (Cafaro *et al.,* 2016). When not engaged in nesting and breeding, the population is widely dispersed in the Mediterranean and Black Sea basins, and it is often sighted in large flights (Snow & Perrins, 1998).

Caretta caretta (loggerhead sea turtle) is a species with a Mediterranean subpopulation whose distribution covers the entire basin, being mainly present in the eastern sector. Like most sea turtles, *C. caretta* is highly migratory and uses a wide range of broadly separated localities and habitats during its lifetime (Bolten & Witherington, 2003). This species nests on insular and peninsular sandy beaches, and upon leaving the nesting beach, it begins a pelagic phase. Upon attaining sexual maturity, it undertakes breeding migrations between foraging grounds and nesting areas (Schroeder *et al.,* 2003; Hays *et al.,* 2010). *C. caretta's* Mediterranean subpopulation is classified by the IUCN Red List under the category of "least concern" (IUCN, 2016).

The distributions of top predators are expected to act as indicators of an ecosystem's status and performance (Boyd *et al.,* 2006; Würtz, 2010), allowing the identification of highly productive areas in need of protection (Alessi & Fiori, 2014; Cafaro *et al.,* 2016). From this perspective, the role played by seamounts may reveal the importance of these topographic structures in the wider context of the Mediterranean basin.

The distribution of the considered species in the Tyrrhenian basin (NW sector of the Mediterranean Sea) was investigated by means of random forest regression, taking into consideration several morphologic parameters of the basin together with the presence of the seamounts.

In the last few decades, the advances in regression analyses have allowed the development of more and more reliable ecological models, increasing understanding of ecological systems (Guisan *et al.,* 2002). More recently, regression based on the random forest technique (Breiman, 2001) was applied and compared to other regression techniques and proved to be more reliable and accurate in predicting habitat distribution (Cutler *et al.,* 2007; Virkkala *et al.,* 2010; Marini *et al.,* 2015; Carlucci *et al.,* 2016). In particular, recent developments in spatial modeling have made it possible to predict the presence/absence or the abundance of a species by means of a set of predictor variables, highlighting the relative importance of habitats (Baumgartner, 1997; Phillips *et al.,* 2006; Pitchford *et al.,* 2015; Redfern *et al.,* 2006; Thorne *et al.,* 2012; Carlucci *et al.,* 2018). These approaches are increasingly becoming essential to identify critical habitats in order to enhance the protection of threatened species, mostly in coastal areas where the potential for conflicts is high (Best *et al.,* 2012; Edren *et al.,* 2010).

The main targets of the research are (1) to determine the distribution of suitable habitats for the investigated top predator species, (2) to identify the role played by seamounts in shaping the distribution of top predators, (3) to investigate the seamounts' characteristics most appreciated by top predators, and (4) to discuss the importance of seamounts in terms of protection, conservation, and related management implications.

Materials and Methods

Study area

The study area covers the entire Tyrrhenian basin, a morphologically complex sea area of extensional tectonisms between Africa and Europe. From a geological perspective, the basin's formation happened in a very limited time frame, and one of the main consequences is the presence of a large number of seamounts in the basin. In this area, 64 different seamounts have been identified (Rovere *et al.,* 2015) (Table 1).

Morphological characteristics such as maximum and minimum depth, absolute and relative elevation, base area, and maximum and minimum slope were calculated for each seamount as reported in Table 2 and Figure 1, aiming at the identification of the influence of seamount topographic features on the attraction effect of pelagic species.

Table 1. Seamounts considered in this study.

Name	Lon	Lat	Peak depth	Base depth	Min slope	Max slope	Base area	Elevation	Relative elevation
			m	m			km²	m	
Aceste/Tiberio	11.52	38.42	120	800	13.7	137.6	38.9	680	0.85
Albano	12.06	41.36	250	590	35.2	71.2	5.5	340	0.58
Albatros/Cicerone	13.18	40.40	1390	2310	159.7	352.1	2.7	920	0.4
Alcione	15.30	39.27	920	1760	277.6	418.6	0.9	840	0.48
Anchise	12.82	38.69	510	1150	40.4	213.6	6.0	640	0.56
Augusto	12.50	39.13	1950	2250	74.4	246.0	1.3	300	0.13
Baronie/K	10.24	40.60	160	1320	23.0	308.5	15.9	1160	0.88
Cassinis	11.72	40.77	1090	1690	26.4	512.1	3.1	600	0.36
Catullo	12.92	39.36	2880	3200	71.5	366.6	1.9	320	0.1
Cialdi	10.60	41.85	300	1220	46.1	383.8	3.5	920	0.75
Cornacya	10.24	39.11	1240	1540	34.6	213.2	4.9	300	0.19
Cornaglia	10.65	39.70	1030	2530	82.0	370.9	8.0	1500	0.59
D'Ancona Ridge	12.12	39.93	2710	3330	69.8	351.2	3.3	620	0.19
De Marchi	12.26	40.23	2360	3400	79.1	499.8	3.7	1040	0.31
Diamante	15.30	39.66	400	710	152.4	248.2	0.6	310	0.44
Drepano	12.23	38.61	460	720	23.3	142.8	10.6	260	0.36
Enarete	14.00	38.64	320	1660	239.1	437.1	1.9	1340	0.81
Enea	11.74	39.44	2850	3230	44.4	447.5	3.3	380	0.12
Enotrio	15.34	39.50	290	750	69.7	305.1	2.1	460	0.61
Eolo	14.16	38.56	640	1370	83.3	253.2	2.8	730	0.53
Etruschi	10.37	41.67	310	700	27.1	115.8	5.6	390	0.56
Farfalla	12.48	40.44	2450	3150	54.3	327.5	4.0	700	0.22
Finale struct	14.16	38.30	800	1290	30.9	259.3	8.3	490	0.38
Flavio Gioia	13.05	40.04	2100	2910	81.8	438.1	3.5	810	0.28
G.Cesare/Caesar	11.45	38.62	1150	1620	42.2	167.5	5.7	470	0.29
Garibaldi/Glauco	13.79	39.11	1770	2380	220.9	467.8	3.0	610	0.26
Glabro	15.16	39.51	850	1200	77.6	398.5	1.1	350	0.29
Gortani	12.47	40.27	3110	3470	40.0	314.0	3.2	360	0.1
Ichnusa	9.58	38.75	190	970	22.6	114.2	21.8	780	0.8
Issel	13.66	39.68	1910	2660	30.2	344.6	7.6	750	0.28
Lametino 1	15.40	39.06	950	1820	292.0	417.4	0.7	870	0.48
Lametino 2	15.32	39.01	1370	2150	320.7	442.2	1.0	780	0.36
Lucrezio	13.25	38.98	2680	3320	81.6	353.4	1.8	640	0.19
Major	11.28	39.70	2060	2800	104.9	276.7	3.1	740	0.26
Marsili/Plinio	14.40	39.28	570	3180	92.5	233.6	12.2	2610	0.82
Marussi	10.56	40.61	1040	1530	61.9	542.8	2.7	490	0.32
Monte della Rondine	11.67	40.22	1950	2380	89.6	202.2	1.8	430	0.18
Orazio	13.42	39.33	3000	3340	26.0	166.4	11.9	340	0.1
Ovidio	15.47	39.56	240	380	6.4	197.5	36.0	140	0.37
Palinuro/Strabo	14.83	39.48	70	1580	62.7	312.1	12.7	1510	0.96
Pompeo	11.81	38.60	1040	1310	84.4	572.2	1.2	270	0.21
Poseidone	13.84	39.73	1640	2150	35.4	284.8	6.1	510	0.24
Prometeo	13.47	38.63	1830	2150	30.0	299.5	3.2	320	0.15
Quirra	10.32	39.32	890	1600	45.8	323.1	11.0	710	0.44

(continued)

Table 1 continued

Name	Lon	Lat	Peak depth	Base depth	Min slope	Max slope	Base area	Elevation	Relative elevation
			m	m			km^2	m	
Sallustio	10.92	39.76	2410	2740	31.6	389.9	4.9	330	0.12
San Vito Ridge	12.85	38.33	580	730	35.0	125.7	9.8	150	0.21
Sardinia	10.14	40.03	1190	1470	27.6	158.9	5.7	280	0.19
Scuso	12.55	38.27	50	300	32.1	123.9	5.7	250	0.83
Secchi/Adriano	11.70	40.45	1220	2430	98.0	285.2	13.1	1210	0.5
Sele	14.21	40.30	240	730	25.4	116.6	3.4	490	0.67
Selli	11.77	40.23	1980	2380	122.9	319.3	1.1	400	0.17
Sirene	13.92	40.26	660	1060	16.7	183.0	7.0	400	0.38
Sisifo	13.85	38.79	1080	2020	77.1	250.6	4.9	940	0.47
Solunto struct high	13.75	38.42	700	1330	23.8	85.4	20.5	630	0.47
Tacito	13.57	40.19	1150	1530	53.1	222.2	3.0	380	0.25
Tiberino	11.55	41.67	290	780	17.1	130.4	13.7	490	0.63
Tibullo	12.84	39.76	3070	3550	24.9	563.8	6.8	480	0.14
Tito Livio	10.91	39.35	2270	2670	30.2	403.8	6.3	400	0.15
Traiano	12.23	38.99	1920	2300	35.8	203.1	3.4	380	0.17
V.Emanuele/Magnaghi	11.78	39.91	1530	3150	111.0	306.5	8.4	1620	0.51
Vavilov	12.61	39.86	820	3160	131.5	377.7	5.0	2340	0.74
Vercelli	10.91	41.11	60	1010	53.0	395.4	9.8	950	0.94
Vespasiano	12.77	38.79	1530	1860	26.1	216.4	3.8	330	0.18
Virgilio	12.52	39.31	2650	3050	22.6	310.3	7.8	400	0.13

Table 2. Main features characterizing seamounts.

variable	calculation
peak depth	depth of the shallowest point of the seamount (Pd in Figure 1)
base depths	depth of the deepest isobath of the seamount (Bd in Figure 1)
elevation	difference between base and peak depths (Bd-Pd in Figure 1)
relative elevation	ratio between elevation and base depth ((Bd-Pd)/Bd in Figure 1)
base area	surface occupied by the deepest isobath of the seamount (grey area in top view Figure 1)
maximum slope	ratio between elevation and minimum distance from peak to base ((Bd-Pd)/md in Figure 1)
minimum slope	ratio between elevation and maximum distance from peak to base ((Bd-Pd)/Md in Figure 1)

Data collection

Two dedicated sampling campaigns were carried out during August 2013 and 2014. The sampling campaigns were carried out with a 15 m sailing boat with an 80.2 hp diesel outboard engine. Both campaigns followed a planned track developed to both cover the highest part of the basin and sample as many seamounts as possible. 3250 NM were covered overall, while 1620 NM were covered with an onboard crew actively engaged to detect animals' presence on the sea surface (hereinafter, on sighting effort). The remaining track was covered during night or with unfavorable sea state conditions without scanning the sea surface to detect animals' presence. This track was developed to cover both areas close to seamounts (33 seamounts were sampled by sailing above the seamount peak) and areas far from seamounts to get a full coverage of the range of influence of seamounts (Fig. 2).

A previous analysis regarding the distribution of track segments in relation to the distance from the closest seamount revealed that a wide range of distances from seamounts was covered (from 0 to 60 NM), with an average value of 20 NM (Fiori *et al.,* 2015).

During the navigation, track and sighting positions were recorded by Garmin eTrex® GPS and reported on a navigation form. The average cruising speed was maintained at 6 kn. Sighting effort was conducted only under Douglas sea state 3 (i.e., state of the sea: slight or

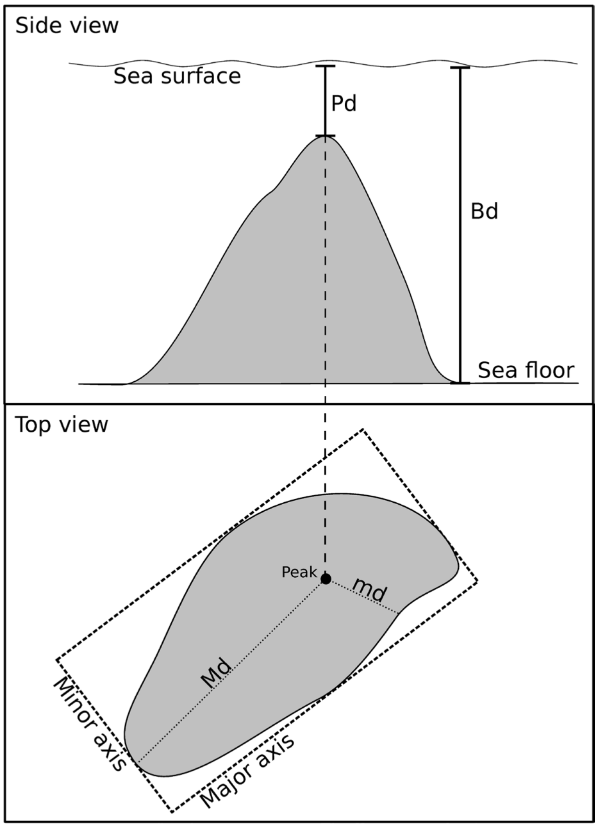

Fig. 1: Main physiographic characteristics of seamounts.

0.5–1.25 m wave height) or lower and during daytime (from 6:00 to 22:00). Visual surveys were conducted by four trained observers. Each observer continuously scanned a specific sector (0° to 90°, 90° to 180°, 180° to 270°, and 270° to 360°). A fifth researcher onboard was dedicated to recording the boat's track using a GPS device and noting details (e.g., species identification, group size, associations with other species, and behavior) when a sighting occurred. During sighting, the planned track was temporarily dropped, and animals were cautiously approached, aiming to clearly identify species and their abundances and main behaviors and to collect photographic documentation. As soon as all the identification procedures were completed, the boat was brought back on the planned track, and the sighting effort protocol was resumed.

The study area, covering the whole Tyrrhenian basin, was divided into a regular grid with 9.955 cells 2x2 NM wide. Four explanatory variables were calculated for each cell: mean depth, distance of the cell center from the coast (calculated as the minimum geodetic distance from the coastline considering both mainland and islands), mean seafloor slope, and distance of the cell's center from the nearest seamount (calculated as the geodetic distance from the nearest seamount peak).

Finally, each cell was identified, for each considered taxon, as a presence cell if at least one sighting occurred during two sampling campaigns (as an absence cell otherwise).

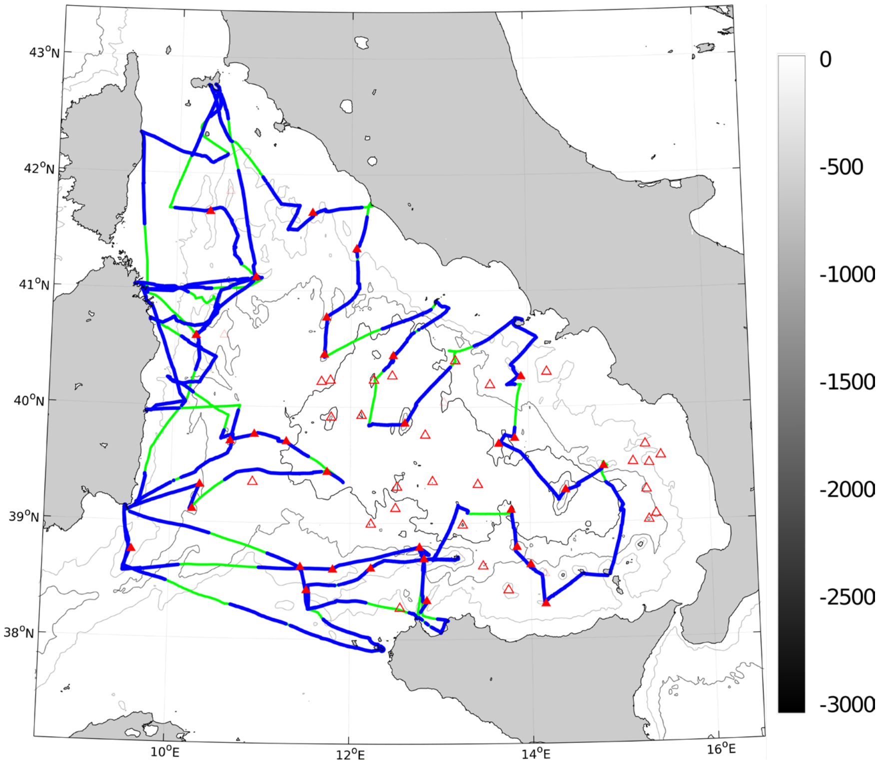

Fig. 2: Track covered during 2013 and 2014 campaigns. Blue lines show tracks covered on active sighting effort (daytime, good weather conditions). Green lines show tracks covered off sighting effort. Seamounts are identified by red triangles. Filled triangles identify sampled seamounts. Gray contours represent depth in meters.

Model development

Random forests (RF; Breiman, 2001) are a combination of tree predictors such that each tree depends on the values of a random vector sampled independently and with the same distribution for all trees in the forest. This is achieved by two means: (a) a random selection of explanatory variables is chosen to increase each tree, and (b) each tree is based on a different random data subset, created by bootstrapping (Efron, 1979). Finally, the optimal "splitting" in comparison with real data is identified and selected as a predictor. Therefore, the number of trees needs to be set sufficiently high (1200 in this case) to guarantee a reliable prediction with the lowest prediction error. Additionally, RF implicitly deals with the over-fitting issue as decision trees are fitted to random samples of the data and perform splits in random subsets of the variable space, while the regression rule is used to predict distribution on the whole dataset (Kehoe *et al.,* 2012). In this study, a model predicting presence probability was developed for each species, always considering the same four explanatory variables (depth, distance from the coast, slope, and distance from the nearest seamount). The most relevant variables were identified for each model. In particular, the importance of each explanatory variable was accounted for as the change in mean square error that was achieved by leaving the variable out of the model. After the most relevant variables have been identified, the next step is to attempt to understand the nature of the dependence of response variables on each explanatory variable. Partial dependence plots (Hastie *et al.,* 2001) are used to graphically characterize relationships between individual explanatory variables and predicted probabilities of presence obtained from RF.

Traditionally, approaches for modeling species distribution have relied on the collection of presence/absence data (Guisan & Zimmermann, 2000; Brotons *et al.,* 2004). However, these methods assume that the absence data are accurate. Obtaining reliable absence data for pelagic species is problematic. Due to the mobility of pelagic predators and their propensity to spend time underwater (and therefore undetectable to observers on the surface), there is always a degree of uncertainty associated with absence data. Recurrent samplings may reduce this uncertainty, but the separation of 'true' absences, where animals are actually absent, from 'false' absences, where animals are present but not detected, is difficult and leads to uncertainty when interpreting results (Hall, 2000; Martin *et al.,* 2005). Statistical adjustments to face this intrinsic uncertainty have been developed, and to this aim, in this study, we applied a correction already proposed in recent applications (Azzellino *et al.,* 2012; Fiori *et al.,* 2014; Marini *et al.,* 2015; Carlucci *et al.,* 2016) consisting of the selection of random sets of cells where absence was recorded equal to the number of presence cells.

Modeling and analysis procedures were implemented by means of the 'randomForest' package (Liaw and Wiener, 2002) in the "R" software package (a free software package for statistical computing). The final result of the model implementation is the estimation of the presence probability of each considered species in each cell of the regular grid covering the study area.

Model verification and identification of suitable habitats

Model performance was evaluated to verify the reliability of predictions. In particular, predicted values were compared to observed values, allowing the compilation of a confusion matrix (Stehman, 1997).

In addition, a set of metrics of model accuracy was calculated, including sensitivity and specificity. Sensitivity is calculated as the ratio between true presences (TP) and total presences (TP+FP), accounting for the probability that the model will correctly classify a presence. Specificity is computed as the ratio between true absences (TN) and total absences (TN+FN), measuring the probability that the model will correctly classify an absence.

Based on these values, the Matthews correlation coefficient (MCC; Matthews, 1975), a reduction of the Pearson correlation coefficient for binary variables (Baldi and Brunak, 2001), is considered a solid criterion of machine learning performance (Bhasin and Raghava, 2004; Chen *et al.,* 2004; Bao and Cui, 2005; Daliakopoulos *et al.,* 2017).

$$MCC = \frac{TP \times TN - FP \times FN}{\sqrt{(TN+FN)(TN+FP)(TP+FN)(TP+FP)}}$$

MCC is particularly useful for imbalanced datasets where the disparity between the numbers of presence and absence samples is significant.

The optimal cutoff probability value was selected by applying the Youden Index method (Fluss *et al.,* 2005) to the receiver operating characteristic (ROC) curve (Fielding & Bell, 1997). The ROC curve is obtained by plotting the true-positive rate (sensitivity) against the false-positive rate (specificity) for various cutoff values. In particular, the Youden Index method allows the determination of the optimal cutoff point using the maximum vertical distance of the ROC curve from the chance line (where false positive rate=true positive rate) (Hajian-Tilaki, 2013).

Once the optimal cutoff was identified, the suitable habitat areas (cells with probability prediction higher than cutoff) were identified and plotted on the study area.

Results

During the sampling campaigns, a total of 3250 NM were covered (2405 on sighting effort). A total of 686 sightings of pelagic predator species were recorded overall (Fig. 3).

The most frequently observed species was *Puffinus yelkouan* (298 sightings), followed by *Caretta caretta* (118 sightings) and *Stenella coeruleoalba* (75 sightings). Finally, *Thunnus thynnus* (48 sightings) was the species

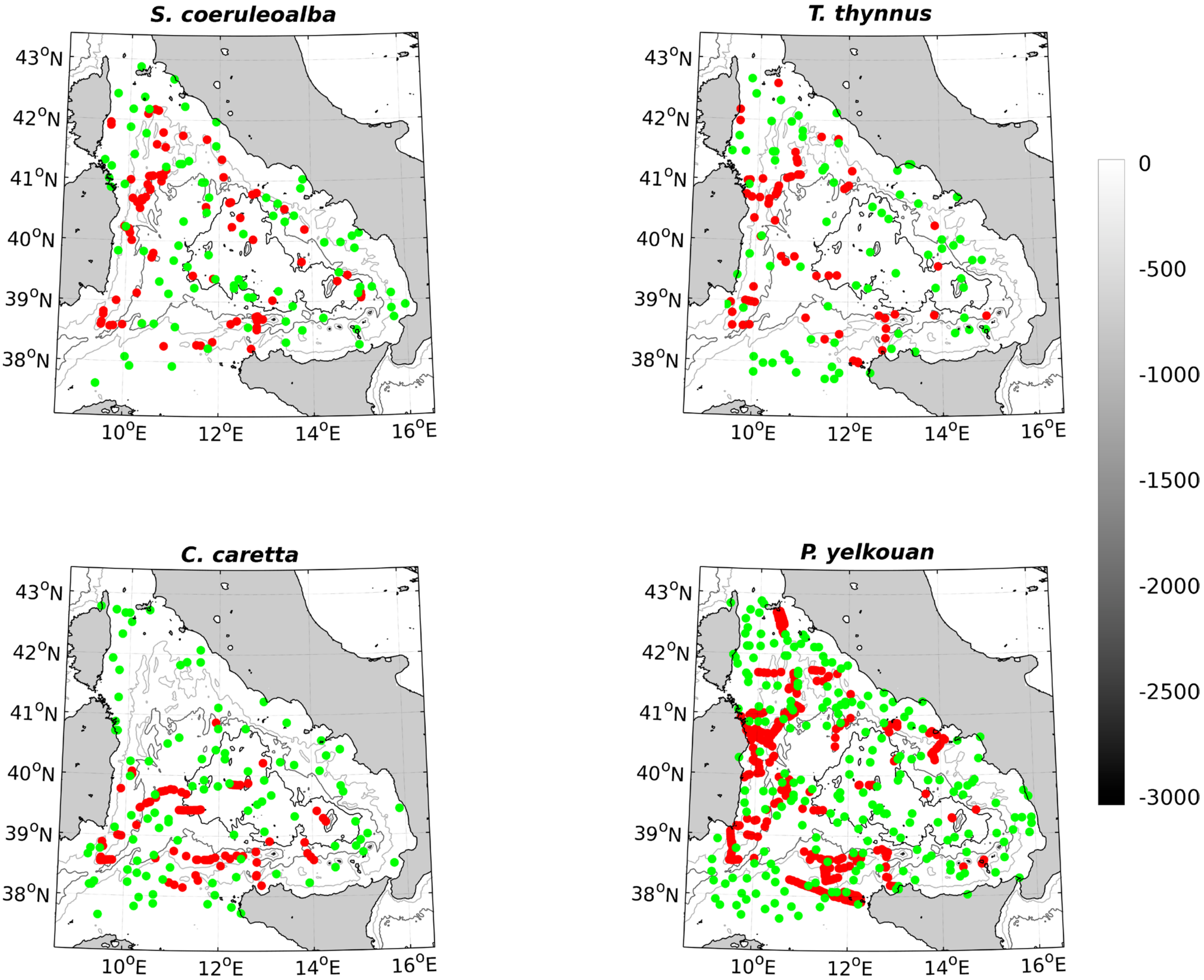

Fig. 3: Spatial distribution of sightings during 2013 and 2014 sampling campaigns. Red dots identify sightings; green dots are the real absences employed during model training. Gray contours represent depth in meters.

with the lowest number of sightings among those here considered.

Habitat use by species

S. coeruleoalba

Striped dolphin distribution is mainly driven by depth greater than 500 m and distance from seamount less than 25 km. Distance from coast displays a non-linear relationship, with the highest presence probabilities at distances between 50 and 80 km (Table 3, Fig. 4). Lower importance is shown by seafloor slope, whose value is not relevant in the determination of the striped dolphin's distribution in the Tyrrhenian Sea (Table 3). As shown in Table 4, the model had a higher sensitivity than specificity, indicating better performance in detecting presences than in detecting absences. The model's overall accuracy was 90% (Table 4). Striped dolphins' habitat preference was found to be widely distributed in the study area, with several patches of suitable habitat. A couple main areas are located between 500 and 1200 m depth off the northern Sicilian coast and east of the Bonifacio strait between Corsica and Sardinia (Fig. 5). Other suitable habitats were detected around Sardinia and in close proximity to a number of seamounts in the central part of the basin.

T. thynnus

RF regression identified first slope and the similar values of depth and distance from seamounts as mainly important for the distribution of *T. thynnus*. Distance from coast evidently has less effect in shaping the habitat (Table 3). The univariate partial dependence plots for *T. thynnus* (Fig. 6) display presence probabilities linked to increasing seafloor slope, depth between 1000 and 2000 m, and distance from seamounts lower than 50 km.

The model had a lower sensitivity than that for the

Table 3. Explanatory variables' importance for each considered species. Mean decrease in accuracy (MDA) is a measure of the accuracy loss in case of exclusion of the variable from the analysis.

	Sightings	**Depth**		**Distance from coast**		**Slope**		**Distance from seamount**	
		MDA	**Rank**	**MDA**	**Rank**	**MDA**	**Rank**	**MDA**	**Rank**
S. coeruleoalba	75	33.2	1	20.3	3	7.6	4	24.8	2
T. thynnus	48	27.2	2	9.3	4	33.4	1	25.1	3
P. yelkouan	298	62.7	1	20.6	4	22.4	3	35.2	2
C. caretta	118	11.4	3	25.1	2	9.8	4	39.9	1

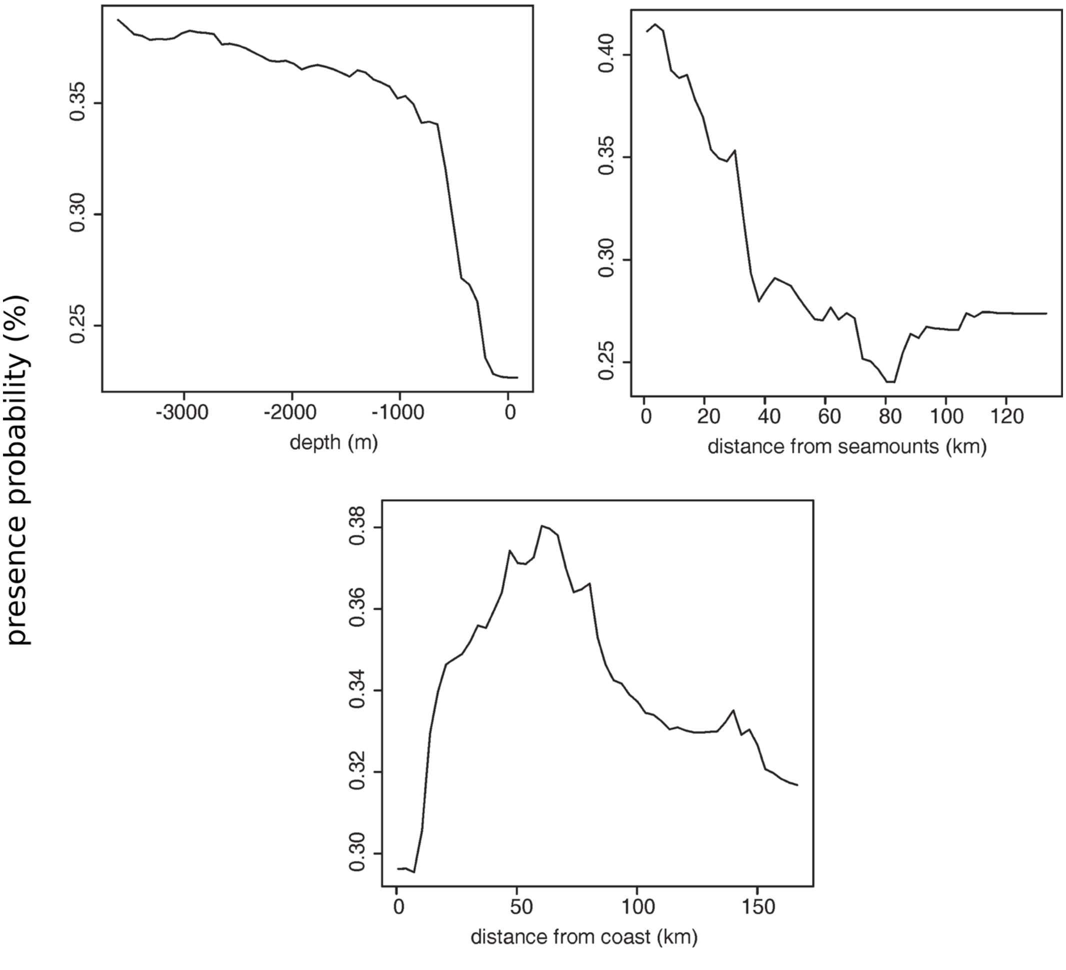

Fig. 4: Partial plots for *S. coeruleoalba.*

striped dolphin and shows better accuracy in detecting absences than in detecting presences. The model's overall accuracy reaches 81% (Table 4), lower than *S. coeruleoalba*'s model. The predicted distribution of *T. thynnus* is characterized by few but evident patches mainly located in the western and southern sectors of the basin (Fig. 5).

P. yelkouan

Seabird distribution depends mainly on depth. Lower importance, even if with relevant effects, is assessed to distance from seamounts, slope, and distance from the coast (Table 3).

Table 4. Confusion matrix with model accuracy metrics.

		Pred. absence	Pred. presence	Cutoff	Sens	Spec	MCC
S. coeruleoalba	**Obs. absence**	140	10	0.58	0.99	0.93	0.90
	Obs. presence	1	74				
T. thynnus	**Obs. absence**	89	7	0.62	0.90	0.93	0.81
	Obs. presence	5	43				
P. yelkouan	**Obs. absence**	530	66	0.47	0.78	0.89	0.67
	Obs. presence	66	232				
C. caretta	**Obs. absence**	227	9	0.59	0.98	0.96	0.93
	Obs. presence	2	116				

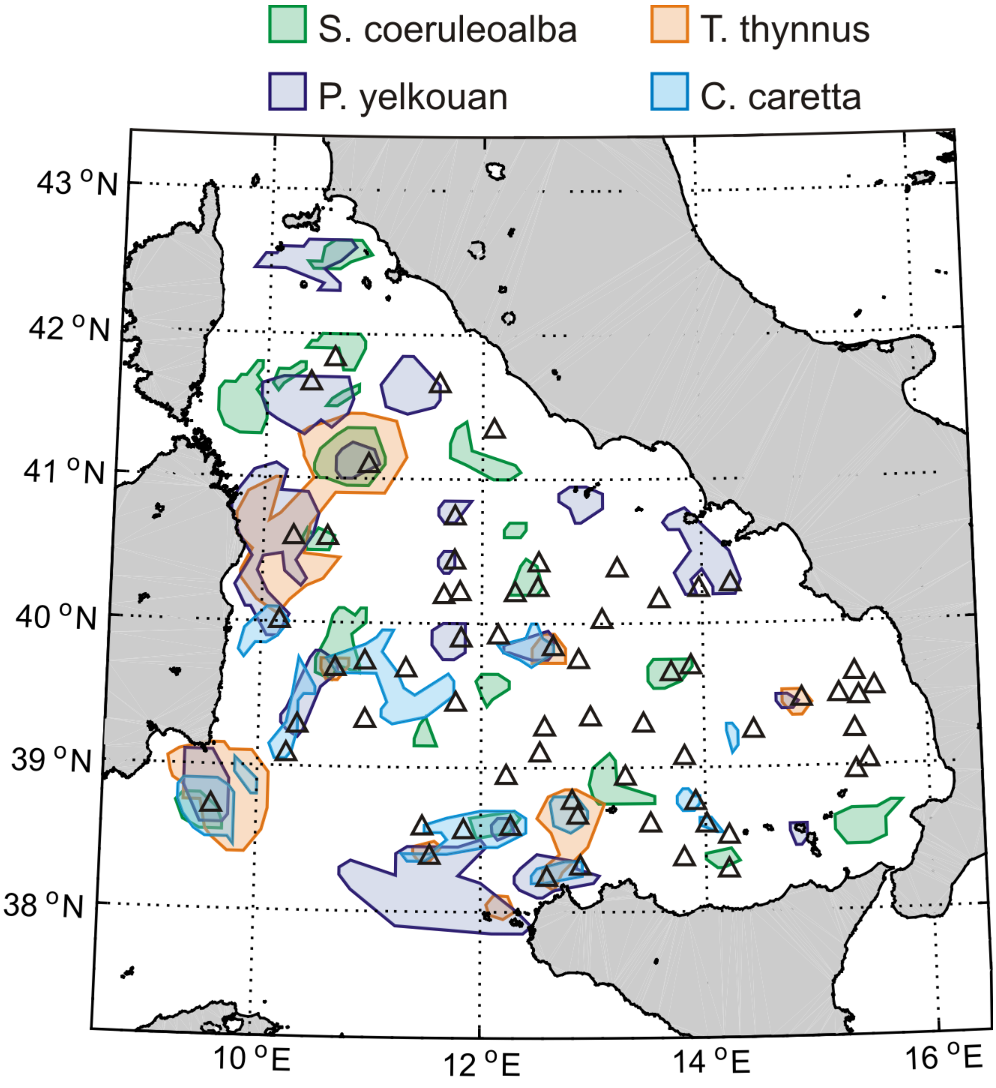

Fig. 5: Distribution map of the suitable habitats of the four considered species. Seamounts are identified by small triangles.

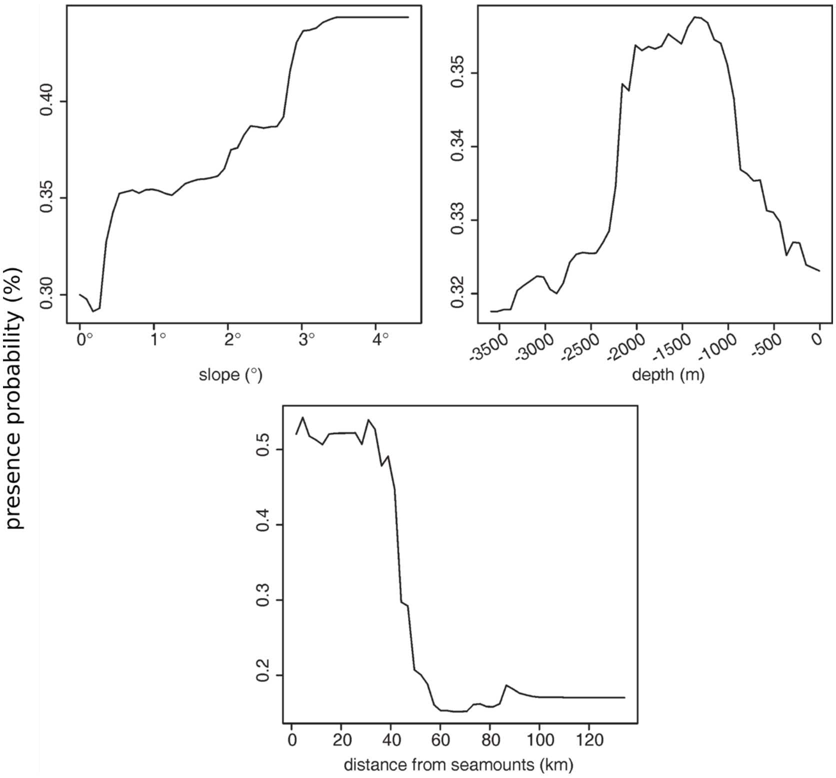

Fig. 6: Partial plots for *T. thynnus.*

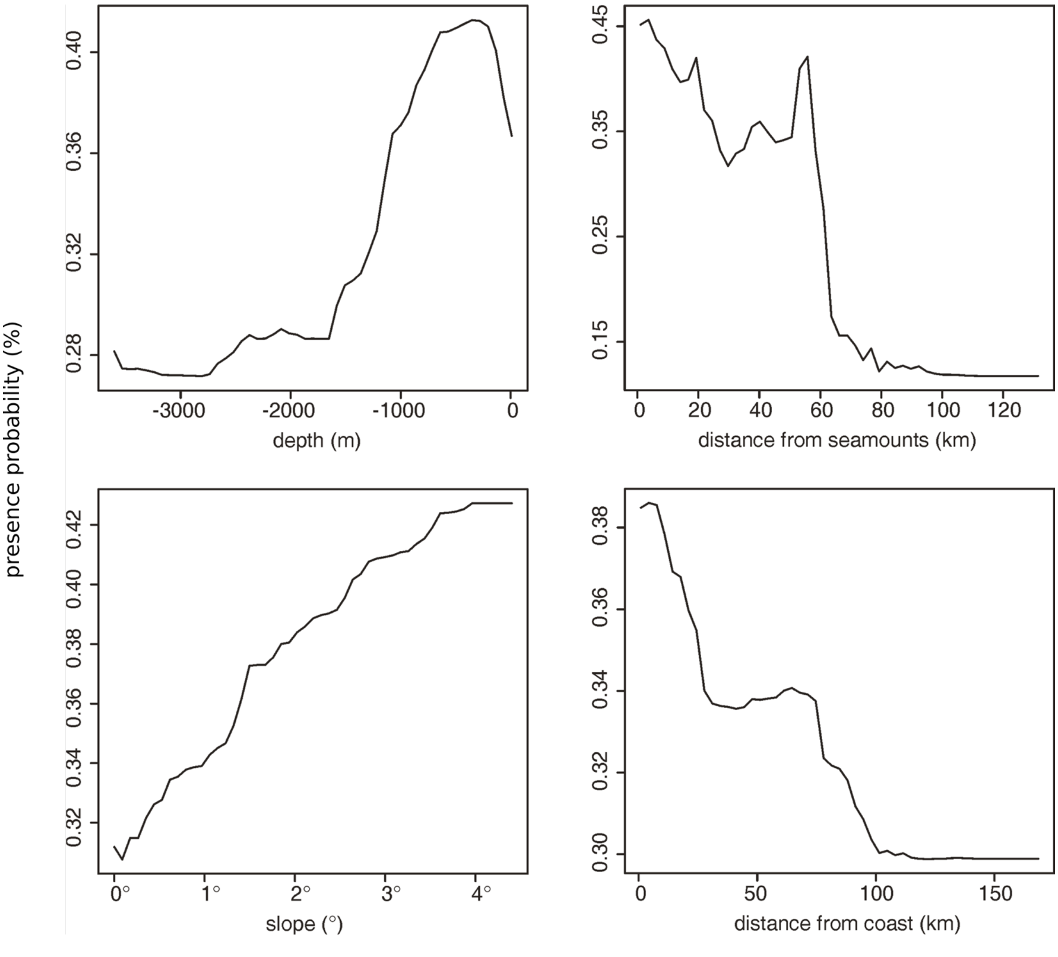

Fig. 7: Partial plots for *P. yelkouan.*

The univariate partial dependence plots for *P. yelkouan* (Fig. 7) display increasing presence probabilities at decreasing depth, distance from seamounts less than 60 km, increasing slope, and decreasing distance from coast, mainly less than 25 km.

The model showed the lowest sensitivity and specificity values and an overall accuracy reaching 67% despite the relatively high number of sightings (Table 4). The predicted spatial distribution shows the suitable habitat located at low depth, mainly close to the coastline with particularly evident patches east of the Sardinian coast and in a corridor between southern Sardinia and western Sicily (Fig. 5). High probability of presence was also detected along the south coast of Isola d'Elba and off the Gulf of Naples (Fig. 5).

C. caretta

Distance from seamounts and distance from the coast are important variables for determining the distribution of sea turtles. Lower importance (less than 10% of accuracy decrease in case of exclusion from the analysis) is shown by both seafloor slope and depth (Table 3).

The univariate partial dependence plots for sea turtles (Fig. 8) display increasing presence probabilities at decreasing distance from seamounts, specifically lower than 25 km, and increasing distance from the coast, with a first plateau at 50 km and a second increment at distances greater than 130 km.

The model showed high values of both sensitivity and specificity and the best overall accuracy, reaching 93% (Table 4). The predicted spatial distribution shows higher probabilities in the southwest quadrant of the Tyrrhenian Sea, mainly between the Sicilian and Sardinian coasts (Fig. 5), and a lack of suitable habitat zones in the northern part of the Tyrrhenian basin.

Seamounts' attraction effect

The habitat distribution depicted in Figure 5 shows that several seamounts are within suitable habitat for more than one species. The number of overlapping suitable habitats is here considered as a measure of the attraction effect of seamounts: The higher the number of suitable habitats, the more attractive the seamount is considered (Fig. 9). The influence of the main characteristics of the seamounts on the attraction effect was investigated by means of a correlation analysis (Table 5). Seamounts' attraction is higher for structures with shallow peak and base depths (lower than 500 and 1300m depth respectively) but wide base areas (more than 13 km^2) and high relative elevations (greater than 60% of water column). On the contrary, the influence of seamount slope and elevation is not relevant to the assessment of the attraction effect.

Discussion and Conclusions

In this study, the distribution of *S. coeruleoalba*, *T. thynnus*, *P. yelkouan*, and *C. caretta* in the Tyrrhenian Sea has been investigated, examining the importance of four physical habitat descriptors: depth, distance from the coast, seafloor slope, and distance from seamounts. Depth and distance from seamounts act as main variables in all the cases except for *T. thynnus* whose distribution resulted mainly driven by seafloor slope which, otherwise, is poorly important for the determination of the presence/absence probability. Distance from coast is mainly important for the distribution of *C. caretta* only. This is in agreement with the rate of turtle by-catch in the Mediterranean, even if this may also be influenced by different fishing strategies (Báez *et al.,* 2007).

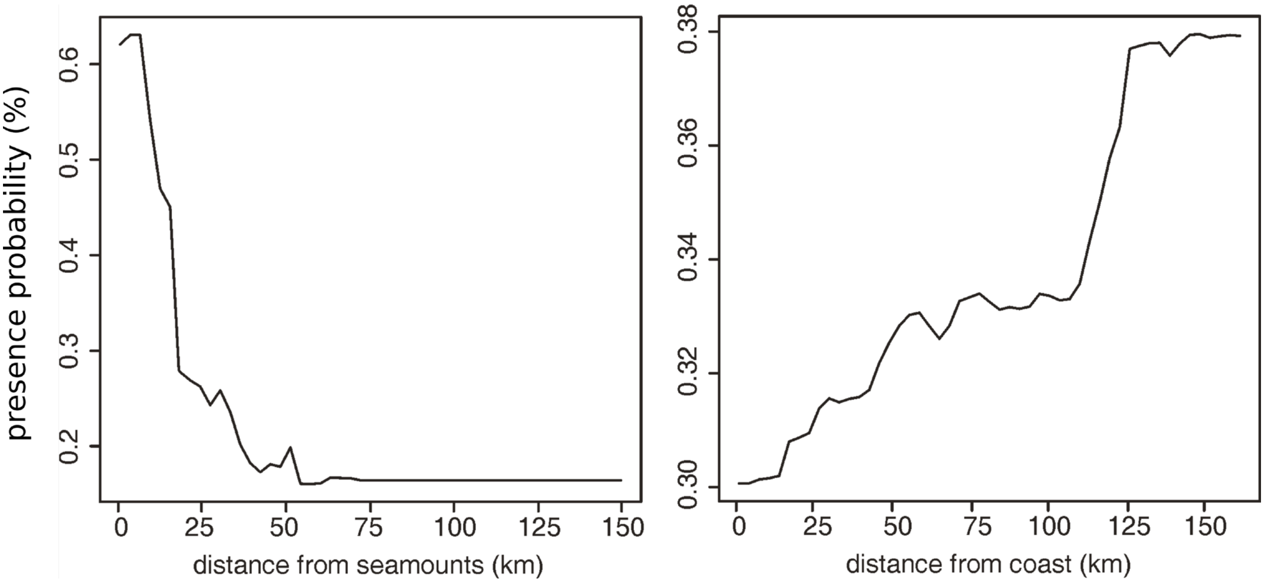

Fig. 8: Partial plots for *C. caretta.*

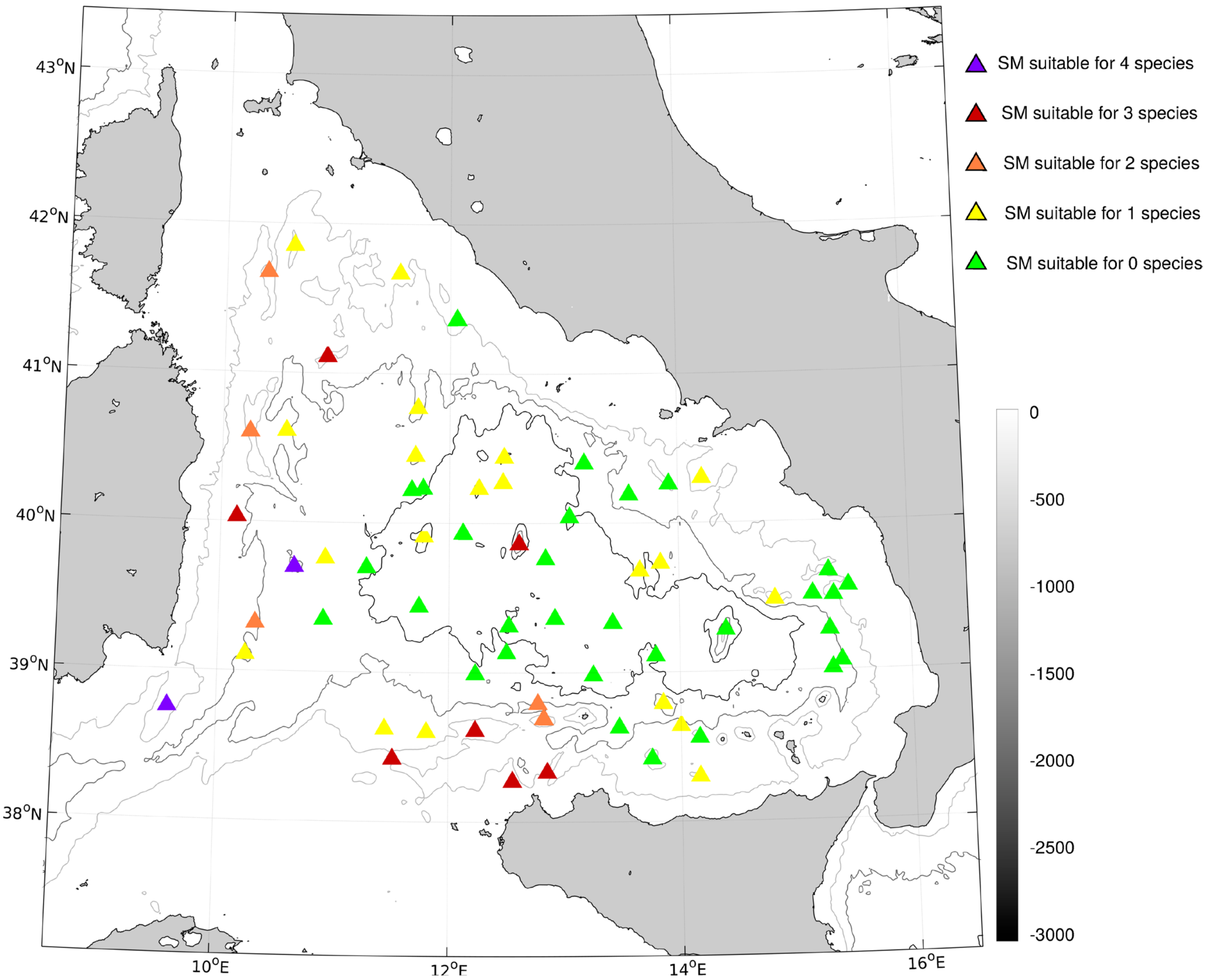

Fig. 9: Attraction effect of 64 Tyrrhenian seamounts. Gray contours represent depth in meters.

Table 5. Correlation matrix among attraction effect and SM main characteristics. Significant correlation values at p<0.01 are reported in bold.

Seamount characteristic	Correlation coefficient
Peak depth	**-0.44**
Base depth	**-0.34**
Min slope	-0.27
Max slope	-0.25
Base area	**0.35**
Elevation	0.18
Relative elevation	**0.45**

The models presented in this study allowed correctly predicting between 78% and 98% of the presence/absence of the studied species (Table 4). The best prediction performances, measured by means of the Matthews correlation coefficient, are displayed by *C. caretta* and *S. coeruleoalba*, taking advantage of the extremely high values of sensitivity. *P. yelkouan* was found to be the species with the weakest habitat preferences since the model's accuracy was the lowest and displayed higher accuracy for predicting the absence rather than the presence cells. These values lower the cutoff threshold, which is the lowest for this species and is due to the wide distribution of the sightings of this species.

All considered species are characterized by evidently patched suitable habitats covering a limited portion of the Tyrrhenian basin. This testifies to the extreme heterogeneity of the study area together with the ecological vulnerability of the considered species, which are able to effectively exploit small sectors of the basin. Despite a low level of overlapping among the considered species in the eastern sector of the basin, a number of overlapped habitats were identified off the coasts of Corse and Sardinia and in the area between Sicily and Sardinia, where, in some cases, all the considered species may find suitable habitats. These overlapping areas are generally centered in close proximity to seamounts because, even though the considered species display a clear separation of preferences for most of the considered parameters, they present a univocal attraction to seamounts that is shown by the increased predicted presence for all the species at decreasing distance from seamounts.

The attraction effect may be both direct and indirect. The direct effect may act on pelagic species that, during migrations, may use seamounts as reference points for where to rest, feed, and aggregate. The indirect effect may be due to the increased availability of prey since seamounts are well known as hot-spots of benthic abundance and diversity (Shank, 2010). Moreover, the influence of seamounts on local circulation may trigger phenomena like upwelling and water enrichment (Würtz & Rovere, 2015; Morato *et al.,* 2016), which may attract species that do not directly interact with seamounts like the ones here taken into consideration. Seamounts have been already identified as important structures for the reclamation of pelagic species (Morato *et al.,* 2010) in an oceanic context, and this study confirms their focal role for top predators in the Mediterranean Sea. Moreover, it is clear that not all seamounts act as hot-spots of large pelagic aggregations. Here, we assumed that the seamounts falling into overlapping habitats are the most attractive structures, and the main features characterizing these seamounts have been investigated. The most attractive seamounts displayed shallow peak and base depths but wide base areas and high relative elevations (in other words, seamounts occupying wide portions of the water column). Seamounts with these characteristics may deserve particular attention in terms of mitigation of anthropic activities on marine environments since these areas are here reckoned to be habitats for many sensitive species. This is particularly relevant since most of the overlapping habitats areas are close to the coast and at relatively short distance from coastal fishing ports. This makes these seamounts particularly attractive for fishery exploitation (Sabatini *et al.,* 2011; Palmas *et al.,* 2015; Lauria *et al.,* 2017) and thus easily subjected to one of the most commonly identified impacts on seamounts (Würtz and Rovere, 2015).

As a matter of fact, the assessment of habitat distribution is critical when planning management and conservation strategies for wild species. Effective management strategies need to consider the habitat requirements of the species of interest, as well as the level of interaction of these habitats at the scale of the basin. From this perspective, the understanding provided by this analysis allows the identification of areas of potential interest, and, in turn, the suggestion of protection measures. Model predictions also indicate areas where future survey efforts should be focused, especially in case of coexistence of high-probability presences and anthropic pressures (e.g., fisheries, ship traffic, noise pollution), aiming at highlighting the potential conflicts with human activities and evaluating the ecosystem's vulnerability (intended as exposure risks) from a risk management perspective.

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