Research Article

Habitat Suitability Modeling in Different Sperm Whale Social Groups

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ABSTRACT The identification of significant habitats for highly mobile marine vertebrates is essential for their conservation. Evidence is often difficult to obtain for deep-diving species such as sperm whales (*Physeter macrocephalus*), where standard visual survey methods are not sufficient to detect the species. Sperm whales rely on sound for most of their activities, so acoustics is a crucial tool to locate them in the environment and collect information about their daily life. We used a maximum entropy (MaxEnt) modeling approach to predict potential habitats for sperm whales during 2007–2015 in an area of the Mediterranean Sea (characterized by submarine canyon systems) where sperm whale singletons, social units of females and calves, and clusters with immature males, were regularly encountered in sympatry. Models to test species' distribution and the potential differences between groups of varying composition and life stages were based on 3 independent variables (depth, slope, and Euclidean distance from the nearest coast) and a combination of presence-only visual and acoustic data from boat-based surveys. One variable (depth) was the strongest predictor in all encounters (pooled data) and clusters, whereas distance from coast and slope best predicted encounters with singletons and social units, respectively. The model predicted suitable locations in areas that were well-known sperm whale habitat and in new regions of previously overlooked habitat, which possibly represent key areas for this endangered species in the Mediterranean. This study highlights that consideration should be taken regarding type of social aggregation when using modeling techniques for generating suitable habitat maps for conservation purposes. © 2018 The Wildlife Society.

KEY WORDS conservation ecology, MaxEnt, Maximum entropy modeling, Mediterranean Sea, *Physeter macrocephalus*.

Effective management decisions and appropriate conservation efforts depend on the population status of a species, which implies knowledge of its distribution and movements, habitat and feeding preferences, trends in abundance, behavior, and threats (Redfern et al. 2006, Sveegaard et al. 2015, Greggor et al. 2016). Such information is often hard to obtain for cryptic and highly mobile marine species that span over large regions and are difficult to survey, particularly deep divers such as sperm whales (*Physeter macrocephalus*) for which standard visual survey methods are not sufficient to detect and study the species. Sperm whales

rely on sound for most of their activities, producing different click types for echolocation and communication (Whitehead 2003). Therefore, underwater acoustics, and passive acoustic monitoring and tracking techniques are indispensable instruments to collect information about sperm whale presence in the environment (e.g., distribution, movements, feeding, socializing behaviors) and can be tools in scientific research (Gannier et al. 2002, Barlow and Taylor 2005, Lewis et al. 2007, Pirotta et al. 2011, Merchant et al. 2015) and conservation efforts (Cato et al. 2005, Nowacek et al. 2016).

The integration of presence data from passive acoustic monitoring and visual observation, coupled with adequate modeling techniques, may offer the most effective approach to identifying suitable habitats for the species based on environmental factors that are relevant for its distribution

(Mikkelsen et al. 2016). In addition, animals' phenotypes (and especially their behavior; Whitehead 2010), life stage, and group composition could play an important role in determining use of the habitat by distinct groups of the same species (van Toor et al. 2011). The sperm whale exhibits a strong sexual body size dimorphism, with males being up to 1.5 times longer and 3 times heavier than females (Lockyer 1981). The size dimorphism, and any kind of sexual dimorphism, including differences in parental investment and use of resources, is assumed to be associated with different degrees of sexual segregation (Ruckstuhl and Neuhaus 2002, Safi et al. 2007, van Toor et al. 2011), a common phenomenon among vertebrates including sperm whales. Adult females and their offspring form stable social units, and males, once they reach puberty, segregate from the units and form small male-only aggregations (bachelor groups), becoming increasingly solitary as they mature and roaming alone for the rest of their lives (excepting short-term associations with social units in mating periods; Whitehead 2003). The reasons for and factors influencing sexual segregation in sperm whales are still under debate, and hypotheses include differences in growth rates (males demand larger search areas to find locations with high prey concentrations), dietary needs and hence habitat preferences, and food competition (group of females prevail over solitary males when feeding on mid-water squids; Whitehead 2003, Jones et al. 2016). On a global scale, this leads to different dispersal patterns and segregation by sex, with male sperm whales feeding in high latitudes and females limited mainly to low latitudes (Lyrholm et al. 1999); on a local (Mediterranean Sea) scale, sperm whale groups by sex class may be found in sympatry (Pirotta et al. 2011, Frantzis et al. 2014, Pace et al. 2014, Rendell and Frantzis 2016), with indications of fine-scale partitioning and different habitat preference of singletons and groups in a given region (Pirotta et al. 2011, Jones et al. 2016). Dissimilarities in habitat choices made by males and females in different social assemblages may have also practical implications for the effective management of a population because differences in spatial distribution and resource use might expose males and females to distinct threats, thus affecting population dynamics through differential mortality risk (Catry et al. 2012).

The International Union for Conservation of Nature (IUCN) Red List classifies the Mediterranean subpopulation of sperm whale as Endangered and infers that their numbers are declining from significant anthropogenic threats (Notarbartolo di Sciara et al. 2012). These whales are likely to be genetically isolated from the Atlantic population (Engelhaupt et al. 2009). The species is subject to several threats including bycatches in fishing gear, ship strikes, disturbance, noise, and chemical contaminants with several potential negative effects at the population level (Notarbartolo di Sciara 2014, Pace et al. 2015). The European Union (EU)-Habitats Directive (Council Directive 92/43/EEC [European Economic Community] on the Conservation of natural habitats and of wild fauna and flora), which has created the Natura 2000 network of Special Areas of Conservation (SACs) including

areas with particular habitats or hosting particular species as identified by each Member State, listed all cetacean species under the Annex IV. This obliges Member States to "establish and implement an effective system of strict protection" (i.e., "a set of coherent and coordinated measures of a preventive nature contributing to the aim of maintaining the species in the long term or restoring its population in its habitat;" European Commission 2007:27).

Habitat suitability models can be useful when prioritizing between areas to reach certain conservation and management goals because they estimate the relationship between species records at specific locations and the environmental characteristics of the same sites (Mikkelsen et al. 2016). The maximum entropy modeling technique (MaxEnt) was specifically developed for presence-only data (Phillips et al. 2006). The general approach of MaxEnt is to estimate a probability distribution (i.e., relative likelihood of presence; McClellan et al. 2014) for a species over the pixels in a grid of the study area by contrasting occurrence data with background data rather than true absence data (Smith et al. 2012, Thorne et al. 2012). MaxEnt does not assume that absence precludes the likelihood of occurrence, because absence may indicate either an unsuitable area or suitable habitat into which the species has not yet distributed (Jarnevich et al. 2015). The output of MaxEnt is an index of probability distribution (Sillero 2011), where higher values correspond to a prediction of better conditions and a higher probability of occurrence (Phillips et al. 2006, Phillips and Dudík 2008, Elith et al. 2011).

We used a MaxEnt technique to investigate if sperm whale singletons and social groups selected for different habitats. We analyzed a combination of visual and acoustic sperm whale occurrence data (i.e., presence-only records) collected in 2007–2015 around Ischia and Ventotene Islands (Tyrrhenian Sea, Italy), a small key Mediterranean site where sperm whale singletons, social units and groups of immature males were regularly encountered (Mussi et al. 2014, Pace et al. 2014, Pace 2016). Our objective was to deliver prediction maps to better understand habitat requirement in relation to the species' sexual segregation and to predict its distribution in a region surrounding the study area where conditions are potentially suitable for the survival of the species (Phillips et al. 2004). Our final goal was to identify the essential scale of management for effective conservation of sperm whales in the framework of the EU Habitats Directive.

STUDY AREA

The site of investigation was in the central Tyrrhenian Sea (Italy), a zone featuring one of the most complex structures in the seas surrounding the Italian peninsula. The study region covered about 4,900 km^2 and included the Pontine Archipelago, consisting of 5 islands (Ponza, Palmarola, Zannone, Ventotene, and Santo Stefano), and the Campanian Archipelago in the Gulf of Naples, incorporating the islands of Ischia, Procida, Vivara, Nisida, and Capri (Fig. 1). The typical Mediterranean climate characterized the area, with temperature fluctuating between 5 and 12°C in winter months and between 25 and 30°C in the summer season.
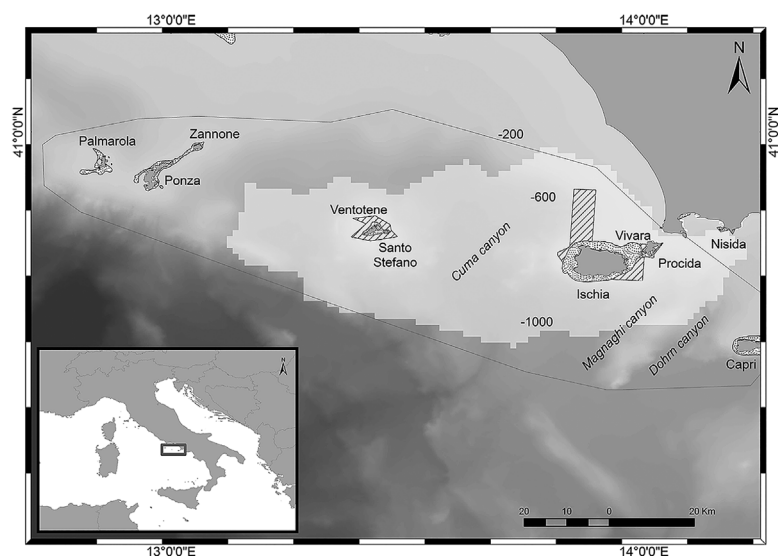
Figure 1. The study site is situated in the central Mediterranean Sea (Tyrrhenian Sea, Italy) and includes the Pontine Archipelago (Ponza, Palmarola, Zannone, Ventotene, and Santo Stefano Islands) and the Campanian Archipelago (Ischia, Procida, Vivara, Nisida, and Capri Islands). The areas with parallel lines define the 2 Marine Protected Areas. The zones with dots represent the Sites of Community Importance ranges. The Important Marine Mammal Area is marked by the gray line around all the islands. The light gray area highlights the surveyed area used as background to build a MaxEnt model for sperm whale habitat suitability, 2007–2015. The position of the Cuma, Magnaghi, and Dohrn submarine canyons are also indicated. The numbers define 200-m, 600-m, and 1,000-m bathymetries.

The number of marine species recorded in the area is representative of more than 70% of the total species known for the Mediterranean Sea and almost all typical Mediterranean habitats are present in the region: seagrass meadows; hard bottom communities with coastal banks, cliffs, and caves; sand; and muds (detritic muds, which in some areas typically form rhodolith facies; Warwick et al. 2003). The entire area also provides an important and thriving economic and recreational resource, supporting commercial and leisure activities that may detrimentally influence its ecosystems. Among these, tourism and fisheries are the most evident factors during summer, when the frequency of maritime (mostly ferries and fast ferries) and recreational boat traffic, and the intensity of the fishing effort, usually increase (Pace et al. 2012).

Coastal seabed portions of all islands were designated as Sites of Community Importance (SCIs; Fig. 1) under the Natura 2000 network primarily for the presence of meadows of the endemic Mediterranean seagrass (*Posidonia oceanica*) and the existence of coralligenous habitat. In addition, 2 Marine Protected Areas (MPAs) were established (Fig. 1) to protect biodiversity and mitigate some of the effects that the large amount of human activity in the region could have on marine species: the MPA embracing the island of Ventotene and the nearby volcanic islet of Santo Stefano, and the Regno di Nettuno (i.e., Neptune's Kingdom; Gambi et al. 2003) comprising the islands of Ischia, Procida, and Vivara. The more pelagic area of the Neptune's Kingdom MPA was modeled specifically after the area identified as a critical habitat for the endangered short-beaked common dolphin (*Delphinus delphis*; Reeves et al. 2003). However, comparison of short-beaked common dolphin habitat to sperm whale habitat in the waters surrounding Ischia (Pace et al. 2012, Mussi et al. 2014)

shows a vast, unprotected stretch of water that could be a critical area for the currently endangered sperm whale. Recently, the area including Pontino and Campano Archipelagos was acknowledged as an Important Marine Mammal Area (IMMA; discrete portions of habitat, important to marine mammal species, that have the potential to be delineated and managed for conservation) for the sperm whale in the Mediterranean Sea by the IUCN Marine Mammal Protected Areas Task Force (IUCN-MMPATF 2017; Fig. 1).

The study region was principally located in the waters surrounding Ischia and Ventotene islands and characterized by the presence of complex and varied geological structures including submarine canyons (de Alteriis and Toscano 2003, Pace et al. 2012). The site is mostly furrowed by the Cuma canyon (Fig. 1), a topographical system including the northwest part of Ischia Island and extending out to the submarine valley between Ischia and Ventotene (de Alteriis and Toscano 2003, Pace et al. 2012, Mussi et al. 2014). In the Gulf of Naples, between Ischia and Capri, the shelf is interrupted by 2 other large canyons: the Magnaghi (southeast Ischia) and the Dohrn (west-northwest Capri), which comprise the Magnaghi-Dohrn structure (Fig. 1; D'Argenio et al. 2004 and Di Fiore et al. 2011). The highly variable seascapes within canyons influence oceanographic processes that concentrate nutrients and shape prey availability vertically in the water column (i.e., upwelling phenomena), sustaining diverse assemblages of species that play different ecological roles (Fernandez-Arcaya et al. 2017). The intricate topography of the study region and the canyon systems were proposed as influencing factors of the sperm whale local presence, possibly influencing the species' distribution and affecting feeding activities (Mussi et al. 2014, Pace 2016).

METHODS

Surveys

We used visual and acoustic data collected in the field from 2007 to 2015. We followed the American Society of Mammalogists research guidelines on live animals (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016). We made daily survey trips during our field season (Jun–Oct each yr, with a few sporadic trips in Nov and Dec) aboard a 17.7-m sailing vessel in daylight hours and in suitable sea states (≤ 4 on the Beaufort scale), covering approximately 60×74 km of area and limited by the distances that could be traveled by the vessel within a single day. We followed random sampling procedures (La Manna et al. 2016). We established survey tracks to provide an approximately even coverage of the study area, considering bottom topography and depth, although tracks were constrained by weather conditions and vessel limitations. We surveyed 16,469.55 nautical miles during 660 days at sea (5,282 hr) between 2007 and 2015 in the study area.

We conducted searches for sperm whales by continuously scanning the water surface with the naked eye or with 8–16×50 power binoculars, and using 2 hydrophones (100 Hz–22 kHz bandwidth, ENEA-UT-APRAD Radiation Sources Laboratory, Frascati, Rome, Italy) spaced 3 m apart and towed on 50 m and 100 m cables, with 2 pre-amps (ASD-Schaller, Postbauer-Heng, Germany). We connected the system to the laptop through an audio interface (RME-Fireface 400, Haimhausen, Germany; sample rates up to 192 kHz; selected sample rates: 44.1 and 48 kHz). We connected the output signal to headphones and a pair of stereo speakers located in the pilothouse. We listened continuously for sounds from the array while the vessel was underway. During all surveys, we used the data logging software Logger (http://www.marineconservationresearch. co.uk/downloads/logger-2000-rainbowclick-software-downloads/) on a laptop connected to the global positioning system (GPS) receiver to record the position of the research vessel every 180 seconds. We used Rainbow Click for audio recording and acoustic data collection; the software is designed to locate and analyze sperm whale clicks and other odontocete acoustics (Gillespie 1997). Once we detected sperm whales, we maneuvered the vessel route to estimate the relative bearing of vocalizing animal(s) and tracked them until emersion and sighting at surface. Rainbow Click analyzed the stereo signal using time of arrival differences between the same clicks on the 2 channels to estimate a bearing to each click source (De Vos et al. 2012). We considered only clear and loud acoustic detections for the analysis.

When at the surface, we approached whales with extreme caution. Once the whales were within 300 m, we decreased the speed of the vessel and stopped behind the whales. We used a digital camera equipped with a high-quality image stabilized telephoto zoom lens (100–400 mm F4.5–5.6) to take photo-identification images. We first estimated the number of whales comprising a group visually and then acoustically. We assessed group composition in the field considering direct observation of the whales' genital area and size estimates, then confirmed afterwards through the analysis of photo-identification images and underwater videos. We classified whales as singletons, clusters, and social units. A singleton was a single large-size individual estimated to be ≥ 12 m in length with no other sperm whales visually or acoustically detectable around. A cluster was a set of 2–5 presumed or confirmed male whales staying or moving together in a coordinated fashion over hours (Whitehead 2003). Clusters included bachelor groups (i.e., aggregations of similar sized or aged whales comprising immature males estimated at 9–11 m). Social units were all whale groups that included calves (i.e., whales having a visually estimated length of about 4–5 m, $\leq$ half the length of an accompanying animal) or juveniles (i.e., whales having a visually estimated length of about 7 m, > half the length of an accompanying animal but less than full size).

Data and Variables

We stored raw data collected in the field with Logger 2000 in a database (Postgresql 9.1) and used PostGIS 2.0 geographical extension and the PL/R library with R 2.14 (R Foundation for Statistical Computing, Vienna, Austria) to implement spatial and statistical analysis. We assigned presence data to a fine spatial resolution grid of 8,800 0.0125×0.0125-degree cells at the level of field seasons pooled across years. We considered this was an adequate choice to attain an overall representation of the distribution of long-lived, mobile animals such as sperm whales in the scale of our study area.

We used 3 fixed environmental variables to generate distribution models: depth, slope, and Euclidean distance from the shoreline. We selected these variables as proxies of environmental characteristics that could affect the distribution of sperm whales or their prey and, given the fine scale of the investigated area, the ones that better represent its peculiar topography (slope gradients and depth profiles significantly vary along submarine canyon axis; Li et al. 2016). Even if variables do not have a direct physiological effect on species distribution, indirect variables are often used because they can replace a combination of different resource and direct variables in a simple way (Guisan and Thuiller 2005). The chosen variables were commonly used in other works involving the cetacean habitat modeling, suggesting that they might be relevant predictors of their distribution (Edrén et al. 2010, Bombosch et al. 2014, Correia et al. 2015, Gómez and Cassini 2015, Breen et al. 2016). The environmental variables were obtained from a geographic information system (GIS) raster layers at the same resolution of the grid used for the analyses.

Habitat Modeling

We used the MaxEnt presence-only modeling technique, which combines general-purpose machine learning with statistical methods, to model the relationships between environmental predictors and the occurrence record of sperm whale by groups of varying composition and life stages. We selected MaxEnt because accurate absence records for

cetaceans are not always available and may be unreliable in some cases because logistic, ecological, and behavioral effects may influence the species' absences even though the environment was suitable (Mandleberg 2004, Pearson 2010). In our study, the separation of true absences, where animals were actually absent, from false absences, where animals were present but not detected (for instances when animals made acoustic pauses) was difficult to assess, potentially leading to uncertainty when interpreting results. Thus, for our study absence data was not suited to habitat modeling using presence-absence methods. MaxEnt is among the best performing methods for presence-only data, demonstrating comparable ability to predict a species' distribution to presence-absence methods (Elith et al. 2006, Wisz et al. 2008, Duan et al. 2014). In addition, MaxEnt was reported to outperform these other methods when data were characterized by small sample size (Wisz et al. 2008), spatial positioning errors (Graham et al. 2008), and a mismatch between the spatial resolution of observations and environmental variables (Guisan et al. 2007).

We used the software MaxEnt (version 3.3.3, http://www.cs.princeton.edu/~schapire/maxent/) to build models. Because the purpose of the study was to investigate if habitat selection differed by sex or life stage, we used occurrence data (visual sightings at surface combined with the entire acoustic tracks while tracking the animals) to create 4 species distribution models by pooling together all encounters and stratifying data per different group composition (singletons, clusters, social units). The study area for predictions and model outputs included the surveyed area, which comprised adequate environmental variability giving the ecology of the species, and the surrounding zone containing similar ecological characteristics (Fig. 1).

MaxEnt allows accounting for sampling biases inherent in the sightings data via available correction features that consider sampling effort (which is then used to bias the selection of the background points; Phillips et al. 2009). We used the bias file feature to input a layer representing the area of the sampling effort. Instead of randomly selecting the background points from the study area, this option allows MaxEnt to select points that reflect the sampling distribution of collection effort; thus, selection of background points is subjected to the same bias as the occurrence data (Stolan and Nielsen 2015). In this study, we controlled sampling bias by including a specific bias created from all georeferenced occurrence data, considering the minimum convex polygon of the surveyed section across the area of investigation, and applying it as a template for the extraction of background points in zones of search effort (Elith et al. 2010, Bombosch et al. 2014, Fourcade et al. 2014). We applied this bias to build all 4 final models. We then associated each background and presence location with the set of continuous environmental variables. Because we used only fixed variables (so that the same location has identical environmental variable associated in different time), we set MaxEnt to remove duplicates in the same location to reduce pseudo-replications and spatial autocorrelation of samples.

We ran distinct MaxEnt models by pooling together all encounters and stratifying data per different group composition (singletons, clusters, social units) using subsamples to split training (i.e., model building) and test (i.e., model validating) data. We ran 15 replicates of each model using default regularization parameters, with maximum iteration up to 5,000 to reach convergence, and randomly selecting 70% of the presence records as training data and 30% as test data. We adopted the same settings to allow different models to be comparable (Moura et al. 2012) and restricted MaxEnt to using only linear, quadratic, and product feature classes (i.e., functional forms), constraining it to produce relatively simple models that do not over-fit the training data (Merow et al. 2013, Syfert et al. 2013). We used a minimum of 10 presence points for training (Pearson et al. 2007).

We evaluated each MaxEnt prediction using the area under the curve (AUC) of the receiver operator characteristic (ROC) on training and test data (Thorne et al. 2012). We selected the AUC because is one of the most widely used threshold-independent evaluators of model discriminatory power (Fielding and Bell 1997), and because it determines model discriminatory power by comparing model sensitivity (i.e., true positives) against model specificity (i.e., false positives). The AUC values range from 0 to 1; an AUC of 0.5 implies that the model was no better than random at discriminating habitat, whereas higher values denote improving precision. We estimated the relative contribution of individual environmental variables to each of the resulting models by jackknife analysis of the average AUC with training and test data, and estimated average percent contribution and permutation importance (Baldwin 2009). Jackknife analysis included creating a model excluding 1 environmental variable, followed by the generation of a model using only the omitted individual variable (Moura et al. 2012), thus providing an indication of how well the model performed when an environmental variable was omitted and additionally how each variable contributed to the model individually (Bombosch et al. 2014). Finally, we visually inspected all models for sign of overfitting (Bombosch et al. 2014) and evaluated models by computing the difference between average AUC training values from AUC test values.

Using ArcGIS version 10.2.2 (Environmental Systems Research Institute, Redlands, CA, USA) we generated spatial prediction maps of habitat suitability based on MaxEnt outputs, which depict habitat suitability across the investigated region with values ranging from 0 (very unsuitable habitats) to 1 (very suitable habitats). We used the same classification scale for all maps.

RESULTS

We had 103 visual encounters with sperm whales (34, 63, and 6 encounters with singletons, clusters, and social units, respectively) and 208.5 hours of acoustic tracking. Both accounted for 3,982 presence locations, mainly composed of acoustic points. After the removal of duplicates, we used 1,808 points out of 3,982 to determine MaxEnt distribution (background and presence points).

All 15 runs for training and testing data of MaxEnt final models obtained mean AUC scores >0.7 (with the only

exception of test data in singletons), with small standard deviations for training and test data (Table 1), which suggests very good predictive power of the fitted model (Lobo et al. 2008) compared with the value (0.5) expected from a random prediction. We did not find evidence of overfitting, suggesting that we applied the appropriate default settings.

The estimates of relative contributions and permutation importance of the environmental variables to the MaxEnt model (Table 2) provided estimates of variable importance measuring the model's predictive ability. Overall, for the variables used in these analyses, depth had the greatest explanatory (predictive) power for all encounters pooled together and for clusters throughout the study period. The highest logistic probability for finding sperm whales was between 500 m and 800 m in depth, with a peak around 600 m for social encounters (clusters and social units) and >1,000 m for singletons. Distance from coast and slope best predicted encounters with singletons and social units, respectively, with a higher probability of finding singletons at a distance >5 km from the nearest coast, and of locating social units at slope steepness >15%. All MaxEnt outputs are available online (Pace 2017).

The predictive map of habitat suitability for all sperm whale encounters pooled identified an extremely suitable area along the Dohrn canyon and south Capri Island (Fig. 2a), together with zones in south Ischia, and southeast Ponza to southwest Palmarola. In addition, an extended area including the Cuma Canyon, the waters surrounding Ventotene Island, and a zone northwest of Palmarola were highly suitable too. When stratifying data per different sex or age group, the maps revealed a predicted wide-ranging pattern of suitability in sperm whale singletons (Fig. 2b). The areas of highest suitability for clusters were located in the near the Dohrn Canyon heads, north Ventotene Island, and northwest Palmarola (Fig. 2c). The best predicted conditions for social units were in an important extension through an almost uninvestigated area in the western and southern part of the islands of Ponza and Palmarola, south of Capri, the deepest part of the Dohrn Canyon west-southwest of Capri, and the southern part of Ischia (Fig. 2d).

DISCUSSION

The use of the MaxEnt modeling technique was successful in predicting the distribution of habitat important to sperm whale groups by sex or age class in an area of the Mediterranean Sea during the time of our study and made

predictions beyond surveyed areas. Although the main strengths of the MaxEnt method lie in its ability to efficiently handle complex relationships (Phillips and Dudìk 2008), its robustness at small sample sizes (Hernandez et al. 2006, Wisz et al. 2008, Williams et al. 2009), and its adaptability to a range of data types and sources, known limitations must be considered when results gained through this modeling technique are proposed or adopted as possible conservation instruments as in this study (Hastie and Fithian 2013, Yackulic et al. 2013, Monk 2014). For example, MaxEnt is not immune to the obstacles posed by imperfect detectability (Dorazio 2012) and it does not provide measures of occupancy; MaxEnt merely yields relative maps of suitability (Phillips et al. 2006). In the presence of detection heterogeneity, however, MaxEnt has been suggested as an adequate avenue for analysis of cryptic species (Rota et al. 2011, Tsai-Yu et al. 2012), resulting in a reliable option for this sperm whale study.

We attempted to minimize limitations of this modeling exercise. First, because one of the fundamental limits is that sample selection bias (whereby some areas are sampled more intensively than others) has a strong effect on presence-only data, we used the bias file feature within the MaxEnt framework, as recommended by Stolan and Nielsen (2015). Syfert et al. (2013) demonstrated the importance and efficacy of the bias file option and reported that correcting for bias had more of an effect on model fit than the type of response curves permitted to train the model. Second, to decrease the influence of duplicate points and reduce spatial autocorrelation, we removed very closely clustered points from our dataset (Hammond et al. 2016). Even though we used rather grouped presence points considering the fine spatial scale of this study, we are fairly confident that our models were not highly biased for overfitting; constraining MaxEnt to using only linear, quadratic, and product functional forms minimized the likelihood of overfitting the training data because our models were relatively simple (Merckx et al. 2011, Merow et al. 2013, Syfert et al. 2013). Finally, we used an evaluator of model discriminatory power (AUC), estimated the relative contribution of individual environmental variables to each of the resulting models using jackknife analysis of the average AUC, ran the model multiple times ($n = 15$) to measure the amount of variability in the model, and checked and weighed our findings with various pieces of available evidence in our empirical data, to reach a balanced inference from that evidence.

Although our modeling exercise may improve knowledge of the species distribution in the investigated region during our survey season, study limitations must be highlighted, and results interpreted with caution, because accuracy of model predictions is not always easy to achieve (there is often a large amount of variability surrounding the measurements of response and environmental variables, and this variability could lead to uncertainty in the predictions; Pennino et al. 2017). In addition, we principally conducted surveys during summer and early autumn, when weather conditions were most suitable, thus restricting the ability to quantify long-term cross-seasonal trends in sperm whale distribution and

Table 1. Mean and standard deviation (SD) results of the area under the curve (AUC training and test) of the receiver operated characteristic (ROC) plots for MaxEnt models applied to sperm whale occurrence data collected in the central Mediterranean Sea between 2007 and 2015. All plots are available online (Pace 2017).

|	AUC training	AUC test	SD training	SD test
All encounters	0.7530	0.7136	0.0047	0.0093
Singletons	0.7304	0.6562	0.0351	0.0889
Clusters	0.8414	0.7330	0.0222	0.0409
Social units	0.9006	0.8528	0.0189	0.0576

Table 2. Estimates of relative contribution (%) and permutation importance of the environmental variables to the MaxEnt models applied to sperm whale occurrence data collected in the central Mediterranean Sea between 2007 and 2015.

	% contribution			Permutation importance		
	Depth (m)	Distance to coast (km)	Slope (%)	Depth (m)	Distance to coast (km)	Slope (%)
All encounters	85.8	12.1	2.1	62.8	31.9	5.4
Singletons	37.4	47.0	15.6	16.6	52.1	31.3
Clusters	78.3	11.8	9.9	68.2	15.8	16.0
Social units	27.6	18.9	53.5	45.6	26.9	27.5

resulting in a seasonal bias in species occurrence data. However, in the study area, sperm whale occurrence was documented from March to December (Mussi et al. 2014, Pace 2016), suggesting an almost persistent presence during the year. Seasonality of the environment may play a major role in species distributions by altering the presence of individuals in a given place at a stated time (Murray et al. 2013); seasonal habitat use can be influenced by modifications in ecological processes and by biological functions such as growth, feeding, and reproduction (Lambert et al. 2017). In the Mediterranean, few and scattered long-term systematic year-round studies useful to assess sperm whale seasonality in patterns of occurrence have been conducted, with high heterogeneity of survey efforts and methodologies, thus making problematic possible inferences in our study

area. In the Ligurian Sea, sperm whale presence was recorded almost throughout the year (Laran and Gannier 2006, Laran and Drouot-Dulau 2007), with no suggestions of strong seasonal patterns or variations in abundance (Laran et al. 2017). In the Sardinian-Balearic sector, sperm whales were detected especially during summer and autumn, whereas in the central Tyrrhenian Sea the species was never detected in autumn, but it was recorded during other seasons (Arcangeli et al. 2017).

In this study, results of environmental variables showed that depth was the most important predictor of habitat suitability for all sperm whales in the study area. Within the Mediterranean, sperm whales were principally found in waters deeper than 1,000 m to 2,500 m (Cañadas et al. 2002 [Alboran Sea], Pirotta et al. 2011, Arcangeli et al. 2017
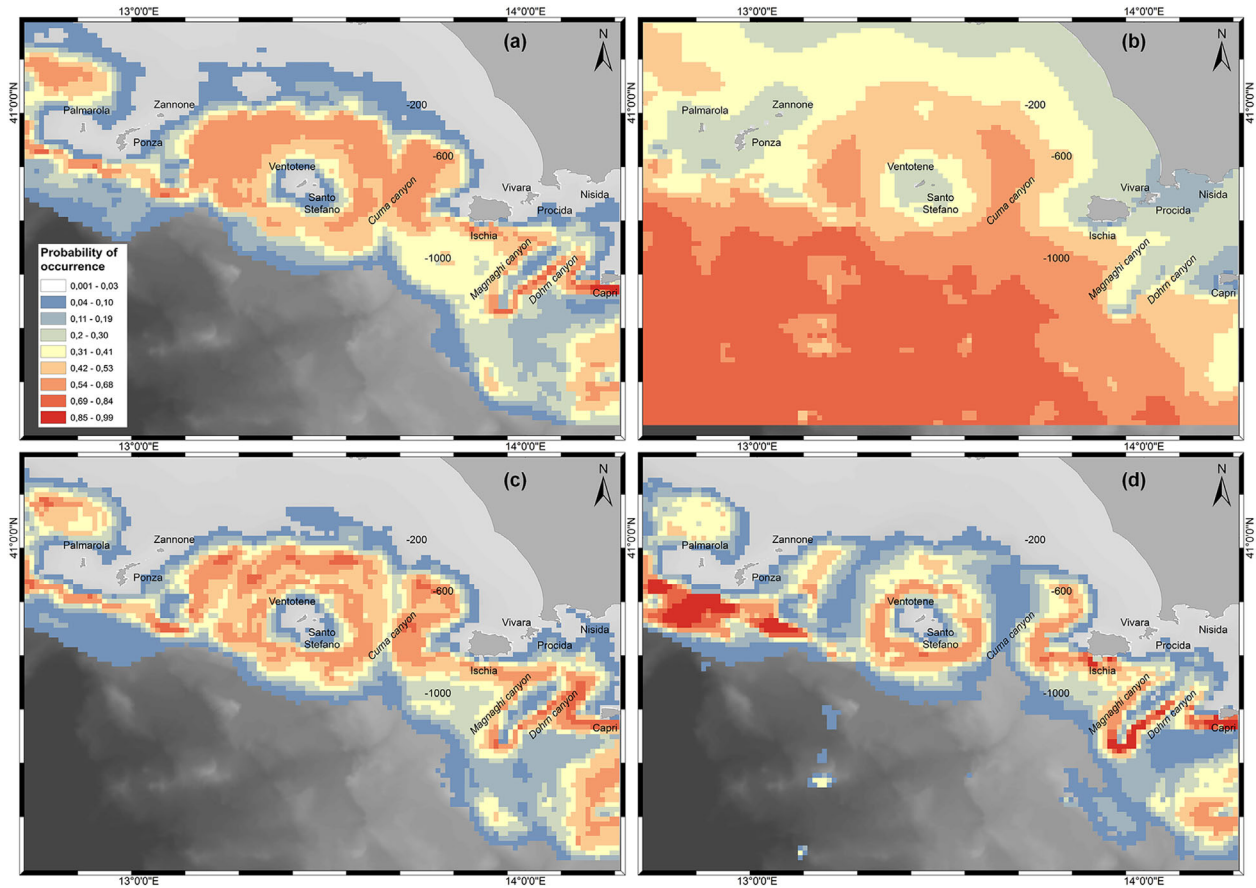
Figure 2. Suitability habitat maps for all sperm whale encounters (a), singletons (b), clusters (c), and social units (d) in the central Mediterranean Sea, 2007–2015. Colors were classified on 9 classes based on natural brakes in the probability of occurrence. Warmer colors show areas with better predicted conditions.

[Balearic Archipelago and Sardinian-Balearic sector], Fiori et al. 2014 [Pelagos Sanctuary, Ligurian Sea]). In this study, the species tended to be sighted at water depths of 500–800 m but was also present over the 300–1,000 m contour. A spatially bimodal distribution for the sperm whale in the western Mediterranean was proposed because of its opportunistic feeding strategy (Gannier et al. 2002, Gannier and Praca 2007), a hypothesis that was reinforced in the Pelagos Sanctuary (Azzellino et al. 2008) and that is possibly pertinent in our study as well considering predictions outside the surveyed area. The species was sighted over the continental slope, where topographies such as canyons are considered main influences for habitat selection, and in the offshore waters, where the presence of the animals appears to be linked to the position of downwelling or upwelling water movements associated with frontal zones (Gannier and Praca 2007, Arcangeli et al. 2017). In this way, sperm whales would be able to capitalize on the food resources available in both areas by shifting to different prey targets (Gannier et al. 2002). The interaction between complex seafloor characteristics and water circulation appears to be relevant to the species' distribution in the Mediterranean Sea and in other regions (Davis et al. 2002, Skov et al. 2008). As shown, topographical features characterize the continental slope of the study area, incised by large scars and a network of canyons or tributary channels, which likely enhance primary productivity and sustain a richer biomass along the entire trophic web (Pace et al. 2012). Given their local importance, these canyons may represent hotspots for cetacean species in the Ligurian Sea (Azzellino et al. 2008, 2012; David and Di-Meglio 2012) and the Tyrrhenian Sea (Bittau and Manconi 2011, Pace et al. 2012). These canyons are relevant regional sources of marine biodiversity and ecosystem function, supporting diverse assemblages of species that play a variety of ecological roles, often across small spatial scales (McClain and Barry 2010, Leduc et al. 2014).

In this study, bottom depth significantly influenced sperm whale distribution, being presumably associated with the bathymetric zonation of its prey (i.e., cephalopod assemblages; Quetglas et al. 2000). The cephalopod fauna in the southern Tyrrhenian Sea seems to be dominated by Sepiolidae (in terms of abundance in epipelagic and mesopelagic zones, at 200–300 m; Romeo et al. 2012), Ommastrephidae, and Onychoteuthidae (in terms of biomass, at depth >500 m; Romeo et al. 2012). These factors highlight the importance of these widely distributed cephalopod families as key species in the Mediterranean pelagic food web and in the ecosystem of the area. Moreover, Ommastrephidae and Onychoteuthidae, muscular high-speed swimming squids, are fast-growing, active predators that efficiently convert their prey into biomass (Clarke 1996), therefore representing a primary source of food and energy for large marine predators (Romeo et al. 2012). Sperm whales in the study area may benefit from the occurrence of these cephalopod assemblages, as also suggested by the concomitant presence of top predators considered efficient cephalopod collectors (Romeo et al. 2012) such as swordfish (*Xiphias gladius*), bluefin tuna (*Thunnus thynnus*), albacore (*Thunnus alalunga*), and Mediterranean spearfish (*Tetrapturus belone*). However, direct information on the availability and movements of sperm whale prey would be beneficial for a better understanding of the relationship of this species with its environment (Jaquet and Gendron 2002).

Although depth showed a high level of reliability for the prediction of habitat suitability for all sperm whale encounter types in the study area, particularly for clusters, we also found a relevant relationship with the slope steepness >15% (which has been deemed crucial in aggregating prey; Praca et al. 2009) and the distribution of social units. Furthermore, in contrast to groups (clusters and social units), we observed an increased probability in the presence of singletons with distances >5 km from the nearest coast, suggesting individuals have different ecological requirements and habitat preferences related to different behaviors, such as searching and feeding activities and socializing. Although sperm whales spend a considerable amount of time foraging at depth, they are highly social mammals (Whitehead 2003) and sociality was reported to be an important component for animals encountered in the study area (Pace et al. 2014, Pace 2016). Although singletons can focus their habitat choice on prey availability (Pirotta et al. 2011), significantly moving within the study area to find suitable food patches far from anthropogenic disturbance near the coasts, individuals in clusters and social units might be required to trade-off foraging efficiency for benefits of social interactions. Some of the benefits of sociality, such as increased predator detection and offspring survival, are intimately linked to an individual's energy budget and could lead individuals in sperm whale groups to target other prey species with different spatial distributions (Whitehead 2003) than singletons. In addition, it was suggested (Whitehead 2003) that female sperm whale occurrence and movements are better explained by the model of a nomadic animal moving in response to changes in food availability, and the presence of immature individuals is known to heavily affect the behavior of adults (Whitehead 1996). The output of the MaxEnt model for social units seems to underlie these evidences by mostly showing suitable areas where upwelling phenomena are more likely to occur (steep slope zones). It was recently proposed that the restricted latitudinal range available in the Mediterranean does not allow for the segregation among age and sex classes observed at the oceanic scale (Rendell and Frantzis 2016), and it appears to be the norm for these age and sex classes to inhabit the same waters (Pirotta et al. 2011, Frantzis et al. 2014, Pace et al. 2014, Pace 2016). The coexistence of age and sex classes seen in these studies suggests a sympatry of males and female groups and such overlapping ranges could alter the way that they divide ecological niches, in theory leading to increased competition for resources between female groups and solitary or clusters of maturing males (Rendell and Frantzis 2016). The habitat partitioning emerged in this study between singletons and groups, also observed in the Western Mediterranean (Pirotta et al. 2011), should be considered when evaluating the area used by sperm whales for conservation purposes. Besides the known

presence hotspots in the Cuma's Canyon area, our results suggested that other areas were highly suitable habitats for the endangered sperm whale, particularly for social groups. These new regions comprise the area south of the Palmarola and Ponza islands in the northwest, the area of the Dohrn Canyon in the southeast, and the southern part of Capri Island. In future conservation planning, it is advisable to increase the research effort through systematic surveys, to collect additional data of the different sperm whale groups to test the reliability of the model, and to ascertain that the new areas, defined by the model as being suitable, fit with the prediction. Based on published data regarding animals using the area (Mussi et al. 2014, Pace et al. 2014, Pace 2016), the entire region seems to be vital for foraging, breeding, social cohesion, mixing, and possibly mating, therefore containing critical habitat (i.e., a habitat scientifically important and critical to the survival of listed threatened species or ecological communities) for sperm whales. Cetaceans, such as sperm whales, occupy an extensive range and there is a strong potential that by protecting their critical habitat, a wide variety of other species that regularly occur within the area and ecosystem processes will be protected (Hoyt 2011). Thus, this modeling exercise may serve as a valuable starting point relative to recognizing submarine canyons as hotspot regions in the Mediterranean to be managed according to sperm whale groups.

MANAGEMENT IMPLICATIONS

Our findings underlined that consideration should be taken regarding type of social aggregation, group composition, and life stage when using modeling techniques for generating suitable habitat maps for conservation purposes. To date, ours is one of the very small number of studies that will allow future management and conservation planning to be based on the comprehensive integration of the spatial ecology of the species' sexual segregation and group differences.

In addition, the dive cycle and the vocalizations produced by sperm whales make it a suitable species to apply passive acoustic techniques to monitor its habitat use and can be used to understand its abundance. Based on the results of the study, it is recommended to incorporate a future passive acoustic monitoring program for sperm whales in Pontino and Campanian Archipelagos to assess the presence of the species year-round, to evaluate potential seasonal patterns, and to measure the effects of anthropogenic activities and their interactions with the species, so that any possible deleterious human impacts can be evaluated and mitigated.

Finally, the recent IMMA status of the Pontino and Campano Archipelagos, assessed thanks to sperm whale occurrence and distribution data (IUCN-MMPATF 2017), may be of great importance to clearly identify the area as highly valuable in terms of biodiversity, and could become an effective way of building institutional capacity to make substantial contributions to the sperm whale conservation needs. This is particularly relevant in this region where 2 coastal MPAs exist, one of them (Neptune's Kingdom around Ischia Island) including a pelagic environment largely inadequate for sperm whale conservation because it does not match with the distribution of the species.

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