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Combining multispecies home range and distribution models aids assessment of MPA effectiveness

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ABSTRACT: Marine protected areas (MPAs) are today's most important tools for the spatial management and conservation of marine species. Yet, the true protection that they provide to individual fish is unknown, leading to uncertainty associated with MPA effectiveness. In this study, conducted in a recently established coastal MPA in Portugal, we combined the results of individual home range estimation and population distribution models for 3 species of commercial importance and contrasting life histories to infer (1) the size of suitable areas where they would be fully protected and (2) the vulnerability to fishing mortality of each species. Results show that the relationship between MPA size and effective protection is strongly modulated by both the species' home range and the distribution of suitable habitat inside and outside the MPA. This approach provides a better insight into the true potential of MPAs in effectively protecting marine species, since it can reveal the size and location of the areas where protection is most effective and a clear, quantitative estimation of the vulnerability to fishing throughout an entire MPA.

KEY WORDS: Cuttlefish · Maxent · Marine reserve · Sole · Vulnerability to fishing · White seabream

INTRODUCTION

Marine protected areas (MPAs) have become a key spatial management and conservation tool for coastal nations worldwide, but their effectiveness is largely uncertain in most, if not all, cases (Kaiser 2011). In fact, the size of the areas where the different species are effectively protected and the amount of time they are available to the fishery is typically unknown.

The adequate design and management of MPAs is highly dependent on the quality of the baseline ecological information. Of particular relevance is the knowledge of the species' site fidelity, distribution and habitat use (Glazer & Delgado 2006, Le Quesne & Codling 2009, Grüss et al. 2011, Schmiing et al. 2013). These data can not only help determine the initial location and correct size of MPAs based on the species' habitat requirements but also provide relevant information for the adaptive management of already implemented MPAs.

Recent studies have presented quantitative models to assess the efficiency of MPAs (Walters et al. 2007, Le Quesne & Codling 2009, Moffitt et al. 2009). However, these models do not consider that no-take areas do not, in most cases, consist of 100% of suitable habitats. It is therefore possible that a no-take area several times larger than the species' home range does not offer adequate protection.

Acoustic telemetry is one of the most widely used methods to track marine species, as it provides long-term, fine-scale spatio-temporal data on individual movement and home range (e.g. Afonso et al. 2009, Abecasis et al. 2013b). However, there is no consensus on how to translate such individual data, the typ-

*Corresponding author: davidbecas@gmail.com ical output of telemetry studies, into the more relevant population-scale projection when evaluating the effectiveness of protection provided from existing MPAs or forecasting their optimal designs.

This study offers evidence that home range areas and habitat suitability should be addressed when designing MPAs. This was achieved by combining information about species home range areas with species distribution models to calculate the effective protection provided to 3 species with contrasting life histories by a small coastal MPA, the Luiz Saldanha Marine Park (LSMP), Portugal. In particular, this study focused on analysing the vulnerability to fishing of the 3 species — cuttlefish *Sepia officinalis*, Senegalese sole *Solea senegalensis* and white seabream *Diplodus sargus* — and on estimating the size of suitable areas where these species are in fact protected from local fisheries. Arguably, an MPA design based on the requirements of only 3 species is unlikely to ensure the full protection of all local marine species. Nevertheless, the contrasting life histories of these 3 species, all of which are also of key commercial importance for the region, ensure the wide spectrum needed to demonstrate the wider applicability of this study towards this MPA. This study is also innovative in combining typical finfish with cephalopods and flatfishes, which are seldom used in MPA studies (Lester et al. 2009, Horta e Costa et al. 2013).

Species distribution models (SDMs) have become an important tool for studies in biogeography, ecology, species management, conservation biology and climate change (Guisan & Zimmermann 2000, Guisan & Thuiller 2005, Elith & Leathwick 2009b, Bean et al. 2012). These statistical methods associate species data (presence, presence/absence or abundance) with mapped environmental predictor variables and/or geographical information to provide information on the presence of species across the entire area of interest (Guisan & Zimmermann 2000). Recent developments in the field of SDMs have produced multiple methods (Elith et al. 2006, Elith & Graham 2009) which are now commonly used to predict species distribution (Elith & Leathwick 2009a, Newbold 2009). The low data requirements and the ease of integration with GIS analysis have made Maxent one of the most widely used software programs for SDMs (Elith et al. 2006, Elith & Leathwick 2009b). Different comparative studies using a wide range of data demonstrated that Maxent is consistently among the best performing methods (Elith et al. 2006, Hernandez et al. 2006, Navarro-Cerrillo et al. 2011). Maxent is a machine-learning method that predicts potentially suitable environmental conditions for the species using presence records and a set of environmental variables, continuous and/or categorical, that are likely to influence the species' fitness and long-term persistence (Phillips et al. 2006, Phillips & Dudík 2008).

The main objectives of this study were to (1) determine the amount of suitable habitats where 3 of the most commercially important fish species are effectively protected and (2) determine the vulnerability of these species to fishing throughout the LSMP.

MATERIALS AND METHODS

Study area

This study took place in the LSMP, which was established in 1998 yet only fully implemented in 2009. Located on the Portuguese western coast, this MPA covers an area of approximately 53 km^2 stretching over 38 km of coastline (Fig. 1). It includes a narrow stretch of rocky reef habitats down to a depth of 15 m and a wider stretch of soft substrates (sand and mud) down to 100 m. The LSMP regulations entail different zones and limitations to extractive activities. Commercial fisheries have different limitations within the different zones: all fisheries are excluded from a full-protection (no-take) area of about 4.2 km^2; octopus traps and jigs are allowed beyond 200 m from the coastline within the 4 partial-protection areas, totalling 21 km^2; and commercial fishing boats less than 7 m long are allowed to operate using traditional fishing gear within the 3 buffer areas, totalling 28 km^2 (Fig. 1). Spearfishing is prohibited within the entire area of the LSMP, whereas recreational angling is only allowed within the 3 buffer areas. With these regulations, the cuttlefish is only fully protected from fishing (trammel nets and jigs) within the no-take zone, whereas the white seabream and the Senegalese sole are fully protected from fishing (longlines and nets, respectively) within both the no-take zone and partial-protection areas.

Studied species

This study focused on 3 species: the sparid *Diplodus sargus* (white seabream), the flatfish *Solea senegalensis* (Senegalese sole) and the cephalopod *Sepia officinalis* (cuttlefish). The 3 species are very distinctive from each other, as they present contrasting ecological traits and life histories, but share high economic value across southern Europe. In the LSMP area, both the cuttlefish and the Senegalese sole are targeted by the

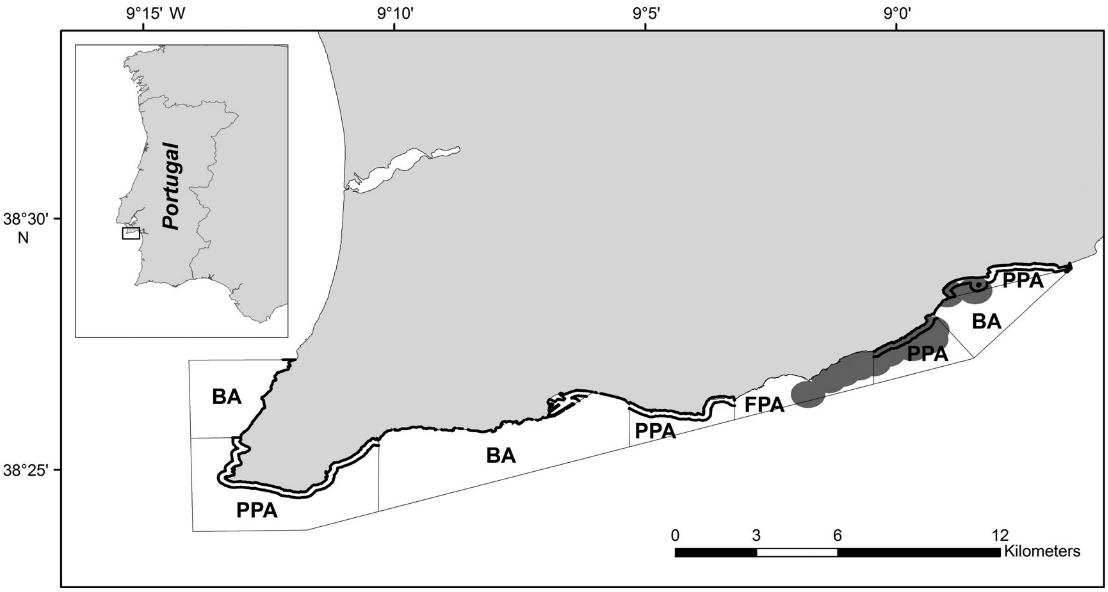

Fig. 1. Study area, showing the 3 different protection levels: buffer areas (BAs), partial-protection areas (PPAs) and a full-protection or no-take area (FPA). The dark grey area represents the monitored area during the acoustic telemetry studies. The black line in the PPAs indicates 200 m from the coastline

local small-scale commercial vessels that operate mainly with trammel nets (Batista et al. 2009), whereas the white seabream is mainly captured by artisanal longlines and recreational fishing (Veiga et al. 2010). Their habitat preferences are also very distinct: the Senegalese sole is a benthonic species that occupies soft substrates (Quéro et al. 1986), the white seabream is a demersal species that prefers hard substrates such as rocky reefs but also forages on soft substrates (Abecasis et al. 2013b) and the cuttlefish is a nektonic-benthonic species that makes use of different types of substrates (Guerra 2006). All 3 species have very different life histories, even though they all use estuaries as nursery areas and later move to marine coastal areas. The cuttlefish is a semelparous species with a maximum lifetime of about 2 yr (Le Goff & Daguzan 1991), whereas the Senegalese sole and the white seabream are iteroparous species that can reach 8 and 18 yr old, respectively (Abecasis et al. 2008, Teixeira & Cabral 2010). By focusing on species that present such different biological, ecological and economic characteristics, this study should allow us to shed light on the benefits and performance of this MPA for a wider range of species.

Species distribution modelling

To model species distribution, we used Maxent software version 3.3.3k (available from www.cs.princeton.edu/~schapire/maxent/), with the maximum number of iterations set to 5000. Based on the ecological knowledge of the 3 species and the availability of environmental data for the area, we selected the following variables as explanatory variables in the model: 'habitat', 'bathymetry', 'curvature', 'slope', 'aspect' and 'distance to rock'. The variables 'curvature', 'slope' and 'aspect' represent the surface curvature, the rate of maximum change in depth from each cell and the direction that the slope is facing (north, south, east, west), respectively. The variables 'habitat' and 'aspect' were set as categorical variables, whereas the remaining variables were set as continuous. Information on 'habitat' was collected using acoustic and video surveys and comprised 11 different habitats (unknown, mud to sandy mud, muddy fine sand, muddy medium sand, coarse sand, rocky outcrops, fine sand, medium sand, algae on rock, nearshore reefs and mixed sands). These data were presented in raster format with a cell size of approximately 40 × 40 m. The variable 'bathymetry' was estimated by combining data from a recent bathymetric survey. In addition, we estimated the variable 'distance to rock' by calculating the Euclidean distance to the nearest rocky bottom.

We used presence data from previous acoustic telemetry studies on these 3 species (Abecasis 2013, Abecasis et al. 2013a, 2014) as training data for the SDMs. Presence locations for each species were obtained by triangulation of detections in multiple receivers, with overlapping range, over 30 min periods (Simpfendorfer et al. 2002). Acoustic detections of Senegalese sole and white seabream occurred for up to 290 d, whereas detections of cuttlefish only occurred during the months of November and December. The total number of detections was 36 657 for cuttlefish, 385 371 for Senegalese sole and 176 499 for white seabream. To avoid autocorrelation of presence locations, consecutive locations of the same animal used in the models had a minimum interval of 24 h (Reynolds & Laundre 1990). The final number of presence locations was 103 from 5 cuttlefish, 353 from 22 Senegalese sole and 118 from 20 white seabream. A sampling bias file with the extension of the acoustically monitored area was used to remove sampling distribution bias (Phillips et al. 2009, Syfert et al. 2013, Yackulic et al. 2013). Data from experimental trammel net monitoring surveys, carried out throughout the LSMP, were used as independent test data for cuttlefish and Senegalese sole (Abecasis 2013, Abecasis et al. 2013a, 2014). For the cuttlefish, however, given that the acoustic telemetry data presented a short temporal extent (November to December), we only considered the trammel net surveys carried out during autumn, which correspond to approximately the same time frame. For the white seabream, we obtained test data from underwater visual observations, given that this species is rarely caught by the trammel nets (for more details, see Horta e Costa et al. 2013). We ran models with regularization multipliers of 1, 2, 2.5 and 3 and compared them using the small sample size-corrected Akaike's information criterion (AICc), estimated using ENMTools (Warren & Seifert 2011), as recommended by Rodda et al. (2011). The regularization multiplier parameter affects how closely fitted the output distribution is. The default of 1.0 will result in a closer fit to the given presence records, while a larger regularization multiplier will give a more spread out, less localized prediction and is less prone to overfitting (Warren & Seifert 2011). The AICc approach weights model fit with the number of included variables to provide a relative score for each model. Different types of features, which correspond to how Maxent treats each predictor variable, were also tested. We tested hinge features, which combine linear and step functions; linear and quadratic features, where Maxent uses simple linear coefficients and squared predictor values; and also auto features, where Maxent automates the task of choosing feature types using an empirical algorithm based on sample size. Following comparison of the different models with the AICc approach, we proceeded with the jackknife test of variable importance (implemented in Maxent) to see if any of the variables could be removed without sacrificing model performance. We started with all variables and then removed each variable one by one based on the drop of the regularized training gain.

The area under the receiver operating characteristic curve (AUC) was used for model evaluation (Elith 2002). Although Lobo et al. (2008) considered that AUC was not appropriate for model comparison, Elith et al. (2011) found it suitable to test for the model's predictive performance. The AUC statistic ranges between 0 and 1, with 1 representing a perfect model, and 0.5 representing a model no different from random. AUC values above 0.7 are considered usable, with values above 0.8 considered good, and values above 0.9 considered very good (Swets 1988). We compared the AUC value against a null distribution of AUC values, based on random sampling, to test the model significance against a random model (Raes & ter Steege 2007). We generated 100 sets of sample points randomly drawn from background points for each species. Since the number of presence locations varied with each species, we generated data sets with a random number of points equal to the number of points available for each species. Because the presence locations were biased, the randomly drawn points were selected from the acoustically monitored area to avoid higher chances of significantly deviating from the null model (Raes & ter Steege 2007). The AUC values obtained for the null models were used to create a frequency distribution. The calculated AUC value for each species model was then compared with the 95th percentile AUC of the null frequency distribution. A model performs better than random and is considered significant if its AUC is greater than the 95th percentile AUC of the null distribution (Raes & ter Steege 2007).

Because Maxent produces continuous outputs, thresholds were adopted to make a distinction between suitable and unsuitable habitat areas. Although the use of presence/absence is more uncertain than relying on presence probabilities (Meynard & Kaplan 2012), the use of binary models was the most straightforward for the estimation of vulnerability to fishing. Two thresholds were applied, the lowest presence threshold (LPT) and the maximum sensitivity plus specificity threshold (MSST). Sensitivity is the proportion of observed presences that are correctly predicted and therefore quantifies omission errors. Specificity is the proportion of observed absences that are predicted as such and therefore quantifies commission errors. The LPT, also known as minimum training presence, is the lowest prediction value returned by Maxent for a location with observed presence of the species and is one of the most commonly used thresholds (Pearson et al. 2007, Thorn et al. 2009, Bean et al. 2012). The MSST threshold is one of the better performers among the various sensitivity-specificity methods and has been shown to achieve better results than LPT (Liu et al. 2005, Hernandez et al. 2006, Bean et al. 2012). The performance of the binary models was measured using the true skill statistic (TSS). The TSS is independent of prevalence, and its results are highly correlated with the AUC statistic (Allouche et al. 2006). TSS varies between −1 and 1, where values below 0 represent models that perform no better than random, and values close to 1 represent perfect agreement. Landis & Koch (1977) consider TSS values of 0 to 0.20 as slight, 0.21 to 0.40 as fair, 0.41 to 0.60 as moderate, 0.61 to 0.80 as substantial and 0.81 to 1 as almost perfect agreement.

We combined information provided by the SDMs with home range information to determine the effective protection provided by the LSMP to the 3 study species. The minimum, average and maximum length of home range for each species was obtained from previous acoustic telemetry studies conducted in the area (Abecasis 2013, Abecasis et al. 2013a, 2014). From the SDMs, we calculated the size of the suitable areas where species were fully protected (no-take zone for cuttlefish and no-take plus partial-protection zones for Senegalese sole and white seabream). Vulnerability to fishing (V_x) was estimated for each discrete point (x) along the coast of the LSMP for an individual, with its home range centered at x (Moffitt et al. 2009). This vulnerability to fishing equals the fraction of the home range that overlaps the fished areas and is estimated by:

$$V_x = \frac{1}{H}\sum_{i-\left(\frac{H}{2}\right)}^{i+\left(\frac{H}{2}\right)} c_x + i \qquad (1)$$

where H is the home range length in reserve length units, i defines all the locations included in the home range along the coastline and c is the coastline, defined as:

$$c_x \begin{cases} 0 & \text{reserve} \\ 1 & \text{non-reserve} \end{cases} \qquad (2)$$

RESULTS

Cuttlefish

The cuttlefish distribution model with the regularization parameter of 3 presented the highest AUC value. Nevertheless, the AICc revealed that the model using the regularization parameter of 1 was the most adequate from a parsimonious perspective (Table 1). The cuttlefish distribution model using auto features performed better than the models using only hinge features or linear plus quadratic features (Table 1). The AUC value for the models with different predictor variables was higher for the model containing the variables 'bathymetry', 'distance to rock', 'aspect' and 'slope' (Table 1). However, the AICc analysis suggests that the best performance was achieved when using all variables except 'slope' (Table 1).

The jackknife test revealed that 'bathymetry' was the variable that contributed the most to the model, given that removing this variable resulted in the largest reduction of the regularized training gain.

The relationship between 'bathymetry' and 'presence suitability' resembles a bell-shaped curve that peaks around a depth of 15 m (Fig. 2). The response curve of the relationship between 'suitability' and 'distance to rocky bottoms' suggests that, at least during the months of November and December, the suitability of areas farther than 450 m away from rocky bottoms is very low for cuttlefish (Fig. 2). Medium sand (Category 7) and algae on rock (Category 8) were the habitats that presented the highest suitability for cuttlefish (Fig. 2B).

The final suitability map for cuttlefish in the LSMP during the months of November and December (Fig. 3A) achieved an AUC of 0.963, which exceeds the 95th percentile of the AUC of the biased-corrected null model distribution (0.962), indicating that it is significantly better than a random model. The binary map of suitable and unsuitable areas based on the LPT achieved a TSS of 0.376 (Fig. 3B), while the map using the MSST achieved a TSS of 0.146 (Fig. 3C).

Senegalese sole

The Senegalese sole distribution model with a regularization parameter of 1 achieved the best AUC and AICc values (Table 1). The distribution model using auto features performed better than the models using only hinge features or linear plus quadratic features (Table 1). According to the AICc, the best model was achieved when considering the variables 'bathymetry', 'habitat', 'aspect', 'slope' and 'curvature'. The jackknife test revealed that 'bathymetry' was the variable that contributed the most to the model. Removal of this variable resulted in the largest reduction of the regularized training gain, indicating that bathymetry is the variable with the most useful information and also the one that appears to have the most information that is absent in the other variables.

Table 1. Sample size-corrected Akaike's information criterion (AICc) and area under the receiver operating characteristic curve (AUC) results for the *Sepia officinalis*, *Solea senegalensis* and *Diplodus sargus* distribution models estimated with Maxent. *S. officinalis* models were estimated with 103 presence points from 5 ind., *S. senegalensis* models were estimated with 353 presence points from 22 ind., *D. sargus* models were estimated with 118 presence points from 20 ind. All individuals were tagged with acoustic transmitters. A = 'aspect', B = 'bathymetry', C = 'curvature', D = 'distance to rock', H = 'habitat', S = 'slope'

		AICc	Test AUC	Training AUC	No. of parameters
Regularization multiplier					
Sepia officinalis	1	2089.050	0.757	0.963	27
	2	2106.396	0.766	0.961	21
	2.5	2118.178	0.770	0.960	21
	3	2121.860	0.773	0.958	19
Solea senegalensis	1	6154.368	0.769	0.946	56
	2	6178.760	0.760	0.944	36
	2.5	6219.291	0.762	0.943	39
	3	6243.030	0.763	0.941	35
Diplodus sargus	1	1860.726	0.820	0.985	42
	2	1859.498	0.854	0.982	25
	2.5	1876.307	0.865	0.981	24
	3	1882.392	0.877	0.980	21
Feature					
Sepia officinalis	Auto	2089.050	0.757	0.963	27
	Hinge	2186.138	0.790	0.958	36
	Linear and quadratic	2140.644	0.785	0.954	14
Solea senegalensis	Auto	6154.368	0.769	0.946	56
	Hinge	6431.699	0.783	0.939	67
	Linear and quadratic	6480.751	0.776	0.928	19
Diplodus sargus	Auto	1859.498	0.854	0.982	25
	Hinge	1937.731	0.780	0.978	32
	Linear and quadratic	1970.980	0.941	0.971	14
Variable					
Sepia officinalis	B, H, D, A, C and S	2089.050	0.757	0.963	27
	B, H, D, A and C	2087.975	0.787	0.963	27
	B, H, D and A	2121.283	0.789	0.960	21
	B, H and D	2158.772	0.788	0.953	23
	B and H	2246.013	0.765	0.933	15
	B	2274.929	0.764	0.920	11
Solea senegalensis	B, H, A, S and C	6154.368	0.769	0.946	56
	B, H, A and S	6164.712	0.785	0.944	43
	B, A and S	6207.511	0.784	0.940	37
	B and S	6338.511	0.770	0.926	32
	B	6464.368	0.785	0.921	18
Diplodus sargus	B, H, D, A, C and S	1859.498	0.854	0.982	25
	B, D, A, C and S	1854.470	0.851	0.982	23
	B, D; A and S	1853.764	0.842	0.981	20
	B, D and A	1855.285	0.840	0.981	16
	B and D	1901.842	0.823	0.977	13
	B	1980.530	0.814	0.961	8

The study area suitability for Senegalese sole, according to the different variables, is shown in Fig. 2. The highest suitability occurred between the bathymetries of 5 and 25 m; sea bottoms facing east, southeast and south; fine sands and medium sands habitats; and flatter sea bottoms in general, with slope angles between 0.3 and 5°.

The map of the final model suitability for Senegalese sole in the LSMP area shows that the highest suitability was found within the no-take zone and adjacent partial-protection areas (Fig. 4A). The AUC obtained for this model (0.946) was higher than the 95the percentile of the AUC of the biased-corrected null model distribution (0.944), indicating that it is significantly better than random. The binary map of suitable and unsuitable areas based on the LPT achieved a TSS of 0.285 (Fig. 4B), while the map using the MSST achieved a TSS of 0.421 (Fig. 4C).

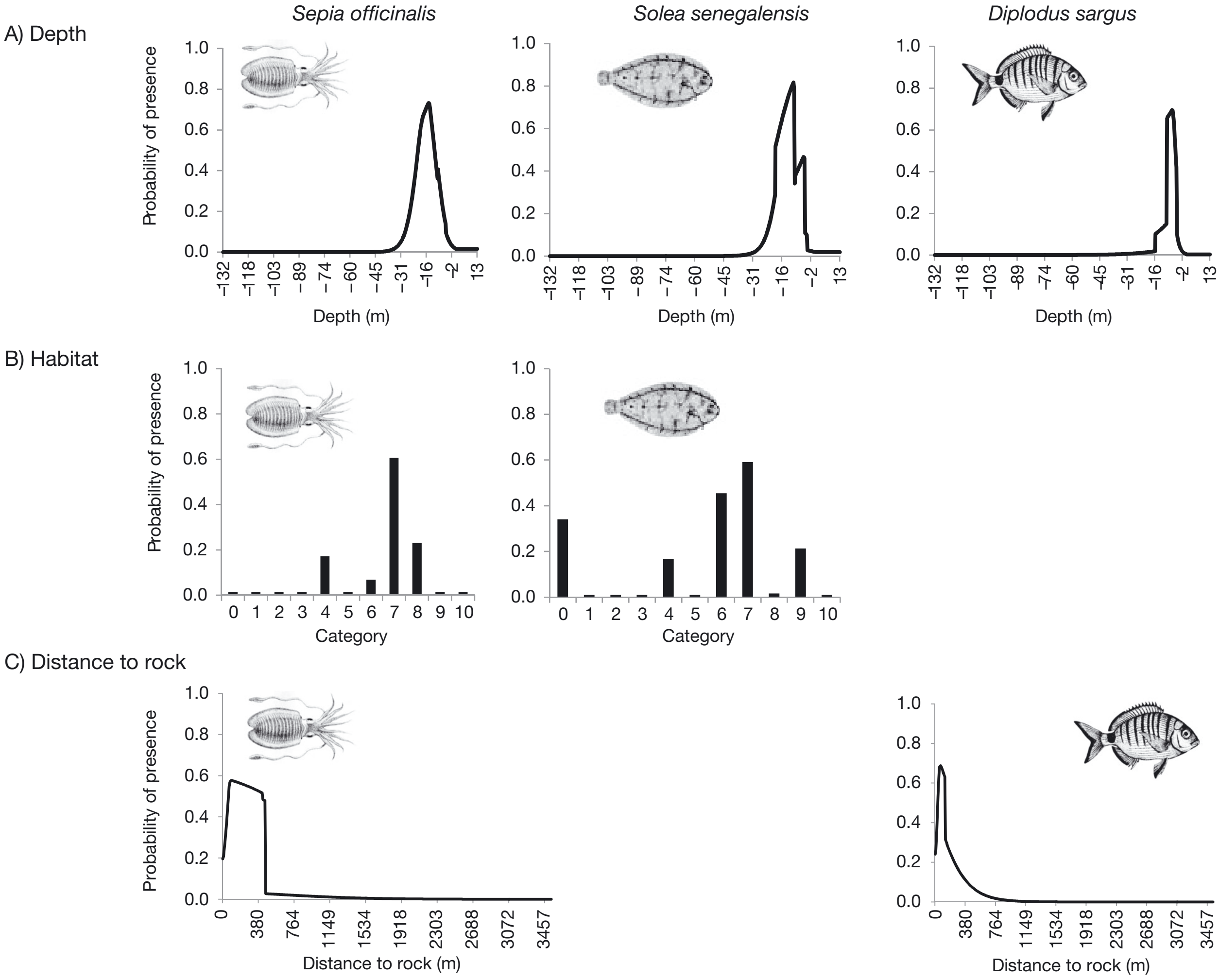

Fig. 2. Response curves of the different variables for *Sepia officinalis*, *Solea senegalensis* and *Diplodus sargus* distribution models estimated with Maxent. (A) Depth, (B) habitat, (C) distance to rock, (D) aspect, (E) curvature, and (F) slope. Habitat categories in (B): 0 = unknown, 1 = mud to sandy mud, 2 = muddy fine sand, 3 = muddy medium sand, 4 = coarse sand, 5 = rocky outcrops, 6 = fine sand, 7 = medium sand, 8 = algae on rock, 9 = nearshore reefs, 10 = mixed sands. Aspect categories in (D): 1 = flat, 2 = north, 3 = northeast, 4 = east, 5 = southeast, 6 = south, 7 = southwest, 8 = west, 9 = northwest, 10 = north. Missing panels are when the variables were not used in the final model (figure continues on next page)

White seabream

Although the best training AUC results were obtained for the model that used a regularization parameter of 0.5, from a parsimonious point of view the most adequate model was achieved when using a regularization parameter of 2 (Table 1). When the features used were changed, the best model, in terms of AICc, was achieved when using the auto features option (Table 1). According to the AICc results, the best model was achieved when only the variables 'bathymetry', 'distance to rock', 'aspect' and 'slope' were used (Table 1).

As for the previous species, 'bathymetry' was the variable that contributed the most to the model, according to the jackknife analysis of variable importance. Besides providing the most useful information, this variable seems to present information that is absent for other variables.

According to the final distribution model obtained for white seabream, the highest suitability occurs between the depths of 5 and 10 m and when the distance to rock is less than 120 m (Fig. 2). The map of the final model suitability for white seabream in the LSMP area demonstrates that the areas with highest suitability were located near rocky shore

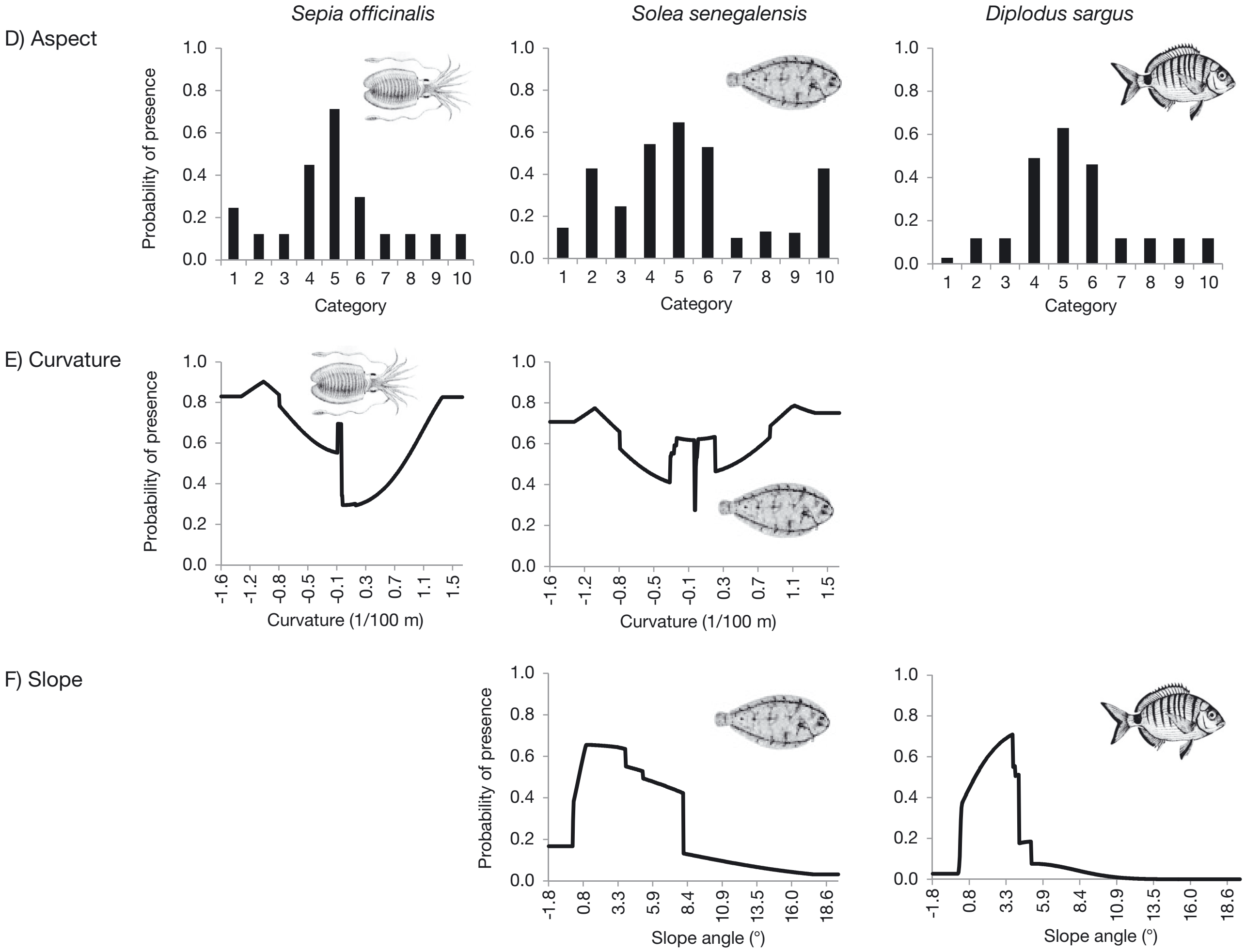

Fig. 2 (continued)

areas throughout the entire MPA (Fig. 5A). The AUC obtained for this model (0.981) was higher than the 95th percentile of the AUC of the biased-corrected null model distribution (0.959), indicating that it is significantly better than random. The binary map of suitable and unsuitable areas based on the LPT achieved a TSS of 0.494 (Fig. 5B), while the map using the MSST achieved a TSS of 0.260 (Fig. 5C).

The area with suitable habitats for all of the studied species is limited to areas close to the coastline and where the coast is facing south (Fig. 6).

Vulnerability to fishing

The regulated zones where both the Senegalese sole and the white seabream are protected from fishing are larger than 25 km^2 in total (fully protected plus partially protected areas). For cuttlefish, the area where it is fully protected from fisheries is the no-take (full-protection) area, which corresponds to approximately 4.2 km^2. Although cuttlefish are also protected in the first 200 m from the coastline in partially protected areas, these areas were not considered, given their small size. Nevertheless, only a small proportion of these protected areas corresponds to suitable habitats for these species (Table 2). In fact, of the entire LSMP, less than 8% presents suitable habitats for the 3 species, with the highest percentage being found in the fully protected area (Table 3). The vulnerability to fishing, considering an individual's home range centered in the middle of the no-take area, was 0.0 for every species and home range considered (Fig. 7). In the western partial-protection area, the vulnerability to fishing was 0.0 for white seabream and Senegalese sole except when considering the maximum home range for Senegalese sole, where it reached a minimum of 0.05 (Fig. 7).

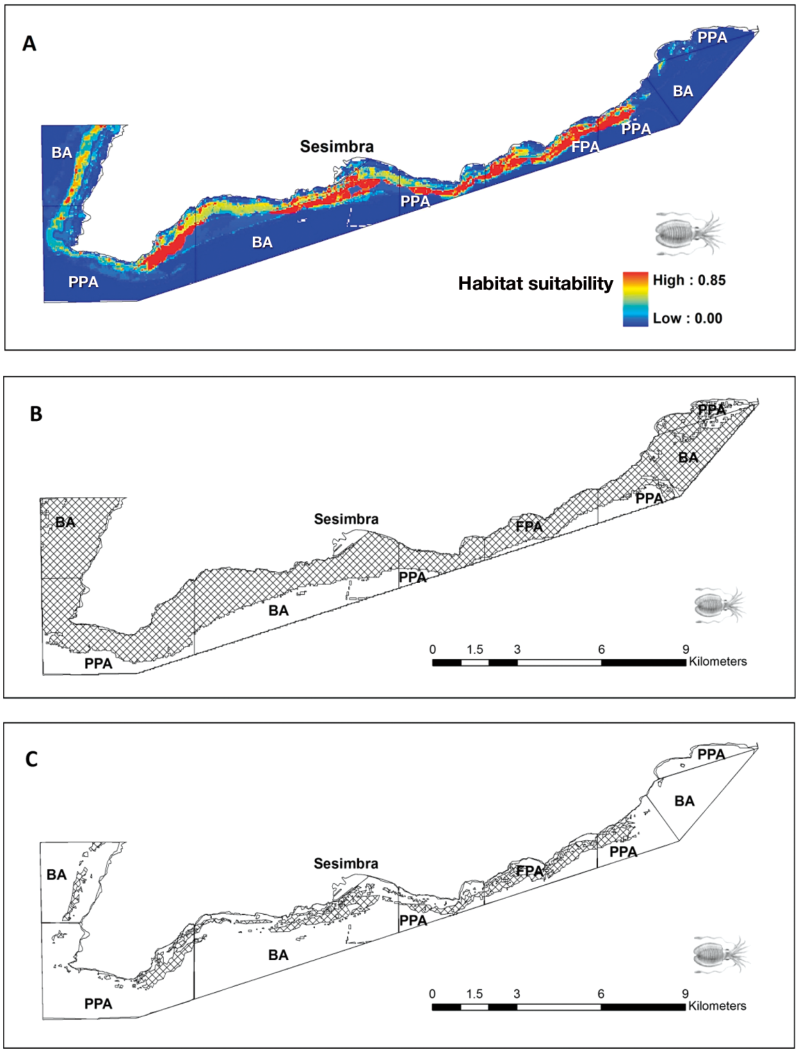

Fig. 3. (A) Habitat suitability map estimated with Maxent and (B,C) binary suitability maps using (B) the lowest presence threshold and (C) the maximum sensitivity plus specificity threshold of *Sepia officinalis* in the Luiz Saldanha Marine Park during the months of November and December. Cross-hatched areas in (B,C) represent suitable habitats. BA = buffer area, PPA = partial-protection area, FPA = full-protection area

DISCUSSION

The results of the home range studies, together with the adequacy of the resulting models, allow us to draw important conclusions about the design suitability of the LSMP for cuttlefish, Senegalese sole and white seabream and the extent of protection offered by the MPA to these 3 species combined. Importantly, this study goes a step further when compared with previous studies using home range areas only (e.g. Moffitt et al. 2009, Grüss et al. 2011) by combining this information with species distribution and indirect habitat preference throughout the study area.

Model adequacy

The values of AUC obtained for the SDMs, when compared with the AUC value of the null models, are evidence that the final models obtained through Maxent are adequate and likely useful instruments (Swets 1988, Elith 2002) for the evaluation of the protection offered by MPA and the vulnerability to fishing. Additionally, a qualitative visual analysis of the resulting maps, made by local scientists and fishermen, also suggested that these models are helpful.

Although not frequently used in previous SDM studies, correcting for sampling bias decreases the number of false presences and false absences (Syfert et al. 2013). As in other studies (e.g. Phillips & Dudík 2008, Radosavljevic & Anderson 2014), we show that species-specific tuning of model parameters can improve model performance. In addition, we used a totally independent test data set, which is considered the most adequate approach to approximate optimal model complexity via tuning experiments (Phillips & Dudík 2008, Peterson et al. 2011). All of these measures are known to reduce model overfitting and improve performance (Phillips & Dudík 2008, Radosavljevic & Anderson 2014). Nevertheless, the AUC and TSS values obtained are only marginally good, and some of the response curves (e.g. curvature) are complex, which could indicate model overfitting, probably because of data limitations (Elith & Graham 2009). Yet the AUC value itself should not be used as a guide to model utility, since it can be misleading (Lobo et al. 2008).

It could be argued that other potentially relevant input variables (e.g. hydrodynamics and prey distribution and abundance) could also prove useful to improve the predictive power of the spatial distribution models of these species. However, information on such variables was either absent or unavailable at adequate spatial scales for this area.

Importantly, the 6 variables that were selected to run the SDMs reflect various environmental factors known to influence marine species distributions.

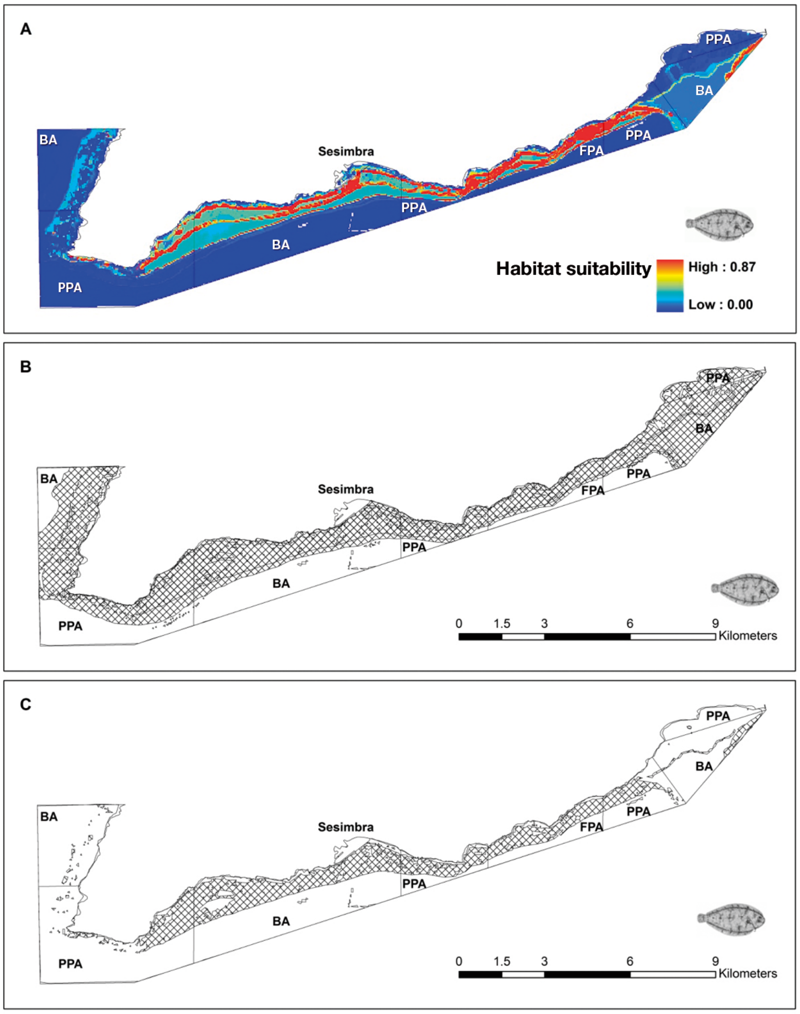

Fig. 4. (A) Habitat suitability map estimated with Maxent and (B,C) binary habitat suitability maps using (B) the lowest presence threshold and (C) the maximum sensitivity plus specificity threshold of *Solea senegalensis* in the Luiz Saldanha Marine Park. Cross-hatched areas in (B,C) represent suitable habitats. Area abbreviations defined in Fig. 3

The variable 'habitat' was used because marine species are known to prefer specific and sometimes distinct habitats throughout their life cycle. The variable 'bathymetry' is widely used as an indirect proxy for several proximal factors such as temperature, light and pressure (Elith & Leathwick 2009b). The variable 'aspect' was selected as a proxy for hydrodynamic variables, since in this specific case bottoms oriented to the southern and western quadrants are more influenced by strong winds and high seas, whereas those facing the northern and eastern quadrants are more sheltered. The variables 'slope' and 'curvature' were also considered because these have been used as predictor variables for several marine species (Leathwick et al. 2008, Owens et al. 2012, Schmiing et al. 2013). The variable 'distance to rock' could be interpreted differently, depending on the studied species. Adult white seabream, for instance, are known to prefer rocky bottom habitats (Abecasis et al. 2013b), and therefore 'distance to rock' is likely to simply stand for distance to its preferred habitat. In the particular case of the cuttlefish, however, it can be interpreted as distance to spawning grounds, since this species prefers soft substrate but attaches its eggs to hard substrates like seaweeds, shells and debris (Ezzeddine-Najai 1997), and such substrates are also frequently found near shallow rocky bottoms. In fact, egg clutches were frequently observed in the acoustic receivers' mooring structures, particularly in those located in vast sandy areas farthest away from rocky bottoms (Abecasis et al. 2013a), where other hard substrates are absent or rare. These observations support the hypothesis that cuttlefish use habitats closer to rocky bottoms during the spawning season because it is easier to find adequate substrates to attach their eggs. It also explains why the variables 'distance to rock' and 'bathymetry' were the most important for the final cuttlefish's SDM, especially considering that data collection took place during the migration/spawning months of November and December.

The response curves obtained for the predictor variables were, in some cases, very complex. Although this could indicate an unrealistic fit of the model, the AUC and TSS results obtained show their adequacy. This is especially relevant because a low number of false negatives is highly desirable in the particular case of conservation spatial planning because false negatives could lead to potentially suitable areas being left out of management plans (Araújo & Guisan 2006).

The SDMs for Senegalese sole and white seabream were estimated with presence locations obtained throughout almost the entire year. Therefore, it is likely that the suitability maps represent an accurate picture for habitat selection of adults of

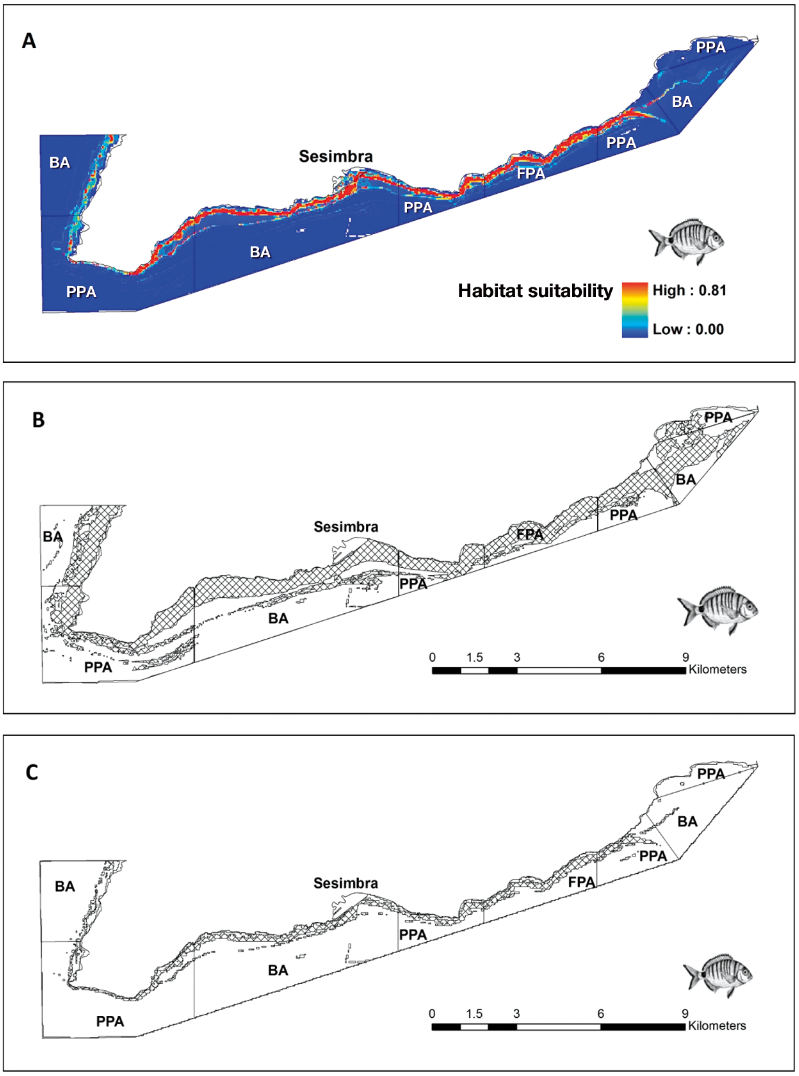

Fig. 5. (A) Habitat suitability map estimated with Maxent and (B,C) binary habitat suitability maps using (B) the lowest presence threshold and (C) the maximum sensitivity plus specificity threshold of *Diplodus sargus* in the Luiz Saldanha Marine Park. Cross-hatched areas in (B,C) represent suitable habitats. Area abbreviations defined in Fig. 3

both species in the LSMP. However, this was not the case for cuttlefish, for which presence data were only obtained for a shorter period of time (for more details, see Abecasis et al. 2013a). Considering that the cuttlefish is a migratory species that inhabits a wide range of habitats, it is highly probable that the distribution model obtained underestimates the true distribution for this species during its adult phase. Instead, the information provided by the model should be interpreted as an SDM for the cuttlefish's spawning period because presence data were obtained from adults during this period (Abecasis et al. 2013a).

Habitat suitability

The suitability maps revealed that the LSMP area facing south contains the largest area of suitable habitats for all 3 species. The sheltering of this area from the dominant north winds and ocean swell has been put forward as one of the reasons for its high biodiversity (Gonçalves et al. 2003).

Despite the fair to moderate TSS values associated with the obtained SDMs, the results for white seabream might be slightly biased, given that the areas defined as suitable when using the MSST expanded farther away from rocky bottoms than anticipated, considering the results of experimental fishing trials. Some bias related to less accurate positions used as training data may have occurred, and as a result, several sandy bottom areas relatively distant from rocky bottoms scored high suitability. Additionally, the method used to obtain the fishes' fine-scale positions limited the capability to distinguish between a true position over rocky bottoms and an assumed position over sandy bottoms. The reason for this limitation is that the acoustic receivers were located in line with each other, parallel to the coast, and on sandy bottoms. Consequently, nearly all locations were associated with sandy bottoms when, in fact, fish were likely roving over the nearby rocky bottoms within the detection range. This possibility is supported by the inclusion of 'distance to rock' as the second most important variable for the white seabream distribution model, confirming previous studies that demonstrated this species' preference for rocky bottoms, even though excursions to sandy bottoms may be frequent (Abecasis et al. 2013b). Regarding the Senegalese sole, the SDM model suggests that fine and medium sands are the habitats with the highest suitability, which is consistent with the results of habitat selection studies (Abecasis et al. 2014).

As in other studies of marine fish species (e.g. Leathwick et al. 2008, Lefkaditou et al. 2008), 'bathymetry' was the variable that most contributed to the distribution models. According to our models, the depth interval in which the white seabream and the

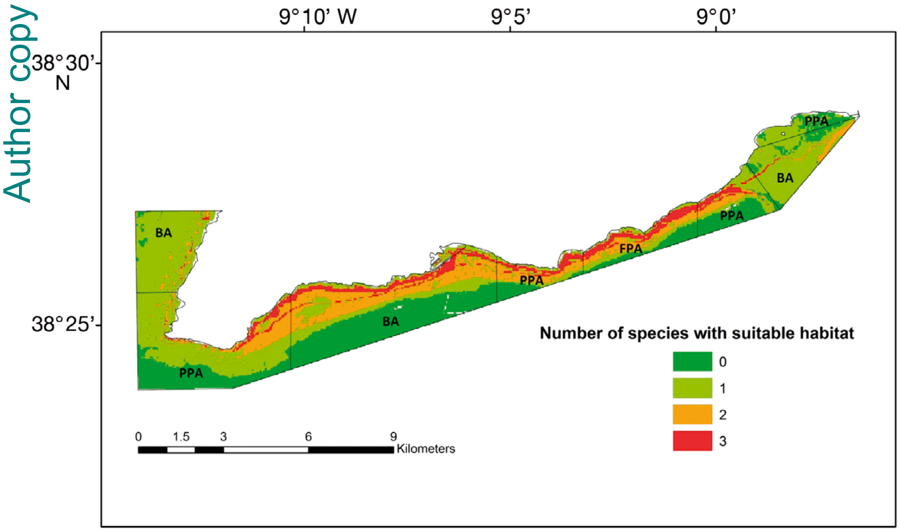

Fig. 6. Overlap of the binary suitability maps that achieved the highest true skill statistic for the study species (*Sepia officinalis*, *Solea senegalensis* and *Diplodus sargus*). BA = buffer area, PPA = partial-protection area, FPA = full-protection area

Table 2. Average home range area (Avg. HR), size of full-protection areas (FPA) and full-protection suitable areas (FPSA) for *Sepia officinalis*, *Solea senegalensis* and *Diplodus sargus*. LPT indicates habitat suitability maps based on the lowest presence threshold; MSST indicates habitat suitability maps based on maximum sensitivity plus specificity threshold. For *S. senegalensis* and *D. sargus*, the marine reserve area includes the full-protection and partial-protection areas. For *S. officinalis*, the marine reserve area only includes the full-protection area

Variable	*S. officinalis*		*S. senegalensis*		*D. sargus*	
	LPT	MSST	LPT	MSST	LPT	MSST
Avg. HR (km^2)	1.26[a]	1.26[a]	1.19	1.19	0.65	0.65
FPA (km^2)	4.2	4.2	25.3	25.3	25.3	25.3
FPSA (km^2)	3.2	1.5	14.7	6.4	10.4	2.9
Minimum length HR (km)	0.9	0.9	0.9	0.9	0.9	0.9
Avg. length HR (km)	2.26	2.26	1.89	1.89	1.39	1.39
Maximum length HR (km)	3.5	3.5	2.8	2.8	3.4	3.4

[a] Home range areas based on minimum convex polygon

Table 3. Percentage of suitable habitat for 0, 1, 2 and 3 of the study species (*Sepia officinalis*, *Diplodus sargus* and *Solea senegalensis*) in the entire marine protected area (MPA) and in each protection level

No. of species	Entire MPA (%)	Full-protection area (%)	Partial-protection area (%)	Buffer area (%)
0	29.47	22.94	31.54	29.03
1	44.29	26.19	44.64	46.77
2	18.85	28.27	16.76	19.03
3	7.39	22.60	7.07	5.17

Senegalese sole were more common is consistent with the results obtained during the experimental fishing (Cunha et al. 2011). For the cuttlefish, the model suggested that suitable habitats were limited to the interval between 0 and 40 m deep. However, this might not reflect the true bathymetric distribution of this species, which is known to occur at depths up to 200 m (Guerra 2006), particularly because the area monitored during the acoustic telemetry campaigns was confined to shallower habitats because of the limited number of receivers available. Moreover, the presence locations were obtained during a short period of time that overlapped the spawning season, during which time cuttlefish have been reported to migrate into shallower waters (Ezzeddine-Najai 1997, Gauvrit et al. 1997, Wang et al. 2003).

Protection

Our results demonstrate that the LSMP offers different levels of protection, depending on species. This is not only the result of the different regulations applied to each of the LSMP's zones (e.g. the fishery targeting cuttlefish is only forbidden within the no-take zone, whereas the fisheries targeting Senegalese sole and white seabream are forbidden in both the no-take and partially protected zones) but also a consequence of the different movement patterns and home range areas required by each species.

Overall, the LSMP appears to provide full protection from fisheries to individuals of white seabream and Senegalese sole that have their home ranges centered anywhere in the no-take area or in central areas of partial-protection zones. In fact, the results of a recent study suggest that the white seabream may already be benefiting from implementation of the LSMP, given the increase in its abundance and biomass (Horta e Costa et al. 2013). For the Senegalese sole, the LSMP seems to

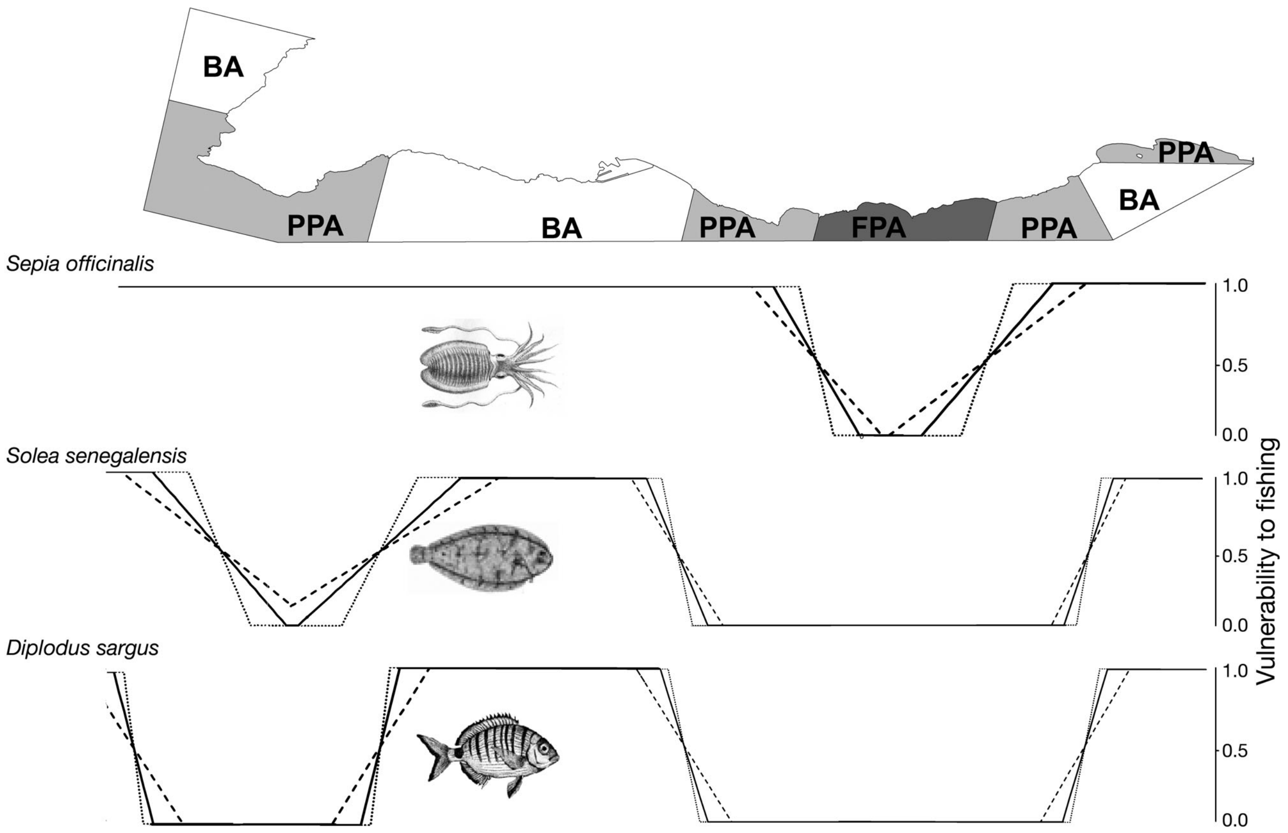

Fig. 7. Vulnerability to fishing for *Sepia officinalis*, *Solea senegalensis* and *Diplodus sargus* in the Luiz Saldanha Marine Park. The dotted line indicates vulnerability estimates considering the minimum home range, the black line indicates vulnerability considering the average home range and the dashed line indicates vulnerability considering the maximum home range. BA = buffer area, PPA = partial-protection area, FPA = full-protection area

play an important role in the protection of local populations, given the large size of suitable areas for this species located within areas where the species is fully protected. However, the effects of protection to this species are yet to be detected (Abecasis et al. 2014).

The cuttlefish, in contrast, appears to benefit less from protection, as our results indicate higher vulnerability to fishing throughout the LSMP. Previous studies suggest that this species presents low site fidelity and undertakes large migrations (Wang et al. 2003, Abecasis et al. 2013a), which is consistent with the short periods of time in which tagged cuttlefish remained within the study area. Therefore, despite the protection provided by the no-take area to cuttlefish, this result might be misleading, since this species presents no site fidelity.

This study focuses on adult individuals only. In fact, some life history stages of the study species are not common in the study area. Important factors such as larval dispersal, early life history periods and recruitment should be considered when overall MPA efficiency is assessed, especially when species persistence is considered. Nevertheless, this study provides important information regarding the protection of commercially important fish species and how habitat suitability should be taken into account.

CONCLUSIONS

This study demonstrates that the combined use of home range areas and SDMs allows for an estimate of the increase in vulnerability to fishing as a function of the species' habitat use and shape of the reserve units. It shows that such an increase will vary substantially, depending on the species' behaviour, and can be modulated by the distribution of their preferred habitat patches within the reserve. This study differs from previous classical works analysing the implications of fish biotelemetry to spatial management by upscaling from individual telemetry data to the population scale of relevance for the assessment of MPA effectiveness and optimal design. Also, contrary to most conceptual modeling MPA studies, our approach is driven by individual movement and habitat use data rather than by previously defined behavioural patterns for the species and is thus a better representation of their behavioural patterns and implications of reserve scenarios and vice versa.

This methodology can and should be used in identifying multispecies MPA designs, whether this is done *a priori* or as part of an adaptive management strategy of MPAs. In the particular case of the LSMP, the levels of protection suggest that this MPA may provide adequate protection for the Senegalese sole and the white seabream if compliance is adequate, but this is not the case for the cuttlefish, given this species' higher levels of exposure to fisheries and very low residency. Nevertheless, to determine the effectiveness of an MPA to achieve species persistence factors such as larval dispersal, fishing effort outside the MPA, recruitment parameters and minimum population size must also be considered.

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