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Assessing *Octopus vulgaris* distribution using presence-only model methods

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Abstract The distribution of the common octopus (*Octopus vulgaris*) in the Mediterranean and Eastern Atlantic waters is evaluated using two presence-only analyses: The maximum entropy model (Maxent) and the ecological niche factor analysis (ENFA). Maxent predicts those geographical areas that satisfy the environmental or abiotic requirements of a species while ENFA explores the niche and habitat preferences of *O. vulgaris*. The analyses were implemented recovering the spatial information from 213 octopus presence data collected from surveys and bibliographical records. Together, these analyses provided reasonable estimates of the species distribution and the octopus habitat. Among the gathered set of explanatory environmental variables, sea bottom temperature, sea bottom salinity, surface dissolved oxygen and sea surface chlorophyll-α appear as the main variables involved in *O. vulgaris* distribution. These results were confronted with the available literature.

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Introduction

The comprehension of the geographical distribution of a species is one of the most important aspects for the study of its populations, ecology and management. In marine species, the relationships between species distribution and environmental factors are essential to comprehend many aspects of their ecology towards effective conservation and management and assessment of possible impacts from anthropogenic activities (MacLeod et al., 2008; Valavanis et al., 2008). However, in many cases, the distribution limits of a species are difficult to define due to inherent difficulties in detecting marine species. As indicated by Tsoar et al. (2007) for most regions and taxa, detailed data on species distribution are usually not available and collecting such data is costly and labour intensive (Prendergast et al., 1999; Bowker, 2000; Ottaviani et al., 2004).

One solution to this lack of distributional data is the use of mathematical approaches to investigate the relationships between environmental variables and species occurrence modelling the species distribution and habitat. These relationships can be used to predict the areas where species most likely occur (e.g. Elith et al., 2006; Basille et al., 2008; MacLeod et al., 2008; Ready et al., 2010). However, many potential techniques require both accurate presence and absence data that not always can be available, particularly for marine species that are difficult to detect due to their mobility and habitat preferences or inadequate sampling procedures. In this sense, the alternative presence-only approaches are of special interest for modelling marine species distributions (Tsoar et al., 2007; MacLeod et al., 2008) and the use of such models to study marine species with poorly known or limited presence records facilitates the generation of distributional maps that can be used as a tool for studying in danger or protected species where sampling is limited (Hirzel et al., 2002a; Ready et al., 2010).

One of these approaches is the maximum entropy model (Maxent), developed by Phillips et al. (2006) to assess species geographic distributions in relation to environmental variables with limited presence-only data. Maxent takes as input a set of commonly georeferenced gridded layers or environmental variables as well as a set of species occurrence locations and produces a model of the species distribution (Phillips et al., 2004, 2006; Phillips & Dudík, 2008). Maxent has been used to study the distribution of terrestrial (Elith et al., 2006; Phillips et al., 2006; Basille et al., 2008; Veloz, 2009) and marine (Lefkaditou et al., 2008; Ready et al., 2010) species.

Another approach to evaluate the relationship with environmental variables using presence-only data is the ecological niche factor analysis (ENFA), developed by Hirzel et al. (2002b), based in Hutchinson's niche concept (Hutchinson, 1957). Specifically, Basille et al. (2008) have conceived and implemented ENFA in R (R Development Core Team, 2010) as an exploratory tool to identify the variables regulating the niche of the species and to distinguish between the available conditions and the habitat selected by the species.

One marine species with unresolved distribution and habitat preferences in European waters is the common octopus, *Octopus vulgaris* Cuvier, 1797, despite the fact it is the most important harvested octopus species from the Atlantic and the Mediterranean waters reaching global catches of more than 37,000 tonnes in 2007 (Josupeit, 2000; FAO, 2009). A great amount of knowledge is available on several aspects of its biology and ecology (e.g. Mangold, 1983; Guerra, 1992; Domain et al., 2000; Hernández-López et al., 2001; Otero et al., 2008, 2009; Hermosilla et al., 2010), although, some aspects like its geographical distribution are still poorly known. Furthermore, its populations show notable yearly fluctuations on abundance and catch due to the high paralarval and settlement mortality (Otero et al., 2008, 2009) as well as species' rapid response to environmental variation (Sobrino et al., 2002; González et al., 2005). Production fluctuations can be detected even in nearby ports in the same season, a fact that has been reported by Murphy et al. (2002) in Northern and Southern Sahara Bank and Mauritania.

In the past, the presence of *O. vulgaris* has been recorded in several regions of the world suggesting that this was a cosmopolitan species (Mangold, 1983; Roper et al., 1984; Warnke et al., 2004). However, this statement has been questioned by other authors (Mangold, 1998; Mangold & Hochberg, 1991) that suggest *O. vulgaris* is one member of a species complex (Norman, 2000) and its distribution is only limited to east Atlantic and Mediterranean waters (Guerra, 1992; Mangold, 1998). Remarkably, recent evidences support the previous assertions suggesting *O. vulgaris* distribution is probably cosmopolitan and extending to Mediterranean Sea, Eastern Atlantic Ocean (from South England to Southwest African waters), Azores, Canary, Cape Verde, St. Helena, Tristan da Cunha Islands, southern Brazil, Isla Margarita (Venezuela), southeastern coast of South Africa, Japanese and Taiwanese waters in the Pacific and Saint Paul and Amsterdam Islands in the Indian Ocean (Warnke et al., 2004; Pardo-Gandarillas et al., 2009; Guerra et al., 2010). In any case, the most probable situation of *O. vulgaris* could be that its distribution is wider than the Mediterranean and Eastern Atlantic and that it overlaps the distributions of other similar species forming a species complex.

In this study, we used two complementary presence-only analyses, Maxent and ENFA, to model the spatial distribution of *O. vulgaris* in the Mediterranean and Eastern Atlantic waters and to reveal its habitat preferences, respectively. Since these two analyses approach species distribution modelling in a different manner, it is interesting to determine which environmental variables are more relevant in each analysis for the octopus.

Materials and methods

Octopus data sets

Two data sets were used in this study, following the indications of Fielding & Bell (1997) and Veloz (2009). The first data set was used to develop both models and hence, was called the training data. It consists of 213 *O. vulgaris* records (Fig. 1) from different sources, including sampling data collected from 2006 to 2008 as well as bibliographical records (Table 1). An independent (non-correlated) data set was used to test and validate the Maxent and ENFA models. This data set was kindly provided by I. Sobrino, P. Pascual and L. Gil de Sola from Instituto Español de Oceanografía and consists of a set of *O. vulgaris* presence data obtained during several research surveys in the Gulf of Cadiz (survey years from 1993 to 2009), Morocco coast (survey years from 1989 to 1990), Mauritania coast (survey years from 2006 to 2007) and Mediterranean Sea (Alborán Sea and Vera Gulf, from MEDITS survey, 2005–2008). These data sets were too large and redundant. Thus, for each data set only 57 presence records were selected avoiding repetitions and bias. When more presence records were available in a data set, only 57 of them were randomly selected using R. In consequence, a total test sample size of 171 octopus presence records was used to test models. The independent test sample size is smaller than the training data set used to develop the models ($n = 213$) because the test sample represents a smaller area than that represented by the training data set.

Environmental variables

A total of 17 environmental or abiotic variables were assembled and utilized in this study, selected because they were directly or indirectly related to octopus biology and ecology. Whereas it is true that more variables are related to its biology, habitat preferences and distribution, there are not public datasets available for all variables that we would like to include. In other cases, when the data set exist, it does not cover the complete area included in the study.

From the 17 environment variables, only five of them were used in the final model development: dissolved oxygen (DO0 and DO200 in ml O_2/l, at 0 and 200 m depth, respectively), sea bottom salinity (SBS ‰), sea bottom temperature (SBT in °C) and chlorophyll-α (CHLA in mg/m^3). All the variables were assembled as climatological (long-term) averages, except from CHLA, which was assembled as annual average for 2006 (most of sampling data were collected during that year). Long-term averages were used because this is the first attempt to create a picture of the distribution of the species in a wide area utilizing the wide extent of satellite data (the use of time-stamps according to samples dates would not allow to produce a wide-area map).

The other variables examined (estuary area, euphotic depth, mean primary production, precipitation, sea

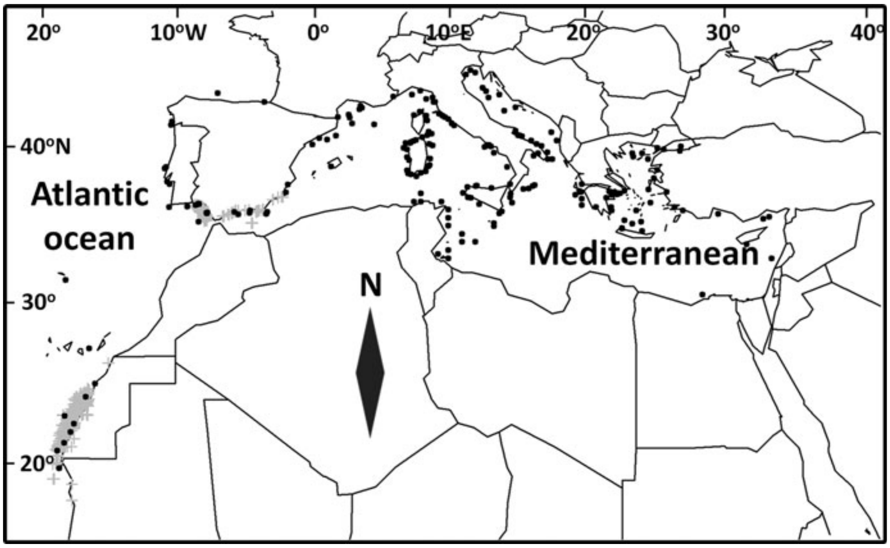


Fig. 1 Map showing the location of *O. vulgaris* presence data utilized in this study. *Black dots* represent presence data used in Maxent and ENFA models. *Grey crosses* represent test data used in Maxent model

Table 1 List of survey data and bibliographical records used in this study

Source	Area sampled
This study	A total of 12 sampling localities in: Spain (Vigo, Vilanova i la Geltrú, Málaga, Cádiz, Bilbao); Southern Portugal; Italy (Bari, Sicily, Naples); Greece (Lesbos and Crete), and; Mauritania (Atlantic)
Belcari et al. (2002)	Mediterranean region: Alborán Sea; Alicante region; Catalonian Sea; Morocco; Gulf of Lion; Corsican Sea; Ligurian Sea; Sardinian Sea; Tyrrhenian Sea; Sicilian Channel; Adriatic Sea; Ionian Sea; Argosaronikos region; Aegean Sea
Borges-Seixas et al. (2002)	Portuguese Atlantic Coast: Viana do Castelo and Cascais
Byrne et al. (2002)	Mediterranean coast of France (Corse: Stareso, Calvi) and Italy (Bay of Naples)
Cabranes et al. (2008)	Spanish Atlantic Coast (Asturias, Galicia and Portugal); Atlantic (Canary Island); Mediterranean (Murcia)
Catalán et al. (2006)	Spanish Atlantic coast: Gulf of Cadiz
Cerezo-Valverde & García-García (2005)	Spanish Mediterranean coast: coast of Murcia
Chapela et al. (2006)	Spanish Atlantic coast: Vigo
Costa et al. (2004)	Portuguese Atlantic coast: Peniche (NW) and Olhâo (South)
Ezzeddine & El-Abed (2004)	Mediterranean region: Tunisia (Gulf of Gabès)
Faraj & Bez (2007)	Atlantic Coast of Africa: Southern Morroco (26°N to 21°N)
Hernández-López et al. (2001)	Atlantic waters: Canary Islands (Spain)
Katsanevakis & Verriopoulos (2004b)	Mediterranean region: Aegean Sea
Katsanevakis & Verriopoulos (2006b)	Mediterranean region: Aegean Sea
Lefkaditou et al. (2003)	Mediterranean region: Ionian Sea
Madan & Wells (1996)	Mediterranean region: Coast of France
Maltagliati et al. (2002)	Mediterranean region: Spain (Vilanova i la Gertrú); Italy (Western Sardinia, Gulf of Olbia, Leghorn and Porto Santo Stefano in Tuscany, Gulf of Naples, Porto Palo in Sicily), Greece (Crete north of Heraklion)
Miliou et al. (2005)	Mediterranean region: Saronicos Gulf (Aegean Sea)
Quetglas et al. (1998)	Mediterranean region: Palma de Mallorca (Spain)
Rodriguez-Rúa et al. (2005)	Spanish Atlantic coast: Huelva and Bay of Cadiz
Salman et al. (2002)	Mediterranean region: Turkish coastal waters: Sea of Marmara, Aegean sea and eastern Mediterranean

surface salinity, sea surface temperature, sediment type, tidal range, wind speed, wind direction) were discarded from analysis due to low contribution to model development (data not shown). In addition, bathymetry and shelf area were also evaluated preliminary (data not shown) but since *O. vulgaris* is a species known to live in the continental shelf, i.e. in shallow waters, these variables were not included in the analysis, in order to reveal less obvious factors that affect octopus distribution and habitat preferences. Furthermore, it is known that bathymetry and shelf area are correlated with other variables selected in the final analysis, such as DO, which generally declines with depth, SBT and SBS (the deeper, the colder and saltier), therefore, since it is not recommended to incorporate highly correlated variables into Maxent we did not include them into the analysis.

Data were obtained from NASA's OceanColor website (CHLA, oceancolor.gsfc.nasa.gov), Aquamaps (SBS, SBT, Kaschner et al., 2008, http://www.aquamaps.org/) and World Ocean Atlas 2005 (DO0 and DO200, Garcia et al., 2006, http://www.nodc.noaa.gov/OC5/WOA05/pr_woa05.html). All data were converted to ESRI's ArcGIS grids and resampled under a common spatial resolution (0.05° or 5 km approximately) covering the Mediterranean and Eastern Atlantic (17°–48°N, 19°W–42°E using SAGA-GIS software (Conrad, 2006).

Maxent model

Maxent analysis was carried out using Maxent software (V. 3.3.2) and downloaded from the 'Maxent software for species habitat modelling' web page (www.cs.princeton.edu/~schapire/maxent). As previously mentioned, 171 independent data points were used to test the reliability of the model using a binomial test of omission to evaluate the statistical significance of the prediction.

The importance of each environmental variable in the model was evaluated by means of a heuristic estimation during training of the model and by means of a jackknife test. The latter test was executed initially running the model by excluding one variable in each run, then running the model with only one variable and finally, including all variables in the model. Next, the performance of the different models was evaluated. Response curves were created for each environmental variable showing the effect of every environmental variable on the logistic prediction, i.e. the marginal effect of changing one variable in the model, by keeping the remaining variables at their average value. The model was evaluated with the threshold-independent receiver operating characteristic (ROC) approach, by calculating the area under the ROC curve (AUC) as the measure of the prediction success. The ROC curve is obtained by plotting all true positive values (sensitivity fraction) against their equivalent false positive values (1-specificity fraction, Phillips et al., 2006). Analysis was performed 10 times to generate 95% confidence intervals.

ENFA model

The ENFA analysis compares the total area combinations of habitat variables available to the species with the combinations of habitat variables at the locations where the species is found by means of the terms marginality and specialization. Marginality is a measure of the separation between this optimal habitat combinations (those of the actual presence sites) and the average available environmental conditions within the study area; specialization contrasts the global distribution variance with the species habitat variance, i.e. it measures how restricted is the species niche in comparison with available habitat combinations (Hirzel et al., 2002a; Basille et al., 2008).

ENFA is implemented in the Adehabitat package (Calenge, 2006) of R software (R Development Core Team, 2010). The analysis performs a principal-component analysis-like analysis, calculating factors that have biological meaning. The first factor explains marginality (m) and the remaining ones explain the specialization (s). Larger values of marginality indicate that the species is not equally distributed in the environment and that the habitats utilized strongly differ from the average conditions in the study area (Hirzel et al., 2002a; Basille et al., 2008). Alternatively, small values of specialization represent less restricted niches on some particular environmental variable (Basille et al., 2008) and high values of specialization means the species do not tolerate variation in that dimension.

Adehabitat package also provides global marginality (M) and global tolerance (T) of the species to the habitat evaluated: the greater the marginality, the more the niche deviates from the available conditions; the smaller the tolerance, the more restricted is the niche, i.e. more specialized is the species. These global estimations, however, must be used cautiously as they only apply to the specific area covered in a specific study and assumes that the environmental variables do not change over time (Hirzel et al., 2002a; Basille, per. comm.).

Marginality, the specialization axes and tolerance were evaluated with Monte-Carlo tests to assess their significance after 999 replicates (Basille et al., 2008, 2009; Calenge & Basille, 2008). As in Maxent, the analysis was also evaluated with ROC approach. In order to perform this validation, ENFA was applied to a set of 200 random absence points created with Dismo package (Hijmans et al., 2010) of R software, avoiding land areas and areas nearby to presence points to minimize 'false' absences in these points. Then, the predicted suitability of both training and test data was contrasted with the ENFA results performed with the absence points by means of ROCR package (Sing et al., 2009) of R software.

Results

According to the heuristic estimations of Maxent, the variables that mostly contribute to the model are

Table 2 Relative contributions of the environmental variables to the Maxent and ENFA models

Variable	MAXENT	ENFA		
	Percent contribution	Marginality	Specialization 1	Specialization 2
CHLA	6.1	−0.078	0.231	−0.177
DO0	14.7	0.124	−0.575	−0.615
DO200	3.5	0.656	0.763	−0.491
SBS	12.7	1.452	−0.129	−0.319
SBT	63.0	1.700	−0.132	0.498

SBT, DO0 and SBS (63.0, 14.7 and 12.7% of contribution to the model, respectively, Table 2). The jackknife test shows that the variables that produce the greater gain in the model when considered in isolation are SBT, SBS and CHLA (longest dark grey bars in Fig. 2), which therefore appear to be more relevant for the octopus distribution; those that mostly decrease the gain of the model when they are omitted is DO0, CHLA and SBT (shortest light grey bars in Fig. 2), which consequently appear to have the most information that is not present in the other variables.

Maxent model indicates that predicted suitability of *O. vulgaris* increases in zones where SBT, DO0, SBS and CHLA range is 15–30°C, 5.0–7.5 ml/l, 30–45‰ and 0–50 mg/m^3, respectively (Fig. 3). The area under the curve (AUC) for the training data was 0.958 and for test data was 0.946 (Fig. 4A), which means that the model prediction is higher than chance (AUC = 0.5). Furthermore, the binomial test of omission was less than 0.0001 indicating the model estimations were significantly better than random predictions. The map generated by Maxent shows the areas with the best predicted conditions for octopus occurrence (Fig. 5) and it is congruent with the known distribution of *O. vulgaris*. In addition, several areas with higher probability of presence are coincident with the current fisheries areas for the species (e.g. Sahara bank, Iberian Peninsula, Italy and Greece).

Global marginality estimated by ENFA was 5.45 ($P = 0.001$), which indicates that the area used by octopus strongly differs from the average conditions in the Mediterranean Sea and Atlantic Ocean (niche centroid shown in Fig. 6) and that it requires a specific niche of habitat. In terms of variable importance, the analysis indicates that SBT and SBS are the main variables that contribute to marginality (Table 2, longest arrow projections on marginality axis in Fig. 6). SBT and SBS have large and positive values, meaning that octopus prefers areas where these variables have an average greater than those of the environment (see Fig. 7).

Two specialization axes were kept in the analysis because they accounted for the main part of specialization (data not shown). They correspond to an eigenvalue of 12.7 ($P = 0.005$) and 9.1 ($P = 0.001$), meaning that the variance of the available

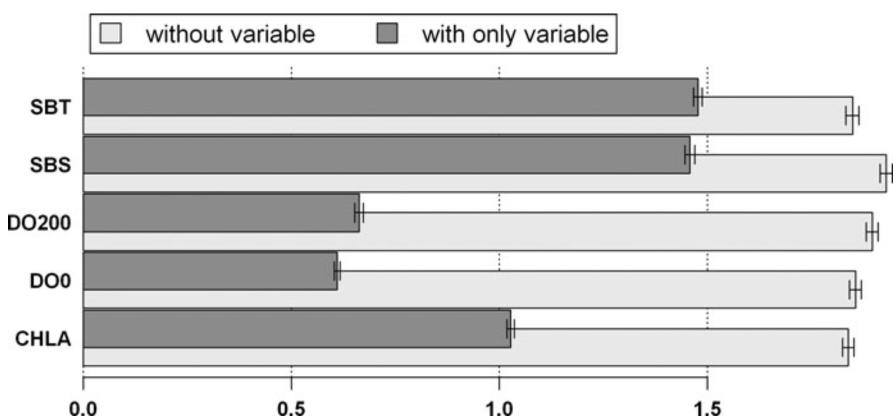
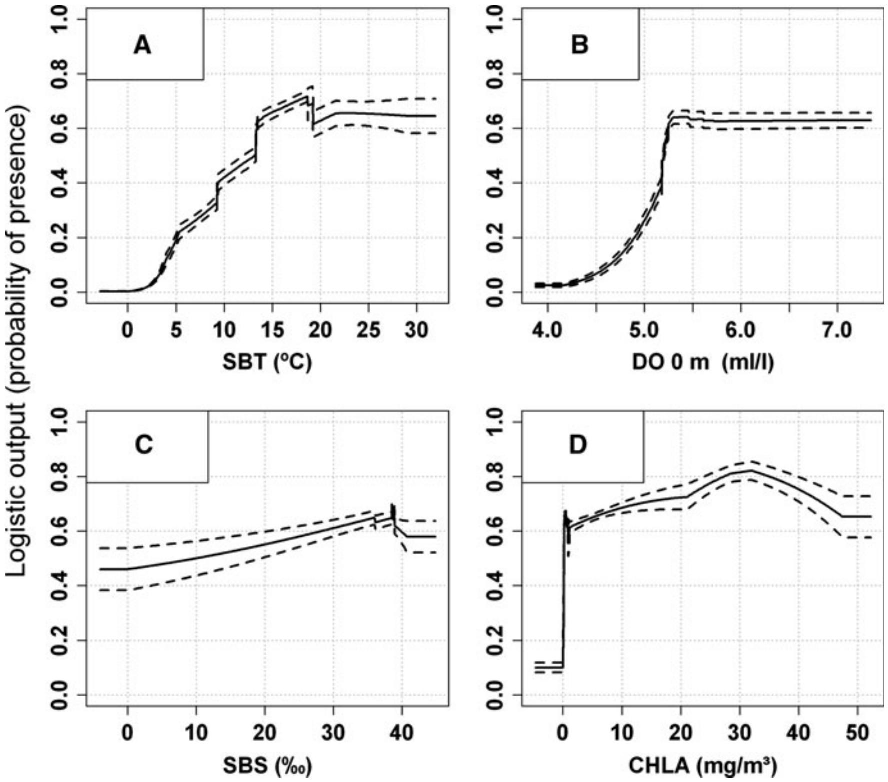


Fig. 2 Results of the jackknife test of variable importance in the Maxent model. In *dark grey*, model gain using only that variable; *light grey*, effect of removing that variable from the model. *Bars* indicate 95% CI

Fig. 3 Response curves for the most important variables of the Maxent model. **A** SBT; **B** DO at 0 m; **C** SBS; **D** CHLA. *Solid lines* represent the effect of the variable on the model; *dashed lines* represent 95% CI



environment is 12.7 and 9.1 times larger than the variance of the ecological niche in each of those dimensions. Hence, the niche appears rather restricted in those dimensions.

Indeed, the biplot of ENFA (Fig. 6) showed that the niche is quite restricted, since low values of tolerance indicate constrained niches (Dolédec et al., 2000; global tolerance is 1.15, $P = 0.001$). At this point, it is worth mentioning that it is not recommended to compare marginalities, specializations and tolerance from different studies, i.e., a tolerance value from a model built with three variables cannot be compared to a tolerance value of a model built with 10 variables (Basille, per. comm.).

DO200 and DO0 are the variables with higher specialization coefficients, thus they are the most critical in terms of habitat selection (longest arrow projection on specialization axis in Figs. 6 and 7, Basille et al., 2008). The AUC for the training data was 0.784 and for test data was 0.659 (Fig. 4B), meaning that the model prediction is also better than randomness (AUC = 0.5), although comparatively, the ability of ENFA to predict suitability areas is inferior to that of Maxent model.

Discussion

This study represents the first attempt to understand *O. vulgaris* habitat preferences and distribution in the Mediterranean and Eastern Atlantic waters using novel techniques such as Maxent modelling and ENFA analysis, which integrate multiple environmental variables with presence-only data. To date, studies have been focused in local abundance and/or fisheries of *O. vulgaris* in relation to some environmental variables like SST, CHLA, Season, Rainfall or Depth and the North Atlantic Oscillation (NAO) (Hernández-López, 2000; Balguerías et al., 2002; González & Sánchez, 2002; Sobrino et al., 2002; Katsanevakis & Verriopoulos, 2004a; Vargas-Yáñez et al., 2009; Caballero-Alfonso et al., 2010). Similar studies showed positive relationships between paralarval abundance and SST and upwelling (Katsanevakis & Verriopoulos, 2006a; Moreno et al., 2009; Otero et al., 2009). This study integrates octopus presence data from a wide distribution range with an extensive number of environmental variables.

Nevertheless, it would be relevant for future studies, to extend the number of training and test

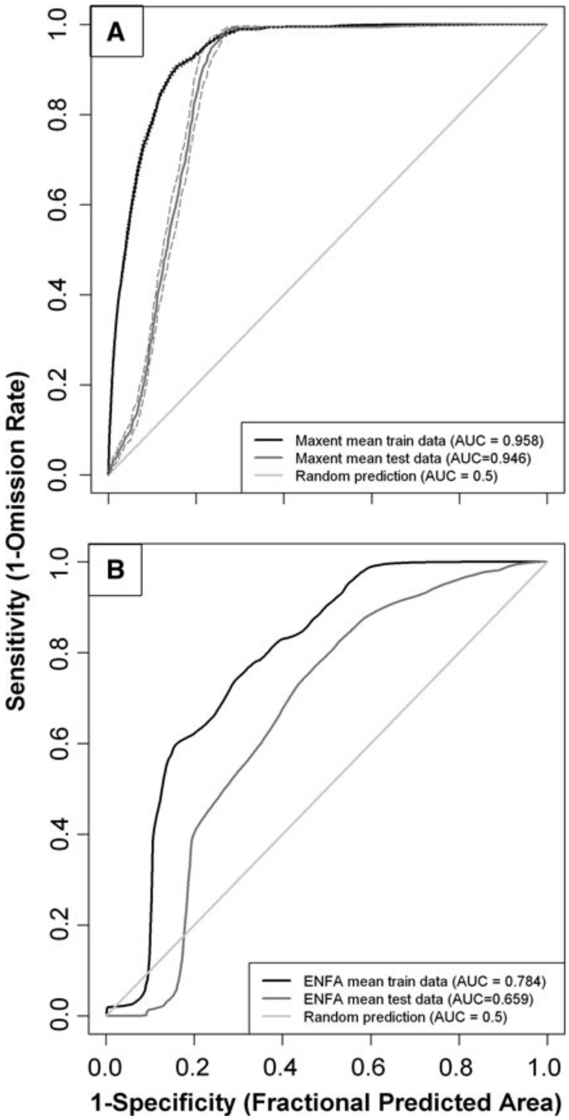


Fig. 4 Receiver operating characteristic (ROC) curve for *O. vulgaris* data using Maxent model (**A**) and ENFA (**B**). *Dashed lines* represent 95% CI

records, avoiding biases due to region misrepresentation. For instance, it is urgent to include more records from eastern and southern Mediterranean, which is clearly less studied. An effort must be made in this sense to carry out more surveys and to publish the results in peer review journals.

In terms of analysis comparison, Maxent model is more robust than ENFA as a predictive tool: both training and test AUC plots confirmed its high performance (Fig. 4A), though test AUC had a lower value because test data did not include the entire area that was incorporated in the training data. In contrast, ENFA had a lower fitness because the absence model was built using random points that covered most of the total available habitat, thus the model could not perform adequately.

Both analyses agreed that SBS and SBT are relevant variables to octopus spatial distribution and habitat preferences (Figs. 2, 6), although they showed a small discrepancy in terms of the remaining variables. For instance, to Maxent, CHLA is a decisive variable (Fig. 2) whereas to ENFA, i.e. to habitat preferences, it does not seem to be a relevant variable (low marginality and specialization value; Fig. 6). This is a reflection of the differences of both analyses. Whereas Maxent deals with spatial distribution, ENFA focuses in habitat preferences. Therefore, to Maxent model, CHLA, a measure of primary production, is essential to spatial distribution of the species, because high levels of CHLA are in direct relationship with high productivity areas and food availability, key element to cephalopod abundance, especially for octopus (Rocha et al., 1999; González et al., 2005; Otero et al., 2009). In the other hand, CHLA is not influential to its habitat preferences, which make sense because a benthic species should not select its (benthonic) habitat according to CHLA values.

Previous studies have shown the importance of SST in octopus habitat preferences, distribution and ecology; however, results have shown both positive correlations (Demarcq & Faure, 2000; Balguerías et al., 2002; Sobrino et al., 2002; Vargas-Yáñez et al., 2009; Caballero-Alfonso et al., 2010) and negative relationships (González & Sánchez, 2002) to abundance and catch. However, results of this study do not show a major effect of SST in *O. vulgaris* distribution; in fact, SST was discarded during preliminary evaluation due to its low contribution to the analyses. Instead, our study places SBT as an important factor in octopus spatial distribution and habitat preferences, in accordance to octopus nature. Most likely, the relevance of SST in regulating adult *O. vulgaris* spatial distribution could have been overestimated, due to its availability as marine environmental variable or due to the limited use of SBT in their analysis.

In this sense, SST can affect mainly octopus paralarvae abundance (Moreno et al., 2009) in their pelagic zooplanktonic habitat where their survival

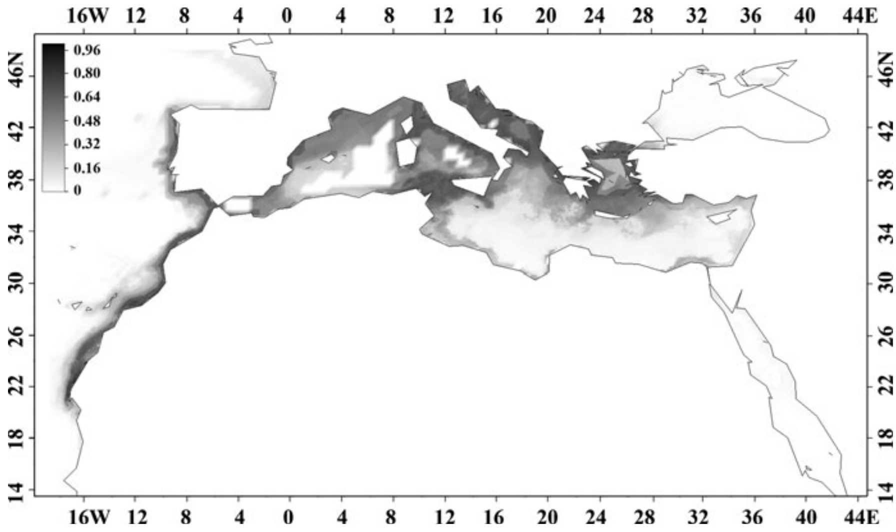


Fig. 5 Distribution representation for *O. vulgaris* using Maxent model. *Darker colours* show areas with better predicted conditions. 1 represents more suitable prediction and 0 represents not suitable prediction for octopus

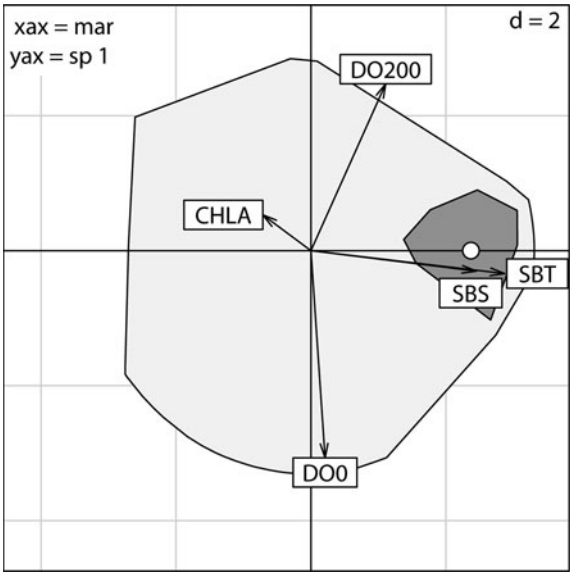


Fig. 6 *Octopus vulgaris* niche display in the study area. Axes represent marginality (*x*-axis) and specialization (*y*-axis). *Light grey* area represents total available area and *dark grey* represents used area (niche). *White dot* represents the niche centroid (centroid of the available area is located at the origin of the coordinates 0,0). *Arrows* represent the projections of the environmental variables on the marginality and specialization axes

depends on sea surface temperature and productivity (Rocha et al., 1999; González et al., 2005). However, when octopus juveniles leave zooplanktonic habitat to live as adult benthonic species (Guerra, 1992; Belcari et al., 2002; González & Sánchez, 2002), the importance of SST could be limited. In consequence, for the spatial distribution and habitat preferences of *O. vulgaris* juveniles and adults, the bottom temperature must be considered an important factor instead of sea surface temperature.

In the other hand, SBS, it is not surprising an essential variable to *O. vulgaris*. This cephalopod is known as a species that cannot tolerate low values of salinity (Vaz-Pires et al., 2004); indeed, low salinity phenomena can be highly stressful or even fatal to this species (Chapela et al., 2006). Therefore, bottom salinity can explain the absence of *O. vulgaris* in low salinity waters, like estuarine environments and Black Sea.

DO0 and DO200 were more relevant to ENFA than to Maxent (Figs. 2, 6), because they contributed the most to the specialization axis, meaning that they do not tolerate drastic changes in DO0 and DO200. This coincides with basic physiological requirements of this species (Vaz-Pires et al., 2004). Besides, DO0 levels estimated by Maxent model (Fig. 3), agreed with results from Cerezo-Valverde & García-García (2005), who report that ventilatory frequency is altered below mean oxygen levels of 4.5 ± 0.95 mg O_2/l (~3.1 ± 0.66 ml O_2/l; mean temperature 20.5°C); above that value, ventilatory frequency is optimal. In addition, mean critical oxygen saturation reported at 2.3 ± 0.57 mg O_2//l (~1.6 ± 0.40 ml O_2/l; mean temperature 20.5°C) (Cerezo-Valverde & García-García, 2005). Consequently and according to results in the present work, octopus is searching for areas with optimal oxygen levels.

Because cephalopods can be easily affected by environmental changes (Lefkaditou et al., 2008;

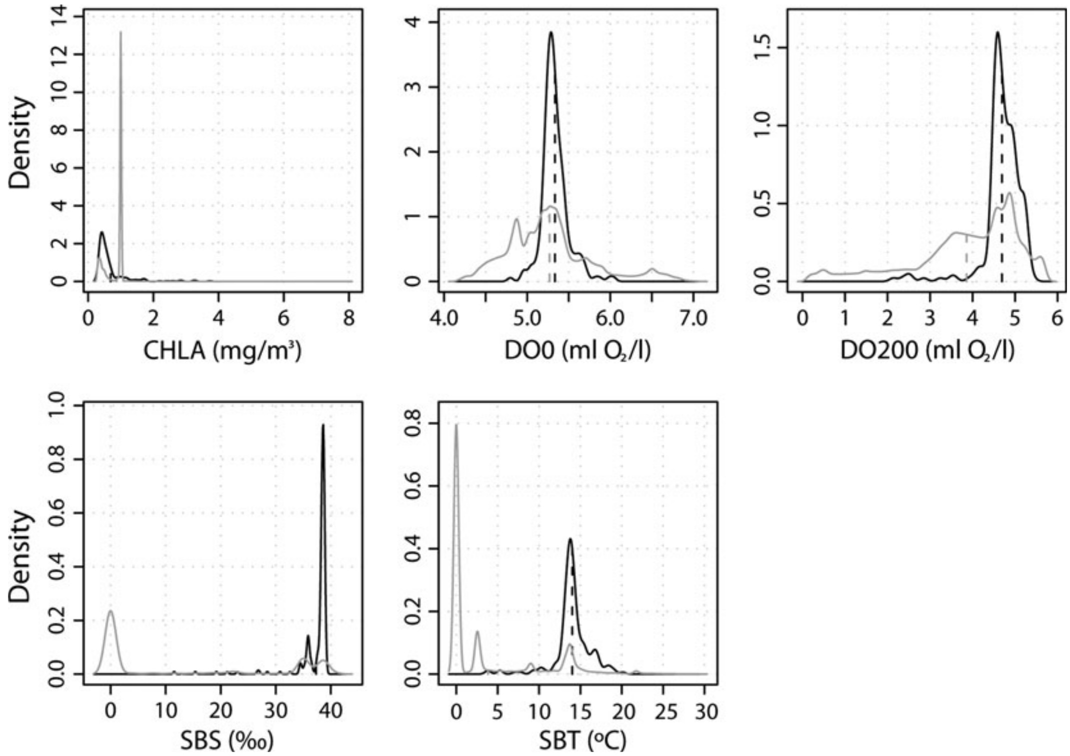


Fig. 7 Representation of the niche–environment system in the study area. *Black lines* represent the used units (the niche) and *grey lines* represent the available resource units (the environment)

Pierce et al., 2008; Tian, 2009), it could be meaningful to carry out the presented analysis on annual basis in order to evaluate variations in octopus spatial distribution and changes in habitat preferences due to environmental fluctuations caused by climate change and global warming. Furthermore, it could be interesting to include other variables in the models, such as the NAO index and sea currents data to further understand the distribution of *O. vulgaris.*

Finally, Maxent, as a tool to assess how environmental variables are related to the *Octopus vulgaris* spatial distribution in the Mediterranean and Eastern Atlantic can be used to generate valid distribution models for this species, given its geographical distribution is poorly known (Elith et al., 2006; Kaschner et al., 2006; FAO, 2010; Ready et al., 2010). In this study, we have tested part of the known distribution of the species in the Mediterranean and Eastern Atlantic producing a robust model, based on environmental variables, capable of predicting its distribution.

In the future, this model can be applied in a wider geographical area to locate other habitable areas for *O. vulgaris*, generating a distributional pattern at global scale. It can also be used to complement the current distribution map provided by FAO (FAO, 2010), adding information about more or less suitable areas for the species and helping to elucidate the possible *O. vulgaris* presence in regions where the actual identity of the species is uncertain and where no genetic and taxonomic studies are possible.

Conclusion

Together, Maxent model and ENFA identified habitat preferences and spatial distribution patterns of *Octopus vulgaris*. Main environmental variables related to them are congruent with known species life history and previous studies. To Maxent, sea bottom temperature, sea bottom salinity and chlorophyll-α are the most relevant variables to its spatial distribution; whereas to ENFA, sea bottom temperature, sea bottom salinity, dissolved oxygen level (at 0 and 200 m) are the key variables in terms of habitat preferences. Maxent can successfully predict octopus spatial distribution with the capability to evaluate which variables are more important to its distribution. This could be very useful to understanding the distributional patterns and ecology of the species. Finally, if these models are generated annually, it could be possible to evaluate variations in octopus distribution due to changes caused by climate change and global warming.

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References

Balguerías, E., C. Hernández-González & C. Perales-Raya, 2002. On the identity of *Octopus vulgaris* Cuvier, 1797 stocks in the Saharan bank (northwest Africa) and their spatio-temporal variations in abundance in relation to some environmental factors. Bulletin of Marine Science 71: 147–163.

Basille, M., C. Calenge, E. Marboutin, R. Andersen & J. M. Gaillard, 2008. Assessing habitat selection using multivariate statistics: some refinements of the ecological-niche factor analysis. Ecological Modelling 211: 233–240.

Basille, M., I. Herfindal, H. Santin-Janin, J. D. C. Linnell, J. Odden, R. Andersen, K. Arild Høgda & J.-M. Gaillard, 2009. What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? Ecography 32: 683–691.

Belcari, P., D. Cuccu, M. González, A. Srairi & P. Vidoris, 2002. Distribution and abundance of *Octopus vulgaris* Cuvier, 1797 (Cephalopoda: Octopoda) in the Mediterranean Sea. Scientia Marina 66(Suppl. 2): 157–166.

Borges-Seixas, S., T. Pinheiro & C. Sousa-Reis, 2002. Lead in octopus (*Octopus vulgaris*) in Portugal: a preliminary study. Bulletin of Marine Science 71: 1091–1093.

Bowker, G. C., 2000. Mapping biodiversity. International Journal of Geographic Information Systems 14: 739–754.

Byrne, R. A., M. Kuba & U. Griebel, 2002. Lateral asymmetry of eye use in *Octopus vulgaris*. Animal Behaviour 64: 461–468.

Caballero-Alfonso, A. M., U. Ganzedo, A. Trujillo-Santanaa, J. Polanco, A. Santana del Pino, G. Ibarra-Berastegi & J. J. Castro-Hernández, 2010. The role of climatic variability on the short-term fluctuations of octopus captures at the Canary Islands. Fisheries Research 102: 258–265.

Cabranes, C., P. Fernandez-Rueda & J. L. Martínez, 2008. Genetic structure of *Octopus vulgaris* around the Iberian Peninsula and Canary Islands as indicated by microsatellite DNA variation. ICES Journal of Marine Science 65: 12–16.

Calenge, C., 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197: 516–519.

Calenge, C. & M. Basille, 2008. A general framework for the statistical exploration of the ecological niche. Journal of Theoretical Biology 252: 674–685.

Catalán, I. A., M. T. Jiménez, J. I. Alconchel, L. Prieto & J. L. Muñoz, 2006. Spatial and temporal changes of coastal demersal assemblages in the Gulf of Cadiz (SW Spain) in relation to environmental conditions. Deep-Sea Research II 53: 1402–1419.

Cerezo-Valverde, J. & B. García-García, 2005. Suitable dissolved oxygen levels for common octopus (*Octopus vulgaris* Cuvier, 1797) at different weights and temperatures: analysis of respiratory behaviour. Aquaculture 244: 303–314.

Chapela, A., A. F. González, E. G. Dave, F. Rocha & A. Guerra, 2006. Growth of common octopus (*Octopus vulgaris*) in cages suspended from rafts. Scientia Marina 70: 121–129.

Conrad, O., 2006. SAGA—program structure and current state of implementation. In Böhner, J., K. R. McCloy & J. Strobl (eds), SAGA—Analysis and Modelling Applications. Göttinger Geographische Abhandlungen, Vol. 115. 130 pp.

Costa, P. R., R. Rosa & M. A. M. Sampayo, 2004. Tissue distribution of the amnesic shellfish toxin, domoic acid, in *Octopus vulgaris* from the Portuguese coast. Marine Biology 144: 971–976.

Demarcq, H. & V. Faure, 2000. Coastal upwelling and associated retention indices derived from satellite SST. Application to Octopus vulgaris recruitment. Oceanologica Acta 23: 391–408.

Dolédec, S., D. Chessel & C. Gimaret-Carpentier, 2000. Niche separation in community analysis: a new method. Ecology 81: 2914–2927.

Domain, F., D. Jouffre & A. Caverivière, 2000. Growth of *Octopus vulgaris* from tagging in Senegalese waters. Journal of the Marine Biological Association of the United Kingdom 80: 699–705.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, Overton J. McC, A. Townsend Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberón, S. Williams, M. S. Wisz & N. E. Zimmermann, 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129–151.

Ezzeddine, S. & A. El-Abed, 2004. Potential biological and environmental influences on the *Octopus vulgaris* population of the Gulf of Gabès (south-eastern Tunisian coast). MedSudMed Technical Documents 2: 42–49.

FAO, 2009. Global production statistics 1950–2007. United Nations Food and Agriculture Organization [available on internet at http://firms.fao.org/gfcm/topic/17105/en]. Accessed October 2009.

FAO, 2010. Species fact sheets, *Octopus vulgaris* (Lamarck, 1798). United Nations Food and Agriculture Organization [available on internet at http://www.fao.org/fishery/species/3571/en]. Accessed July 2010.

Faraj, A. & N. Bez, 2007. Spatial considerations for the Dakhla stock of *Octopus* indicators, patterns, and fisheries interactions. ICES Journal of Marine Science 64: 1820–1828.
Fielding, A. H. & J. F. Bell, 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24: 38–49.
Garcia, H. E., R. A. Locarnini, T. P. Boyer & J. I. Antonov, 2006. World Ocean Atlas 2005, Volume 3: Dissolved Oxygen, Apparent Oxygen Utilization, and Oxygen Saturation. S. Levitus, Ed. NOAA Atlas NESDIS 63, U.S. Government Printing Office, Washington, DC, 342.
González, A. F. & P. Sánchez, 2002. Cephalopod assemblages caught by trawling along the Iberian Peninsula Mediterranean coast. Scientia Marina 66: 199–208.
González, A. F., J. Otero, A. Guerra, R. Prego, F. J. Rocha & A. W. Dale, 2005. Distribution of common octopus and common squid paralarvae in a wind-driven upwelling area (Ria of Vigo, northwestern Spain). Journal of Plankton Research 27: 271–277.
Guerra, A., 1992. Mollusca, Cephalopoda. In Ramos, M. A., J. A. Tercedor, X. Bellés, J. G. Gonsálbez, A. Guerra, E. Macpherson, F. Martín, et al. (eds), Fauna Ibérica, Vol. 1. Nacional de Ciencias Naturales, CSIC, Madrid: 1–327.
Guerra, A., A. Roura, A. F. González, S. Pascual, Y. Cherel & M. Pérez-Losada, 2010. Morphological and genetic evidence that *Octopus vulgaris* Cuvier, 1797 inhabits Amsterdam and Saint Paul Islands (Southern Indian Ocean). ICES Journal of Marine Science 67: 1401–1407.
Hermosilla, C. A., F. Rocha, G. Fiorito, A. F. González & A. Guerra, 2010. Age validation in common octopus *Octopus vulgaris* using stylet increment analysis. ICES Journal of Marine Science 67: 1458–1463.
Hernández-López, J. L., 2000. Biología, ecología y pesca del pulpo común ("*Octopus vulgaris*", Cuvier 1797) en aguas de Gran Canaria. PhD thesis, Universidad de las Palmas de Gran Canaria.
Hernández-López, J. L., J. J. Castro-Hernández & V. Hernández-García, 2001. Age determined from the daily deposition of concentric rings on common octopus (*Octopus vulgaris*) beaks. Fishery Bulletin 99: 679–684.
Hijmans, R., S. Phillips, J. Leathwick & J. Elith, 2010. Dismo: Species distribution modeling. R package version 0.5-4 [available on internet at http://CRAN.R-project.org/package=dismo].
Hirzel, A. H., J. Hausser, D. Chessel & N. Perrin, 2002a. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology 83: 2027–2036.
Hirzel, A. H., J. Hausser, N. Perrin, 2002b. Biomapper 3.1. Lab. for Conservation Biology. Department of Ecology and Evolution, University of Lausanne [available on internet at http://www.unil.ch/biomapper].
Hutchinson, G. E., 1957. Concluding remarks. Cold Spring Harbour Symposium on Quantitative Biology 22: 415–427.
Josupeit, H., 2000. Los mercados mundiales de cefalópodos. Productos del Mar Noviembre-Diciembre: 43-48.
Kaschner, K., J. S. Ready, E. Agbayani, J. Rius, K. Kesner-Reyes, P. D. Eastwood, A. B. South, S. O. Kullander, T. Rees, C. H. Close, R. Watson, D. Pauly & R. Froese, 2008. AquaMaps: predicted range maps for aquatic species. World Wide Web electronic publication, www.aquamaps.org, Version 10/2008.
Kaschner, K., R. Watson, A. W. Trites & D. Pauly, 2006. Mapping world-wide distributions of marine mammal species using a relative environmental suitability (RES) model. Marine Ecology Progress Series 316: 285–310.
Katsanevakis, S. & G. Verriopoulos, 2004a. Abundance of *Octopus vulgaris* on soft sediment. Scientia Marina 68: 553–560.
Katsanevakis, S. & G. Verriopoulos, 2004b. Den ecology of *Octopus vulgaris* Cuvier, 1797, on soft sediment: availability and types of shelter. Scientia Marina 68: 147–157.
Katsanevakis, S. & G. Verriopoulos, 2006a. Modelling the effect of temperature on hatching and settlement patterns of meroplanktonic organisms: the case of the octopus. Scientia Marina 70: 699–708.
Katsanevakis, S. & G. Verriopoulos, 2006b. Seasonal population dynamics of *Octopus vulgaris* in the eastern Mediterranean. ICES Journal of Marine Science 63: 151–160.
Lefkaditou, E., C. H. Mytilineou, P. Maiorano & G. D'onghia, 2003. Cephalopod species captured by deep-water exploratory trawling in the north-eastern Ionian Sea. Journal of Northwest Atlantic Fishery Science 31: 431–440.
Lefkaditou, E., C.-Y. Politou, A. Palialexis, J. Dokos, P. Cosmopoulos & V. D. Valavanis, 2008. Influences of environmental variability on the population structure and distribution patterns of the short-fin squid *Illex coindetii* (Cephalopoda: Ommastrephidae) in the Eastern Ionian Sea. Hydrobiologia 612: 71–90.
MacLeod, C. D., L. Mandleberg, C. Schweder, S. M. Bannon & G. J. Pierce, 2008. A comparison of approaches for modelling the occurrence of marine animals. Hydrobiologia 612: 21–32.
Madan, J. J. & M. J. Wells, 1996. Cutaneous respiration in *Octopus vulgaris*. The Journal of Experimental Biology 199: 2477–2483.
Maltagliati, F., P. Belcari, D. Casu, M. Casu, P. Sartor, G. Vargiu & A. Castelli, 2002. Allozyme genetic variability and gene flow in *Octopus vulgaris* (Cephalopoda, Octopodidae) from the Mediterranean Sea. Bulletin of Marine Science 71: 473–486.
Mangold, K., 1983. Octopus vulgaris. In Boyle, P. R. (ed.), Cephalopod Life Cycles, Vol. 1. Species Accounts. Academic Press, London, United Kingdom: 335–364.
Mangold, K., 1998. The Octopodinae from the Eastern Atlantic Ocean and the Mediterranean Sea. Smithsonian Contributions to Zoology 586: 521–528.
Mangold, K. & F. G. Hochberg, 1991. Defining the genus *Octopus*: redescription of *Octopus vulgaris*. Bulletin of Marine Science 49: 665.
Miliou, H., M. Fintikaki, T. Kountouris & G. Verriopoulos, 2005. Combined effects of temperature and body weight on growth and protein utilization of the common octopus, *Octopus vulgaris*. Aquaculture 249: 245–256.
Moreno, A., A. dos Santos, U. Piatkowski, A. M. P. Santos & H. Cabral, 2009. Distribution of cephalopod paralarvae in relation to the regional oceanography of the western Iberia. Journal of Plankton Research 31: 73–91.
Murphy, J. M., E. Balguerías, L. N. Key & P. R. Boyle, 2002. Microsatellite DNA markers discriminate between two

Octopus vulgaris (Cephalopoda: Octopoda) fisheries along the northwest African coast. Bulletin of Marine Science 71: 545–553.

Norman, M., 2000. Cephalopods—A World Guide. ConchBooks, Hackenheim, Germany.

Otero, J., X. A. Álvarez-Salgado, A. F. González, A. Miranda, S. B. Groom, J. M. Cabanas, G. Casas, B. Wheatley & A. Guerra, 2008. Bottom-up control of common octopus *Octopus vulgaris* in the Galician upwelling system, northeast Atlantic Ocean. Marine Ecology Progress Series 362: 181–192.

Otero, J., X. A. Álvarez-Salgado, A. F. González, M. Gilcoto & A. Guerra, 2009. High frequency coastal upwelling events influence *Octopus vulgaris* larval dynamics on the NW Iberian shelf. Marine Ecology Progress Series 386: 123–132.

Ottaviani, D., G. J. Lasinio & L. Boitani, 2004. Two statistical methods to validate habitat suitability models using presence-only data. Ecological Modelling 179: 417–443.

Pardo-Gandarillas, M. C., C. M. Ibáñez, A. T. Palma & E. Poulin, 2009. Origin and molecular divergence of *Octopus crusoe*, octopus endemic to the Juan Fernandez Archipelago. In Guerra, A. & A. F. González (eds), Abstract Book, Cephalopod International Advisory Council, CIAC Symposium. Vigo, Spain: 33.

Phillips, S. J. & M. Dudík, 2008. Modelling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31: 161–175.

Phillips, S. J., M. Dudík & R. E. Schapire, 2004. A Maximum entropy approach to species distribution modelling. In Brodley, C. (ed), Proceedings of the Twenty-First International Conference on Machine learning, Banff, Canada: 655–662.

Phillips, S. J., R. P. Anderson & R. E. Schapire, 2006. Maximum entropy modelling of species geographic distributions. Ecological Modelling 190: 231–259.

Pierce, G. J., V. D. Valavanis, A. Guerra, P. Jereb, L. Orsi-Relini, J. M. Bellido, I. Katara, U. Piatkowski, J. Pereira, E. Balguerias, I. Sobrino, E. Lefkaditou, J. Wang, M. Santurtun, P. R. Boyle, L. C. Hastie, C. D. MacLeod, J. M. Smith, M. Viana, A. F. González & A. F. Zuur, 2008. A review of cephalopod–environment interactions in European Seas. Hydrobiologia 612: 49–70.

Prendergast, J. R., R. M. Quinn & J. H. Lawton, 1999. The gaps between theory and practice in selecting nature reserves. Conservation Biology 13: 484–492.

Quetglas, A., F. Alemany, A. Carbonell, P. Merella & P. Sánchez, 1998. Biology and fishery of *Octopus vulgaris* Cuvier, 1797, caught by trawlers in Mallorca (Balearic Sea, Western Mediterranean). Fisheries Research 36: 237–249.

R Development Core Team, 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0 [available on internet at http://www.R-project.org].

Ready, J., K. Kaschner, A. B. South, P. D. Eastwood, T. Rees, J. Rius, E. Agbayani, S. Kullander & R. Froese, 2010. Predicting the distributions of marine organisms at the global scale. Ecological Modelling 221: 467–478.

Rocha, F., A. Guerra, R. Prego & U. Piatkowski, 1999. Cephalopod paralarvae and upwelling conditions off Galician waters (NW Spain). Journal of Plankton Research 21: 21–33.

Rodriguez-Rúa, A., I. Pozuelo, M. A. Prado, M. J. Gómez & M. A. Bruzón, 2005. The gametogenic cycle of *Octopus vulgaris* (Mollusca: Cephalopoda) as observed on the Atlantic coast of Andalusia (south of Spain). Marine Biology 147: 927–933.

Roper, C. F. E., M. J. Sweeney & C. E. Nauen, 1984. FAO species catalogue. Vol. 3. Cephalopods of the world. An annotated and illustrated catalogue of interest to fisheries. FAO Fisheries Synopsis 125: 1–277.

Salman, A., T. Katagan & H. A. Benli, 2002. Cephalopod fauna of the eastern Mediterranean. Turkish Journal of Zoology 26: 47–52.

Sing, T., O. Sander, N. Beerenwinkel & T. Lengauer, 2009. ROCR: Visualizing the performance of scoring classifiers. R package version 1.0-4 [available on internet at http://CRAN.R-project.org/package=ROCR].

Sobrino, I., L. Silva, J. M. Bellido & F. Ramos, 2002. Rainfall, river discharges and sea temperature as factors affecting abundance of two coastal benthic cephalopod species in the Gulf of Cadiz (SW Spain). Bulletin of Marine Science 71: 851–865.

Tian, Y., 2009. Interannual-interdecadal variations of spear squid Loligo bleekeri abundance in the southwestern Japan Sea during 1975–2006: impact of the trawl fishing and recommendations for management under the different climate regimes. Fisheries Research 100: 78–85.

Tsoar, A., O. Allouche, O. Steinitz, D. Rotem & R. Kadmon, 2007. A comparative evaluation of presence-only methods for modelling species distribution. Diversity and Distribution 13: 397–405.

Valavanis, V. D., G. J. Pierce, A. F. Zuur, A. Palialexis, A. Saveliev, I. Katara & J. Wang, 2008. Modelling of essential fish habitat based on remote sensing, spatial analysis and GIS. Hydrobiologia 612: 5–20.

Vargas-Yáñez, M., F. Moya, M. García-Martínez, J. Rey, M. González & P. Zunino, 2009. Relationships between *Octopus vulgaris* landings and environmental factors in the northern Alboran Sea (Southwestern Mediterranean). Fisheries Research 99: 159–167.

Vaz-Pires, P., P. Seixas & A. Barbosa, 2004. Aquaculture potential of the common octopus (*Octopus vulgaris* Cuvier, 1797): a review. Aquaculture 238: 221–238.

Veloz, S. D., 2009. Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. Journal of Biogeography 36: 2290–2299.

Warnke, K., R. Söller, D. Blohm & U. Saint-Paul, 2004. A new look at geographic and phylogenetic relationships within the species group surrounding *Octopus vulgaris* (Mollusca, Cephalopoda): indications of very wide distribution from mitochondrial DNA sequences. Journal of Zoological Systematics and Evolutionary Research 42: 306–312.