

# Predictive distribution models of European hake in the south-central Mediterranean Sea

G. Garofalo  · S. Fezzani · F. Gargano · G. Milisenda ·  
O. Ben Abdallah · N. Ben Hadj Hamida · O. Jarboui ·  
B. Chemmam-Abdelkader · W. Khoufi · R. Micallef ·  
R. Mifsud · S. Gancitano · P. Rizzo · S. Zgozi · L. Ceriola ·  
E. Arneri · F. Fiorentino

Received: 15 February 2017 / Revised: 25 July 2017 / Accepted: 31 July 2017 / Published online: 26 September 2017  
© Springer International Publishing AG 2017

**Abstract** The effective management and conservation of fishery resources requires knowledge of their spatial distribution and notably of their critical life history stages. Predictive modelling of the European hake (*Merluccius merluccius* L., 1758) distribution was developed in the south-central Mediterranean Sea by means of historical fisheries-independent databases available in the region. The study area included the international waters of the south-central Mediterranean Sea and the territorial waters of Italy, Malta, Tunisia and Libya. Distribution maps of

predicted population abundance index, and probabilistic occurrence of recruits and large adults were obtained by means of generalized additive models using depth and seafloor characteristics as predictors. Presence/absence data of the two life stages was obtained using threshold values applied to the mean weight of the survey catches. Modelling results largely matched previously reported knowledge on habitat preference of the species and its critical life phases. Hake recruits showed an occurrence peak at 200 m depth with preference for soft bottoms. Large adults preferred deeper and harder bottom substrates. Prediction maps allowed to improve our knowledge on the distributional patterns of one of the most important shared stocks in the south-central Mediterranean. This knowledge is essential for an appropriate development of regional-spatial-based management plans.

---

Guest editors: Angelo Bonanno, Othman Jarboui,  
Salem Wniss Zgozi, Roberta Mifsud & Luca Ceriola / Marine  
Ecosystems and Living Resources in the Central  
Mediterranean Sea

---

Handling editor: Iacopo Bertocci

---

G. Garofalo (✉) · F. Gargano · G. Milisenda ·  
S. Gancitano · P. Rizzo · F. Fiorentino  
Istituto per l'Ambiente Marino Costiero - Consiglio  
Nazionale delle Ricerche, Mazara Del Vallo, TP, Italy  
e-mail: germana.garofalo@iamc.cnr.it

S. Fezzani · B. Chemmam-Abdelkader · W. Khoufi  
Institut National des Sciences et Technologies de la Mer –  
Centre de La Goulette, La Goulette, Tunisia

F. Gargano  
Department of Energy, Information engineering and  
Mathematical models (DEIM), University of Palermo,  
Palermo, Italy

O. Ben Abdallah · N. Ben Hadj Hamida · O. Jarboui  
Institut National des Sciences et Technologies de la Mer –  
Centre de Sfax, Sfax, Tunisia

R. Micallef · R. Mifsud  
Department of Fisheries and Aquaculture - Fisheries  
Resource Unit, MSDEC, Marsa, Malta

S. Zgozi  
Marine Biology Research Centre (MBRC), Tajura, Libya

L. Ceriola · E. Arneri  
Fisheries and Aquaculture Department, FAO  
MedSudMed, Rome, Italy

**Keywords** Species distribution modelling · *Merluccius merluccius* · Generalized additive models · Recruits habitat · Large adults habitat · Seafloor geophysical features · Strait of Sicily

## Introduction

The European hake (*Merluccius merluccius* L., 1758) is a neoto-benthonic fish widely distributed in the northeast Atlantic and throughout the Mediterranean and Black Sea (Papaconstantinou & Stergiou, 1995). The species inhabits a broad range of depth from 20 to 1000 m, preferring different depths according to size and season (Oliver & Massutí, 1995; Papaconstantinou & Stergiou, 1995). On the basis of the literature, a general pattern of relationship between size and depth, due to ontogenetic and reproductive factors, can be outlined, with the smallest hake preferring circalittoral bottoms between 100 and 200 m, while the largest specimens occurring mainly on bathyal bottoms (Zupanovic, 1968; Bouhlal, 1973; Recasens et al., 1998; Bartolino et al., 2008).

European hake is a key commercial species caught in mixed fisheries in the Strait of Sicily (south-central Mediterranean Sea) as well as throughout the Mediterranean Sea, with bottom trawlers exploiting mainly the youngest fraction of the population and gillnet and longline fisheries targeting large adults (Martin et al., 1999). In the Strait of Sicily, the stock of the European hake is shared by Italian, Maltese and Tunisian fisheries. The species is the main commercial bycatch of Italian trawling targeting the deep-water rose shrimp and a target species for artisanal vessels using longlines and gillnets, even though more than 95% of the catch comes from bottom trawling (Fiorentino et al., 2008). Along the Tunisian coasts, it is a target species for both trawling and artisanal fisheries (Khoufi et al., 2010). The average annual landing in the region for the period of years, 2007–2015, was over 3000 tons (Gancitano et al., 2016). Since 2016, fisheries catching the European hake have been subjected to a multi-annual management plan adopted by the FAO General Fisheries Commission for the Mediterranean Sea (GFCM, REC.CM-GFCM/40/2016/4; see FAO, 2016). Latest joint-stock assessment in the Strait of

Sicily highlighted high catches of juveniles and maturing specimens and suggested a condition of overfishing with intermediate levels of relative biomass (Gancitano et al., 2016). As a consequence, reduction of fishing mortality, especially on the juvenile fraction of the stock, through actualization of the management plan, becomes necessary for the improvement of the exploitation of this shared resource. Protecting nursery areas and essential fish habitats important for the stocks of the European hake is a specific objective (REC.CM-GFCM/40/2016/4) of the multi-annual fisheries management plan. To this aim, two fisheries restricted areas (FRA) were already established in 2016 (FAO, 2016) in the northern region of the Strait of Sicily along the Italian-Maltese continental shelf. However, the identification of nurseries across the entire region and particularly off the African coast is still limited (Druon et al., 2015) and can be of utmost importance to provide further reliable advice in support of multi-lateral fisheries management.

In the recent decades, a plenty of scientific literature has emphasized the importance of knowing the spatial distribution of fishery resources and protecting certain life stages to achieve their effective management and conservation (Caddy, 2000; Berkeley et al., 2004; Rice, 2005; Ciannelli et al., 2008; Planque et al., 2011). Spatially explicit management measures, such as temporary or permanent restriction of fishing on nursery and/or spawning areas are considered relevant for achieving reduction of juvenile mortality or preservation of reproductive potential of exploited resources (Caddy, 2000; Caddy & Seijo, 2002; Berkeley et al., 2004). The Council Regulation (EC) 1967/2006 specifically requires the inclusion of spatial management measures such as the establishment of fishing protected areas in order to protect nurseries and/or spawning areas and ultimately ensuring the long-term sustainability of fisheries. Scientific bottom trawl surveys may represent the most valuable source of information for studying and capturing the true spatial pattern of abundance and demography of demersal resources, providing fisheries independent data collected according to statistical sampling design (Cotter et al., 2009). However, owing to the wide distribution of many exploited species and the high cost associated with large-scale bottom surveys, it becomes difficult to monitor species and habitats in a

comprehensive way. With the ever-increasing availability and a variety of environmental data mapped at regional or global scale, the development of species distribution models (SDMs) (Guisan & Zimmermann, 2000; Elith & Leathwick, 2009; Peterson & Soberon, 2012) has acquired rising importance and popularity to fill the gaps in the knowledge of the spatial distribution of species. Indeed, the idea behind most SDM studies is basically (i) to model the link between observed species occurrence or abundance data and a combination of environmental factors usually mapped at higher spatial resolution than biological data and (ii) to use the model to predict the spatial distribution of species across unsampled areas, also by extrapolation in space or time (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Elith & Leathwick, 2009; Schröder & Richter, 1999). Kearney (2006) argued that what is actually modelled by this correlative approach to distributional modelling is the species' habitat, i.e. the biotic and abiotic features of a place where a species live. This concept of habitat is purely descriptive and does not include mechanistic understanding of interactions between the species and its environment (Kearney, 2006). However, many underlying processes governing species' distribution and persistence can result implicitly incorporated in distributional models if the chosen environmental predictors are surrogates for causal processes (Austin, 2007; Kearney & Porter, 2009). Predictive maps of species occurrence are of utmost utility for immediate practical conservation purposes (Austin, 2007) and, in this sense, SDMs have become a key component of the ecosystem-based approach to fisheries management. They have been extensively applied in ecological and fisheries research (see overview in Guisan et al., 2002; Venables & Dichmont, 2004; Johnson et al., 2013), although more research effort is claimed for advancing the field, for example by an increased integration of biotic variables like predation or competition (Johnson et al., 2013).

In recent years, several applications of SDMs applied to demersal species in the Mediterranean have been developed at both basin scale (Colloca et al., 2015; Druon et al., 2015; Keller et al., 2016) and local scale, e.g. the Aegean Sea (Katsanevakis et al., 2009; Damalas et al., 2010; Maravelias et al., 2007, 2012; Tserpes et al., 2008, 2013; Yalçın & Gurbet, 2016) or the Strait of Sicily (Lauria et al.,

2015; Lauria et al., 2016) and Tunisian platform (Hattab et al., 2013). In this Mediterranean context, European hake has been the focus of several studies applying SDMs (Maravelias et al., 2007; Tserpes et al., 2008; Katsanevakis et al., 2009; Hattab et al., 2013; Colloca et al., 2015; Druon et al., 2015; Yalçın & Gurbet, 2016). Considering in particular the south-central Mediterranean Sea, a number of different mapping exercises have already been developed for this species. Persistent habitats for hake recruits have been identified in the northern region of the Strait of Sicily (Fiorentino et al., 2003; Garofalo et al., 2011; Colloca et al., 2015; Druon et al., 2015). Suitable habitats for hake recruits along the Tunisian coasts were predicted applying an ecological niche approach developed at Mediterranean scale using data distributed along the European coasts (Druon et al., 2015). Besides, a preliminary study dealing with the bathymetric distribution of the species was realized basing on the trawl survey in the north of Tunisia (Khouri et al., 2012). Finally, a first attempt was developed to describe the geographical distribution of hake recruits and spawners across the entire region (Garofalo et al., 2008), but the analysis was based on only one year of data from different research surveys that were not standardized. Moreover the work failed to identify nursery areas along the southeastern Tunisian shelf. Substantially, the lack of standardization of available fisheries-independent databases has prevented to date the analysis of survey indices for the European hake on a regional basis. In 2011, an intercalibration experiment was conducted to compare the fishing power of the Italian and Tunisian vessels employed in the region for research purposes and to estimate a correction factor between the catches per unit effort (CPUE) from the two vessels. This allowed the setting up of a regional standardized database of abundance indices for the European hake that was used for the first time in this study.

The objective of this study was to develop correlative approaches of SDMs for predicting the abundance of European hake and the occurrence probability of recruits and large adults in the south-central Mediterranean Sea. Abiotic factors with a strong implication in species distribution, i.e. depth and seafloor features such as slope, aspects, rugosity, etc. (Moore et al. 2009; McArthur et al., 2010; Monk et al., 2010; Pittmann & Brown, 2011; Lecours et al.,

2015) were used as explanatory variables. Temperature and salinity which might play an important role as well were not used due to data limitation. The models developed will contribute to (i) increase knowledge about the attributes of habitat utilized by the species, notably of two critical life history stages, and (ii) provide new information that would be of high utility for the management of this shared species and the development of the GFCM regional spatial management plan (REC.CM-GFCM/40/2016/4; see FAO, 2016).

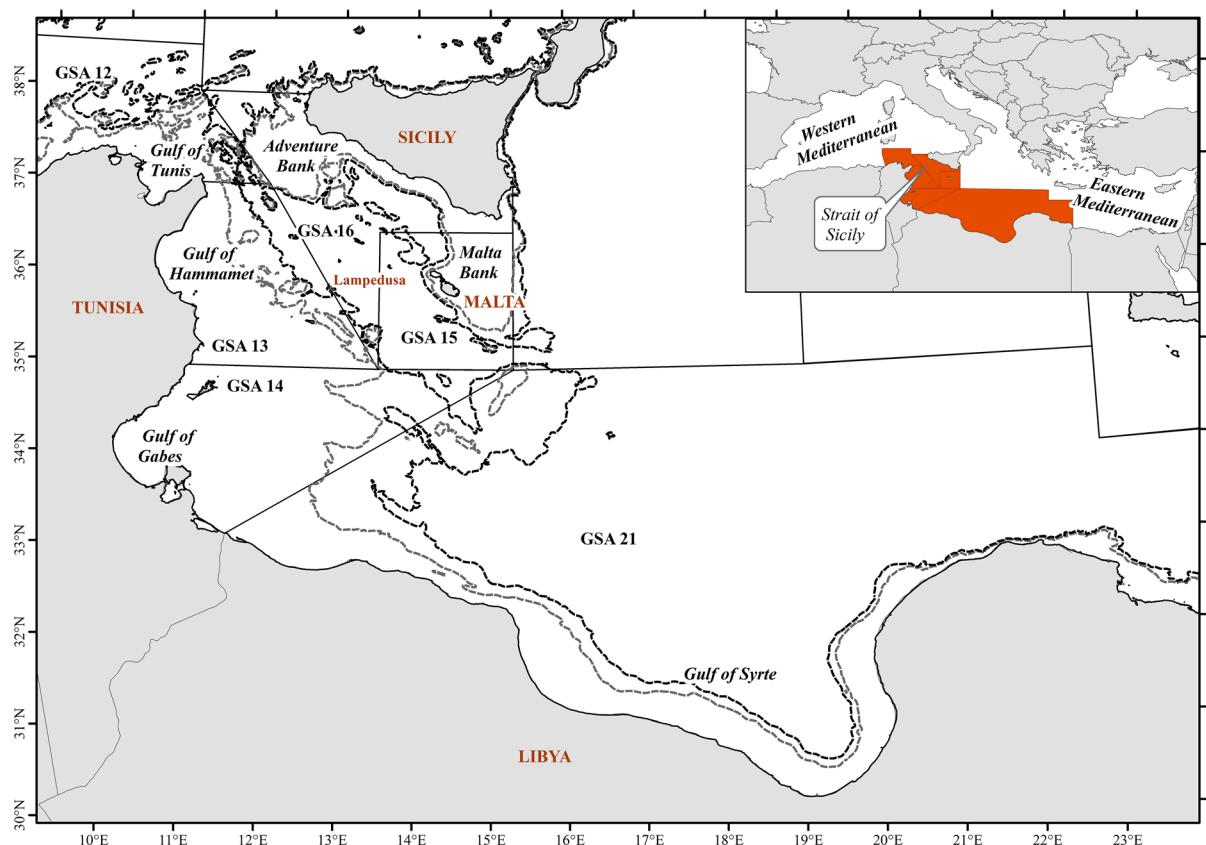
## Materials and methods

### Study area

The study area, Strait of Sicily and adjacent areas (Fig. 1), is located in the south-central Mediterranean and is characterized by a complex bottom

morphology and hydrographical circulation pattern which control the water exchange between the western and eastern Mediterranean basins. The northern part, that is bordered by the southern coast of Sicily and includes the national waters of the Maltese Islands, is characterized by two wide and shallow (<100 m) banks on the west (Adventure Bank) and east (Malta Bank), respectively, separated by a narrow shelf in the middle part. To the south, the continental platform is wide especially along the Tunisian coast where it arrives to extend for more than 100 nautical miles from the coast. The shape of the slope between Sicily and Tunisia is extremely irregular, incised by many canyons, trenches, and steep slopes, whereas it is very gentle between Malta and Libya.

The general pattern of water circulation in the Strait of Sicily can be schematized as a two-layer system with the fresh Modified Atlantic Water flowing eastwards in the upper layer (top 200 m



**Fig. 1** Map of the study area showing the GSAs' borders (solid line) and the bathymetric contours (dashed line) of 200 m (grey) and 400 m (black). In the inset, the position of the study area in the Mediterranean Sea is shown

depth), and the warm and salty Levantine Intermediate Water flowing westwards at depths ranging between 200 and 700 m (Beranger et al., 2004). The entire system is characterized by high spatio-temporal hydrographical variability and climatic differentiation along longitudinal and latitudinal gradients. Climatological maps based on satellite estimates of surface chlorophyll concentration (CHL) and sea surface temperature (SST) exhibit overall meridional gradients, with the southeastern region warmer and less productive than the northern region (Rinaldi et al., 2014).

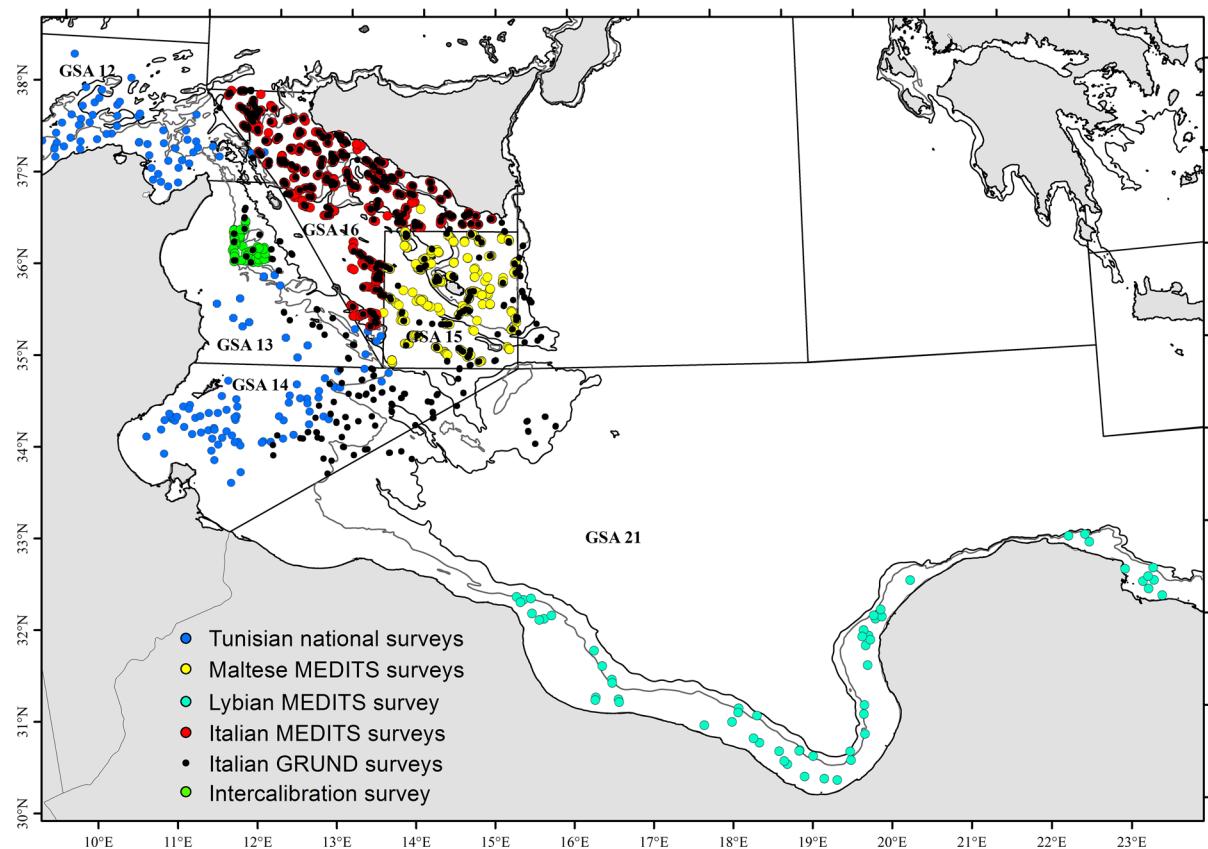
The study area corresponds to six GFCM Geographical Sub Areas (GSA; FAO GFCM, 2009) (Fig. 1): GSA 12 (Northern Tunisia), GSA 13 (Gulf of Hammamet), GSA 14 (Gulf of Gabès), GSA 15 (Malta Island), GSA 16 (South of Sicily), GSA 21 (Libya). On the whole, it spans 8 degree of latitude (from 30.5° to 38° N) and 16 degree of longitude (9°

to 25° E) and the total surface is approximately 150000 km<sup>2</sup>.

## Data

### Surveys data

A number of bottom trawl surveys were conducted by multiple nations (i.e. Italy, Malta, Tunisia and Libya) and vessels in the south-central Mediterranean Sea from 2003 to 2011 (Fig. 2). MEDiterranean International Trawl Surveys (MEDITS; Bertrand et al., 2002) were conducted annually in GSAs 15 and 16 (Malta and Italy, respectively) using the commercial Fishing Vessel “F/V S.Anna” equipped with a high-vertical-opening bottom trawl net (GOC 73:36/40 with codend mesh size of 20 mm) specifically developed for the MEDITS surveys. The MEDITS gear was also used on board the Research Vessel R/V Philia during the survey conducted in GSA 21



**Fig. 2** Distribution of the trawl survey hauls used in the present study, spanning the period of years, 2003–2011. Different colours represent the different survey series

(Libya). The F/V S.Anna equipped with a typical Italian commercial gear carried out surveys within the framework of the Italian national project GRUND (GRUppo Nazionale Demersali; Relini, 2000) in a large area covering GSA 16 and portions of adjacent GSAs. The R/V Hannibal equipped with a high vertical-opening bottom trawl (GOV:42/55 with codend mesh size of 40 mm) carried out surveys in GSAs 12, 13 and 14 (Tunisia).

Differences in catchabilities of gears used in MEDITS and GRUND surveys were evaluated through comparative fishing trials (intercalibration experiment) performed in 1998 (Scalisi et al., 1998), while an analogous experiment was conducted in 2011 to quantify differences in catchabilities between MEDITS gear and Tunisian GOV (Garofalo et al., *in press*). In both experiments, estimates of the fishing power correction factor between catches of any pair of gears were provided. MEDITS was taken as reference survey because it represents the longest and the most standardized series of research surveys in the Mediterranean Sea. Therefore, to standardize the full set of data, the computed correction factors were applied (as multiplicative constants) to adjust catches of hake obtained by GRUND and Tunisian surveys to those which would have been obtained by the standard MEDITS survey.

There was a discrepancy between the years covered by the different surveys in the different areas. Indeed, while data were available for the whole time series in Sicily and Malta, data available for African coastal area (Tunisia and Libya) were discontinuous.

For each survey and each year, georeferenced catches in the number and weight of European hake were adjusted for the area swept by the trawl in each haul, obtaining density indices (DIs) as the number of specimens per square kilometre ( $N/km^2$ ) and biomass indices (BIs) as kilograms per square kilometre ( $kg/km^2$ ).

A total of 2471 georeferenced points (Fig. 2) were collected from all surveys, and about 18% of them gave zero catch for the European hake.

For each haul, the ratio of BI and DI was computed to obtain the mean weight of individuals in the catch. Building on the existing knowledge of growth rate and size at the first maturity of European hake in the south-central Mediterranean (see, overview in Fiorentino et al., 2008), two threshold values

of the mean weight were used to discriminate two fractions of the populations sampled: recruits (i.e. specimens in their first year of life) and adults with full reproductive capacity. A mean weight less than 20 g, corresponding to 15 cm of total length (TL), was considered indicative of the presence of recruits. A mean weight greater than 400 g (corresponding to 38 cm TL) was considered indicative of the presence of adults with full reproductive capacity, called large adults hereafter. Indeed the average size of first maturity ( $L_{50}$ ) reported by Fiorentino et al. (2008) was 35 cm for females (from  $L_{50}$  estimates of years 2002 and 2007). Moreover the authors reported a sex ratio, as number of females out of the total number of sexed specimens, equal to 0.9 for specimens with  $TL > 36$  cm, therefore the population fraction classified as large adults consisted predominantly of mature females.

The population fraction corresponding to the intermediate class of mean weight 20–400 g was not considered for modelling because it was supposed to be composed by mixed age classes.

For each population fraction, relative abundance was recoded as binary observations, i.e. 0 indicated the absence of the class and 1 indicated its presence.

#### Abiotic data

Depth and a suite of seafloor geophysical characteristics were selected as predictive variables to model spatial distribution of the European hake in the study area. As suggested by Monk et al. (2010), seafloor characteristics are either direct or indirect proxies that represent important physiological or ecological limitations, including the availability of territory, food, shelter or the existence of predation or competition. It was decided to not use environmental variables such as sea surface temperature and salinity in this study because these two variables exhibit a strong gradient towards the southeast of the study region (Rinaldi et al., 2014) where the sampling coverage was unbalanced with respect to the north. A brief description is provided explaining the purpose and use of the abiotic variables considered.

Depth: it is known to be one of the most important drivers of spatial distribution of species, related to different ecological factors like light, hydrodynamics, pressure and water density (Kinne, 1970).

Slope: it provides a measure of bottom steepness. It can be indicative of stability of sediments and local acceleration of currents. Its ecological relevance may be related to aspects of food supply, exposure, etc. (Elvenes et al., 2014).

Aspect (eastness and northness): the two measures represent the orientation of the seabed and are therefore proxies for exposure of any given area to dominant and/or local currents from a particular direction. Their ecological relevance may be related to aspects of food supply, larval dispersion, etc. (Monk et al., 2010; Elvenes et al., 2014).

Rugosity or terrain roughness: it is a quantitative measure of topographical heterogeneity. It is considered an index of habitat structural complexity and hence a surrogate of hard substrate (Dunn & Halpin, 2009; Monk et al., 2010). Its ecological relevance may be related to the amount of habitat available for colonization by benthic organisms, and shelter and foraging area for mobile organisms (mainly critical life stages) (Elvenes et al., 2014). According to McArthur et al. (2010) it has a strong surrogacy potential because disturbance in unstable sediments depresses richness and biomass.

In addition to depth and seafloor characteristics, three geographical variables were selected to build the models.

Geographical coordinates, latitude and longitude: they were included in the models because they can act as proxies of specific geographical gradients of direct importance for the species (McArthur et al., 2010) or as indicators of residual spatial variation in the distribution of the species not explained by abiotic parameters included in the models.

Distance to the shore: It represents the relative geographical position across the shelf and is quantified using Euclidean distances to shoreline and islands (Pittmann & Brown, 2011; Hattab et al., 2013).

Depth, slope, northness, eastness and distance to shore were provided by the MARSPEC database (Sbrocco & Barber, 2013), available at <http://www.marspec.org/>. MARSPEC is a global marine database containing a high-resolution (nominal 1-km or 30 arc-second) raster grid representing ocean bathymetry, and seven derived variables which quantify topographical complexity of the seafloor (including slope, aspect and the distance to shore).

Rugosity was derived from the MARSPEC bathymetry layer using the Benthic Terrain Modeller tool in ArcGIS 10.1 (Wright et al., 2012).

## Modelling

Two datasets were created from the original dataset by randomly selecting 75% of the occurrence localities as training data, with the remaining 25% reserved for testing the resulting models.

Relationships between abundance or the presence/absence records of the European hake and their habitat features were estimated using Generalized Additive Models (GAMs; Hastie & Tibshirani, 1990). GAMs are non-parametric regression methods, quite flexibles relative to strictly parametric linear or generalized linear models, where the expected mean value of the response variable is described as:

$$g(\mu) = \beta_0 + \sum_{i=1}^n f_i(x_i) + \varepsilon \text{ with } g(\mu) \text{ denoting the link}$$

function defining the relationship between the response variable and the additive predictors,  $\beta_0$  denoting the intercept term and  $f_i(x_i)$  is, in general, an arbitrary smooth function of i-th predictor  $x_i$  or a function with a specified parametric form (for example a polynomial) (Venables & Dichmont, 2004).

GAMs were considered to be appropriate models because there was no ecological reason for choosing a particular shape (such as linear or quadratic) of the species response to the abiotic variables used in this study. Indeed these variables have only indirect relationships with a species occurrence, through associations with variables more correlated to eco-physiological processes, and these relationships may assume any shape (Austin, 2007).

Models were developed for three response variables: the total abundance of European hake population expressed as DI ( $N/km^2$ ), the presence/absence of recruits, the presence/absence of large adults.

For the response variable DI, a two-stage GAM approach generally known as delta model (Aitchison, 1955; Stefansson, 1996) was applied in order to deal with high number of zero catches and over-dispersion (Gruss et al., 2014). This consists of fitting two independent models, a binomial distribution for the presence/absence data and a zero-truncated distribution, such as lognormal or Gamma distribution, for

**Table 1** Selected predictive models of probability of presence of hake (PPH), non-zero hake abundance (DIH), probability of presence of recruits (PPR) and probability of presence of large adults (PPA)

Model	Adj- $r^2$	Dev %	TPR	$\rho_s$ int.	$\rho_s$ ext.
PPH ~ s(depth) + rugosity + s(lat) + s(lon)	0.40	40.8	0.87	0.54	0.51
DIH ~ s(depth) + slope + s(rugosity) + s(distshore) + s(lat) + s(lon) + s(rugosity)	0.46	47.9		0.62	0.62
PPR ~ s(depth) + slope + rugosity + s(distshore) + s(lat) + s(lon)	0.32	36.0	0.86	0.43	0.39
PPA ~ s(depth) + slope + rugosity + s(eastness)	0.21	34.9	0.80	0.34	0.35

Only the significant predictors are included in the models

Latitude and longitude are abbreviated “lat” and “lon”, respectively; distance to shore is abbreviated “distshore”. The s() indicates a smooth function of the predictor. Adj- $r^2$ , Dev %, and TPR are, respectively, the coefficient of determination, the percentage of deviance explained and the True Positive Rate. The Spearman’s correlation coefficients for internal and external evaluations are indicated as  $\rho_s$  int. and  $\rho_s$  ext., respectively

non-zero abundance data (Stefansson, 1996). The final predictions of species abundance are obtained by multiplying the predictions from the two models. Specifically, a delta-Gamma model was developed fitting a binomial model (logit link function) to predict the probability of presence of European hake (PPH) and a Gamma model (inverse link function) to predict the non-zero abundance (DIH). Binomial models (logit link function) were developed to predict, respectively, the probability of presence of recruits (PPR) and the probability of presence of large adults (PPA).

Smooth terms were represented using penalized regression splines with smoothing parameters selection based on Un-Biased Risk Estimator (UBRE) and generalized cross validation (GCV) criteria (Wood, 2006) for binomial and Gamma model, respectively. Selection of best model was performed by minimization of Akaike’s information criterion (AIC). Deviance explained (Dev %) and coefficient of determination (adj- $r^2$ ) were computed as measures of goodness of fit. To check whether spatial autocorrelation could bias analysis, the strength of the models residuals spatial dependence was explored using Moran’s I coefficient (Legendre & Legendre, 1998). Moran’s I takes values between -1 and 1 with a zero value indicating a random spatial pattern. Correlograms were plotted using spatial lags of 10 km.

To validate models, Spearman’s correlation coefficients (Spearman’s  $\rho$ ’s) between predicted and

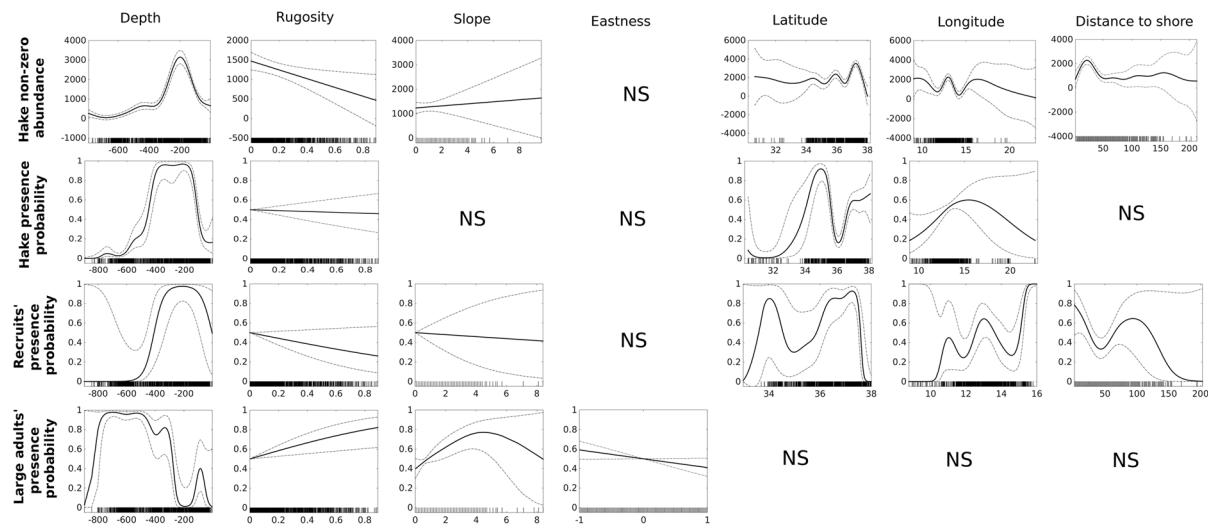
observed values were estimated using both training dataset (internal evaluation) and test dataset (external evaluation).

The predictive performance of the binomial models was evaluated using the true positive rate (TPR) or model sensitivity. It is calculated as proportion of true presence data that are correctly predicted. A perfect predictor would be described as 100% sensitive. Following Cormon et al. (2014), TPR was preferred to the most popular area under the receiver operating characteristic curve (AUC-ROC, where the ROC is the TPR as a function of False Positive Rate), to take into account for imperfect detectability (or catchability) when monitoring marine populations (Katsanevakis et al., 2012).

The selected models were used to generate prediction maps, including unsurveyed cells of the study area, using a grid cell size of 1 × 1 km. Sea bottoms deeper than 800 m were excluded because they were out of the depth range of the training dataset.

Since data from all years were pooled together, results of modelling should be interpreted as mean habitat (*sensu* Kearney, 2006) preference for the species or fractions of its population.

GAM models were developed using the MGCV package (Wood, 2006) of R (R Development Core Team, 2015). Moran’s I coefficient and related correlograms were computed with the SPDEP package (Bivand & Piras, 2015) while ROCR package (Sing et al., 2005) was used to calculate TPR.



**Fig. 3** Smoothed curve of partial effects of predictive variables (columns) on the different models (rows). For each model, the predictors which became significant are shown (NS

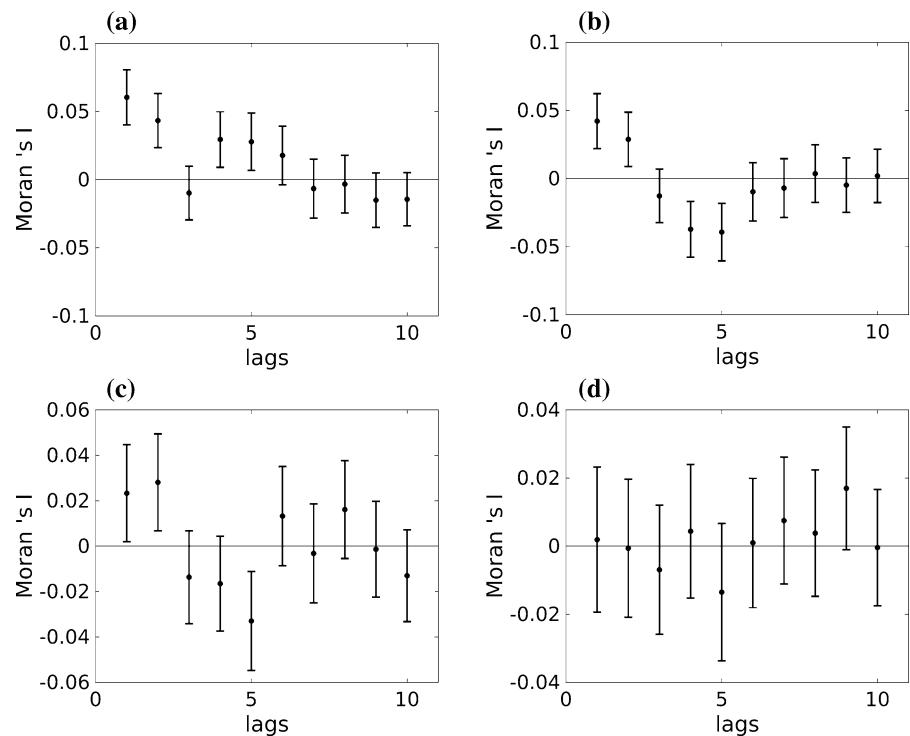
stands for not significant). The smoothed fit (solid line) is shown along with 95% confidence intervals (dotted lines). Data points are shown at the lower axis

## Results

All geographical and seafloor geophysical factors were found to be significant predictors of European

hake distribution (Table 1) with the exception of the aspect characteristics (eastness and northness) for which eastness was only correlated to adult presence. Figure 3 shows the partial effects of significant

**Fig. 4** Moran's I coefficients of spatial autocorrelation in the residuals of the predictive models: **a** non-zero abundance ( $N/km^2$ ), **b** the presence probability, **c** recruit presence probability, **d** large adult presence probability, of European hake

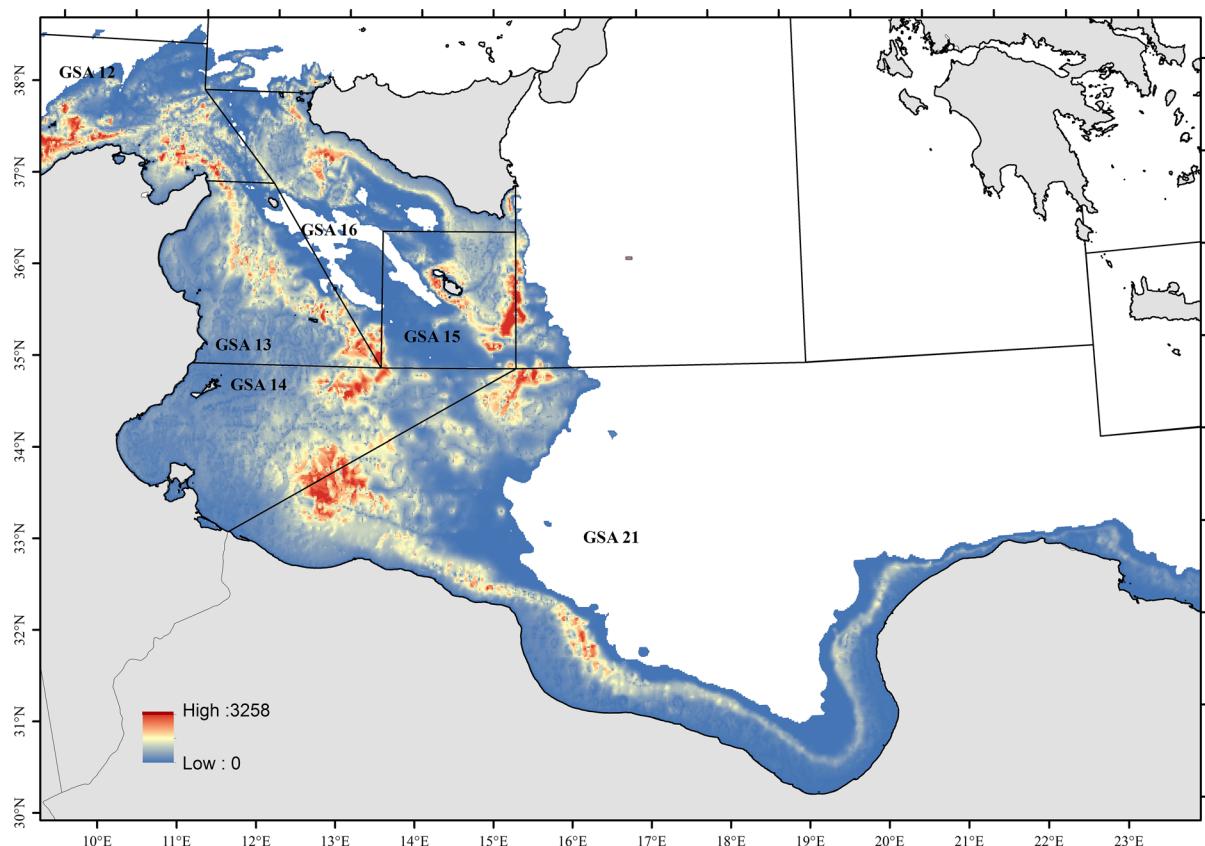


explanatory variables in each model. The water depth was found to be a highly significant ( $P < 0.001$ ) predictor in all models. Rugosity was fitted as linear term in all binomial models (Table 1) showing a negative linear relationship for recruit presence probability (PPR) and a positive one for large adult presence probability (PPA) (Fig. 3). In general, nonlinear response patterns were evident for the three geographical variables: latitude, longitude and distance to shore.

Analysis of correlograms (Fig. 4) showed that Moran's I coefficients of spatial autocorrelation in the residuals were positive and significant to a lag of 20 km for the models of hake presence and abundance (PPH and DIH) and presence of recruits (PPR), although the absolute value of the coefficients was extremely low. Indeed the order of magnitude of Moran's I was  $10^{-2}$  at any lag. These results mean that the above models accounted for much of the

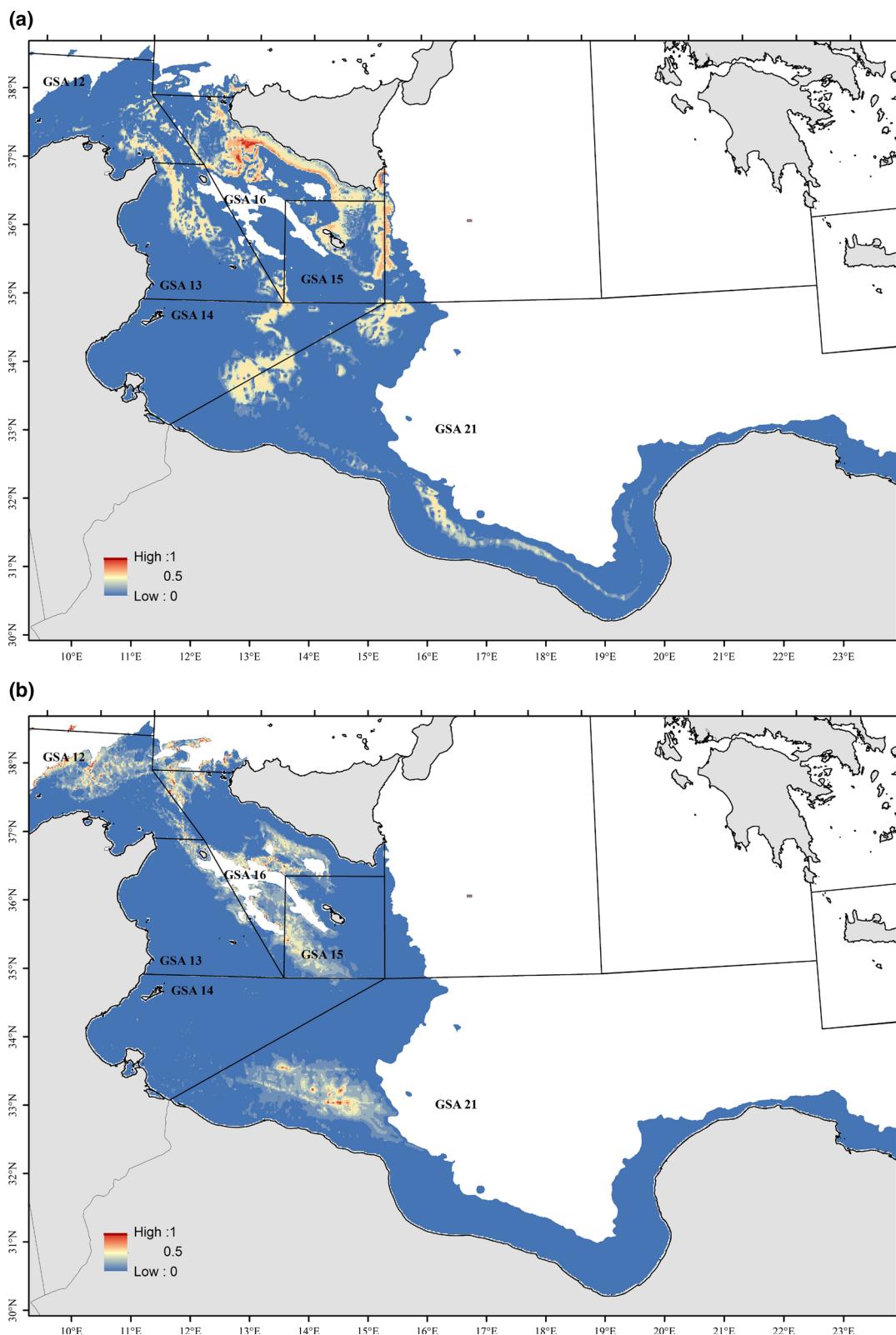
**Fig. 6** Distribution map of the predicted probability of the presence of **a** recruits, **b** large adults, of European hake in the south-central Mediterranean Sea. A graduated colour scale was used to represent low probability values in blue and high probability values in red. The white area in the centre represents bottoms deeper than 800 m where no prediction has been made

spatial variability and autocorrelation of the original data but there still existed some weak pattern not captured by the selected predictors. No spatial pattern in the residuals was evident for the model of large adults (PPA), being the Moran's I coefficients consistently close to 0 at any lag (Fig. 4). Models evaluation showed that the percentage of deviance explained ranged between 34.9 and 47.9% (Table 1) for the different models with the lower value found for PPA model and the highest value for non-zero abundance model (DIH). Spearman's correlation



**Fig. 5** Distribution map of the predicted European hake abundance ( $N/km^2$ ) in the south-central Mediterranean Sea. A graduated colour scale was used to represent low values of

abundance in blue and high values in red. The white area in the centre represents bottoms deeper than 800 m where no prediction has been made



coefficients between predicted and observed values had similar values in internal and external evaluations (Table 1) and showed that models for hake presence and abundance performed better than models for recruits and large adults. All binomial models exhibited high sensitivity as suggested by values of TPR ranging between 0.80 and 0.87. On the whole, goodness of fit and predictive capability proved a little bit worse for PPA model (Table 1) probably due to the low number of the presence data of large adults.

#### European hake abundance

Probability of presence of European hake (PPH) was best described by a model including four factors (depth, rugosity, latitude and longitude), while two more factors appeared to drive the abundance of the species (non-zero abundance, DIH), i.e. slope and distance to shore (Table 1). Hake presence probability was almost uniform between 200 and 400 m, while the abundance attained a maximum at 200 m depth and then decreased up to 600 m depth with a local maximum at 400 m depth (Fig. 3). For DIH, a strong negative linear relationship was observed with rugosity and a positive one with slope. Non-linear relationships were observed with latitude, longitude and distance to the shore with general patterns highlighting the presence of local maxima of abundance (Fig. 3). In the smoother of latitudes, these maxima appeared at the increasing values of DIH when passing from 34° to 38° of latitude (Fig. 3).

The percentage of deviance explained in the models, related to the models goodness of fit, was 40.8% for the presence probability of the hake and 47.9% for non-zero abundance data. The Spearman's correlation coefficients in the external evaluation were 0.51 and 0.62 for PPH and DIH, respectively (Table 1), suggesting a good predictive performance of the whole model for the European hake abundance ( $\text{N}/\text{km}^2$ ).

The map of predicted abundance showed the even distribution of the species along the shelf break-upper slope (up to 400 m depth) of both Italian and African platforms (Fig. 5). Areas of high concentration were observed in the Gulf of Tunis, off the wide Tunisian platform south of Lampedusa island, on the eastern flank of Adventure Bank and Malta Bank, respectively, and in the western sector of Libyan platform.

The abundance of the species considerably decreased off the eastern Libyan coast.

#### Probability of presence of recruits

The highest probability of presence of recruits (PPR) was associated with a depth range between 150 and 250 m (Fig. 3). Negative linear relationships were found with slope and rugosity. In contrast, nonlinear relationships were found with distance to shore, latitude and longitude (Fig. 3) which were highly significant predictors ( $p < 0.0001$ ) for PPR.

The main areas of recruits concentration were located to the east of the Adventure Bank and Malta Bank extending also along the central-southern coast of Sicily (Fig. 6a). Off the Tunisian coasts, recruits' concentration areas were observed in the Gulf of Tunis and Gulf of Hammamet, as well as in the east of the Gulf of Gabès at the border between Libyan coast. Along the Libyan coast, preferential habitat for recruits was found in the western part of the Gulf of Syrte, while the population fraction was very scanty along the Libyan eastern coast (Fig. 6a).

#### Probability of presence of large adults

The probability of presence of large adults (PPA) was significantly influenced by depth and three seafloor characteristics (slope, rugosity and eastness) (Table 1). PPA showed maximum probability in a wide range of depth centred around 600 m depth, abruptly decreased up to 200 m and then showed a relative peak at shallow waters (100 m depth). A positive linear relationship with rugosity was observed, while the nonlinear relationship with slope showed the increasing PPA up to 4° of slope. A negative linear relationship with eastness suggested that large adults in the study area prefer west-facing slopes.

Concerning the geographical distribution, large adults were preferentially distributed in the deep bottoms north of Tunisia and west of the Adventure Bank, and in the deepest bottoms between Italian and Tunisian platforms (Fig. 6b). A further concentration area was observed off the western part of the Libyan coast below 400 m depth.

## Discussion

In the present study, models of the spatial distribution of European hake in the south-central Mediterranean have been developed using, after appropriate standardization, series of bottom trawl surveys carried out in the region from 2003 to 2011. Specifically, a distribution map of the European hake abundance has been produced together with maps of probability of presence of recruits and large adults.

The map of the predicted European hake abundance (described by density N/km<sup>2</sup>) has highlighted the wide distribution of the species in the study area along the shelf break–upper slope of both Italian–Maltese and Tunisian platforms, while the species abundance appeared very scanty in the easternmost Libyan waters. Despite the species being present in a wide bathymetric range (from 50 to 800 m), abundance decreased below 200 m depth, and was negligible below 400 m depth, in agreement with previous studies on the species in the Mediterranean Sea (Orsi Relini et al., 2002; Recasens et al., 1998; Katsanevakis et al., 2009). Orsi Relini et al. (2002) reported that the bathymetric distribution of European hake in the Mediterranean Sea ranges between 25 and 1000 m depth, but the highest abundances are found in the range 100–400 m depth. European hake specimens occurred between 50 and 750 m depth in the north-western Mediterranean, but density was low below 400 m depth (Recasens et al., 1998). In the eastern Mediterranean Sea, the species exhibited a density peak between the lower shelf and the upper continental slope (Katsanevakis et al., 2009).

The type of explanatory factors that best described the probability of presence of recruits and large adults, respectively, as well as the shape of their smoothers revealed diverse habitat requirements of the two population fractions.

Besides depth, the three geographical variables latitude, longitude and distance to shore were highly significant predictors of recruits presence. The non-linear shape of these smoothers with the presence of different relative maxima, suggested that further mesoscale environmental factors could account for the presence of recruits, likely related to their pelagic lifestyle. On the contrary, geographical variables were not included in the model of large adult presence probability which appeared strictly related to specific seafloor habitat characteristics such as

rugosity, slope and orientation of the bottom slope, suggesting the necto-benthonic lifestyle of this component of the population. Carpentieri et al. (2005) described a strong difference in trophic requirements among the European hake size classes in the central Mediterranean sea. Their study showed that during the first year of life (<16 cm), the European hake feed almost exclusively on crustaceans, mainly Euphausiids. Small hake undertakes daily vertical migrations to follow these planktonic crustaceans that migrate to near the surface at night. When juveniles move from nursery areas after the first year of life, their diet changes to fish prey (mainly Clupeiformes) with drastic reduction of Euphausiids consumption and progressively shifts towards a fully piscivorous diet (comprising large fish prey) at the attainment of sexual maturity. Changes in the preferred depth range of the different life stages have been put in relationship to this ontogenesis-related diet shifts (Carpentieri et al., 2005). On the basis of this knowledge, it is evident the importance of exploring biotic-based causal relationships when modelling species distribution in space and time (Johnson et al., 2013). In particular, variables linked to intra- and interspecific competitions and predations are supposed to drive species distribution and abundance (Johnson et al., 2013). In the present study, significant relationships have been found between the presence of recruits and large adults of European hake and abiotic variables which may act as proxy of favourable feeding conditions for the different life stages, but no biotic variables such as prey abundance have been included in the models. The importance of integrating biotic variables in European hake modelling is confirmed by a recent study (Cormon et al., 2014) that found a positive relationship between the species' spatial distribution in the North Sea and the occurrence of potential competitors and preys. Prey-size selectivity can also play a major role in predator-prey interaction and deserves much attention. A significant positive relationship between hake predator length and fish prey length has been found in a study of European hake diet in the Bay of Biscay and the Celtic Sea (Mahe et al., 2007). Furthermore, the potential importance of prey size over prey abundance has been highlighted for the European hake around the Balearic Islands in the Mediterranean (Johnson et al., 2012). Future studies should therefore investigate whether prey abundance and size are key

factors in defining habitat requirements of the different life stages of the European hake in the south-central Mediterranean by including explicitly such biotic variables in the species distribution models.

In the present study, the probability of presence of European hake recruits reached its maximum around 200 m depth which is in agreement with other studies in the Mediterranean. Areas of recruits concentration were observed between 100 and 200 m in the north-western Mediterranean (Recasens et al., 1998; Morfin et al., 2012) and in the eastern–central Mediterranean (Carlucci et al., 2009), around 250 m at the Balearic Islands (Hidalgo et al., 2008) and in the northern sector of the Strait of Sicily (Garofalo et al., 2011). In this latter area, the undersized specimens of European hake represented a predominant fraction of trawl discard at depths between 150 and 300 m (Milisenda et al., 2017). Recruits were instead concentrated at shallower depths (100–150 m) off the Catalan coast (Maynou et al., 2003). The difference with respect to the Balearic island, according to Hidalgo et al. (2008), is explained as being due to the recruits' preference for muddy bottoms with a high content of organic matter (Maynou et al., 2003) which, off the Balearic shelf, are distributed deeper than those off the Catalan coast (with organic matter also increasing with the depth). The recruits' preference for fine sediments has been also observed in the present study. Indeed, the rugosity of the sea floor, providing insight on the bottom hardness was found to be a significant variable to explain (and predict) the probability of presence of European hake recruits. The model indicated an inverse relationship between the occurrence of recruits and both slope and rugosity. Low values of these two variables are indicative of areas of sediment deposition and soft seabed substrata (Lauria et al., 2015) and confirmed recruits' preference for soft sediment habitat. This is consistent with results by Druon et al. (2015) concerning recruits' preferences for low current velocity at sea bottom which would favour the deposition of particulate organic matter, and ultimately the recruits' feeding at seabed during the day.

The observed hotspots of recruits concentration are supposed to be nursery areas. Many studies have investigated the persistence of the nurseries in the northern sector of the Strait of Sicily across the Italian-Maltese platform (Fiorentino et al., 2003; Garofalo et al., 2011; Colloca et al., 2015). Models of

European hake's suitable habitat in the European Mediterranean waters were developed using depth and geographical variables (latitude, longitude and distance to shore) as predictors (Colloca et al., 2015). In agreement with the results of the present study, the nursery areas identified in the Strait of Sicily were mostly located between 100 and 250 m depth, and showed a patchy distribution along the shelf break (Colloca et al., 2015). The location and persistence of the nursery areas in the northern sector of the Strait of Sicily has been related to the bathymetric and oceanographical features that characterize the area (Abella et al., 2008; Garofalo et al., 2011; Colloca et al., 2015), i.e. the presence of wide offshore banks (Adventure Bank and Malta Bank) and the occurrence of considerable upwelling phenomena and mesoscale structures such as eddies and fronts throughout the year (Beranger et al., 2004). One more modelling study was developed by Druon et al. (2015) at Mediterranean scale using an ecological niche approach to predict the mean occurrence of favourable habitat for the European hake recruits ( $\leq 15$  cm total length). In that study, the model was built combining information on biological traits of recruits (duration of life stages, growth, settlement and movement) and environmental variables (depth, chlorophyll-a, sea bottom current and temperature). Those authors suggested that hake nurseries are preferably located where productive fronts, likely enhancing prey availability, frequently occur near the shelf-break area. Notably, the model by Druon et al. (2015) provided for the first time knowledge about the spatial distribution pattern of recruits in the southern sector of the Strait of Sicily, off the African coast. Again, high agreement has been observed with results from the present study.

A different pattern of habitat preference by large adults (individuals with  $TL > 38$  cm) with respect to recruits has emerged in the study area. Their predicted distribution has shown higher probability of occurrence in the deep bottoms (below 400 m depth) with a peak around 600 m. Contrary to recruits, large adults' preference for hard bottom substrates has been suggested by a positive linear relationship with rugosity and slope, which is indicative of stability of sediments (Elvenes et al., 2014). Rugosity is considered a strong surrogate of hard bottoms and fish species richness (Pittman et al., 2007), and therefore, it may suggest enhanced prey

availability for the large European hake specimens. Moreover, a significant relationship has been observed between the occurrence of large adults and the orientation of the seabed, specifically the west-facing slopes. Slope and aspect (eastness and/or northness) together give information on the exposure of the seabed to bottom currents and local accelerations of currents, and can act as proxy of food supply (Elvenes et al., 2014). At the observed depth range of large adults, the predominant current is the Levantine Intermediate Water flowing westwards through the Strait of Sicily. There is no element to infer causal relationships between the large adults distribution and the current flow. However, studies conducted on the Pacific hake in the California Current System (Agostini et al., 2006) suggested that the poleward flowing subsurface California undercurrent defines the habitat of adult hake rather than a specific temperature range, with flow properties facilitating or contrasting the northward migration of the Pacific hake. Those authors hypothesized that the positioning of large adults relative to the current flow provides advantages during migrations, ultimately linked to food supply along the way and reduced energy expenditure (Agostini et al., 2006). The migration pattern of the European hake in the study area is not well known, and it should be investigated whether the species is affected by environmental processes similar to those described above.

Orsi Relini et al. (2002) reported that average body size of European hake increases, in general, as depth increases. However, discrepancies are found in the literature concerning the depth range at which large adults occur. Large European hake individuals (mean length > 33 cm) were found across the whole range of sampled depth from 50 to 750 m in the Gulf of Lions, north-western Mediterranean (Recasens et al., 1998), with high concentrations at 150–300 m in autumn and between 200 and 350 m in winter. Comparison of adult distribution versus juvenile distribution was also performed in the Gulf of Lions (Morfin et al., 2012) where the European hake adults were more concentrated than juveniles, but their distribution was included within the distribution range of the juveniles. At the Balearic Islands, the European hake individuals larger than 26 cm were mainly distributed within the depth range of 250–350 m, while catches of the largest fish (>39 cm) were scarce and independent of depth (Hidalgo et al.,

2008). Off the Catalan coast, adults (>34 cm) mainly occurred between 75 and 150 m in winter and spring and moved offshore (>300 m depth) in summer (Demestre & Sánchez, 1998). In the same area, the distribution of individuals larger than 25 cm was investigated in relation to depth and to the distribution of recruits (Maynou et al., 2003); large specimens were distributed over the entire sampled bathymetric range (50–350 m depth), and did not show any correlation with recruits.

Possible explanation of the differences observed in various studies, including the present study, is the difficulty in obtaining representative samples of mature adult specimens in experimental trawl surveys due to the high avoidance capability of large-sized females to bottom trawls (Abella et al., 1997; Ragonese, 2009). It is known that while trawl catches consist mainly of immature juveniles living on the continental shelf, the reproductive adult portion of European hake stocks is mainly exploited by gillnetters and longliners (Aldebert et al., 1993; Recasens et al., 1998; Martin et al., 1999; Sbrana et al., 2007) operating also in the deep sea (i.e. off the shelf and below 400 m) and in non-trawlable areas. This may explain the scarcity of information on spatial distribution of larger adult specimens compared with juvenile stages (Recasens et al., 1998). In this context, the developed predictive model allowed to obtain valuable information about the distribution of large adults across the south-central Mediterranean Sea. It is worth noting that the model predicted a high probability of presence of large adults in an unsampled area off the western part of the Libyan coast. This area is adjacent to shallower sea bottoms where a very high estimate of pelagic fish biomass was obtained in a recent work (Bonanno et al., 2015). This high biomass was linked to the high primary productivity of the Gulf of Gabes. In particular, the authors hypothesized that the area represents the ‘tail’ of a more extended pelagic fish patch centred in the Gulf of Gabes. Therefore, it could be thought that the area of predicted presence of the European hake large adults located in the westernmost sector of Libyan waters is the nearest compliant area in terms of depth and seafloor characteristics where the species can benefit from a high food availability. Further studies should focus on this geographical area to deepen the existing knowledge on the ecology of the species along the African coast and to investigate its

productivity potential for future management perspectives.

The proxy used in the present study to identify large adults (mean weight of the catches greater than 400 g corresponding to 38 cm of total length) produced an underestimate of the reproductive portion of the population which likely has a more spread distribution and aggregates at shallower depth to spawn (here recruits dominate and can mask adults' presence). Indeed, according to a literature review (Fiorentino et al., 2008), spawning should occur in the outer shelf-upper slope. This was also reported by a previous semi-quantitative work carried out in the same region using a threshold length of 29 cm to identify spawners (Garofalo et al., 2008). Even before, Bouhlal (1973) reported aggregations of mature adults between 100 and 200 m depth in the Gulf of Tunis. But considering that a sex ratio equal to 0.9 has been reported for the European hake specimens with TL > 36 cm (Fiorentino et al., 2008), the produced map could be considered a probability distribution of occurrence of large females. Older mature females provide higher relative reproductive contribution to the population and even a moderate level of protection is considered important under conditions of high juvenile mortality (Caddy & Seijo, 2002).

## Conclusion

The predictive models developed in this study have provided an informative picture about the distribution of the European hake in the south-central Mediterranean sea, highlighting different habitat preferences between recruits and large adults. Surely, the degree of deviance unexplained by the models suggests that other abiotic and biotic factors may contribute to explain the distribution of the species and its critical life stages and ought to be taken into account in future studies. However, findings of the present study largely matched those reported in other studies in the Mediterranean area. Despite the apparent limitation of using threshold values of the mean weight of catches to discriminate the two fractions of the population, results allowed an identification of nurseries comparable to those obtained with more accurate methods on length data (Garofalo et al., 2011; Colloca et al., 2015; Druon et al., 2015).

Considering that trawl surveys routinely collect abundance in number and weight for many hundreds of species, this study provides evidence that the proposed approach could be used to explore the spatial distribution of juveniles of species which are vulnerable to trawl net starting from the smallest sizes.

Overall, these results represent a knowledge base to orient further investigations as well as spatial-based management measures in the south-central Mediterranean. Fisheries restricted areas (FRAs) have been established for the conservation and management of the European hake juveniles (REC.CM-GFCM/40/2016/4; see FAO, 2016) in two areas of the northern region of the Strait of Sicily identified as nurseries in previous studies (Fiorentino et al., 2003; Garofalo et al., 2011; Colloca et al., 2015). The present study contributed to expand our knowledge on nursery grounds of the Tunisian platform where further FRAs could be established in the future within the GFCM regional-spatial management plan.

**Acknowledgements** This work was carried out within the Regional Project “Assessment and Monitoring of the Fishery Resources and the Ecosystems in the Straits of Sicily” (MedSudMed) executed by the Food and Agriculture Organization (FAO) of the United Nations and funded by the Italian Ministry of Agriculture, Food and Forestry Policies (MiPAAF). The authors thank all the technical staff of CNR-IAMC UOS of Mazara del Vallo (Italy) and INSTM in Tunisia involved in data collection and processing. Finally, the authors would like to thank the reviewers for constructive and valuable comments, which were of great help in improving the original manuscript.

## References

- Abella, A., J. F. Caddy & F. Serena, 1997. Do natural mortality and availability decline with age? An alternative yield paradigm for juvenile fisheries, illustrated by the hake *Merluccius merluccius* fishery in the Mediterranean. Aquatic Living Resources 10: 257–269.
- Abella, A., F. Fiorentino, A. Mannini & L. Orsi Relini, 2008. Exploring relationships between recruitment of European hake (*Merluccius merluccius* L. 1758) and environmental factors in the Ligurian Sea and the Strait of Sicily (Central Mediterranean). Journal of Marine Systems 71: 279–293.
- Agostini, V. N., R. C. Francis, A. B. Hollowed, S. D. Pierce, C. Wilson & A. N. Hendrix, 2006. The relationship between Pacific hake (*Merluccius productus*) distribution and poleward subsurface flow in the California Current System. Canadian Journal of Fisheries and Aquatic Sciences 63: 2648–2659.

- Aitchison, J., 1955. On the distribution of a positive random variable having a discrete probability mass at the origin. *Journal of the American Statistical Association* 50: 901–908.
- Aldebert, Y., L. Recasens & J. Lleonart, 1993. Analysis of gear interaction in a hake fishery: The case of the Gulf of Lions (NW Mediterranean). *Scientia Marina* 57: 207–217.
- Austin, M. P., 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecological Modelling* 200: 1–19.
- Bartolino, V., F. Colloca, P. Sartor & G. Ardizzone, 2008. Modeling recruitment dynamics of hake, *Merluccius merluccius*, in the central Mediterranean in relation to key environmental variables. *Fisheries Research* 92: 277–288.
- Beranger, K., L. Mortier, G. P. Gasparini, L. Gervasio, M. Astraldi & M. Crèpon, 2004. The dynamics of the Sicily Strait: a comprehensive study from observations and models. *Deep Sea Research II* 51: 411–440.
- Bertrand, J. A., L. Gil De Sola, C. Papaconstantinou, G. Relini & A. Souplet, 2002. The general specifications of the MEDITIS surveys. *Scientia Marina* 66: 9–17.
- Berkeley, S. A., M. A. Hixon, R. J. Larson & M. S. Love, 2004. Fisheries Sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* 29: 23–32.
- Bivand, R. & G. Piras, 2015. Comparing implementations of estimation methods for spatial econometrics. *Journal of Statistical Software* 63: 1–36.
- Bonanno, A., S. Zgozi, G. Basilone, M. Hamza, M. Barra, S. Genovese, P. Rumolo, A. Nfate, M. Elsger, S. Goncharov, S. Popov, R. Mifsud, T. Bahri, G. Giacalone, I. Fontana, B. Buongiorno Nardelli, S. Aronica, L. Ceriola, B. Patti, R. Ferreri, S. Colella, G. Volpe & S. Mazzola, 2015. Acoustically detected pelagic fish community in relation to environmental conditions observed in the Central Mediterranean sea: a comparison of Libyan and Sicilian Maltese coastal areas. *Hydrobiologia* 755: 209–224.
- Bouhlal, M., 1973. Le merlu des côtes nord de la Tunisie: étude économique et biologique (reproduction, sex ratio et répartition bathymétrique). *Bulletin de l'Institut Océanographique de Pêche Salammbô* 2: 579–603.
- Caddy, J. F., 2000. A fisheries management perspective on marine protected areas in the Mediterranean. *Environmental Conservation* 27: 98–103.
- Caddy, J. F. & J. C. Seijo, 2002. Reproductive contributions foregone with harvesting: a conceptual framework. *Fisheries Research* 59: 17–30.
- Carlucci, R., G. Lembo, P. Maiorano, F. Capezzutto, C. A. Marano, L. Sion, M. T. Spedicato, N. Ungaro, A. Tursi & G. D'Onghia, 2009. Nursery areas of red mullet (*Mullus barbatus*), hake (*Merluccius merluccius*) and deep-water rose shrimp (*Parapenaeus longirostris*) in Eastern-Central Mediterranean Sea. *Estuarine, Coastal and Shelf Science* 83: 529–538.
- Carpentieri, P., F. Colloca, M. Cardinale, A. Belluscio & G. D. Ardizzone, 2005. Feeding habits of European hake (*Merluccius merluccius*) in the central Mediterranean Sea. *Fishery Bulletin* 103: 411–416.
- Ciannelli, L., P. Fauchald, K. S. Chan, V. N. Agostini & G. E. Dingsør, 2008. Spatial fisheries ecology: recent progress and future prospects. *Journal of Marine Systems* 71: 223–236.
- Colloca, F., G. Garofalo, I. Bitetto, M. T. Facchini, F. Grati, A. Martiradonna, et al., 2015. The seascape of demersal fish nursery areas in the North Mediterranean Sea, a first step towards the implementation of Spatial planning for trawl fisheries. *PLoS ONE* 10(3): e0119590.
- Cormon, X., C. Loots, S. Vaz, Y. Vermand & P. Marchal, 2014. Spatial interactions between saithe (*Pollachius virens*) and hake (*Merluccius merluccius*) in the North Sea. *ICES Journal of Marine Science* 71: 1342–1355.
- Cotter, J., P. Petitgas, A. Abella, P. Apostolaki, B. Mesnil, C. Politou, J. Rivoirard, M. J. Rochet, M. T. Spedicato, V. M. Trenkel & M. Woillez, 2009. Towards an ecosystem approach to fisheries management (EAFM) when trawl surveys provide the main source of information. *Aquatic Living Resources* 22: 243–254.
- Damalas, D., C. D. Maravelias, S. Katsanevakis, A. Karageorgis & C. Papaconstantinou, 2010. Seasonal abundance of non-commercial demersal fish in the eastern Mediterranean Sea in relation to hydrographic and sediment characteristics. *Estuarine Coastal and Shelf Science* 89: 107–118.
- Demestre, M. & P. Sánchez, 1998. Spatio-temporal distribution of the European hake *Merluccius merluccius* off the Catalan coast (north-western Mediterranean). *Rapport Commission Internationale pour la Mer Méditerranée* 35: 420–421.
- Druon, J. N., F. Fiorentino, M. Murenu, L. Knittweis, F. Colloca, C. Osio, B. Mérigot, G. Garofalo, A. Mannini, A. Jadaud, M. Sbrana, G. Scarella, G. Tserpes, P. Peristeraki, R. Carlucci & J. Heikkonen, 2015. Modelling of European hake nurseries in the Mediterranean Sea: an ecological niche approach. *Progress in Oceanography* 130: 188–204.
- Dunn, D. & P. Halpin, 2009. Rugosity-based regional modeling of hard-bottom Habitat. *Marine Ecology Progress Series* 377: 1–11.
- Elith, J. & J. R. Leathwick, 2009. Species Distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40: 677–697.
- Elvenes, S., M. F. J. Dolan, P. Buhl-Mortensen & V. K. Bellec, 2014. An evaluation of compiled single-beam bathymetry data as a basis for regional sediment and biotope mapping. *ICES Journal of Marine Science* 71: 867–881.
- FAO, 2016. Report of the fortieth session of the General Fisheries Commission for the Mediterranean (GFCM), St. Julian's, Malta, 30 May–3 June 2016. GFCM Report No. 40. Rome, Italy.
- FAO GFCM, 2009. GFCM Resolution RES-GFCM/33/2009/2 Establishment of Geographical Sub-Areas in the GFCM area amending the resolution GFCM/31/2007/2. In: FAO General Fisheries Commission for the Mediterranean, Report of the thirty-third session. Tunis, 23–27 March 2009. GFCM Report. No. 33. Rome, FAO. 2009.
- Fiorentino, F., G. Garofalo, A. De Santi, G. Bono, G. B. Giusto & G. Norrito, 2003. Spatio-temporal distribution of recruits (0 group) of *Merluccius merluccius* and *Phycis blennoides* (Pisces, Gadiformes) in the Strait of Sicily (Central Mediterranean). *Hydrobiologia* 503: 223–236.

- Fiorentino, F., S. Ben Meriem, T. Bahri, M. Camilleri, M. Dimech, S. Ezzeddine-Naja, F. Massa, O. Jarboui, & S. Zgozi, 2008. Synthesis of information on some target species in the MedSudMed Project area (central Mediterranean). GCP/RER/010/ITA/MSM-TD-15. MedSudMed Technical Documents, 15.
- Gancitano, V., G. Milisenda, S. Ben Meriem, F. Colloca, E. Arneri, L. Ceriola, O. Jarboui, O. Ben Abdallah, M. Gambin, R. Mifsud & F. Fiorentino, 2016. ASSESSMENT OF EUROPEAN HAKE IN GSAs 12–16. In: General Fisheries Commission for the Mediterranean, Scientific Advisory Committee (SAC), Working Group on stock assessment of demersal species (WGSAD)—Rome, Italy, 07–12 November 2016, Final report.
- Garofalo, G., M. Bel Hassen, O. Jarboui, S. Zgozi, M. Gristina, F. Fiorentino, S. Ragonese, & M. Camilleri, 2008. Preliminary results on spatial distribution of abundance indices, nursery and spawning areas of *Merluccius merluccius* and *Mullus barbatus* in the central Mediterranean. GCP/RER/010/ITA/MSM-TD 19. MedSudMed Technical Documents, 19.
- Garofalo, G., T. Fortibuoni, M. Gristina, M. Sinopoli & F. Fiorentino, 2011. Persistence and co-occurrence of demersal nurseries in the Strait of Sicily (Central Mediterranean): implications for fishery management. Journal of Sea Research 66: 29–38.
- Garofalo, G., F. Fiorentino, F. Gargano, O. Jarboui, R. Micallef, R. Mifsud, S. Zgozi, E. Arneri, & L. Ceriola, in press. A cooperative research in the south-central Mediterranean Sea: from inter-calibration of bottom trawl surveys to resources abundance mapping. GCP/RER/010/ITA/MSM-TD 36. MedSudMed Technical Documents, 36.
- Guisan, A. & W. Thuiller, 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8: 993–1009.
- Guisan, A. & N. E. Zimmermann, 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135: 147–186.
- Guisan, A., T. C. Edwards & T. Hastie, 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157: 89–100.
- Gruss, A., M. Drexler & C. H. Ainsworth, 2014. Using delta generalized additive models to produce distribution maps for spatially explicit ecosystem models. Fisheries Research 159: 11–24.
- Hastie, T. J. & R. J. Tibshirani, 1990. Generalised Additive Models. St. Edmundsbury Press Limited, Suffolk.
- Hattab, T., F. Ben Rais Lasram, C. Albouy, C. Sammari, M. S. Romdhane, P. Cury, F. Leprieur & F. Le Loc'h, 2013. The use of a predictive habitat model and a fuzzy logic approach for marine management and planning. PLoS ONE 8(10): e76430.
- Hidalgo, M., E. Massutí, J. Moranta, J. Cartes, J. Lloret, P. Oliver & B. Morales-Nin, 2008. Seasonal and short spatial patterns in European hake (*Merluccius merluccius* L.) recruitment process at the Balearic Islands (western Mediterranean): the role of environment on distribution and condition. Journal of Marine Systems 71: 367–384.
- Johnson, A. F., M. Valls, M. Moranta, S. R. Jenkins, J. G. Hiddink & H. Hinz, 2012. Effect of prey abundance and size on the distribution of demersal fishes. Canadian Journal of Fisheries and Aquatic Sciences 69: 191–200.
- Johnson, A. F., S. T. Jenkins, J. G. Hiddink & H. Hinz, 2013. Linking temperate demersal fish species to habitat: scales, patterns and future directions. Fish and Fisheries 14: 256–280.
- Katsanevakis, S., C. D. Maravelias, D. Damalas, A. P. Karageorgis, E. V. Tsitsika, C. Anagnostou & C. Papaconstantinou, 2009. Spatiotemporal distribution and habitat use of commercial demersal species in the eastern Mediterranean Sea. Fisheries Oceanography 18: 439–457.
- Katsanevakis, S., A. Weber, C. Pipitone, M. Leopold, M. Cronin, M. Scheidat, T. K. Doyle, L. Buhl-Mortensen, P. Buhl-Mortensen, G. D'Anna, I. De Boois, P. Dalpadado, D. Damalas, F. Fiorentino, G. Garofalo, V. M. Giacalone, K. L. Hawley, Y. Issaris, J. Jansen, C. M. Knight, L. Knittweis, I. Kröncke, S. Mirto, I. Muxika, H. Reiss, H. R. Skjoldal & S. Vöge, 2012. Monitoring marine populations and communities: methods dealing with imperfect detectability. Aquatic Biology 16: 31–52.
- Kearney, M., 2006. Habitat, environment and niche: what are we modelling? Oikos 115: 186–191.
- Kearney, M. & W. Porter, 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species ranges. Ecology Letters 12: 1–17.
- Keller, S., V. Bartolino, M. Hidalgo, I. Bitetto, L. Casciaro, A. Esteban, M. C. Follesa, C. Garcia, G. Garofalo, M. Iosifides, A. Jadaud, E. Lefkaditou, P. Maiorano, C. Manfredi, B. Marceta, E. Massutí, R. Micallef, P. Peristeraki, G. Relini, P. Sartor, M. T. Spedicato, G. Tserpes & A. Quetglas, 2016. Large-scale spatio-temporal patterns of Mediterranean cephalopod diversity. PLoS ONE 11(1): e0146469.
- Kinne, O. (Ed.), 1970. Marine ecology—a comprehensive, integrated treatise on life in oceans and coastal waters. Vol I, Environmental factors, Parts 1, 2 and 3. John Wiley & Sons Ltd. 1970.
- Khoufi, W., S. Ben Meriem, & M. S. Romdhane, 2010. Les pêches de *Merluccius merluccius smiridus* (Rafinesque, 1810) des côtes tunisiennes. In: Acta of the international conference on biodiversity of the aquatic Environment (Syria). INOC-Tischreen University Publication: 552–561.
- Khoufi, W., H. Jaziri, S. Elfekhri, S. Ben Meriem & M. S. Romdhane, 2012. Apport de données in situ pour la mise place d'indicateurs biologiques dans le cadre de la gestion du stock Tunisien de *Merluccius merluccius* (Linnaeus, 1758). Journal des Sciences Halieutiques et Aquatiques 5: 161–170.
- Lauria, V., M. Gristina, M. J. Attili, F. Fiorentino & G. Garofalo, 2015. Predictive habitat suitability models to aid conservation of elasmobranch diversity in the central Mediterranean Sea. Scientific Reports 5: 13245.
- Lauria, V., G. Garofalo, M. Gristina & F. Fiorentino, 2016. Contrasting habitat selection amongst cephalopods in the Mediterranean Sea: when the environment makes the difference. Marine Environmental Research 119: 252–266.

- Lecours, V., V. L. Lucieer, M. F. J. Dolan & A. Micallef, 2015. An ocean of possibilities: applications and challenges of marine geomorphometry. In Hengl, T., J. Jasiewicz, Z. Zwolinski & H. Mitasova (eds), Geomorphometry for Geosciences. Bogucki Wydawnictwo Naukowe, Poznan: 23–26.
- Legendre, P. & L. Legendre, 1998. Numerical ecology, developments in environmental modelling 20, 2nd ed. Elsevier, Amsterdam.
- Mahe, K., R. Amara, T. Bryckaert, M. Kacher & J. M. Brylinski, 2007. Ontogenetic and spatial variation in the diet of hake (*Merluccius merluccius*) in the Bay of Biscay and the Celtic Sea. ICES Journal of Marine Science 64: 1210–1219.
- Maravelias, C. D., E. V. Tsitsika & C. Papaconstantinou, 2007. Environmental influences on the spatial distribution of European hake (*Merluccius merluccius*) and red mullet (*Mullus barbatus*) in the Mediterranean. Ecological Research 22: 678–685.
- Maravelias, C. D., G. Tserpes, M. Pantazi & P. Peristeraki, 2012. Habitat selection and temporal abundance fluctuations of demersal cartilaginous species in the Aegean Sea (Eastern Mediterranean). PLoS ONE 7(4): e35474.
- Martin, P., P. Sartor & M. Garcia Rodriguez, 1999. Exploitation patterns of the European hake *Merluccius merluccius*, red mullet *Mullus barbatus* and striped red mullet *Mullus surmuletus* in the western Mediterranean. Journal of Applied Ichthyology 15: 24–28.
- Maynou, F., J. Lleonart & J. E. Cartes, 2003. Seasonal and spatial variability of hake (*Merluccius merluccius* L.) recruitment in the NW Mediterranean. Fisheries Research 60: 65–78.
- McArthur, M., B. P. Brooke, R. Przeslawski, D. A. Ryan, V. L. Lucieer, S. Nichol, A. W. McCallum, C. Mellin, I. D. Cresswell & L. C. Radke, 2010. On the use of abiotic surrogates to describe marine benthic biodiversity. Estuarine, Coastal and Shelf Science 88: 21–32.
- Milisenda, G., S. Vitale, D. Massi, M. Enea, V. Gancitani, G. B. Giusto, C. Badalucco, M. Gristina, G. Garofalo & F. Fiorentino, 2017. Spatio-temporal composition of discard associated with the deep water rose shrimp fisheries (*Parapenaeus longirostris*, Lucas 1846) in the south-central Mediterranean Sea. Mediterranean Marine Science 18: 53–63.
- Monk, J., D. Ierodiaconou, V. L. Versace, A. Bellgrove, E. Harvey, A. Rattray, L. Laurenson & G. P. Quinn, 2010. Habitat suitability for marine fishes using presence-only modelling and multibeam sonar. Marine Ecology Progress Series 420: 157–174.
- Moore, C. H., E. S. Harvey & K. P. Van Niel, 2009. Spatial prediction of demersal fish distributions: enhancing our understanding of species–environment relationships. ICES Journal of Marine Science 66: 2068–2075.
- Morfin, M., J.-M. Fromentin, A. Jadaud & N. Bez, 2012. Spatio-temporal patterns of key exploited marine species in the Northwestern Mediterranean Sea. PLoS ONE 7(5): e37907.
- Oliver, P. & E. Massutí, 1995. Biology and fisheries of western Mediterranean hake (*M. merluccius*). In Alheit, J. & T. J. Pitcher (eds), Hake. Fisheries, Ecology and Markets., Fish and Fisheries Series 15 Chapman & Hall, London: 181–202.
- Orsi Relini, L., C. Papaconstantinou, S. Jukic-Peladic, A. Souplet, L. Gil De Sola, C. Piccinetti, S. Kavadas & M. Rossi, 2002. Distribution of the Mediterranean hake populations (*Merluccius merluccius smiridus* Rafinesque, 1810) (Osteichthyes: Gadiformes) based on six years monitoring by trawl surveys: some implications for management. Scientia Marina 66: 21–38.
- Papaconstantinou, C. & K. I. Stergiou, 1995. Biology and fisheries of western Mediterranean hake (*M. merluccius*). In Alheit, J. & T. J. Pitcher (eds), Hake. Fisheries, Ecology and Markets., Chapman & Hall Fish and Fisheries Series Springer, Netherlands: 149–180.
- Pittman, S. J., J. D. Christensen, C. Caldow, C. Menza & M. E. Monaco, 2007. Predictive mapping of fish species richness across shallow-water seascapes in the Caribbean. Ecological Modelling 204: 9–21.
- Pittmann, S. J. & K. A. Brown, 2011. Multi-scale approach for predicting fish species distributions across Coral Reef Seascapes. PLoS ONE 6(5): e20583.
- Peterson, A. T. & J. Soberon, 2012. Species distribution modeling and ecological niche modeling: getting the concepts right. Nature Conservation 10: 102–107.
- Planque, B., C. Loots, P. Petitgas, U. Lindström & S. Vaz, 2011. Understanding what controls the spatial distribution of fish populations using a multi-model approach. Fisheries Oceanography 20: 1–17.
- R Development Core Team, 2015. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Ragonese, S., 2009. Avoidance within a changing assessment paradigm for Mediterranean Hake stocks. Mediterranean Marine Science 10: 25–130.
- Recasens, L., A. Lombarte, B. Morales-Nin & G. J. Tores, 1998. Spatiotemporal variation in the population structure of the European hake in the NW Mediterranean. Journal of Fish Biology 53: 387–401.
- Relini, G., 2000. Demersal trawl surveys in Italian seas: a short review. In: Demersal Resources in the Mediterranean. Proceedings of the symposium held in Pisa, 18–21 March 1998. Actes de Colloques Vol. 26. J.A. Bertrand & G. Relini (eds). Ifremer, Plouzané: 76–93.
- Rice, J. C., 2005. Understanding fish habitat ecology to achieve conservation. Journal of Fish Biology 67: 1–22.
- Rinaldi, E., B. Buongiorno Nardelli, G. Volpe & R. Santoleri, 2014. Chlorophyll distribution and variability in the Sicily Channel (Mediterranean Sea) as seen by remote sensing data. Continental Shelf Research 77: 61–68.
- Sbrana, M., P. Belcari, S. De Ranieri, P. Sartor & C. Viva, 2007. Comparison of the catches of European hake (*Merluccius merluccius*, L. 1758) taken with experimental gillnets of different mesh sizes in the northern Tyrrhenian Sea (western Mediterranean). Scientia Marina 71: 47–56.
- Sbrocco, E. J. & P. H. Barber, 2013. MARSPEC: ocean climate layers for marine spatial ecology. Ecology 94: 979.
- Scalisi, M., D. Levi, L. Fiorentini, G. B. Giusto, V. Palumbo & P. Rizzo, 1998. Experimental approach to intercalibrate data of trawl surveys conducted with different nets. Biologia Marina Mediterranea 5: 40–51.

- Schröder, B. & O. Richter, 1999. Are habitat models transferable in space and time? *Zeitschrift für Ökologie und Naturschutz* 8: 195–205.
- Sing, T., O. Sander, N. Beerenwinkel & T. Lengauer, 2005. ROCR: visualizing classifier performance in R. *Bioinformatics* 21: 3940–3941.
- Stefansson, G., 1996. Analysis of groundfish survey abundance data: combining the GLM and delta approaches. *ICES Journal of Marine Science* 53: 577–588.
- Tserpes, G., C. Y. Politou, P. Peristeraki, A. Kallianiotis & C. Papaconstantinou, 2008. Identification of hake distribution pattern and nursery grounds in the Hellenic seas by means of generalized additive models. *Hydrobiologia* 612: 125–133.
- Tserpes, G., C. D. Maravelias, M. Pantazi & P. Peristeraki, 2013. Distribution of relatively rare demersal elasmobranchs in the eastern Mediterranean. *Estuarine, Coastal and Shelf Science* 117: 48–53.
- Venables, W. N. & C. M. Dichmont, 2004. GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. *Fisheries Research* 70: 319–337.
- Wood, S. N., 2006. *Generalized Additive Models: An Introduction* with R. Chapman & Hall, London.
- Wright, D. J., M. Pendleton, J. Boulware, S. Walbridge, B. Gerlt, D. Slinger, D. Sampson, & E. Huntley, 2012. ArcGIS Benthic Terrain Modeler (BTM), V. 3.0.
- Yalçın, E. & R. Gurbet, 2016. Environmental influences on the spatio-temporal distribution of European Hake (*Merluccius merluccius*) in Izmir Bay, Aegean Sea. *Turkish Journal of Fisheries and Aquatic Sciences* 16: 01–14.
- Zupanovic, S., 1968. Study of the hake (*Merluccius merluccius* L.) biology and population dynamics in the central Adriatic. *Conseil Général des Pêches pour la Méditerranée Etudes et Revues* 32.