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Habitat suitability modeling for sardine in a highly diverse ecosystem: the Mediterranean Sea

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Information integrated from different parts of the Mediterranean was used in order to model the spatial and temporal variability of the distribution grounds of sardine. Acoustic data as recorded with a 38 kHz split beam echosounder from the Aegean Sea (Eastern Mediterranean), the Adriatic Sea (Central Mediterranean), the Sicily Channel (Central Mediterranean) and the Spanish waters (Western Mediterranean) have been analyzed along with satellite environmental and bathymetry data to model the spatial distribution of sardine during summer, autumn and early winter. Similarly, egg distribution data from the Spanish waters were used to model the potential spawning habitat of sardine during early winter. Satellite data were used as proxies to infer spatial variations of environmental factors and assess possible ecological relationships. Generalized Additive Models were applied in a presence/absence approach. Model results were evaluated based on the estimation of the area under the receiver operating characteristic curves. The environmental factors that were considered to affect sardine habitat during the different periods of year were identified and discussed. Selected model was subsequently used in order to identify those regions within the entire Mediterranean basin having the higher probability of supporting sardine's presence. Habitat suitability maps were produced for the entire Mediterranean basin for each year and period indicating suitable areas for sardine's habitat. The temporal stability of these areas was also examined. The usefulness of such habitat suitability maps in environmental research and fisheries management in a highly diverse environment like the Mediterranean are discussed.

Keywords: Small pelagics, sardine, habitat suitability modeling, Mediterranean Sea

Running head: Potential sardine habitat in the Mediterranean

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INTRODUCTION

Mediterranean has been characterised as a miniature ocean (Lejeusne *et al.* 2010) and although generally considered as oligotrophic, it is highly heterogeneous in terms of hydrography, bathymetry and productivity. It comprises different kinds of ecosystems including areas with strong upwelling like the Alboran Sea and the Sicily Channel, closed basins dominated by shallow waters and high productivity like the Adriatic Sea, coastal areas that are under strong river outflow with subsequent nutritional forcing and human impact like the North-Western Mediterranean or less productive areas like the Aegean Sea, characterised by peculiar topography with many semiclosed basins being under the Black Sea Water influence. These characteristics can make Mediterranean a key area for climate change studies. At the same time, small pelagic fish have been recently considered from the GLOBEC (Global Ocean Ecosystem Dynamics programme) among these target organisms that their population dynamics is considered important for the study of the effect of climate change and the long term temperature increase (Barange *et al.* 2010).

Small pelagic fish (like sardines and anchovies) are known to play a key ecological role in coastal ecosystems, transferring energy from plankton to upper trophic levels (Cury *et al.* 2000). Their relatively low position in the marine food web, together with their short life-span and their reproductive strategy of producing large quantities of pelagic eggs over an extended spawning season, makes them strongly dependent on the environment (Bakun 1996). Understanding the environmental conditions that drive their spatial distribution requires information over large spatial and temporal scales (Mackinson *et al.* 1999, Planque *et al.* 2007).

European sardine (*Sardina pilchardus*) along with anchovy (*Engraulis encrasicolus*), comprise the bulk of small pelagic fish catches in the Mediterranean Sea. Sardine stocks are highly variable in terms of their recruitment, abundance and distribution while Mediterranean sardine fishery in many areas suffers from a high degree of exploitation with most stocks exhibiting declining trends in terms of abundance and an exploitation rate that often exceeds sustainability (Study Group on Mediterranean Fisheries, SGMED 2009, 2010). The latter makes the need to examine the relationship between their spatial distribution and environmental conditions, even more crucial. Sardine in the Mediterranean is mainly fished by purse seiners although midwater pelagic trawls also operate in the Adriatic Sea, in the Sicily Channel and in the French coastal waters (Tičina *et al.* 1999, Lleonart & Maynou 2003, Basilone *et al.* 2006, Machias *et al.* 2008). Both gears operation and fishing practise is based on the spatial detection of major sardine aggregations by means of echosounders.

The increasing interest concerning the climate change effect on fisheries has given the ignition for a number of studies on habitat suitability modelling (e.g. Guisan & Zimmermann 2000, Francis *et al.* 2005, Planque *et al.* 2007, Bellido *et al.* 2008, Giannoulaki *et al.* 2008, Weber & McClatchie 2010). This modelling approach links species location information to environmental data, aiming to quantify the distribution of species on environmental gradients and provide spatial distributions maps for certain species or life stages. Thus we can obtain information on the temporal changes in the spatial extent of the species habitat which is essential for ecological studies, the monitoring of the population status as well as the implementation of effective fisheries management and conservation planning. At the same time it can set a good framework for understanding the effect of climate on marine ecosystems (Franklin 2009).

Defining the potential habitat of sardine practically means determining the combination of these environmental conditions that are suitable for the survival of the species (Guisan & Zimmermann 2000, Planque *et al.* 2007), however in the absence of biotic interactions (like competition or predation, Austin 2002). The majority of the work already done concerning habitat suitability modelling of sardine either address non Mediterranean areas (Agenbag *et al.* 2003, Castro *et al.* 2005, Bellier *et al.* 2007, Planque *et al.* 2007, Zwolinsky *et al.* 2010) or within the Mediterranean they refer to regional scale studies focusing on a particular time of year (Allain *et al.* 2001, Bellido *et al.* 2008, Giannoulaki *et al.* 2007, Tsagarakis *et al.* 2008). Knowing that sardine meso-scale and large scale spatial distribution is driven by environmental forcing (e.g. Tičina *et al.* 2000, Planque *et al.* 2007, Stratoudakis *et al.* 2007, Bernal *et al.* 2007), the aim of the current work is to describe the environmental conditions that are suitable for sardine presence in the Mediterranean and additionally to identify and evaluate those areas that define the potential spatial distribution of sardine at different periods of the year. The idea was to build a simple, robust and effective habitat model based on distribution data of sardine along with satellite environmental data for June (early summer), September (early autumn) and December (early winter), taking advantage of acoustic monitoring surveys. These studies are applied routinely in the most European Mediterranean areas serving mainly stock assessment purposes, being held at different seasons within a year. Such biological surveys are known to yield high-quality data for habitat modelling (Franklin 2009) enabling the provision of spatially explicit presence/absence information on species and recording their precise location. Study periods represent different phases of the sardine population within an annual basis. Sardine is known to spawn during winter in the Mediterranean (Olivar *et al.* 2001, 2003, Somarakis *et al.* 2006, Ganias *et al.* 2007) so, early summer lies within the recruitment period for sardine and a large percentage of the species population is still juveniles. During September sardine population can be considered as fully recruited whereas early winter coincides with the start of the spawning period for the species. So, within the current work we plan to integrate the picture of the sardine habitat in the Mediterranean at different phases of the population, identify what are the environmental parameters that affect species distribution at each period and search for consistent patterns between the meso- or large scale aggregations of sardine (i.e. exceeding the size of several nautical miles) and the environment.

The use of data from a wide range of environmental conditions ensures the availability of a wide range of observed habitat conditions where sardine population occurs. This is ensured as the four study areas largely differentiate in terms of hydrography and productivity (Millot 1990, Lloret *et al.* 2001, Artegiani *et al.* 1997a, 1997b, Zervakis & Georgopoulos 2002, Patti *et al.* 2010). In addition, satellite environmental data are flexible and dynamic in space and time, allowing estimates in various years and regions, operate as proxies or surrogates to causal factors, infer spatial variations of environmental factors and assess possible ecological relationships. Statistical modelling techniques, Generalised Additive Models (GAMs), that were applied in the current work are being widely used in habitat suitability modelling in order to answer questions on temporal habitat dynamics (Osborne & Suarez-Seoane 2007), regional variation in habitat preferences (e.g. Planque *et al.* 2007, Bellido *et al.* 2008, Giannoulaki *et al.* 2008) or spatially predict climate change impacts (Trivedi *et al.* 2008).

Furthermore, the potential habitat of sardine was recreated for each season and year in order to evaluate the seasonal and annual changes in its spatial extent. Results were evaluated in the framework of existing hydrographic and productivity patterns in the study areas. Moreover, the selected GAMs and grids of satellite environmental data were used in order to identify and map the potential distribution grounds for sardine populations in the entire Mediterranean basin for the period 2004-2008, as well as for the determination of the potential spawning habitat sardine for the period 2006-2008. Since the temporal persistence of the characteristics of an area is a basic prerequisite for its selection as a “habitat” area, the stability of areas with high probability of sardine’ presence was examined. For this purpose an index of persistency (Colloca *et al.* 2009) was calculated and mapped for the entire basin, considered as an indirect evidence of the importance of certain areas to the stability of the population.

MATERIALS AND METHODS

Five years of acoustic data from four different areas of the Mediterranean, the Spanish waters (Western Mediterranean), the Adriatic Sea, the Sicily Channel (Central Mediterranean) and the North Aegean Sea (Eastern Mediterranean) were used for habitat modelling purposes. Surveys were held during June, September and December. Moreover within a preliminary approach, three years of sardine egg data from the Spanish Mediterranean waters, collected during the Spanish acoustic surveys by a Continuous Underway Fish Eggs Sampler (CUFES) were used to model potential spawning habitat (PSH, Planque *et al.* 2007) in December for the first time in the Mediterranean. Data were analysed concerning the occurrence of sardine schools or sardine eggs along with bottom depth and satellite environmental data and statistical models were applied.

Study areas

The Mediterranean Sea is a semi-enclosed area with a single natural connection to the Atlantic Ocean, the Strait of Gibraltar. Its hydrography is highly heterogeneous as seen in the following detailed description of the study areas.

Spanish waters

The Spanish Mediterranean waters are located in the Western Mediterranean basin, between the Strait of Gibraltar and the Spanish-French border (Fig. 1A). The continental shelf is narrow, often less than 6 nautical miles (nm, 1 nautical mile = 1852 m) between the Strait of Gibraltar and the Cape of Palos. Northwards, the continental shelf widens till the surroundings of the Ebro River, where the maximum width is reached (33 nm). In the Catalan coast, continental shelf is narrow (less than< 14 nm), indented by submarine canyons. The circulation is dominated by the entrance of the Atlantic waters, the North Current (NC) a cyclonic along-slope front in the north-western Mediterranean and the outflow of large rivers. The NC flows along the continental shelf from northeast to southwest (Font *et al.* 1988), carrying water from the Gulf of Lions to the Catalan coast, and eventually reaches the Alboran Sea (Millot 1999, Font *et al.* 1988). Strong northerly winds, typical in winter, may intensify the NC (Pinot *et al.* 2002). The wide continental shelf and fresh-water run-off from the Rhone and the Ebro rivers further characterise the area. In the Alboran Sea the water circulation is dominated by less saline Atlantic water entering the basin through the Strait of Gibraltar. The surface Atlantic waters, although relatively nutrient-poor, are related with mesoscale features, such as turbulent mixing, anticyclonic gyres, meanders and eddies (Estrada 1996) generating upwelling along the narrow continental shelf and resulting in a local enrichment of nutrients and primary production in the area (Champalbert 1997). Two anticyclonic gyres are generated in the Alboran Sea, the most western gyre is quasi permanent while the eastern one is more variable (Millot 1999).

Adriatic Sea

The Adriatic Sea (Fig. 1C) is an elongated basin, located in the Central Mediterranean, between the Apennine and the Balkan Peninsula. Its northern section is very shallow and gently sloping (average bottom depth of about 35 m). The middle Adriatic is 140 m deep on average but with two depressions reaching 260 m. The southern section is characterised by a wide depression of more than 1200 m. A large number of rivers discharge into the basin, with significant influence on the circulation, particularly the Po River in the northern basin. The northern Adriatic is characterised by a narrow coastal belt along the western coast exhibiting high productivity. On the contrary, the eastern coastal waters are generally areas of moderate production with limited zones of high production. The general circulation in the Adriatic is cyclonic with a flow towards the northwest along the eastern coast (East Adriatic Current) and a return flow (West Adriatic Current) towards the southeast along the western coast (Artegiani *et al.* 1997a, 1997b). In the north Adriatic Sea, the circulation is largely affected by wind stress and river outflows with the formation, particularly in autumn, of a double gyre structure consisting of a larger cyclone offshore Po River Delta (Marini *et al.* 2008) and an anticyclone along the southern Istrian coast (Russo *et al.* 2009). In central and southern Adriatic, the cyclonic gyres are more evident in summer and autumn. Mesoscale eddies are present in Adriatic Sea and cause water masses exchange between western coast and offshore areas.

Sicily Channel

The Sicily channel connects the two major basins of the Mediterranean Sea. The continental shelf is fairly narrow (15 nm) in the middle of the southern coast but it widens both in the most eastern and most western parts reaching 50 nm in extent in Malta shelf (Fig. 1B) (Patti *et al.* 2004). The surface circulation is controlled by the Modified Atlantic Water motion, the so-called Atlantic-Ionian Stream (AIS, Fig. 1B) (Cuttitta *et al.* 2003). The current enters the channel by its west boundary forming two large cyclones. The upwelling generated by the general circulation is reinforced by wind-induced upwelling events (Patti *et al.* 2004, Patti *et al.* 2010). River discharges in the area are very low and thus coastal upwelling is thought to be the main source of nutrient enrichment of surface waters (Patti *et al.* 2004, Patti *et al.* 2010). The inter-annual variability of the AIS seems to have an impact on the extension of upwelling and the formation of frontal structures (Cuttitta *et al.* 2003).

North Aegean Sea

The North Aegean Sea is characterised by high hydrological complexity mostly related to the Black Sea waters (BSW) that enter the Aegean Sea through the Dardanelles strait as a surface current (Zervakis & Georgopoulos 2002). The area is characterised by the presence of two anticyclonic systems: one in the Samothraki plateau (the Samothraki gyre) and another one in the Strymonikos Gulf (Fig. 1D). These gyres are almost permanent features of the area during early summer. The overall circulation is mainly determined by the presence of the Limnos-Imvros stream (LIS), which carries waters of Black Sea origin onto the Samothraki plateau (Somarakis *et al.* 2002). The outflow of BSW (salinity < 30) enhances local productivity and its advection in the Aegean Sea induces high hydrological and biological complexity (Isari *et al.* 2006, Somarakis & Nikolioudakis 2007). This is further enhanced by the presence of a series of rivers that end in semi-closed gulfs such as Thermaikos and Strymonikos Gulfs (Stergiou *et al.* 1997, Isari *et al.* 2006).

Data Sampling

Acoustic Sampling

Acoustic sampling was performed by means of scientific split-beam echosounders (Simrad EK500, Simrad EK60 and Biosonic DT-X depending on the survey) working at 38 kHz and calibrated following standard techniques (Foote *et al.* 1987). Acoustic data were recorded at constant speed of 8-10 nm h^{-1}. Minimum sampling depth varied between 10 to 30 m depending on the area. The size of the Elementary Distance Sampling Unit (EDSU) was one nautical mile. We considered as sardine presence any school or echo assigned to sardine based either on echo trace classification or attributed to sardine based on the catch output of identification hauls (Simmonds & MacLennan 2005). No discrimination between adults and juveniles was made.

Midwater pelagic trawl sampling was used to identify and verify sardine echo traces. Acoustic data analysis was performed using the Myriax Echoview software besides the Eastern Adriatic where the BI60 SIMRAD software was used. Further details on acoustic sampling per study area are described below.

Specifically, in the Spanish waters acoustic sampling was performed in early winter, between the end of November and mid December, from 2003 to 2008, on board the RV Cornide de Saavedra. Sampling design consisted of parallel equidistant transects, perpendicular to the bottom depth, covering the continental shelf up to 200 m depth (Fig. 1A). Inter-transect distance was 4 nm in the most northern and southern parts, where the continental shelf is narrow, and 8 nm in the middle part, where the continental shelf is wider. In the Sicily Channel acoustic data were collected on board the R/V Dallaporta during June 2003 to 2008. Sampling design consisted of parallel equidistant transects, perpendicular to the coastline with an inter-transect distance of 5 to 8 nm, depending on the width of the continental shelf (Fig. 1B).

In the Western Adriatic acoustic data were collected on board the R/V Dallaporta during September, from 2004 to 2008. Acoustic surveys were carried out along predetermined zigzagged transects (Fig. 1C). In the Eastern Adriatic Sea acoustic data were collected on board the R/V BIOS during September 2004 to 2008. Acoustic surveys were carried out along predetermined parallel transects with 10 nm inter-transect distance while transects in the inner part (i.e. between the islands) were positioned regarding to the topographic features of these areas. Details of the surveys, sampling methodology and data collected have already been described (Tičina *et al.* 2006) (Fig. 1C). In the North Aegean Sea acoustic data were collected on board the R/V Philia during June 2004-2006 and 2008. Acoustic surveys were carried out along predetermined parallel transects with 10 nm intertransect distance in open areas whereas zigzagged transects were sampled inside gulfs (Fig. 1D). Details of the surveys, sampling methodology and data collected have already been described (Giannoulaki *et al.* 2008).

Eggs sampling

In the Spanish Mediterranean waters, fish eggs were collected simultaneously to acoustic surveys using on board installed CUFES unit (Model C-120, Ocean Instruments Inc.) during early winter of 2006 to 2008. Sampling scheme followed the same transect scheme previously mentioned for the Spanish acoustic surveys. Water was continuously pumped at 600-700 l min^{-1} from 5 m below the sea surface. The mesh size of the concentrator and collector was 335 μm. Samples were taken every 3 nm following the acoustic sampling design in parallel transects described above. In case that the most offshore CUFES station was positive for sardine eggs transect was continued further offshore till a null station of sardine eggs was found (no presence of sardine eggs). The collected eggs were stored in 4% seawater-buffered formalin solution. Sardine eggs were then sorted and counted by species, and stored in preservation solution. Sardine-egg concentration along the survey transects was recorded as numbers of eggs per 10 m^3 at a depth of 5 m and integrated every 3 nm. In the Western Mediterranean, sardine eggs are known to be distributed from the sea surface until 80 m deep in the water column, with the maximum abundance found between 10-20 m (Olivar *et al.* 2001, Sabatés 2004). Thus, unlike the possible underestimation of the eggs' abundance due to CUFES sampling, the major centres of sardine spawning are generally considered to be captured adequately by the sampling range and the presence-absence estimates of sardine eggs (Lynn 2003).

Environmental data

Satellite environmental data as well as bathymetry data were used as explanatory variables to model the habitat of sardine in the Mediterranean basin. Mediterranean Sea is an area well monitored in terms of monthly satellite imagery (summarised in Table 1). Specifically, the sea surface temperature distribution (SST in ^{o}C), the sea surface chorophyll concentration (CHLA in mg m^{-3}), the Photosynthetically Active Radiation (PAR in Ein m^{-2} day^{-1}), the sea surface salinity distribution (SSS based on the BCC GODAS model, Behringer and Xue, 2004) and the sea level anomaly (SLA in cm) were downloaded from respective databases (see Table 1) and used. These aforementioned parameters might be important either as predictors for food availability and physiological suitability of the habitat and thus having direct influence on the distribution of sardine echo abundance and eggs (e.g. SST, CHLA) or as a proxy for causal factors (Bellido *et al.* 2001). For example SLA describes ocean processes, such as gyres, meanders and eddies (Pujol & Larnicol 2005), which enhance productivity and often function as physical barriers differentiating the distribution of species or species life stages. Indirect factors such as bathymetry was also used, calculated through processing (kriging) of a point dataset derived from a blending of depth soundings collected from ships with detailed gravity anomaly information obtained from the Geosat and ERS-1 satellite altimetry missions (Smith & Sandwell 1997). All monthly-averaged satellite images were processed as regular grids under a Geographic Information System (GIS) environment using ArcInfo GRID software (ESRI 1994). The mean environmental monthly values for June, September and December of each respective year and area were estimated for all surveyed points of data based on the spatial resolution of 1.5 km for satellite data (Valavanis *et al.* 2004), which is close to the applied EDSU of acoustic data and define environmental spatial heterogeneity adequately.

Data analysis

Model selection

Generalized Additive Models (GAMs) were used in order to define the set of the environmental factors that describe sardine's distribution in the North Aegean Sea, Sicily Channel, Adriatic Sea and the Spanish Mediterranean waters. GAMs are widely used in habitat suitability modelling and spatial prediction (by searching the proper combination of conditions) because they tend to have high accuracy (Franklin 2009). The output of the GAMs is smoothed fits for each environmental variable. GAMs were applied using the 'MGCV' library in the R statistical software (R Development Core Team, 2009). The binomial error distribution with the logit link function was used. Also the natural cubic spline smoother was used for the independent variables smoothing. Each fit was analysed with regards to the Akaike's Information Criterion (AIC, the lower the better) and the confidence region for the smooth (which should not include zero throughout the range of the predictor). The degree of smoothing was also chosen based on the observed data and the Generalized Cross Validation (GCV) method (Woods 2006). The GCV method is known to have some tendency for over-fitting, thus the number of knots in the cubic splines was limited to 4 and the penalty per degree of freedom fit to each term was increased by a factor $\gamma = 1.4$, a technique that largely corrects this problem without compromising model fit (Wood 2006, Katsanevakis *et al.* 2009, Weber & McClatchie 2010).

Moreover, since collinearity in the independent variables is a crucial problem in GAMs application, associated with stepwise model selection (Guisan *et al.* 2002, Wood 2006), the best model was chosen based on a stepwise forward selection method that reduces the collinearity problem starting from a simple initial model with few explanatory variables (Sacau *et al.* 2005, Giannoulaki *et al.* 2008). Specifically, models were compared using the estimated AIC value, the environmental variables were ranked and selection of the final model was based on the minimization of the AIC criterion.

As response variable (y) we used the presence/absence of sardine echo or sardine eggs. As independent variables we used: the cubic root of the bottom depth (to achieve a uniform distribution of bottom depth), the natural logarithm of CHLA (to achieve a uniform distribution of CHLA), the SST, the SSS, the SLA and the PAR. Bottom depth (DEP) and CHLA presented high variability in their original values, thus transformation was necessary in order to achieve uniform distribution for GAM application (Hastie & Tibshirani 1990). The appropriate type of transformation was based on the inspection of Quantile-Quantile plots (QQ-plots) to verify whether variables under certain transformations follow the normal distribution.

Regarding sardine habitat, three models were constructed and validated based on pooled acoustic data derived from: a) the Sicily Channel and the North Aegean Sea in June 2003 to 2008, b) the eastern and the western part of the Adriatic Sea in September from 2004 to 2008 and c) the Spanish waters in December 2003 to 2008. Data from the coastal areas inside the gulfs of the Eastern Adriatic were excluded from the analysis due to the poor satellite data resolution in these locations. Regarding sardine spawning habitat, one model was constructed based on pooled CUFES data from 2006 to 2008 derived from Spanish Mediterranean waters in December. Data from the different years were collated in order to catch the temporal variability in sardine distribution area, obtain more possible observed conditions and ensure potentiality (ICES 2005, Planque *et al.* 2007, Giannoulaki *et al.* 2008). Following the selection of the main effects of the model, all first order interactions of the parameters included in the final model were tested (Wood 2006). Validation graphs (e.g. residual plot versus fitted values, QQ-plot and residual plot against the original explanatory variables) were plotted in order to detect model misspecification.

Model validation

The selected GAM model was applied in order to estimate the probability of habitat use by sardine or eggs at each point of the study areas for each year, based on the available mean monthly values of environmental data. Selected GAM models were also applied for other areas and years where sardine data were available but were not included in the model estimation. In a subsequent step, each selected model was tested and evaluated with the estimation of the area under the Receiver Operating Characteristic Curve (AUC) (Hanley & McNeil 1982, Guisan & Zimmerman 2000). AUC is a threshold-independent metric, moderately affected by factors like species prevalence (Franklin 2009), measuring the ability of a model to discriminate between those sites where a species is present, versus those where it is absent (Hanley & McNeil 1982). The values of AUC ranges from 0 to 1, where a score of 1 indicates perfect discrimination, a score of 0.5 implies predictive ability that is no better than a random guess (Boyce *et al.* 2002, Elith *et al.* 2006). AUC values of 0.7-0.9 are considered moderate and >0.9 high model performance (Franklin 2009). AUC was estimated for each area and year included in the models. Additionally, AUC was estimated for areas and periods that were not included in the model estimation using data derived from a) the Spanish Mediterranean waters in December 2003 b) the Sicilian Channel in June 2003, c) the western Adriatic Sea in September 2004 and 2005 and d) the eastern Adriatic Sea in September 2004.

The final GAM model for each period was applied into new environmental grids describing the mean monthly satellite values measured for the entire Mediterranean basin, resampled at a spatial resolution of 4 km for June, September and December from 2004 to 2008.

The model was used in order to search over these grids for the specific set of satellite conditions associated to different probabilities of sardine or sardine eggs' presence. Finally, habitat suitability maps indicating the locations with this specific set of satellite conditions were plotted as maps using the ArcGIS software.

Monthly and annual differences in the potential habitat of sardine

Monthly and annual differences in the area of the potential habitat of sardine were examined within each study area (North Aegean Sea, Sicily Channel, Adriatic Sea and Spanish Mediterranean waters, Fig. 1) by means of a two factor analysis of variance (ANOVA test). The area of the potential habitat of sardine was estimated as the number of grid cells (i.e. each cell represents an area of 16 km^2) corresponding to different probability of finding suitable environmental conditions for sardine presence. Subsequently, there was a discrimination among (a) the wider distribution area of sardine or otherwise sardine basin habitat defined as the area presenting probability >0.25 (A025), (b) the area of increased likelihood of suitable environmental conditions presenting probability >0.50 (A050) and (c) the area of high probability of suitable conditions for sardine's presence (or otherwise hot-spot areas) defined as those areas indicating values >0.75 (A075). Tukey multiple range test was applied when a significant statistical difference was estimated (Zar 1984).

Index of persistency

An Index of Persistence (I_i) of sardine measuring the relative persistence of each grid cell *i* as an annual sardine habitat (Colloca *et al.* 2009) was calculated for each grid cell in the entire Mediterranean Sea. Let $\delta ikj = 1$ if the grid cell *i* is included in sardine habitat in year *j* and in survey *k*, and $\delta ikj = 0$ otherwise. I_i was computed as follows:

$$I_i = \frac{1}{n}\sum_{k=1}^{n}\delta_{ikj}$$

where *n* is the number of surveys considered. I_i ranges between 0 (cell *i* never included in an annual sardine potential habitat area) and 1 (cell *i* always included in an annual sardine potential habitat area) for each cell in the study area. Using different levels of I_i, the area occupied by sardine habitat area was calculated. In the case of sardine eggs no persistency maps were plotted as data were considered preliminary due to the short time series available and the nature of the sampling.

RESULTS

Habitat modelling

Model selection

The results of the final selected GAMs are presented in Table 2 and the effect of the environmental parameters on sardine presence is shown as plots of the best-fitting smooths (Fig. 2). The 95% confidence intervals are also plotted around the best-fitting smooths for the main effects. Interaction effects are shown as a perspective plot without error bounds. The y-axis reflects the relative importance of each parameter of the model and for the interaction effects this is presented on the z-axis. The rug under the single variable effects plots indicates the density of points for different variable values. It should be noted that the effect of each variable is the conditional effect, i.e. the effect of this variable, given that the other variables are included in the model. Inspection of the validation graphs (not shown) indicated a distinct pattern regarding the plot of residuals versus fitted values due to the presence/absence nature of the data (no indication of a lack of fit). Deviance explained varied from 30% to 43% of the total deviance depending on the model (Table 2).

June sardine model

The final selected GAM based on pooled data from North Aegean Sea and the Sicily Channel from 2004 to 2008 included as main effects: SST and Depth (cubic root transformed) as well as the interactive effect of SLA with CHLA (log transformed). All variables selected in the final model were statistically significant. SST is the variable that was initially entered into the model explaining most of the total variation (Table 2). Plots of the best fitting smooths indicate a higher probability of finding sardine present in SST values below 22 ^{o}C (within the available values), shallow waters (less than 65 m) but sharply reduced in deeper waters. The interaction plot between SLA and CHLA also indicates higher probability of finding sardine present at SLA values of -10 to -4 cm when co-existing with CHLA values of 0.08 to 0.37 mg m^{-3} (Fig. 2), within the available ones. High probability for sardine presence was also indicated at SLA values of -3 to 0 cm when co-existing with high CHLA values (greater than 1 mg m^{-3}).

September sardine model

The final selected GAM based on pooled data from the western and the eastern part of the Adriatic Sea from 2004 to 2008 included the interactive effect of depth (cubic root transformed) with SST as well as the interactive effect of SLA with CHLA (log transformed). All variables selected in the final model were statistically significant. Depth is the variable that was initially entered into the model, explaining most of the total variation (Table 2). Plots of the best fitting smooths indicate a higher probability of finding sardine present in SST values of 20 to 26 ^{o}C and at waters less than 110 m depth. The interaction plot between SLA and CHLA also indicates higher probability of finding sardine present at SLA values of 2 to 10 cm when co-existing with CHLA values of 0.13 to 1.49 mg m^{-3} (Fig. 2), within the available ones.

December sardine model

The final selected GAM based on pooled data from the Spanish Mediterranean waters from 2004 to 2008 included as main effects: Depth (cubic root transformed), CHLA (log transformed) as well as the interactive effect of SLA with SST. All variables selected in the final model were statistically significant. Depth is the variable that was initially entered into the model explaining most of the total variation (Table 2). Plots of the best fitting smooths indicate a higher probability of finding sardine present in CHLA values greater than 0.45 mg m^{-3} and less than 4.5 mg m^{-3} (within the available ones) and at waters less than 90 m depth. The interaction plot between SLA and SST also indicates higher probability of finding sardine present at SST values of 14 to 17 ^{o}C when co-existing with SLA values of -5 to 0 cm (Fig. 2), within the available ones. Moreover, high probability for sardine presence was also indicated at SST values of 16 to 18.5 ^{o}C when co-existing with SLA values of 1 to 5 cm.

December sardine eggs' model

The final selected GAM based on pooled data from the Spanish Mediterranean waters from 2006 to 2008 included as main effects: Depth (cubic root transformed) and SLA as well as the interactive effect of CHLA (log transformed) with SST. All variables selected in the final model were statistically significant. SST is the variable that was initially entered into the model explaining most of the total variation (Table 2). Plots of the best fitting smooths indicate a higher probability of finding sardine eggs present in SLA values greater than -1.5 cm and less than 4.9 cm (within the available ones) and at waters within 30 and 110 m depth. The interaction plot between CHLA and SST also indicates higher probability of finding sardine eggs present at SST values of 14 to 17 ^{o}C when co-existing with CHLA values within 1 to 2.7 mg m^{-3} (Fig. 2), within the available ones.

Model validation

Each model was evaluated based on the estimated AUC values concerning areas and years included in the model estimation as well as areas and years that were not included in the GAM estimation. Results are shown in Table 3. The selected models showed moderate to good prediction ability as the estimated AUC value was >0.70 in most cases (Elith *et al.* 2006, Franklin 2009). In a subsequent step, habitat suitability maps for the study regions and the entire Mediterranean Sea were estimated for June, September and December 2004-2008 (Figs 3 to 5) where areas associated with a specific probability of suitable conditions for sardine presence are indicated. Annual variability was observed in all study regions concerning the areas indicated as potential sardine habitat (A025, A050 and A075), however the ANOVA test concerning the extent of the potential habitat area showed no significant differences between years (Table 4) although a significant difference between months was found (Table 5).

A significant increase in the extent of the suitable areas (A050) was generally observed from June to December (Table 5). In Spanish waters, maps indicated suitable areas for sardine habitat in the coastal waters of the Catalan Sea, south the Ebro River and the North Alboran Sea. (Figs. 3 to 5). In the Adriatic Sea suitable areas for sardine were indicated in the coastal waters of the east and the western part with the highest suitability areas to increase progressively, covering most of the continental shelf at the North Adriatic Sea from June to December (Figs. 3 to 5). The observed absence of suitable areas in the north part of the Adriatic Sea in December 2008 is due to the lack of satellite data for this month. In the Sicily Channel suitable areas were also identified in the coastal waters, being more extended in the southwest part and in the continental shelf between Sicily and Malta (Figs 3 to 5, Table 5). Moreover, in the Aegean Sea suitable areas for sardine were mainly located in the coastal waters of the continental shelf, covering most part of the gulfs that dominate the Greek coastline (Figs. 3 to 5).

Besides the study areas, suitable areas for sardine habitat were also indicated in other parts of the Western and Eastern Mediterranean as well as in various areas of the coastal waters of Africa (Figs. 3 to 5). During September the A075 potential sardine habitat in the coastal waters of Africa appears greatly reduced compared to June and December (Fig. 3 to 5). This could be attributed either to the local shrinkage of suitable areas or to the September model deficiencies due to the existence of large differences between the environmental conditions of the Adriatic (i.e. model calibration dataset) and those of the coastal waters of Africa.

Similarly, based on the PSH maps during early winter, areas suitable for sardine spawning were consistently identified in the surroundings of the Ebro River Delta and the North Alboran Sea (Fig. 6), a pattern that matches the actual sardine spawning grounds in the Spanish waters (Pérez de Rubín 1996, Olivar *et al.* 2001, Vargas-Yáñez & Sabatés, 2007). Suitable spawning areas visually correspond to the sardine adult potential distribution as expected since early winter coincides with the beginning of the spawning season for sardine in the Mediterranean (García *et al.* 2006 and references there in, Somarakis *et al.* 2006). PSH areas were also indicated in other parts of the Mediterranean as well as in the coastal waters of Africa (Fig. 6).

Monthly and annual differences in the potential habitat of sardine

No statistical difference was found between years in the potential habitat area of sardine (Table 4). Two factor analysis of variance results indicated a statistical difference between seasons in the extent of the A050 area in all study areas besides the Sicily Channel (Table 4). The Tukey multiple range test, as applied for the month effect, indicated a statistical significant increase of the potential habitat A050 during December (Table 5). No statistical difference was found for the extent of the A025 area in any study area. The extent A075 was found significantly different between seasons in the Spanish Mediterranean waters only.

Index of persistency

Maps for the entire Mediterranean were created for June, July, September and December, indicating the index of persistency (Colloca *et al.* 2009) for each potential habitat grid cell (Fig. 7). Specifically, the areas with probability of sardine presence greater than 50% (i.e. A050) presenting low persistency (i.e. 0.25 to 0.50), intermediate (i.e. 0.50 to 0.75) and high persistency (i.e. >0,75) are shown. Resulted maps indicate that, although the spatial extent of areas with a high probability of sardine presence might vary in an annual basis, there are areas that are quite persistent as potential habitat (Fig. 7). Generally, maps indicated that persistent favourable areas were almost consistently associated with river run off such as the Ebro and the Rhone Rivers in the Western Mediterranean, the Po River in the north-west part of the Adriatic Sea and the Nile Delta region during all seasons, as well as with upwelling areas such as the Alboran Sea and the southern coasts of Sicily (Fig. 7).

DISCUSSION

Fisheries acoustics surveys data that are regularly sampled for stock monitoring purposes in different Mediterranean areas for the last decade can be used beyond fish abundance estimation, integrating environmental information to model fish spatial distribution towards an ecosystem based management approach. The intention of this work was to take advantage of such surveys for habitat modelling purposes. Spatial patterns of small pelagic in the Mediterranean are less well studied compared to large upwelling ecosystems (e.g., van der Lingen *et al.* 2001, Twata *et al.* 2005, Lynn 2003, Planque *et al.* 2007, Bertrand *et al.* 2008, Coetzee *et al.* 2008, Barange *et al.* 2009). In order to capture the temporal as well as the spatial variability of sardine grounds in the Mediterranean, acoustic data were integrated along with environmental information from four different areas: the Spanish waters (Western Mediterranean), the Adriatic Sea, the Sicily Channel (Central Mediterranean) and the North Aegean Sea (Eastern Mediterranean) at three different seasons (early summer, early autumn and early winter). The aim of the work was to search for consistent patterns in the spatial distribution of the meso- or large-scale aggregations of sardine and the environment. At a meso-scale level, physical processes that are known to increase productivity are considered mostly responsible for the spatial organisation of plankton concentration and subsequently drive the spatial distribution of sardine. At a larger scale, the distribution of sardine population is mostly related to the overall existing abiotic conditions and the species tolerance limits (Bertrand *et al.* 2008). Therefore, the idea of this study was to build an effective, general habitat model that would integrate modelling techniques, satellite environmental data, acoustic or egg distribution data in order to aid the understanding of the ecology of sardine as well as to identify the potential distribution areas for the species in the Mediterranean.

Habitat suitability and seasonal patterns

Three different models were constructed, one addressing each study period. Depth, SLA, SST and CHLA were those environmental parameters that were found important in all cases. Differences in the three models could be attributed either to the variation of the environmental characteristics in the four areas and/or in the different preferences of sardine in relation to early summer, early autumn and early winter environmental conditions. Bottom depth and SST were the two variables that explained most of the deviance in all models.

However, SST was the main explicative variable in the summer model and in the eggs model whereas the bottom depth effect explained most of the variation in the autumn and winter model. Generally, concerning the effect of the bottom depth there was a higher probability of finding sardine present at shallow waters (less than 65 m depth) during summer but reaching deeper waters, up to 100 m depth, in autumn and winter.

During June, in North Aegean Sea and in the Sicily Channel, model results indicated a higher probability of finding suitable areas for sardine in shallow coastal waters characterised with low SST values (less than 22^{o}C), associated with either strong downwelling movement of lower productivity water or located in the periphery of downwelling formations that present higher productivity. Associated maps indicated as potential habitat areas for sardine the gulfs and the closed basins of the North Aegean Sea where shallow waters dominate, rivers outflow and the BSW input characterise these areas. BSW induces high hydrological complexity in the area, resulting in the formation of strong currents, fronts and anticyclonic systems that are permanent features during summer known to enhance local productivity (Isari *et al.* 2006, Somarakis & Nikolioudakis 2007). Results also indicated as potential habitat for sardine the coastal waters of the Sicily Channel extending up to the plateau between Sicily and Malta at certain years. This is generally in good agreement with past knowledge on the known spatial distribution of sardine in the area during summer (Patti *et al.* 2004). During June in the Adriatic, maps indicated potential "hot-spot" areas (i.e. areas with increased probability of sardine presence) mainly located at the north part of the basin in association with the wider Po River Delta region that is in good agreement with previous knowledge on sardine distribution in that area (Tičina *et al.* 2000). In the central part of the Adriatic potential habitat was indicated in the coastal waters of the eastern area. Findings are in accordance with known information on the spatial distribution of sardine (Morello & Arneri 2009 and references therein). In the Western Mediterranean potential habitat areas were mainly identified in the coastal waters, being wider in extent when associated with the Rhone and the Ebro River area as well as in the Balearic Islands plateau. No information is available for the spatial distribution of the species in the Spanish waters during summer, however estimated potential habitat generally agrees with the known distribution grounds of sardine population during other seasons (Pérez de Rubín 1996, Abad *et al.* 1998, Iglesias *et al.* 2006).

During early autumn in the Adriatic Sea, the higher probability for sardine presence was associated with SST values between 20 to 26 ^{o}C when combined with coastal waters up to 110 m depth and moderate upwelling (cyclonic) water movement when combined with moderate CHLA values. Sardine's potential habitat seems to expand compared to the summer period beyond the Po River Delta region covering most of the continental shelf in the North Adriatic. In the central part of the basin sardine potential habitat areas were identified along the coastal waters of the Italian peninsula as well as in the eastern part of the Adriatic along the Slovenian and Croatian coastal zone, extending also offshore around the exterior part of the mid-Dalmatian islands. During September in the North Aegean Sea an expansion of the potential habitat over the continental shelf was also observed. No marked differences were observed in the Sicily Channel, whereas in the Western Mediterranean the potential habitat areas were mainly identified in the coastal waters, similar to the summer period, but exhibiting higher interannual variability, especially concerning the most suitable areas for sardine presence (i.e. A050 and A075, Fig. 4).

During early winter in the Spanish Mediterranean waters, model results seem to reflect the oceanographic complexity of the area. The study area comprises both an upwelling area, the Alboran Sea as well as an area with extended continental shelf subjected to the outflow of the Ebro River. Subsequently, higher probability for sardine presence was observed at a wide range of CHLA values (0.43 to 4.5 mg m^{-3}) and at SLA values of moderate downwelling water movements combined with SST values of 14 to 17 ^{o}C as well as moderate upwelling formations combined with warmer waters (16 to 18.5 ^{o}C). An increase of the potential sardine habitat is observed, mostly reflected in the expansion of the areas with increased probability in December. Potential distribution areas generally coincide with the locations estimated by previous habitat modelling work done in the Spanish Mediterranean waters (Bellido *et al.* 2008) and the actual fish distribution as estimated by acoustic surveys (Abad *et al.* 1998, Iglesias *et al.* 2006). A similar expansion of the A050 areas was also observed in North Aegean Sea and in the Adriatic.

Potential distribution areas generally reflect the known spatial distribution of sardine during early winter, indicating high probabilities of suitable conditions inside the gulfs and the inshore waters of the North Aegean Sea (Somarakis *et al.* 2006). Moreover, in the Adriatic Sea sardine potential habitat covers most of the continental shelf of the North Adriatic, extending southward along the coastal waters of the western and the eastern part of the Adriatic, covering consistently the exterior part of the mid-Dalmatian islands in agreement with the recorded spatial distribution of the species in the 80's (Morello & Arneri 2009 and references therein). No significant increase of the potential habitat area was observed in the Sicily Channel.

Summarising the seasonal patterns in the potential habitat of sardine, an expansion of the suitable habitat areas from summer to winter in all study areas was consistently noticed, besides the Sicily Channel. However, this habitat area expansion is not visible in sardine basin habitat (i.e. A025) but it was found significant only for areas characterised by increased probability of having suitable environmental conditions for supporting sardine presence (i.e. A050). On the other hand, the increase in the habitat area presenting high probability for suitable environmental conditions for sardine presence (i.e. A075) was found not significant in most cases. These high probability areas most likely do not exhibit a consistent pattern in their extent, as they can largely vary, depending on other features besides environmental parameters (i.e. the presence of high concentrations of zooplankton, the occurrence of competitors or predators, even the spatial distribution of the fishing fleet). Habitat expansion from early summer to early winter could be attributed to the population characteristics and the seasonal offshore migratory behaviour of sardine. Sardine is known to spawn in the Mediterranean Sea mainly from October to April (e.g. Regner *et al.* 1987, Sinovčić 2001, Olivar *et al.* 2001, 2003, Palomera *et al.* 2007, Somarakis *et al.* 2006, Ganias *et al.* 2007). Therefore, during early summer sardine population is a mixture of juveniles and adults and summer distribution grounds reflect both nurseries and feeding areas. This could explain why suitable areas are mostly located at inshore waters. Moreover, the potential spatial distribution of the population looks patchier as it reflects the species-environment relationship that is getting more complex with contradicting affinities between co-existing aggregations of young and older fish. Autumn and winter habitat reflects mainly feeding and spawning grounds of the fully recruited population. During autumn and winter, sardine is known to present migratory offshore behaviour that serves spawning purposes. In various upwelling areas this offshore migration is very extended (e.g. California, Lynn 2003) whereas in the Mediterranean (Morello & Arneri 2009 and references therein) and in the coastal Atlantic waters (Furnestin & Furnestin 1959, Bernal *et al.* 2007, Stratoudakis *et al.* 2007) this offshore migration is restricted up to 100 m depth, stressing the idea of coastal spawning. The expansion of the potential habitat of sardine as indicated in the current work is likely to support this migratory behaviour.

The case of the Sicily Channel that showed no significant seasonal variation is most likely attributed to the peculiarities of the specific ecosystem. Sicily Channel is characterised by a narrow continental shelf (15 nm) that widens in the most eastern and most western parts, reaching 50 nm in the Malta shelf, therefore largely determining the available space for a coastal species like sardine. The local sardine stock presents a fairly uniform distribution along the southern coast of Sicily and large interannual variability in abundance, varying even more than 80% from year to year (Patti *et al.* 2004, SGMED 2009). This is most likely associated to the carrying capacity of the ecosystem, largely determined by the year-to-year variability of the Atlantic-Ionian Stream (AIS) that dominates the surface circulation in the area, affecting the extension of the upwelling and the formation of frontal structures (Cuttitta *et al.* 2003, Patti *et al.* 2004). Subsequently, this is reflected to the estimated potential habitat that unavoidably covers most of the suitable and available space, presenting small seasonal variability.

Suitable areas that could serve as sardine habitat in the Mediterranean were also indicated outside the study regions. In the Western Mediterranean these were identified in known distribution grounds for sardine like the Gulf of Lions (Guennegan *et al.* 2000, Bigot 2007) and the coastal waters of the Ligurian Sea (Romanelli & Giovanardi 2000, Romanelli *et al.* 2002). Potential habitat areas were also indicated around the islands of Corsica and Sardinia. Moreover, areas of increased probability were consistently shown along the North African coast, mainly in the extended continental shelf of the Gulf of Gabes in Tunisia and in the Nile Delta region, during early summer. During the winter the potential distribution grounds were more extended, also covering most of the Moroccan and Algerian coast. During September however, suitable habitat areas along the North African coast and in the Levantine are generally lacking, probably due to model deficiencies. September is a transitional season, in which parameters such as SST and CHLA can vary greatly between the different parts of the Mediterranean and especially between the northern and southern parts. Therefore, data from the south and the western part of the Mediterranean are most likely required for the estimation of a more accurate model, applicable to the entire basin.

Potential spawning habitat (PSH)

An attempt was made to model the PSH of sardine, for the first time in the Mediterranean, based on three years of eggs data collected in Spanish waters during December. Higher probability for sardine egg presence was observed at areas with water depth up to 110 m combined with SLA of moderate downwelling or upwelling movement as well as at SST values of 14 to 17 ^{o}C when co-existing with moderate CHLA values. Sardine spawning is known to be related to temperature (e.g. Regner *et al.* 1987, Olivar *et al.* 2001, 2003, Palomera *et al.* 2007, Ganias *et al.* 2007, Stratoudakis *et al.* 2007). Specifically in the Mediterranean, sardine is known to spawn when surface temperature falls well below 20ºC (Olivar *et al.* 2001, 2003). Studies in the Catalan sea have showed a preference for temperatures between 12 and 14ºC but also spawning occurring between 16 and 19ºC (Palomera *et al.* 2007). Studies in the Aegean Sea have shown a similar temperature preference range 17 to 19 ^{o}C during December (Somarakis *et al.* 2006). In the Adriatic, the temperature preferendum lies within 12 to 16 ^{o}C based on studies held mainly in the ’70 and the ‘80s (Morello & Arneri 2009 and references therein). During the 90s a study also indicated that sardines leave shallow areas of the most northern part of the Adriatic Sea with low temperatures (< 10.5ºC) searching for PSH areas with more stable and suitable environmental conditions to spawn (Tičina *et al.* 2000).

In the Spanish Mediterranean waters, PSH areas for sardine generally agree with those indicated based on the December model from acoustic data, like the narrow shelf of the North Alboran Sea, the Ebro River area, the Catalan Sea and the Balearic plateau, verifying that the patchiness of the eggs closely reflects the patchiness of the spawning adults. However, eggs can also be found to deeper waters than adults due to their passive transportation offshore with currents. Although published information on the spatial distribution of the spawning grounds of sardine in the area is limited, referring mostly to Catalan Sea (Olivar *et al.* 2001, 2003) there are also known spawning grounds in the northern coast of the Alboran Sea and the Ebro River area (Pérez de Rubín 1996, García *et al.* 2006, Vargas-Yánez & Sabatés 2007). Annual variation in the PSH in the North Alboran Sea is associated to the variability of the local upwelling and the way it affects the circulation in the area (Pérez de Rubín 1996). In the Adriatic, spawning grounds were indicated in the extended continental shelf of the North Adriatic as well as at coastal waters of the western and the eastern part (Morello & Arneri 2009 and references therein), generally matching the species observed distribution during spawning in the 70s and 80s. The sharp decrease in the north part of the basin in 2007 and 2008 was due to the lack of satellite coverage of the area during the respective December period. In Aegean and eastern Ionian Sea, potential spawning grounds were more persistent inside the coastal waters and the gulfs of the western part. Although the information concerning sardine spawning grounds in these areas is limited, these areas generally coincide with the known spawning grounds of sardine in the early 00's (Somarakis *et al.* 2006). No information is available on the spatial distribution of sardine spawning grounds in the Sicily Channel but they generally match the potential habitat of adults.

Habitat modelling concerning the PSH of sardine has also been applied in the European Atlantic waters indicating a relationship of sardine eggs abundance mainly with bottom depth and temperature (Bernal *et al.* 2007, Planque *et al.* 2007). However, optimal temperature for spawning sardine seems to vary greatly between regions. In the Bay of Biscay sardine spawning has been observed between 12.5 to 15 ^{o}C (Sola *et al.* 1990, Planque *et al.* 2007) whereas in the Moroccan Atlantic waters spawning was observed within the temperature range 16–18.5 ^{o}C (Furnestin & Furnestin 1959, Ettahiri *et al.* 2003). In the North Pacific, the thermal range for sardine, *Sardinops sagax* is described between 13.5 to 17 ^{o}C (Parrish *et al.* 1989, Lluch-Belda *et al.* 1991) whereas Lynn (2003) reports spawning in colder temperature of 12–13 ^{o}C off southern and central California. Similar to the Mediterranean, in the Benguela upwelling system, the range of temperature for spawning sardine (*S. sagax*) is bimodal, with a major peak at 15.5–17.5 ^{o}C and a secondary peak between 18.7 and 20.5 ^{o}C (van der Lingen *et al.* 2001).

Apparently, adding data from areas of the North African region is necessary to estimate an effective habitat model especially when addressing transitional seasons like autumn and spring. Known distribution and/or fishing grounds of sardine exist along the Moroccan and Algerian coast (Djabali *et al.* 1991, Ramzi *et al.* 2006, Bedairia & Djebar 2009), Tunisian and Libyan coastal waters as well as the Nile Delta region along the Egyptian coast (El-Haweet 2001, Ben Abdallah & Gaamour 2005). Further east, the information on the spatial distribution grounds of sardine in the Levantine basin is currently lacking. However, local landings composition denotes sardine presence in the area (Bariche *et al.* 2006, 2007).

Future perspective

Habitat suitability maps resulted from this work can provide large scale essential species distribution information for environmental research, resource management and conservation planning, population viability analysis, environmental risk assessment and ecosystem modelling. This work is the first attempt to construct such models on different life stages (e.g. eggs, juveniles, adults) and integrate knowledge on how environmental parameters affect the spatial distribution of these different life stages. In a next step, it is of particular interest from an ecological aspect to condition these models by climate change scenarios in order to assess the potential changes in the life cycle patterns. In the case of small pelagic, habitat suitability maps can be a simple way to visualise possible regime shifts between species as reflected in the shrinkage and the expansion of the suitable habitat for each species regime shifts in biomass, which are known to occur between small pelagic such as anchovy and sardine or sardine and sardinella *Sardinella aurita* (Cury and Shannon 2004). Furthermore from a management perspective, large-scale conservation planning requires the identification of priority areas in which species have a high likelihood of long-term persistence. This usually requires high spatial resolution data on species and the identification of persistent distribution areas that can serve for the identification of these priority areas. Going further, the overlapping of habitat maps between pelagic, other fish species (e.g. predators or competitors) and zooplankton can provide essential information for the ecosystem approach to fisheries and comprise the basis for the development of indicators to spatially characterise the coastal Mediterranean ecosystems. Incorporating this knowledge into spatial dynamic models like Ecospace (Pauly *et al.* 2000) can eventually result into a very effective, highly dynamic management tool.

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Table 1. Environmental satellite parameters and their characteristics.

PARAMETER	ABBREVIATION	SENSOR/MODEL	RESOLUTION	SOURCE
Sea Surface Chlorophyll-a	CHLO	MODISA	4 km	oceancolor.gsfc.nasa.gov
Sea Surface Temperature	SST	AVHRR	1.5km	eoweb.dlr.de:8080
Photosynthetically Active Radiation	PAR	SeaWiFS	9 km	oceancolor.gsfc.nasa.gov
Sea Level Anomaly	SLA	Merged Jason-1, Envisat, ERS-2, GFO, T/P	0.25° (interpolated to 1.5km using ArcInfo's topogrid)	www.jason.oceanobs.com
Sea Surface Salinity	SSS	NOAA NCEP EMC CMB GODAS model	0.5° (interpolated to 1.5km using ArcInfo's topogrid)	iridl.ldeo.columbia.edu

Table 2. GAM model results for adults and eggs: analysis of deviance for GAM covariates and their interactions of the final models fitted.

Parameter	Res. Df	Res. Deviance	Deviance explained %	AIC	P-value
Pooled Sicily Channel and N. Aegean Sea model (June)					
Null model	3496.00	4265.41		4267.41	
s(SST)	3492.10	3854.00	9.65%	3863.81	<<0.000
s(SST)+s(SLA)	3488.38	3675.45	13.8%	3692.69	<<0.000
s(SST)+s(SLA)+s(Depth)	3540.74	3515.56	17.6%	3484.41	<<0.000
s(SST)+s(SLA)+s(Depth)+s(CHLA)	3374.02	3341.17	21.7%	3480.57	<<0.000
s(SLA, CHLA)+s(SST)+s(Depth)	3461.42	2923.80	31.5%	2994.96	<<0.000
Total variation % explained			31.5%		
Adriatic Sea model (September)					
Null model	8286.00	8399.57		8401.57	
s(Depth)	8623.05	7287.97	13.2%	7289.87	<<0.000
s(Depth)+s(CHLA)	8259.24	6987.14	16.7%	7004.65	<<0.000
s(Depth)+s(SLA)+s(CHLA)	8255.63	6733.51	19.8%	6758.24	<<0.000
s(Depth)+s(SLA)+ s(SST)+s(CHLA)	8252.26	6647.02	20.8%	5951.47	<<0.000
s(Depth)+s(SST)+s(SLA,CHLA)	8230.23	5875.94	30.0%	5636.05	<<0.000
s(Depth,SST)+s(SLA,CHLA)	8209.94	5730.90	31.7%	5847.03	<<0.000
Total variation % explained			31.7%		
Spanish waters (December)					
Null model	5000.00	6926.87		6928.87	
s(Depth)	4979.64	5710.87	17.3%	5727.60	<<0.000
s(Depth)+s(CHLA)	4940.95	5444.28	20.7%	5478.39	<<0.000
s(Depth)+s(CHLA)+s(SLA)	4854.73	4963.30	26.6%	5013.83	<<0.000
s(Depth)+s(CHLA)+s(SLA)+s(SST)	4764.91	4712.16	29.1%	4780.33	<<0.000
s(Depth)+s(CHLA)+s(SLA, SST)	4766.67	4624.58	30.5%	4689.24	<<0.000
Total variation % explained			30.5%		
Spanish waters Sardine eggs' (December)					
Null model	834.00	1041.99			
s(SST)	770.71	793.11	17.5%	811.70	<<0.000
s(SST)+s(CHLA)	765.39	694.84	27.7%	724.06	<<0.000
s(SST)+s(CHLA)+s(SLA)	742.75	607.74	35.5%	644.25	<<0.000
s(SST)+s(CHLA)+s(SLA)+s(Depth)	740.13	574.37	39.1%	616.12	<<0.000
s(CHLA, SST)+s(SLA)+s(Depth)	729.13	537.56	43.0%	601.30	<<0.000
Total variation % explained			43.0%		

Table 3. Validation parameters for sardine adults' GAM models: estimated area under the Receiver Operating Curve (AUC), N=number of records per area and year. Bold indicates data from areas/or years not included in the model selection.

Model	**Year**	**Area**	**N**	**AUC**
June	2004	N. Aegean Sea	510	0.78
	2005	N. Aegean Sea	555	0.73
	2006	N. Aegean Sea	1044	0.73
	2008	N. Aegean Sea	358	0.76
	2003	**Sicily Channel**	**478**	**0.62**
	2005	Sicily Channel	514	0.78
	2006	Sicily Channel	516	0.78
September	**2004**	**West Adriatic**	**1005**	**0.82**
	2004	**East Adriatic**	**865**	**0.76**
	2005	**West Adriatic**	**1439**	**0.82**
	2006	West Adriatic	1425	0.94
	2006	East Adriatic	1094	0.85
	2007	West Adriatic	1399	0.87
	2007	East Adriatic	1088	0.89
	2008	West Adriatic	634	0.81
	2008	East Adriatic	1069	0.90
	2006	South-West Adriatic	404	0.83
	2007	South-West Adriatic	510	0.84
December	2003	N. & S. Spanish Mediterranean	1264	0.77
	2004	N. & S. Spanish Mediterranean	1090	0.81
	2005	N. & S. Spanish Mediterranean	1090	0.85
	2006	N. & S. Spanish Mediterranean	952	0.88
	2007	N. Spanish Mediterranean	669	0.87
	2008	N. & S. Spanish Mediterranean	998	0.77
December eggs	2006	N. & S. Spanish Mediterranean	281	0.82
	2007	N. Spanish Mediterranean	186	0.83
	2008	N. & S. Spanish Mediterranean	294	0.93

Table 4. Results of the analysis of variance of the suitable habitat area (A025, A050, A075) per study region. Significant differences are indicated in bold.

Study area	Suitable habitat area	Source	Sum of Squares	Df	Mean Square	F-ratio	p-value
Aegean Sea	A025	Month	69892.9	2	34946.5	3.62	0.076
		Year	16542.4	4	4135.6	0.43	0.785
		Residual	77178.4	8	9647.3		
	A050	**Month**	**772007**	**2**	**386003**	**10.81**	**0.005**
		Year	82483.1	4	20620.8	0.58	0.687
		Residual	285591	8	35698.8		
	A075	Month	96834.1	2	48417.1	1.55	0.269
		Year	63193.7	4	15798.4	0.51	0.733
		Residual	249372	8	31171.5		
Sicily Channel	A025	Month	34476.1	2	17238.1	1.38	0.304
		Year	24130.3	4	6032.57	0.48	0.747
		Residual	99600.5	8	12450.1		
	A050	Month	245636	2	122818	1.73	0.237
		Year	121782	4	30445.4	0.43	0.784
		Residual	567305	8	70913.1		
	A075	Month	20990.8	2	10495.4	1.89	0.213
		Year	9545.07	4	2386.27	0.43	0.784
		Residual	44404.5	8	5550.57		
Adriatic Sea	A025	Month	539593	2	269796	2.09	0.194
		Year	536375	4	134094	1.04	0.450
		Residual	902175	7	128882		
	A050	**Month**	**5048020**	**2**	**2.52E+06**	**4.85**	**0.048**
		Year	2199770	4	549943	1.06	0.443
		Residual	3640550	7	520079		
	A075	Month	967265	2	483633	1.75	0.242
		Year	1517520	4	379380	1.37	0.335
		Residual	1936660	7	276666		
Spanish Medit. waters	A025	Month	17353.7	2	8676.87	0.25	0.786
		Year	64679.7	4	16169.9	0.46	0.761
		Residual	279194	8	34899.3		
	A050	**Month**	**1947730**	**2**	**973864**	**9.84**	**0.007**
		Year	78033.7	4	19508.4	0.20	0.933
		Residual	792101	8	99012.6		
	A075	**Month**	**769491**	**2**	**384745**	**11.52**	**0.004**
		Year	138595	4	34648.8	1.04	0.445
		Residual	267213	8	33401.6		

Table 5. Results of analysis of the Tukey multiple range test for the suitable habitat area (A025, A050, A075) concerning the monthly differences per study region. * Denotes statistical significant difference.

Study area	Suitable habitat area	Contrast in Months	Difference from the mean	Limits
Aegean Sea	A025	June-September	-82.6	149.525
		June-December	***-167.2**	**149.525**
		September-December	-84.6	149.525
	A050	June-September	-231.0	296.321
		June-December	***-553.2**	**296.321**
		September-December	***-322.2**	**296.321**
	A075	June-September	-96.8	273.065
		June-December	-196.8	273.065
		September-December	-100.0	273.065
Sicily Channel	A025	June-September	52.2	171.804
		June-December	-65.0	171.804
		September-December	-117.2	171.804
	A050	June-September	203.6	405.445
		June-December	-104.6	405.445
		September-December	-308.2	405.445
	A075	June-September	74.0	113.446
		June-December	-9.8	113.446
		September-December	-83.8	113.446
Adriatic Sea	A025	June-September	-457.2	618.972
		June-December	-330.5	656.519
		September-December	126.7	656.519
	A050	June-September	-980.2	1247.17
		June-December	***-1564.25**	**1322.83**
		September-December	-584.05	1322.83
	A075	June-September	-301.8	959.139
		June-December	-719.25	1017.32
		September-December	-417.45	1017.32
Spanish Medit. waters	A025	June-September	81.8	286.414
		June-December	54.6	286.414
		September-December	-27.2	286.414
	A050	June-September	209.8	455.605
		June-December	***-637.6**	**455.605**
		September-December	***-847.4**	**455.605**
	A075	June-September	84.2	311.14
		June-December	***-432.8**	**311.14**
		September-December	***-517.0**	**311.14**

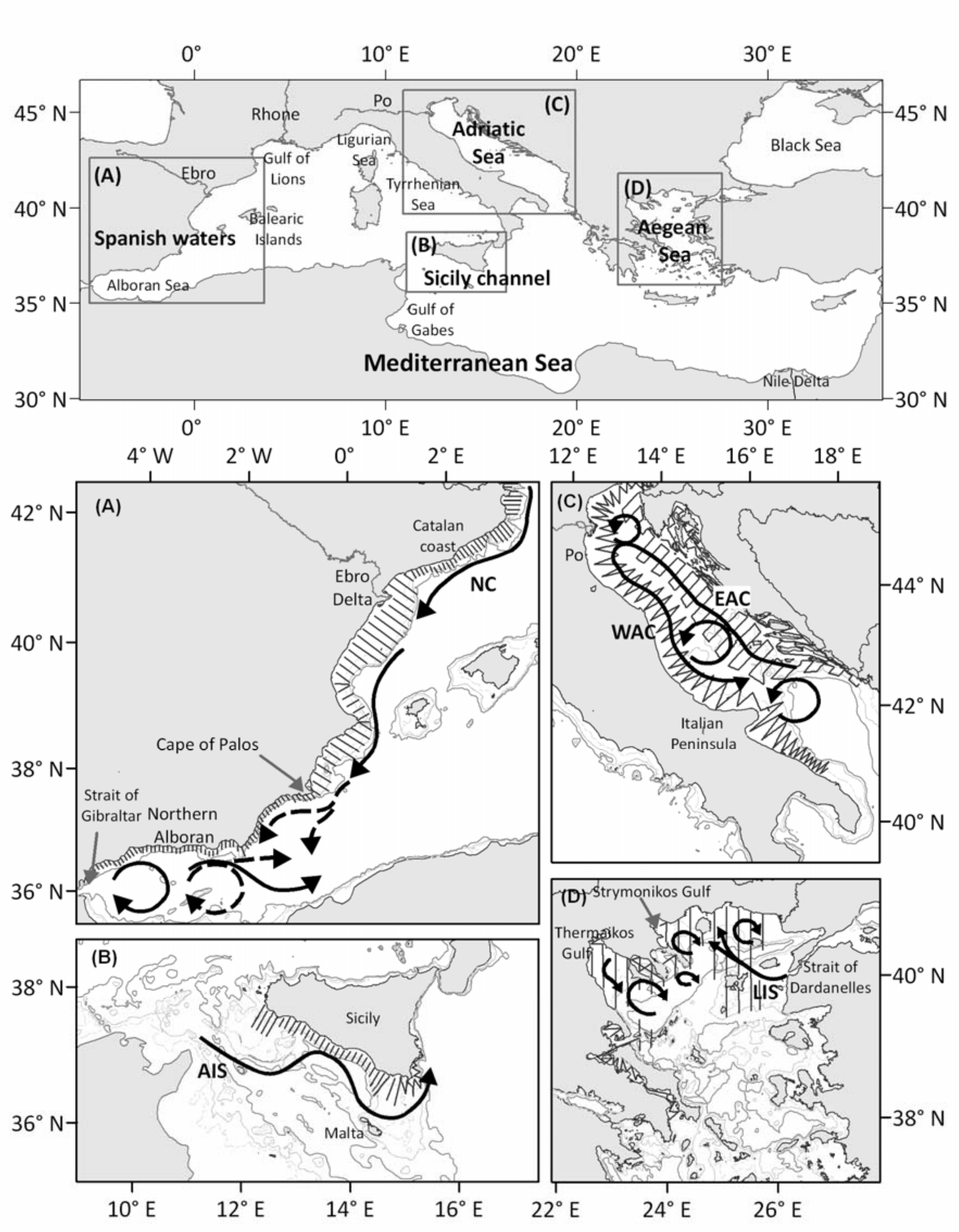

Fig. 1. Map of the study areas where also transects of acoustic sampling are shown. Water circulation is also shown. Arrows indicate the presence of fronts and gyres (redrawn from Millot 1990, Somarakis *et al.*, 2002, Artegianni 1997, Patti *et al.*, 2004). LIS: Limnos–Imvros Stream, NC; Northern Current, AIS: Atlantic Ionian Current, WAC: West Adriatic Current, EAC: East Adriatic Current. Positions of the main rivers in the area are also shown. Bathymetry is also indicated. Toponyms mentioned in the text are also indicated.

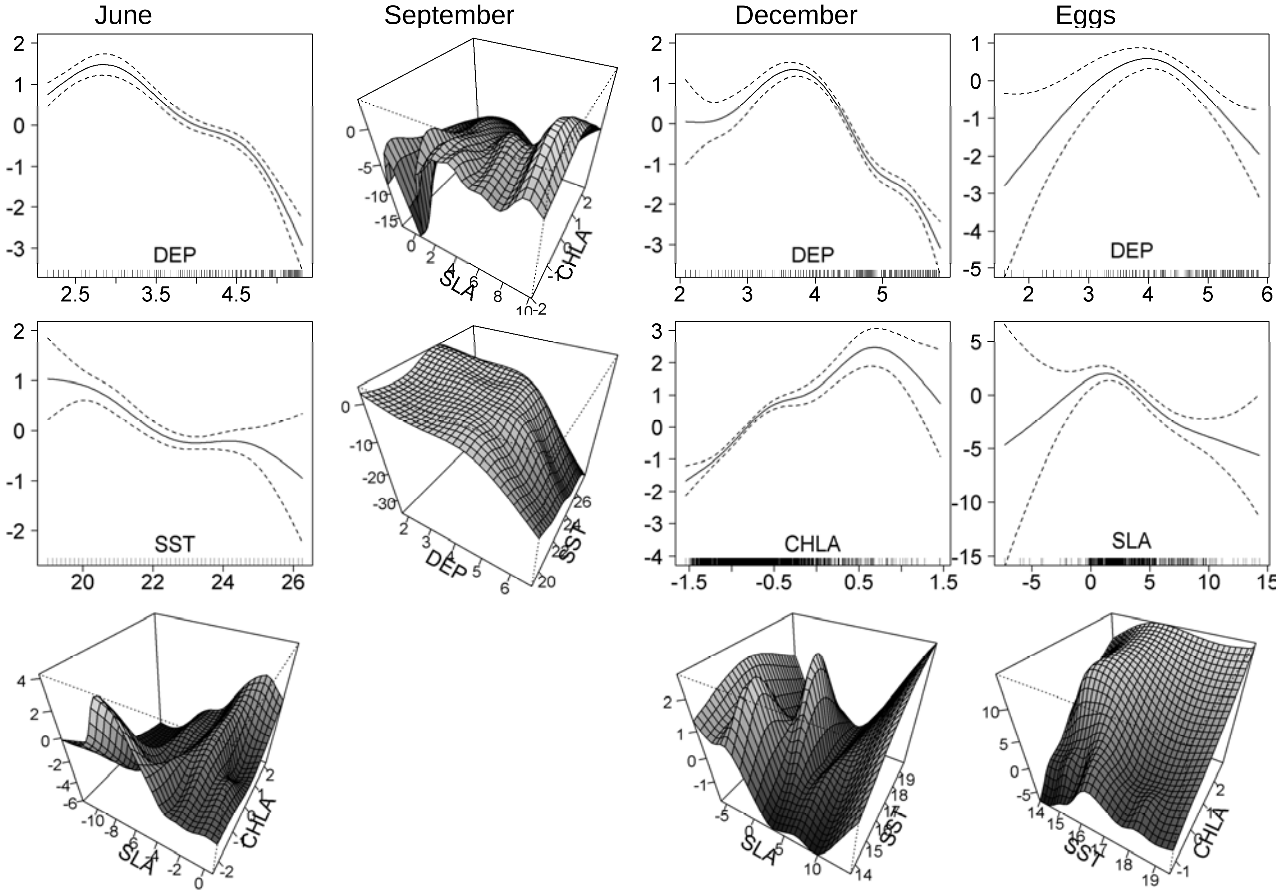

Fig. 2. Coefficients of the Generalized Additive Models (GAMs) for each model. The interaction plots are also shown. Black thick lines indicate the value of GAMs coefficient, dotted lines represent the confidence intervals at $p = 0.05$.

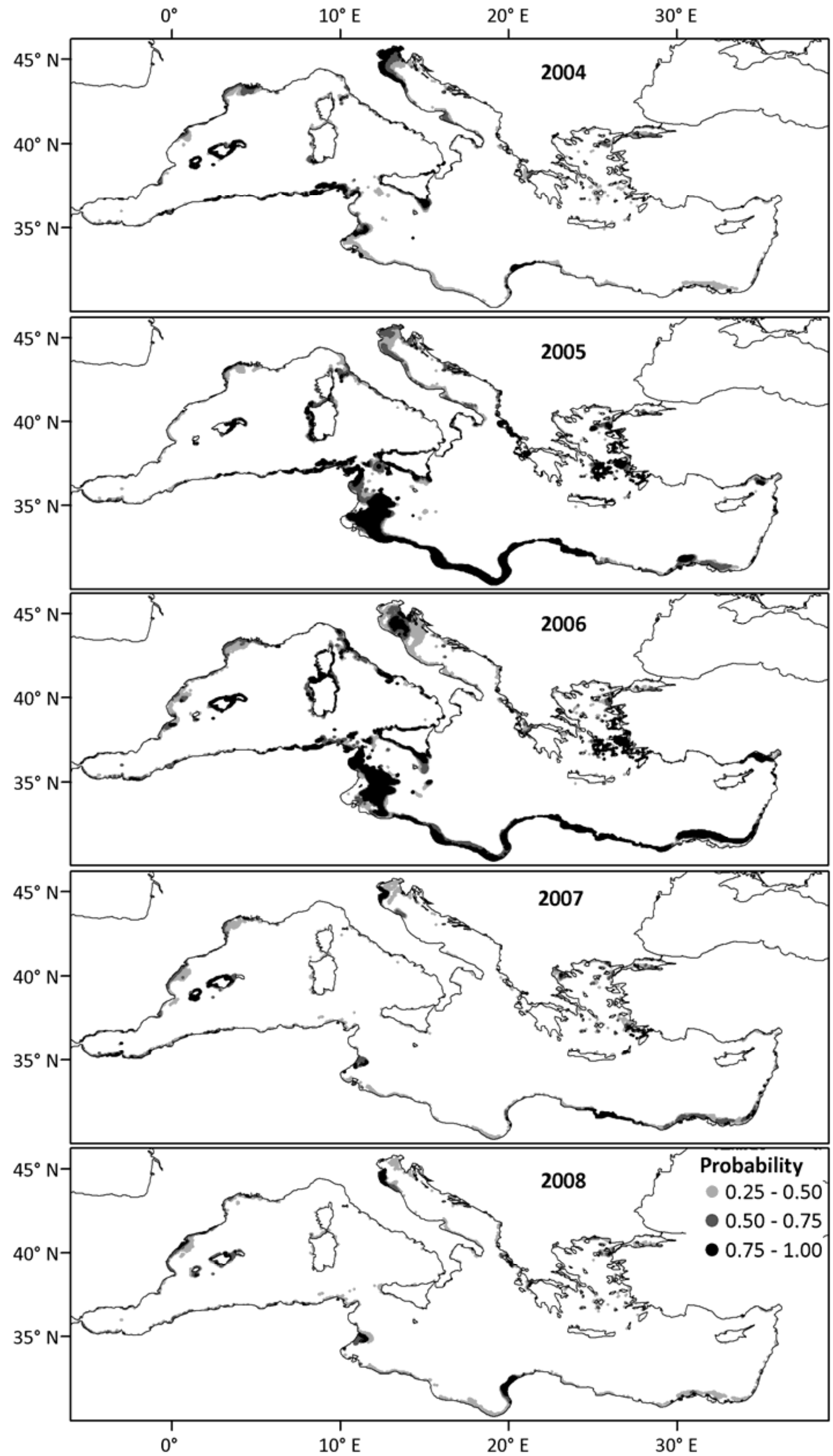

Fig 3. Habitat suitability maps indicating the probability of sardine presence in the Mediterranean Sea based on the selected GAM model in June. Spatial resolution used for prediction was 4 km of mean monthly satellite values from June 2004 to 2008. The scale indicates probability ranges

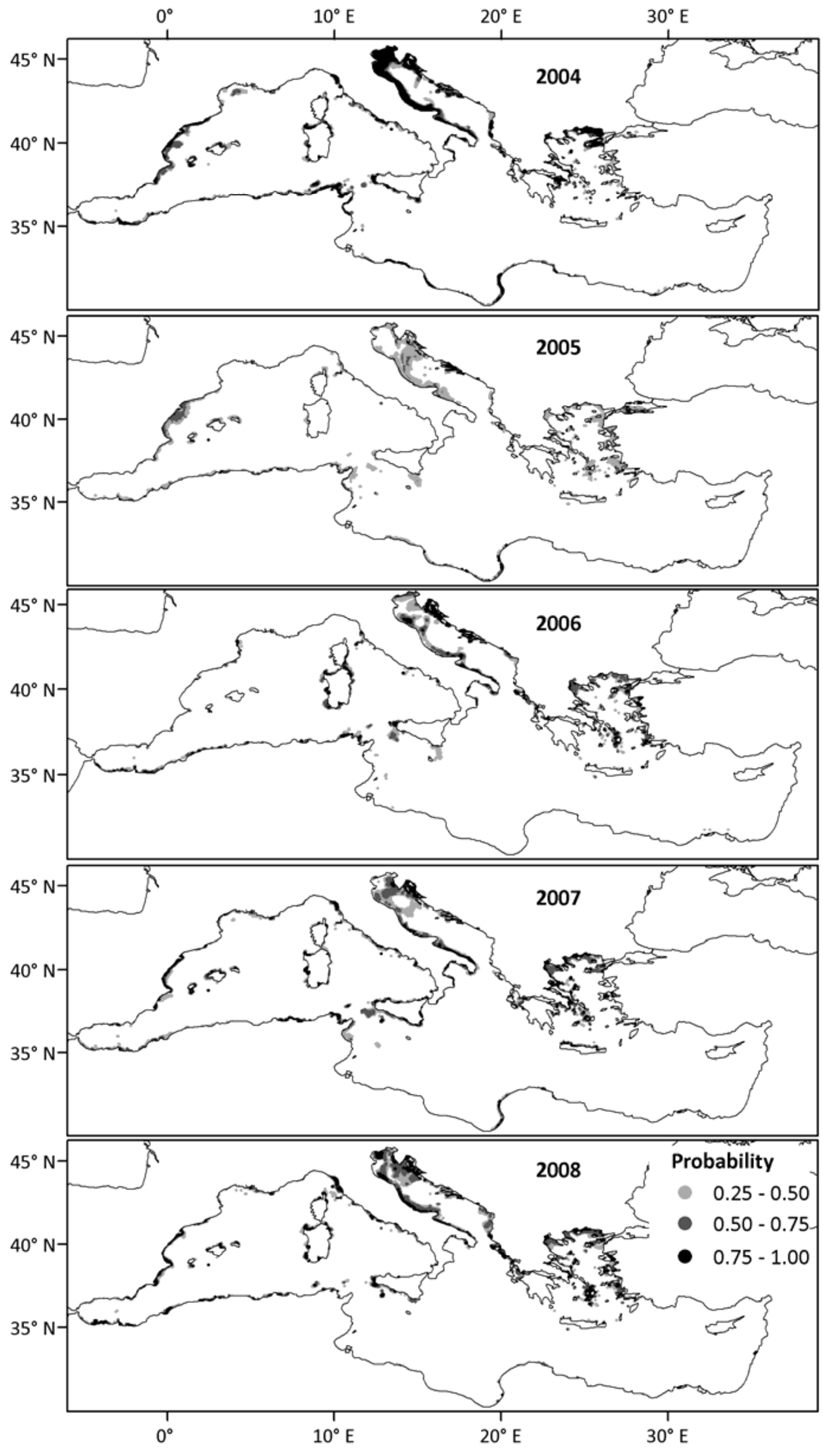

Fig 4. Habitat suitability maps indicating the probability of sardine presence in the Mediterranean Sea based on the selected GAM model in September. Spatial resolution used for prediction was 4 km of mean monthly satellite values from September 2004 to 2008. The scale indicates probability ranges.

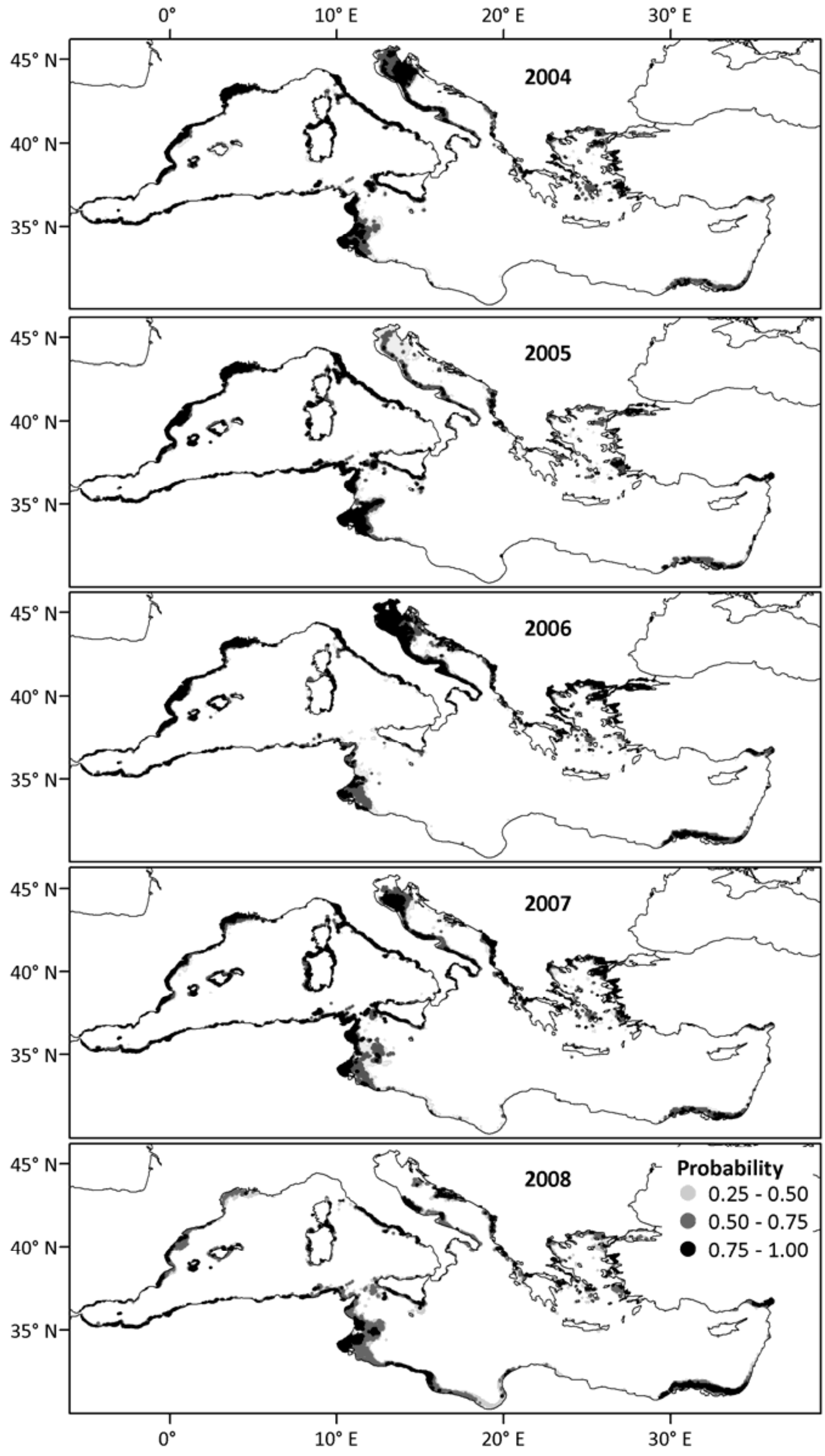

Fig 5. Habitat suitability maps indicating the probability of sardine presence in the Mediterranean Sea based on the selected GAM model in December. Spatial resolution used for prediction was 4 km of mean monthly satellite values from December 2004 to 2008. The scale indicates probability ranges.

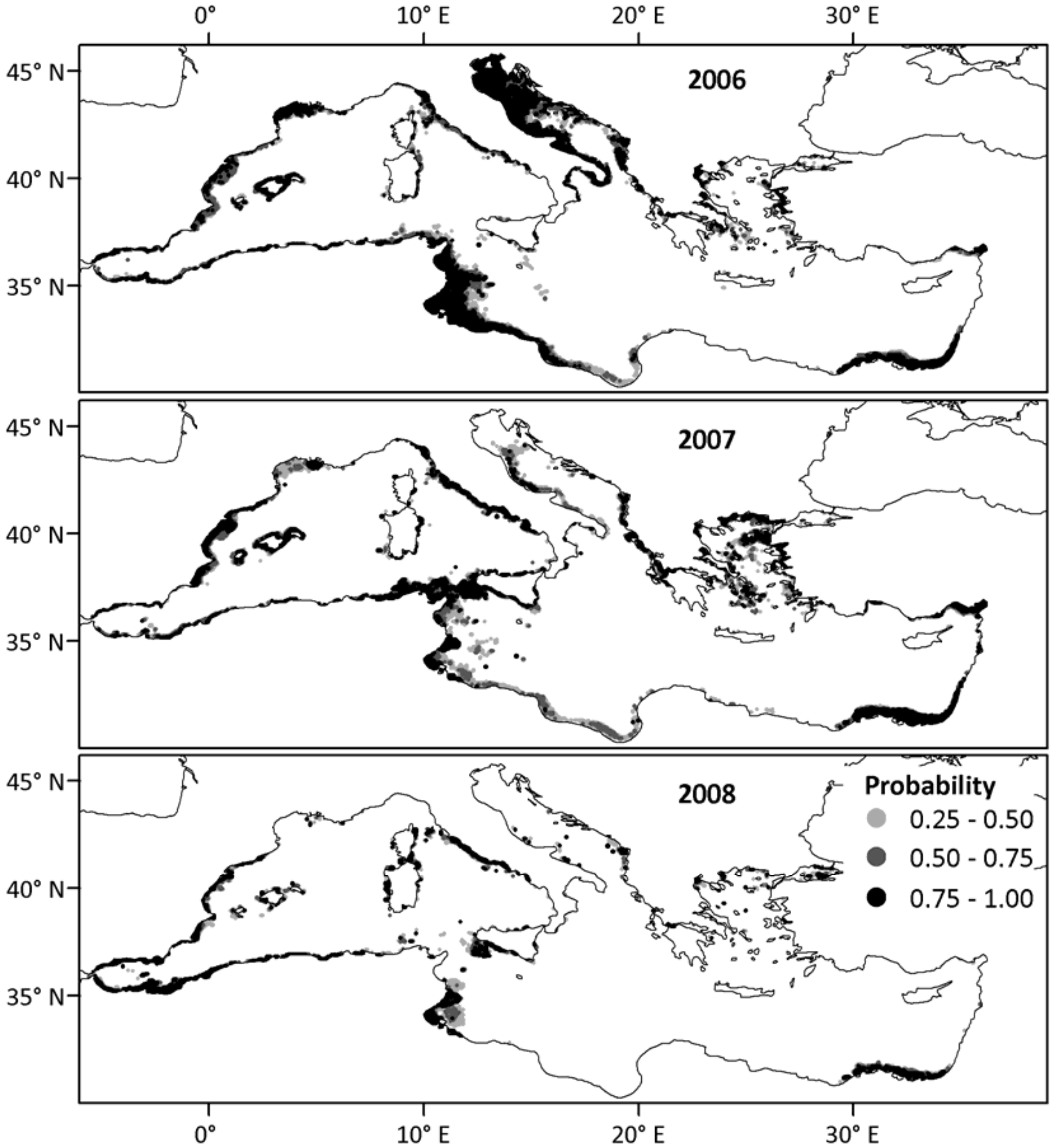

Fig. 6. Habitat suitability maps indicating the probability of sardine eggs' presence in the Mediterranean Sea based on the selected GAM model in December. Spatial resolution used for prediction was 4 km of mean monthly satellite values from December 2006 to 2008. The scale indicates probability ranges.

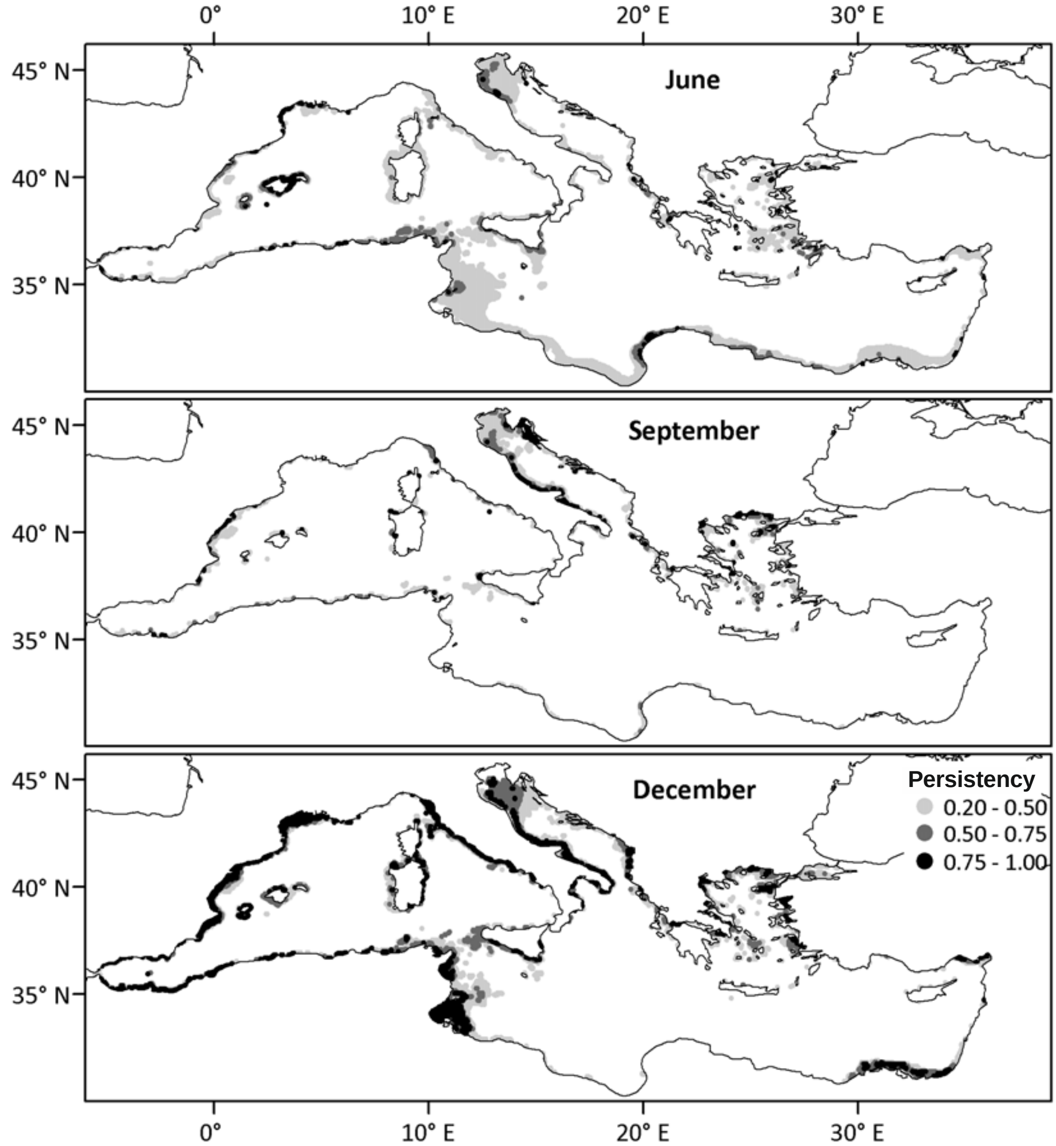

Fig 7. Potential habitat persistency maps for sardine in the Mediterranean Sea during June, September and December. Areas with low (PI: 0.20 to 0.50), medium (PI: 0.50 to 0.75) and high persistency (PI: >0.75) are shown in all cases.