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Identifying the potential habitat of anchovy *Engraulis encrasicolus* at different life stages in 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 anchovy at different life stages. Acoustic data from the Aegean Sea (Eastern Mediterranean), the Adriatic Sea and the Sicily Channel (Central Mediterranean), the Spanish waters and the Gulf of Lions (Western Mediterranean) have been analyzed along with satellite environmental and bathymetry data to model the spatial distribution of adult anchovy during summer and early autumn and the spatial distribution of juvenile anchovy during late autumn and winter. Similarly, egg distribution data from summer surveys were used to model the potential spawning habitat of anchovy in June and July. Generalized Additive Models were applied in a presence/absence approach. Selected models were used to produce potential habitat maps for the entire Mediterranean basin for each year and period, indicating areas presenting the highest probability of supporting the presence of anchovy adults, juveniles and spawning grounds. The temporal stability of these areas was examined. Bottom depth and productivity were the most important parameters found in all models. An expansion of anchovy adult habitat area was observed from summer to early autumn in all study regions. Potential juvenile grounds were identified within the continental shelf in association to high productivity waters, presenting a more extended distribution towards deeper waters in late autumn and moving to more inshore waters in winter. Potential spawning grounds presented a high degree of overlapping between June and July, being more extended compared to the adult grounds in summer.

Keywords: Small pelagics, anchovy, habitat suitability modeling, anchovy potential nurseries, Mediterranean Sea

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INTRODUCTION

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 their population 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 anchovy (*Engraulis encrasicolus*) along with sardine (*Sardina pilchardus*) and to a lesser extent round sardinella (*Sardinella aurita*), comprise the bulk of small pelagic fish catches in the Mediterranean Sea (FAO, 2009). Anchovy stocks are highly variable in terms of their recruitment, abundance and distribution while Mediterranean anchovy fishery in many areas suffers from a high degree of exploitation with most stocks exhibiting declining trends in terms of abundance (Study Group on Mediterranean Fisheries, SGMED 2009, 2010). This makes the examination of the relationship between species spatial distribution and environmental conditions vital. Small pelagic 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 and Maynou, 2003; Basilone *et al.,* 2006; Machias *et al.,* 2008). Both gears operation and fishing practise are based on the spatial detection of major anchovy and sardine aggregations by means of echosounders.

Mediterranean Sea 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.

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 and Zimmermann, 2000; Francis *et al.,* 2005; Planque *et al.,* 2007; Bellido *et al.,* 2008; Giannoulaki *et al.,* 2008; Weber and McClatchie, 2010). This approach links species location information to environmental data, quantifying the distribution of species on environmental gradients and can provide spatial distributions maps for certain species or life stages. Practically, fish habitat corresponds to geographic areas within which the range of environmental factors can define the presence of a particular species.

Therefore, modelling the potential habitat of anchovy practically means determining the combination of these environmental conditions that are suitable for the survival of the species (Guisan and Zimmermann, 2000; Planque *et al.,* 2007), however in the absence of biotic interactions (like competition or predation). The majority of the work already done concerning the habitat modelling of anchovy either address non Mediterranean areas (e.g. Allain *et al.,* 2007; Bellier *et al.,* 2007; Planque *et al.,* 2007; Weber and McClatchie, 2010) or within the Mediterranean they refer to regional scale studies focusing on a particular time of year (e.g. Basilone *et al.,* 2006; Bellido *et al.,* 2008; Giannoulaki *et al.,* 2008; Schismenou *et al.,* 2008; Grammauta *et al.,* 2008). The aim of the current work is to identify and evaluate those areas that define the potential spatial distribution of the species at different life stages and different periods of the year.

Specifically, current work takes advantage of acoustic and ichthyoplankton studies that are applied routinely in most European Mediterranean areas, serving mainly stock assessment purposes but 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. Since such surveys are being held at different periods, derived models are considered to represent different phases of the anchovy population within an annual basis. Anchovy spawns in the Mediterranean from May till September, presenting a maximum during June and July (Somarakis *et al.,* 2006; Palomera *et al.,* 2007) therefore during early summer anchovy population is dominated by spawners whereas during autumn or winter it contains a large number of the young of the year. Thus, within the current work we aim to identify which environmental parameters affect species distribution at each period and life stage as well as integrate the picture of the anchovy habitat in the Mediterranean at different seasons and at different life stages.

Using data from a wide range of environmental conditions ensures the availability of a wide range of observed habitat conditions where anchovy population occurs. This is depicted at the study areas (i.e. north western Mediterranean, Adriatic Sea, Sicily Channel and North Aegean Sea), which largely differentiate in terms of hydrography and productivity (Millot, 1990; Lloret *et al.,* 2001; Artegiani *et al.,* 1997a, 1997b; Zervakis and Georgopoulos, 2002; Patti *et al.,* 2010). In addition, satellite environmental data are dynamic in space and time, allowing estimates in various years and regions, operating as proxies or surrogates to causal factors, inferring spatial variations of environmental factors and assessing possible ecological relationships. Statistical modelling techniques, Generalised Additive Models (GAMs), that were applied in the current work are widely used in habitat suitability modelling in order to answer questions on temporal habitat dynamics (Osborne and Suarez-Seoane,

2007) or regional variation in habitat preferences (e.g. Planque *et al.,* 2007; Bellido *et al.,* 2008; Giannoulaki *et al.,* 2008).

Furthermore, the potential habitat of anchovy was recreated for each season and year in order to evaluate the seasonal and annual changes of habitat's spatial extent. Results were evaluated in the framework of existing hydrographic and productivity patterns in the study areas. Moreover, the estimated GAMs and grids of satellite environmental data were used in order to identify and map the potential distribution as well as spawning grounds for anchovy populations in the entire Mediterranean basin for the period 2004-2008. 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 anchovy's 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

Anchovy habitat at different life stages (i.e. eggs, juveniles, adults) was modelled using data from various areas of the Mediterranean. Specifically, the habitat of adult anchovy was modelled based on data from the Adriatic Sea, the Sicily Channel (Central Mediterranean) and the North Aegean Sea (Eastern Mediterranean). Surveys were held during June and September. The juvenile habitat of anchovy was also modelled based on acoustic data from the Spanish Mediterranean waters, the Adriatic Sea, the Gulf of Lions and the North Aegean Sea. Surveys were held during early winter (November-December) and winter (January-February). Additionally, anchovy egg data collected within the framework of ichthyoplankton surveys held in the North Aegean Sea and the Sicily Channel were used to model the potential spawning habitat of anchovy in June and July. Statistical models were applied to analyse the occurrence of anchovy schools (adults or juveniles) or anchovy eggs along with bottom depth and satellite environmental data.

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 (nmi, 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 nmi), 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). 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).

Gulf of Lions

The Gulf of Lions (Fig. 1B) is one of the most productive zones of the western Mediterranean Sea owing to a number of hydrographic features, including a wide shelf, river run-off, strong vertical mixing in winter, and occasional coastal upwelling (Millot, 1990; Lloret *et al.,* 2001). The large freshwater input in the area comes mainly from the Rhone River. Intense water mixing is induced by the predominant, strong, dry and cold north-westerly winds (i.e. Tramuntane and Mistral, Lloret *et al.*, 2001). Mixed north and north westerly wind systems, occurring during the summer, result in inhomogeneous surface winds over the Gulf of Lions, exhibiting high temporal variability. Furthermore, these winds present high spatial variability, due to existing complex orographic effects, generating upwelling (Forget and Andre, 2007).

Sicily Channel

The Sicily channel connects the two major basins of the Mediterranean Sea. The continental shelf is fairly narrow (15 nmi) in the middle of the southern coast but it widens both in the most eastern and most western parts reaching 50 nmi, extending to Malta shelf (Fig. 1C) (Patti *et al.,* 2004). The surface circulation is controlled by the Modified Atlantic Water motion, the so-called Atlantic-Ionian Stream (AIS, Fig. 1C) (Cuttitta *et al.,* 2003). The current enters the channel by its west boundary forming two large cyclones and the induced upwelling is further reinforced by strong winds (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).

Adriatic Sea

The Adriatic Sea (Fig. 1D) 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 (and an associated thermal-density front) 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.

North Aegean Sea

The North Aegean Sea (Fig. 1E) 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 and 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. 1E). 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 psu) enhances local productivity and its advection in the Aegean Sea induces high hydrological and biological complexity (Isari *et al.,* 2006; Somarakis and Nikolioudakis, 2007). This is further enhanced by the presence of a series of rivers that outflow in semi-closed gulfs such as Thermaikos and Strymonikos Gulfs (Stergiou *et al.,* 1997; Isari *et al.,* 2006).

Data 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 nmi 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 anchovy presence any school or echo assigned to anchovy based either on echo trace classification or attributed to anchovy based on the catch output of identification hauls (Simmonds and MacLennan, 2005). Midwater pelagic trawl sampling was used to identify and verify anchovy echo traces (see Table 2 for details). Acoustic data analysis was performed using the Myriax Echoview software besides the Eastern Adriatic where the BI60 SIMRAD software and the Gulf of Lions where the Movies+ software were used. Further details on acoustic sampling per study area are described below.

Acoustic Sampling (Adults)

Concerning the habitat modelling of adult anchovy acoustic data were used, collected within the framework of regular monitoring surveys, held for the estimation of small pelagic fish abundance.

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. 1D). 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 nmi inter-transect distance while transects in the inner part (i.e. between the islands) were positioned in respect 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. 1D). 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 nmi, depending on the width of the continental shelf (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 nmi intertransect distance in open areas whereas zigzagged transects were sampled inside gulfs (Fig. 1E). Details of the surveys, sampling methodology and data collected have already been described (Giannoulaki *et al.,* 2008).

Acoustic Sampling (Juveniles)

Acoustic data for modelling the habitat of anchovy juveniles were collected either within the framework of regular monitoring surveys in the Spanish Mediterranean waters or within the framework of targeted acoustic juveniles surveys held in the Gulf of Lions, the Adriatic Sea and the North Aegean Sea in 2007 and 2009. Specifically:

Acoustic surveys were held in Mediterranean Spanish waters, during mid November to mid December from 2003 to 2008 (i.e late autumn), on board the R/V Cornide de Saavedra. Sampling design consisted of parallel equidistant transects, perpendicular to the coastline, covering the continental shelf up to 200 m depth (Fig. 1A). Inter-transect distance was 4 nmi in the most northern (Catalan coast) and southern parts (Northern Alboran Sea), where the continental shelf is narrow, and 8 nmi in the middle part, where the continental shelf is wider. Echo was assigned to anchovy juveniles based on the catches of pelagic hauls that were held within the framework of the acoustic surveys (Table 2). The age structure of the catches revealed that the majority of the fish were age 0 (unpublished data of the Institute Espanol Oceanografico).

In a preliminary approach acoustic data from targeted juveniles surveys held in the Adriatic Sea, the Gulf of Lions and the North Aegean Sea (mid January 2009 to mid February

2009) were also used to model the anchovy juvenile habitat in the winter period. Additionally data from targeted juveniles' acoustic surveys held in the Adriatic Sea, the Gulf of Lions and the North Aegean Sea during mid November to mid December 2007 were used for validation purposes of the late autumn model.

Acoustic data collected within the targeted juvenile surveys were sampled following the general acoustic sampling as described above but minimum sampling depth was set at 10 m during these surveys. Anchovy juveniles' echoes discrimination was based on the characteristic echogram shape of the schools and the catch composition of pelagic trawling (Table 2) held in the surveyed area (Simmonds and MacLennan, 2005). Anchovy specimens smaller than 105 mm were considered as juveniles based on the estimated approximate length at first maturity in the Mediterranean for anchovy (Somarakis *et al*., 2006).

Eggs sampling

Eggs data were collected in the North Aegean Sea during ichthyoplankton surveys that were carried out with the R/V PHILIA in June 2003–2006 and 2008. The sampling scheme was based on the same transect scheme used for acoustic sampling and stations were located at 5nmi intervals on each transect (Table 2, see details in Somarakis *et al.,* 2007; Schismenou *et al.,* 2008). The sampling protocol was the same during all DEPM surveys. Standard vertical plankton tows were made at each station using a WP2 sampler (mouth opening: 0.255 m^2, mesh-size: 0.200 mm). Plankton samples were preserved in 10% buffered formalin. In the laboratory, ichthyoplankton was sorted from the plankton samples and anchovy eggs were counted (Somarakis *et al.,* 2007; Schismenou *et al.,* 2008).

Similarly, eggs data were collected in the Sicily Channel during ichthyoplankton surveys that were carried out on board the R/V Urania in the Strait of Sicily in July 2003–2008. Plankton samples were collected on the continental shelf of the southern Sicilian coast from stations based on a of 4×4 nmi grid in sea zones closer to the coasts and a grid of 12×12 nmi for the off-shore areas (Table 2). Ichthyoplankton samples were obtained using Bongo oblique hauls carried out using a 200 μm mesh size net for both sides of the frame. Hauls were towed from the bottom to the surface or from 100 m to the surface where depth was more than 100 m, with a constant speed of 2 nmi h^{-1} (Cuttitta *et al.,* 2003; Grammauta *et al.,* 2008). Biological samples were preserved in 4% buffered formaldehyde and seawater solution. Sorting of ichthyoplankton was performed in the laboratory by means of a stereo binocular at ×12 magnification and anchovy eggs were extracted and counted.

Environmental data

Satellite environmental data as well as bathymetry data were used as explanatory variables to model the habitat of anchovy in the Mediterranean basin. The area is well monitored in terms of monthly satellite imagery (summarised in Table 1). Specifically, sea surface temperature distribution (SST in ^{o}C), sea surface chlorophyll concentration (CHLA in mg m^{-3}), photosynthetically active radiation (PAR in Ein m^{-2} day^{-1}), sea surface salinity distribution (SSS based on the BCC GODAS model, Behringer and Xue, 2004) and sea level anomaly (SLA in cm) were downloaded from respective databases (see Table 1) and used. These aforementioned parameters act either as predictors for food availability and physiological suitability of the habitat and thus having direct influence on the distribution of anchovy 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 and 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 and 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 each sampling period of each respective year and area were estimated for all surveyed points 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 anchovy's distribution in the study areas. 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 (Wood, 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 and 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 anchovy echo or anchovy 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 and 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. In each case the following models were constructed:

Anchovy potential adult habitat

Two models were selected concerning anchovy adults habitat and validated based on pooled acoustic data derived from: a) the North Aegean Sea in June 2004 to 2008, and b) the eastern and the western part of the Adriatic Sea in September 2004 to 2008. Especially, in the case of North Aegean Sea a published model was used (Giannoulaki *et al.,* 2008) and re-evaluated. Moreover, 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.

Anchovy potential juveniles' habitat

Two models were selected concerning the anchovy juveniles habitat and validated using pooled acoustic data derived from a) the Spanish Mediterranean waters from late autumn (mid November to mid December 2004 to 2008), and b) the North Aegean Sea, the Adriatic Sea and the Gulf of Lions during winter (mid January to mid February 2009).

Anchovy potential spawning habitat

Two models were selected concerning the anchovy spawning habitat and validated using pooled egg presence/absence data derived from a) the North Aegean Sea in June 2003 to 2008 and b) the Sicily Channel during July 2003 to 2008. Especially in the case of the North Aegean Sea a published model was used (Schismenou *et al.,* 2008) and re-evaluated.

Model validation

The selected GAM model was applied in order to estimate the probability of habitat suitability for each point of the study areas and each year based on the available mean monthly values of environmental data. In a subsequent step, each selected model was tested and evaluated with the estimation of the Area under the receiver operator characteristic curve (AUC) (Hanley and McNeil, 1982; Guisan and 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 and McNeil, 1982), practically estimating the proportion of positive outcomes that were predicted correctly (true positive rate) as a function of the proportion of negative outcomes that were predicted incorrectly (false negative rate).The values of AUC ranges from 0 to 1, where a score of 1 indicates perfect discrimination and 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 the areas and years included in each model as well as for periods or areas that were not included in the model estimation. Areas not included in the GAM models estimation concerning the potential habitat of adult anchovy were a) the North Aegean Sea in June 2008, b) the Sicily Channel in June 2003, 2005 and 2006, and c) the western Adriatic Sea for September 2006 and 2008. Additionally, the GAM referring to the potential anchovy juvenile habitat in mid November – mid December was validated with data from the Gulf of Lions, the Adriatic Sea and the North Aegean Sea for the same period in 2007. Similarly, the GAMs referring to the potential spawning habitat of anchovy was validated for data from a) the North Aegean Sea in 2008 and b) the Sicily Channel in July 2006.

Each estimated GAM model 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 each sampling period. The model was used in order to search over these grids for the specific set of satellite conditions associated to different probabilities of anchovy or anchovy eggs' presence. Specifically, there was a discrimination among (a) the wider distribution area of anchovy or otherwise anchovy basin habitat defined as the area presenting probability 25% (A025), (b) the area of increased likelihood of suitable environmental conditions presenting probability >50% (A050) and (c) the area of high probability of suitable conditions for anchovy's presence (or otherwise hot-spot areas) defined as those areas indicating values 75% (A075). Habitat suitability maps indicating the locations with this specific set of satellite conditions were plotted as maps using the ArcGIS software.

Index of persistency

An Index of Persistency (I_i) of anchovy measuring the relative persistence of each grid cell i as an annual anchovy 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 anchovy 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 anchovy potential habitat area) and 1 (cell i always included in an annual anchovy potential habitat area) for each cell in the study area. Using different levels of I_i, the area occupied by anchovy habitat area was calculated.

RESULTS

Habitat modelling

Model selection

The results of the final selected GAMs are presented in Tables 3 to 5 and the effect of the environmental parameters on anchovy presence is shown as plots of the best-fitting smooths (Fig. 2 to 4). 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 25% to 42% of the total deviance depending on the model (Tables 3 to 5).

June anchovy adults' model

The selected GAM was based on a previously published model based on data from North Aegean Sea from 2004 to 2006 (Giannoulaki *et al.,* 2008) and included as main effects: Depth (cubic root transformed), PAR and the interactive effect of SLA with CHLA (log transformed). Depth was the variable that was initially entered the model explaining most of the total variation (Table 3). As noted in Giannoulaki *et al.,* (2008) the results of this model indicated a higher probability of finding anchovy present in shallow waters (less than 65 m) and PAR values less than 56 Ein m^{-2} day^{-1}. The interaction plot between SLA and SST indicated higher probability of finding anchovy present at (Fig. 2) SST less than 22 ^{o}C when combined with -40 cm to -12 cm SLA values (i.e. implying downwelling water movement), within the available ones.

Additionally to the areas and periods that were included in the model estimation within the current work, this model was also validated with presence/absence data derived from the acoustic survey held in North Aegean Sea in 2008 and with the presence/absence data derived from acoustic surveys held in the Strait of Sicily from 2003 to 2006. Validation results indicated moderate model performance with AUC ranging from 0.68 to 0.75.

September anchovy adults' model

The selected GAM was based on anchovy presence/absence acoustic data from the Adriatic Sea from 2004 to 2008 and included as main effects: Depth (cubic root transformed) and the interactive effect of SLA with CHLA (log transformed). Depth was the variable that was initially entered into the model explaining most of the total variation (Table 3). Model results indicated a higher probability of finding anchovy present in waters less than 170 m depth and at SLA values of 5 to 12 cm (i.e. implying preference to upwelling water movement) when co-existing with CHLA values of 0.36 to 7.4 mg m^{-3} (Fig. 2), within the available ones.

Additionally to the areas and periods that were included in the model estimation, the model was validated with presence/absence data derived from acoustic survey held in the western Adriatic during September 2006 and 2008. Validation results based on the estimation of the AUC indicated moderate to good model performance ranging from 0.67 to 0.89.

Late autumn anchovy juveniles' model

The selected GAM was based on anchovy presence/absence acoustic data from the Spanish Mediterranean waters from 2004 to 2008 and included as main effects: Depth (cubic root transformed) and the interactive effect of SLA with CHLA (log transformed). Depth was the variable that was initially entered the model explaining most of the total variation (Table 4). Model results indicated a higher probability of finding anchovy present in waters less than 150 m combined with SLA values of -5 to 5 cm and at SST values 17 to 19 ^{o}C when co-exist with CHLA values of 0.36 to 2 mg m^{-3} (Fig. 3), within the available ones. Besides the area that was included in the model estimation, the model was validated with presence/absence data derived from acoustic survey held at the North Aegean Sea, the Adriatic Sea and the Gulf of Lions in the mid November to mid December 2007. Validation results based on the estimation of the AUC indicated moderate to high model performance ranging from 0.75 in Aegean Sea to 0.97 in the Gulf of Lions.

Winter anchovy juveniles' model

The selected GAM was based on anchovy presence/absence pooled acoustic data from the western part of the Adriatic Sea, the Gulf of Lions and the North Aegean Sea in mid January to mid February 2009. The final model included the effect of CHLA (log transformed) as well as the interactive effect of the SST with Depth (cubic root transformed). SST was the variable that was initially entered into the model explaining most of the total variation (Table 4). Model results indicated a higher probability of finding anchovy present in waters of 15m to 90 m depth combined with SST values of 10 to 14 ^{o}C and at CHLA values of 1 to 4.5 mg m^{-3} (Fig. 3), within the available ones. Due to the lack of adequate number of data the model was validated only for those areas and periods that were included in the model estimation. Validation results indicated moderate model performance with AUC ranging from 0.72 to 0.80.

June anchovy eggs' model

The selected GAM was based on a previously published model based on data from North Aegean Sea from 2004 to 2006 (Schismenou *et al.,* 2008) included as main effects: SST and the interactive effect of Depth (cubic root transformed) with CHLA (log transformed). Depth was the variable that was initially entered into the model explaining most of the total variation (Table 5). As noted in Schismenou *et al,* (2008) model results indicated a higher probability of spawning with increasing SST. The interaction plot of Depth and CHLA indicated increasing probability of spawning with increasing values of CHLA and 40 m to 160 m of water depth (Fig. 4). Besides the areas that were included in the model estimation, this model was validated within the current work with presence/absence data derived from ichthyoplankton survey held in North Aegean Sea in 2008. Validation results indicated moderate to high model performance with AUC ranging from 0.77 to 0.91.

July anchovy eggs' model

The selected GAM was based on anchovy eggs presence/absence data from ichthyoplankton surveys held in the Sicily Channel in July 2003 to 2008. The final model included as main effects Depth (cubic root transformed), CHLA (log transformed) and SST. Depth was the variable that initially entered into the model explaining most of the total variation (Table 5). Model results indicated a higher probability of anchovy spawning with increasing values of CHLA, at waters of 40 to 160 m depth but at lower values of SST within the available ones (Fig. 4).

Within the current work this model was validated with presence/absence data derived from ichthyoplankton survey held in the Sicily Channel in July 2006. Validation results, based on data from the areas used for the estimation of the model indicated moderate to high model performance with AUC ranging from 0.80 to 0.91.

Index of persistency

Maps for the entire Mediterranean were estimated concerning (a) the adult habitat, (b) the juvenile habitat and (c) the spawning habitat of anchovy for each study period, indicating the index of persistency (Colloca *et al.,* 2009) for each potential habitat grid cell (Fig. 5 to 7). Specifically, those areas presenting probability of anchovy presence greater than 50% (i.e. A050 areas) 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 anchovy presence might vary in an annual basis, there are areas that are quite persistently indicated as potential spawning, juvenile or adult habitat (Figs. 5 to 7).

Persistency maps of anchovy spawning habitat showed similar favourable areas in both June and July, with areas of high persistency indicated in the coastal waters and the gulfs of Aegean Sea, the north part of the Adriatic Sea and the coastal waters of the western Mediterranean like the Gulf of Lions and the Catalan Sea. Moreover persistent potential spawning habitat areas were indicated in the coastal waters of the Sicily Strait, the Gulf of Gabes in Tunisia and the Nile Delta region (Fig. 5). Favourable juvenile areas were consistently associated with coastal productive waters and river run off areas such as the Po, Ebro and Rhone Rivers (Fig. 6). Moreover, maps implied a tendency that more suitable juveniles' areas to move towards more coastal and shallow waters from late autumn to the winter period, as indicated by the persistency map drawn for late autumn (Fig 6A) and the probability map drawn for the winter period, when only one year of data were available (Fig. 6B). Persistency maps of anchovy adult grounds indicated an increase in area extent from June to September. Indicated adult locations in June were generally similar to the indicated spawning grounds during summer, but being much narrower in extent (Fig. 7).

DISCUSSION

For the first time in the Mediterranean this study aims to take advantage of surveys targeting the same species but being held at different areas and periods within the year, focusing on different life stages in order to obtain a more global perspective on the potential distribution areas for anchovy in the basin. Specifically, data from the Western, the Central and the Eastern part of the Mediterranean were used. Surveys were held at different seasons (summer, early autumn, late autumn and winter) whereas both acoustic and ichthyoplankton data were used.

Adult Potential Habitat

Two different models were constructed for the determination of anchovy adult habitat, one addressing each study period. Depth and SLA were those environmental parameters that were found important in all cases. Bottom depth was the variable that explained most of the deviance in all models. Generally, concerning the effect of the bottom depth there was a higher probability of finding anchovy present at less than 100 m depth during summer but reaching deeper waters, up to 150 m depth in autumn.

Model results referring to the potential habitat of adult anchovy during June, in North Aegean Sea, have shown higher probability of finding suitable areas for anchovy in waters up to 100 m depth, lower SST values within the available ones combined with downwelling water movements. Associated maps indicated as persistent habitat areas for anchovy the gulfs and the coastal areas of the North Aegean Sea characterised by river outflows and the Black Sea Water input. This is in agreement with the known distribution of the species in the area (Giannoulaki *et al.,* 2005; 2006; 2008). BSW is known to induce 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 and Nikolioudakis, 2007). Results also indicated as potential habitat for anchovy 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 the known spatial distribution of anchovy in the area during summer (Cuttitta *et al.*, 2003; Patti *et al.*, 2004; 2005; Bonanno *et al.,* 2005; Patti *et al.,* 2010). In the Adriatic during June, maps indicated that suitable areas cover most of the north part of the basin in association with the wider Po River Delta region, extending southwards along the coastal waters of the eastern and the western part of the Adriatic, which is in accordance with the known information on the spatial distribution of anchovy (Tičina *et al.,* 2005; Leonori *et al.,* 2007; Morello and 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 anchovy population during other seasons (Abad *et al.,* 1998; Guennegan *et al.,* 2000; Alemany *et al.,* 2002; Giráldez and Alemany, 2002; Iglesias *et al.,* 2006; Palomera *et al.,* 2007; Giráldez *et al.,* 2007).

During early autumn (i.e. September) in the Adriatic Sea, the higher probability for anchovy presence was associated with coastal waters up to 150 m depth and moderate upwelling (cyclonic) water movement. Anchovy's potential habitat seems to expand compared to the summer period southwards, covering most of the continental shelf in the North Adriatic. In the central part of the basin anchovy 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. Similarly, in the Sicily Channel potential habitat expansion was observed over the parts where the continental shelf widens, in the most eastern and most western parts of the area. In the Western Mediterranean the potential habitat areas were also extending, covering most of the continental shelf compared to the summer suitable areas.

Suitable areas that could serve as anchovy habitat in the Mediterranean were also indicated outside the study regions like the known distribution grounds for anchovy the Gulf of Lions (Guennegan *et al.,* 2000; Bigot, 2007). Moreover, areas of increased probability were consistently shown in the Ligurian Sea, 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 early autumn the potential distribution grounds were more extended, also covering most of the Moroccan and Algerian coast.

Apparently, adding data from more years and other areas e.g. from the North Africa region, is necessary to improve the accuracy and the performance of the habitat model especially when addressing transitional seasons like autumn and spring. Known distribution and/or fishing grounds of anchovy exist along the Moroccan and Algerian coast (Djabali *et al.,* 1991), Tunisian and Libyan coastal waters as well as the Nile Delta region along the Egyptian coast (El-Haweet 2001; Ben Abdallah and Gaamour, 2005). Further east, the information on the spatial distribution grounds of anchovy in the Levantine basin is currently lacking. However, local landings composition denotes anchovy presence in the area (Bariche *et al.,* 2006; 2007).

Potential Juvenile Habitat

Anchovy spawns in the Mediterranean from May till August (Palomera *et al.,* 2007; Somarakis *et al.,* 2006) presenting a maximum during June and July, therefore late autumn and winter are periods that anchovy juveniles could be found in the population in high abundances. Within the current work, the potential juvenile habitat of anchovy was modelled for the first time in the Mediterranean, based mainly on acoustic data collected in the Spanish Mediterranean waters during late autumn (mid November to mid December). Data from targeted juveniles' surveys in the Adriatic Sea, the North Aegean Sea and the Gulf of Lions were used for the validation of the model. Additionally, the anchovy juvenile habitat in winter (mid January to mid February), was modelled based on pooled information from the Adriatic Sea, the Gulf of Lions and the North Aegean Sea but limited to one year of data.

During late autumn in the Spanish Mediterranean waters, model results indicated higher probability for anchovy juveniles presence at waters up to 160 m depth exhibiting moderate downwelling or upwelling formations (-5 to 5 cm SLA values) as well as intermediate CHLA values combined with intermediate SST values (17 to 21 ^{o}C) within the available ones. Potential juvenile habitat areas presented higher interannual variability compared to the potential adult grounds in June and September, implying the vulnerability of these areas to changing environmental conditions. Suitable 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). Potential distribution areas in the North Aegean Sea generally reflect the known spatial distribution of anchovy during late autumn, indicating high probabilities of suitable conditions inside the gulfs and the inshore waters of the region

(Giannoulaki *et al.,* 2006). Moreover, in the Adriatic Sea anchovy juvenile 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 basin, in agreement with known juvenile grounds in the area (Morello and Arneri, 2009 and references therein). Suitable areas in the Sicily Channel were also located in coastal waters extending in the north and south part where the continental shelf is wider.

During mid January to mid February higher probability for anchovy juveniles' presence was estimated at more shallow waters, from 15 m to 90 m depth combined with warmer (i.e. SST 11 to 13 ^{o}C within the available ones) and more productive waters (higher CHLA values). Indicated locations were similar in all cases, differing mainly in the area extent. Potential anchovy nurseries were indicated mainly in the inner part of the continental shelf in the coastal part of North Adriatic Sea but closely associated to the Po river outflow area, extending also southwards along the coastal waters of the western and the eastern part of the Adriatic Sea. In the North Aegean Sea suitable nursery areas were indicated mainly inside gulfs and closed basins, associated mainly to the more productive coastal waters. In the Western Mediterranean anchovy potential nursery areas were indicated in association with rivers outflow like the Rhone river in the gulf of Lions and the Ebro river southwards in the Spanish waters. Potential nurseries were also indicated along the North Africa coast in the Gulf of Gabes in Tunisia and in the Nile Delta region. River discharge is known to impact anchovy recruitment (Lloret *et al.,* 2001; Lloret *et al.,* 2004) in the Western Mediterranean and anchovy nurseries are known to be located in the vicinity of rivers outflows or shallow productive waters (Lloret *et al.,* 2004; Morello and Arneri, 2009 and references there in) that comprise areas of high food concentration and retention.

In all cases, suitable juvenile areas are characterised by high productivity waters within the continental shelf. Suitable areas were wider in extent during late autumn compared to later in season, presenting a progressive preference towards more shallow and coastal waters from late autumn towards the winter period. Possibly, the coastal, warmer waters can serve both as protected refuges, with high food concentration as weather conditions become worse. At the same time as season progresses a part of the young of the year are grown enough to be recruited to the adult stock therefore their behaviour in respect to environmental conditions can change accordingly (Petitgas *et al.,* 2004). Current results agree with the general argument that pelagic fish nurseries are located in areas of favourable food concentrations. Year-to-year fluctuations in their spatial distribution are due to the variation in the oceanographic factors that should combine favourably within an optimal environmental window (Cury and Roy, 1989; Guisande *et al.,* 2004; Fréon *et al.,* 2005) in order to build good conditions for feeding and growth or otherwise reflect optimal species decisions in respect to environmental factors at various scales. No extended off shelf anchovy recruitment seems to occur in the Mediterranean unlike the Bay of Biscay (Petitgas *et al.,* 2004; Allain *et al.,* 2007; Irigoien *et al.,* 2008), possibly due to the differences in the spatial distribution of the productivity in the two areas. The Bay of Biscay although a non upwelling area, it is more homogeneous from a productivity perspective (Allain *et al.,* 2007) compared to the Mediterranean where productivity "hot spots" are localised within a generally oligotrophic basin (Bosc *et al.,* 2004; Lejeusne *et al.,* 2010). Therefore, suitable nursery areas are located in the shelf, generated by enrichment processes like river outflows, fronts or upwellings, exhibiting persistent locations that expand or contract depending on the annual variation of the environmental parameters.

Potential Spawning Habitat

Two different models were constructed for the determination of anchovy spawning habitat addressing June and July, respectively. Depth, SST and CHLA were those environmental parameters that were found important in both cases. A common preference for intermediate water depth 40 to 160 m and more productive waters was indicated. SST preference in each model is most likely related to the available range of values in each area that are associated with the more productive waters. Maps produced from each model presented a high degree of overlapping, generally indicating the same areas, which depict reasonably well the species' spawning grounds as known from past studies and publications.

In North Aegean Sea both models indicated areas that are in agreement with the spatial distribution of eggs from previous surveys (Somarakis *et al.,* 2004; Somarakis, 2005; Somarakis *et al.,* 2006). The North Aegean Sea ecosystem is largely influenced by the BSW and river runoffs, producing favourable conditions for anchovy spawning (Agostini and Bakun, 2002; Somarakis *et al.,* 2002; Isari *et al.,* 2006; Somarakis and Nikolioudakis, 2007). Spawning spots have also been identified in the coastal areas of Asia Minor, along the Turkish coasts (e.g., Izmir Bay), which have been reported as anchovy fishing areas (Turan *et al.,* 2004). In the Adriatic Sea, areas with higher probability of anchovy spawning were consistently indicated in the northern and the western part of the basin as well as around the coastal waters of the mid-Dalmatian islands in the east part. These are areas are characterised by river outflows and increased primary production, being in good agreement with the known anchovy spawning grounds in the area (Regner, 1996; Morello and Arneri, 2009 and references therein). Anchovy potential spawning grounds were consistently indicated along the coastal waters of the Sicily Channel, being more extended in the north and south part during July which comes in agreement with the known spatial distribution of eggs from previous work in the area (Cuttitta *et al.,* 2003; Basilone *et al.,* 2006; Grammauta *et al.,* 2008). An upwelling driven by the Atlantic Ionian Current (AIS) is observed along the southern coast of Sicily that depending on the year tends to modify the temperature regime of the surface waters, differentiating the suitable conditions for anchovy spawning (García Lafuente *et al.,* 2002). In the western Mediterranean, suitable areas for anchovy spawning were indicated in the Gulf of Lions and the Catalan coast, the Alboran Sea, and, to a lesser extent, along the Italian coasts of the Ligurian and Tyrrhenian Seas. These areas coincide with the main anchovy spawning grounds in the western Mediterranean (García and Palomera, 1996; Olivar *et al.,* 2001; Palomera *et al.,* 2007). Anchovy potential spawning areas were further indicated along the Gulf of Gabes in Tunisia, the coasts of Egypt and the northeastern corner of the Levantine Basin. Anchovy known eggs distribution from these areas is very limited (e.g., Zarrad *et al.,* 2006). However, it is known that anchovy represents a significant proportion of the pelagic fish catch in Tunis (Gaamour *et al.,* 2005), Egypt (Wassef *et al.,* 1985) and the Turkish coast of the Levantine (Turan *et al.,* 2004). Moreover, both models indicated also the Black Sea as a major anchovy spawning ground. Indeed, anchovy is the most abundant species in the Black Sea and spawns all over the basin but spawning grounds are more extended in the north part (Niermann *et al.,* 1994; Kideys *et al.,* 1999).

Potential spawning grounds in June and July look more extended compared to the adult potential habitat in June which seems reasonable since eggs could be broadly dispersed away from the spawning sites (Smith *et al.,* 1985). Depth was a major factor in all models independently of the life stage examined but CHLA was also important especially when it comes to juveniles and eggs indicating a preference towards more productive waters. SST was more important in the case of anchovy juveniles in winter, presenting a preference to warmer waters (> 11 ^{o}C) as well as concerning anchovy spawning grounds in June where a choice towards higher temperatures (> 23 ^{o}C) was shown within the available ones.

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 addressing different life stages (e.g. eggs, juveniles, adults) of anchovy and integrate knowledge on how environmental parameters affect the spatial distribution of the species at different life stages. In a next step, it will be of particular interest to search for a relationship between the area extent of the potential habitat with the variability in landings or abundance, given that a longer time series of data is available. This could help the idea of setting an ecological, spatial indicator (*sensu* Woillez *et al.,* 2009) that can potentially alarm for a decline in abundance or landings when it falls below a certain threshold. Moreover, it presents special interest from an ecological aspect to condition these models with climate change scenarios in order to assess the potential changes in the life cycle patterns. In the case of small pelagic, habitat suitability maps could also be a simple way to visualise possible regime shifts between species as reflected in the shrinkage and the expansion of the suitable habitat, which are known to occur between small pelagic fish (Cury and Shannon, 2004).

From a management perspective, large-scale conservation planning requires the identification of sensitive or priority areas in which species have a high likelihood of long-term persistence, areas of particular importance for the maintenance of the stock. Habitat modelling can provide this sort of information and by incorporating this knowledge into spatial dynamic models like Ecospace (Pauly *et al.,* 2000) can eventually result into a very effective, highly dynamic management tool providing new insights into the current needs of the Ecosystem Management Approach.

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REFERENCES

Abad, R., Miquel, J., Iglesias, M., and Álvarez, F. 1998. Acoustic estimation of abundance and distribution of anchovy in the NW Mediterranean. Sci. Mar. 62 (1-2): 37-43

Agostini, V. N. and Bakun, A. 2002. ‘‘Ocean triads’’ in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat sustainability (with example application to European anchovy, *Engraulis encrasicolus*). Fish. Oceanog. 11: 129–142

Alemany, F., Bigot, J. L., Giráldez, A., Guenegan, Y., Liorzou, B., Miguel, J., and Palomera, I. 2002. Preliminary results on anchovy shared stock in the Gulf of Lions. WD to the GFCM SCSA, Working Group on the Small Pelagic, Rome 20–22 March 2002

Allain, G., Petitgas, P., Lazure, P., and Grellier, P. 2007 Biophysical modelling of larval drift, growth and survival for the prediction of anchovy (*Engraulis encrasicolus*) recruitment in the Bay of Biscay (NE Atlantic). Fish. Oceanog. 16 (6): 489-505

Artegiani, A., Bregant, D., Paschini, E., Pinardi, N., Raicich, F., and Russo, A. 1997a. The Adriatic Sea General circulation. Part I: Air–Sea Interactions and Water Mass Structure. J. Phys. Oceanogr. 27:1515–1532

Artegiani, A., Bregant, D., Paschini, E., Pinardi, N., Raicich, F., and Russo, A. 1997b. The Adriatic Sea General circulation. Part II: Baroclinic Circulation Structure. J. Phys. Oceanogr. 27:1492–1514

Bakun, A. 1996. Patterns in the ocean: ocean processes and marine population dynamics. University of California Sea Grant, San Diego, California, USA, and Centro de Investigaciones Biológicas de Noroeste, La Paz, Baja California Sur, México

Bariche, M., Alwan, N., and El-Fadel, M. 2006. Structure and biological characteristics of purse seine landings off the Lebanese coast (eastern Mediterranean). Fish. Res. 82:246–252

Bariche, M., Sadek, R., Al-Zein, M.S., and El-Fadel, M. 2007. Diversity of juvenile fish assemblages in the pelagic waters of Lebanon (eastern Mediterranean). Hydrobiologia 580:109–115

Basilone, G., Guisande, C., Patti, B., Mazzola, S., Cuttitta, A., Bonanno, A., Vergara, A.R., and Maneiro, I. 2006. Effect of habitat conditions on reproduction of the European anchovy (*Engraulis encrasicolus*) in the Strait of Sicily. Fish. Oceanogr. 15:4: 271–280

Behringer, D.W., and Xue, Y. 2004. Evaluation of the global ocean data assimilation system at NCEP: The Pacific Ocean. Eighth Symposium on Integrated Observing and Assimilation Systems for Atmosphere, Oceans, and Land Surface. American

Meteorological Society. 84th Annual Meeting Proceedings, Washington State Convention and Trade Center, Seattle, Washington, p.11-15

Bellido, J.M., Pierce, G., and Wang, J. 2001. Modelling intraanual variation in abundance of squid *Loligo forbesi* in Scottish waters using generalised additive models. Fish. Res. 52:23–39

Bellido, J.M., Brown, A.M., Graham, J.P., Iglesias, M., and Palialexis, A. 2008. Identifying essential fish habitat for small pelagic species in Spanish Mediterranean waters. Hydrobiologia 612:171–184

Bellier, E., Planque, B., and Petitgas, P. 2007. Historical fluctuations in spawning location of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in the Bay of Biscay during 1967–73 and 2000–2004. Fish. Oceanogr. 16:1: 1–15

Ben Abdallah, L., and Gaamour, A. 2005. Répartition geographique et estimation de la biomasse des petits pélagiques des cotes tunisiennes. MedSudMed Tec Doc 5: 28–38

Bigot, J.L. 2007. Stock Assessment form regarding *Sardina pilchardus* in the Gulf of Lions (GSA07). Working paper, GFCM, SCSA, Working Group on the Small Pelagic

Bonanno, A., Patti, B., Goncharov, S., Basilone, G., Cuttitta, A., Buscaino, G., García Lafuente, J., García, A., Palumbo, V., Cancemi,, M. and Mazzola, S. 2005. Fluctuation of sardine and anchovy abundance in the Strait of Sicily investigated by acoustic surveys. MedSudMed Technical Documents 5: 39–47

Bosc, E., Bricaud, A., and Antoine, D. 2004. Seasonal and interannual variability in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations. Global Biogeochem. Cycles 18:1-17

Boyce, M.S., Vernier, P.R., Nielsen, S.E., and Schmiegelow, F.K.A. 2002. Evaluating resource selection functions. Ecol. Model. 157:281–300

Champalbert, G. 1997. Characteristics of zooplankton standing stock and communities in the Western Mediterranean Sea: Relations to hydrology. Sci. Mar. 60 (Supl. 2): 97-113

Colloca, F., Bartolino, V., Lasinio, G.J., Maiorano, L., Sartor, P., Ardizzone, G. 2009. Identifying fish nurseries using density and persistence measures. Mar. Ecol. Prog. Ser. 381:287-296

Cury, P., and Roy, C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can. J. Fish. Aquat. Sci. 46: 670–680

Cury, P., Bakun, A., Crawford, R.J.M., Jarre-Teichmann, A., Quinones, R., Shannon, L.J., Verheye, H.M. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES J. Mar. Sci. 57:603–618

Cury, P., and Shannon, L. 2004. Regime shifts in upwelling ecosystems: Observed changes and possible mechanisms in the northern and southern Benguela. Prog. Oceanogr. 60 (2-4):223-243

Cuttitta, A., Carini, V., Patti, B., Bonanno, A., Basilone, G., Mazzola, S., García-Lafuente, J., García, A., Buscaino, G., Aguzzi, L., Roll, L., Morizzo, G., and Cavalcante, C. 2003. Anchovy egg and larval distribution in relation to biological and physical oceanography in the Strait of Sicily. Hydrobiologia 503:117–120

Djabali, F., Boudraa, S., Bouhdid, A., Bousbia, H., Bouchelaghem, E.H, Brahmi, B., Dob, M., Derdiche, O., Djekrir, F., Kadri, L., Mammasse, M., Stamboull, A., Tehami, B. 1991. Travoux realises sur les stocks pelagiques et demersaux de la region de Beni-saf. FAO Fish. Rep. 447:160-170

El Haweet, A. 2001. Catch composition and management of daytime purse seine fishery on the Southern Mediterranean Sea Coast, Abu Qir Bay, Egypt. Medit. Mar. Sci. 2 (2):119-126

Elith, J., Graham, C.H., Anderson, R.P., Dudık, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McCoverton, J., Peterson, A.T., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Soberon, J., Williams, S., Wisz, M.S., and Zimmermann, N.E. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151

ESRI. 1994. ARC Macro Language. Environmental Systems Research Institute Inc, Redlands, CA, USA: 3–37

Estrada, M. 1996. Primary production in the northwestern Mediterranean. Sci. Mar. 60 (Supl. 2): 55-64

FAO. 2009. FishStat Plus: Universal software for fishery statistical time series. Version 2.3. FAO Fisheries Department, Fishery Information, Data and Statistics Unit. (http://www.fao.org/fishery/statistics/software/fishstat).

Font, J., Salat, J., and Tintoré, J. 1988. Permanent features of the circulation in the Catalan Sea. Oceanologica Acta, Nº SP. In Oceanographie pelagique mediterranéenne, Edit. H.J. Minas and P. Nival

Foote, K.G., Knudsen, H.P., Vestnes, G., MacLennan, D.N., and Simmonds, E.J. 1987. Calibration of Acoustic Instruments for Fish Density Estimation: A Practical Guide. ICES Coop. Res. Rep. 144:82 pp

Forget, P.; André, G. (2007) Can satellite-derived chlorophyll imagery be used to trace surface dynamics in coastal zone? A case study in the northwestern Mediterranean Sea. Sensors, **7:** 884-904.

Francis, M.P., Morrison, M.A., Leathwick, J., Walsh, C., and Middleton, C. 2005. Predictive models of small fish presence and abundance in northern New Zealand harbours. Est. Coast. Shelf. Sci. 64:419–435

Franklin, J. 2009. Mapping Species Distributions. Spatial Inference and Prediction. New York: Cambridge University Press, 320pp

Fréon, P., Drapeau, L., David, J. H. M., Fernández Moreno, A., Leslie, R. W., Oosthuizen, W. H., Shannon, L. J. and van der Lingen, C. D. 2005. Spatialized ecosystem indicators in the southern Benguela. ICES J. Mar. Sci. 62: 459–468

Gaamour, A., Ben-Abdallah, L., Khemiri, S., and Mili, S. 2005. Etudes de la biologie et de l'exploitation des petits pe´lagiques en Tunisie. MedSudMed Technical Documents 5

García, A. and Palomera, I. 1996. Anchovy early life history and its relation to its surrounding environment in the Western Mediterranean basin. Sci. Mar. 60: 155–166

García Lafuente, J., García, A., Mazzola, S., Quintanilla, L., Delgado, J., Cuttita, A., and Patti, B. 2002. Hydrographic phenomena influencing early life stages of the Sicilian Channel anchovy. Fish. Oceanog. 11: 31–44

Giannoulaki, M., Machias, A., Somarakis, S., and Tsimenides, N. 2005. The spatial distribution of anchovy and sardine in the northern Aegean Sea in relation to hydrographic regimes. Belg. J. Zool. 135: 151–156

Giannoulaki, M., Machias, A., Koutsikopoulos, C., and Somarakis, S. 2006 The effect of coastal topography on the spatial structure of anchovy and sardine. ICES J. Mar. Sci., 63 (4): 650-662

Giannoulaki, M., Valavanis, V.D., Palialexis, A., Tsagarakis, K., Machias, A., Somarakis, S., and Papaconstantinou, C. 2008. Modelling the presence of anchovy *Engraulis encrasicolus* in the Aegean Sea during early summer, based on satellite environmental data. Hydrobiologia 612:225–240

Giráldez, A., and Alemany, F. 2002. Echo-survey estimations of anchovy, sardine, gilt sardine, bogue and horse mackerel populations in the NW Mediterranean Sea (from Creus Cape to La Nao Cape). Working Paper, Working Group on the Small Pelagic

Giráldez, A., Iglesias, M., Miquel, J., Díaz, N., and Torres, P. 2007. Anchovy (*Engraulis encrasicolus*) Stock Assessment by Acoustic Methods in the GFCM Geographical Sub-Area 06, Northern Spain. WD to the GFCM SCSA, Working Group on the Small Pelagic, Athens 13–14 September 2007

Grammauta, R., Molteni D., Basilone G., Guisande, C., Bonanno A., Aronica S., Giacalone, G., Fontana I., Zora M., Patti B., Cuttitta, A., Buscaino G., Sorgente R., and S. Mazzola S., 2008. Linking air-sea energy exchanges and European anchovy potential spawning ground. Eur. Phys. J. B 65, 459–467

Guennegan, Y., Liorzou, B., and Bigot, J.L. 2000. Exploitation des petites pelagique dans le Golf du Lion et suivi de l'evolution des stocks par echo-integration de 1999 a 2000. Paper Presented at WG of Small Pelagics. Fuengirola (Spain) 1–3 March 2000: 27

Guisan, A., Edwards, T.C.Jr, and Hastie, T. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol. Model. 157:89–100

Guisan, A., and Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135:147-186

Guisande, C., Ulla, A., and Thejll, P. 2004. Solar activity governs abundance of Atlantic Iberian sardine *Sardina pilchardus*. Mar Ecol Prog Ser. Vol. 269: 297–301

Hanley, J.A., and McNeil, B.J. 1982. The meaning and use of the area under a Receiver Operating Characteristic (ROC) curve. Radiology 143:29–36

Hastie, T., and Tibshirani, R. 1990. Generalized Additive Models. Chapman and Hall, London

Iglesias, M., Miquel, J., Oñate, D., Giráldez, A., Díaz, N., and Tugores, P. 2006. ECOMED Acoustic Surveys: Methodology, Results and Scope. Working Group on Small Pelagic Species, Sub-Committee for Stock Assessment, Scientific Advisory Committee of the General Fisheries Commission for the Mediterranean (GFCM), 11-14 Septiembre

Irigoien, X., Cotano, U., Boyra, G., Santos, M., Alvarez, P., Otheguy, P., Etxebeste, E., Uriarte, A., Ferrer, L., and Ibaibarriaga, L. 2008 From egg to juvenile in the Bay of Biscay: Spatial patterns of anchovy (*Engraulis encrasicolus*) recruitment in a non-upwelling region. Fish. Oceanog., 17 (6): 446-462

Isari, S., Ramfos, A., Somarakis, S., Koutsikopoulos, C., Kallianiotis, A., Fragopoulou, N. 2006. Mesozooplankton Aegean Sea, Eastern Mediterranean. J. Plankton Res. 28:241–255

Katsanevakis, S., Maravelias, C.D., Damalas, D., Karageorgis, A.P., Tsitsika, E.V., Anagnostou, C., and Papaconstantinou, C. 2009. Spatiotemporal distribution and habitat use of commercial demersal species in the eastern Mediterranean Sea. Fish. Oceanogr. 18(6):439-457

Kideys, A. E., Gordina, A.D., Bingel, F., and Niermann, U. 1999. The effect of environmental conditions on the distribution of eggs and larvae of anchovy (*Engraulis encrasicolus* L.) in the Black Sea. ICES J. Mar. Sci. 56: 58–64

Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C.F., Pérez, T. 2010. Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. Trends Ecol. Evol. 25(4):250-260

Leonori, I., Azzali, M. and De Felice, A. 2007b. Assessment of small pelagic fish by acoustic methods in north western Adriatic Sea. WD to the GFCM SCSA, Working Group on the Small Pelagic, Athens 13–14 September 2007

Lleonart, J., and Maynou, F. 2003. Fish stock assessments in the Mediterranean: state of the art. Sci. Mar. 67(Suppl. 1): 37-49

Lloret, J., Lleonart, J., Solé, I., and Fromentin, J-M. 2001. Fluctuations of landings and environmental conditions in the north-western Mediterranean Sea. Fish. Oceanogr. 10(1):33-50

Lloret, J., Palomera, I., Salat, J., and Sole, I. 2004. Impact of freshwater input and wind on landings of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf waters surrounding the Ebre (Ebro) River delta (north-western Mediterranean). Fish. Oceanog. 13 (2): 102-110

Machias, A., Stergiou, K.I., Somarakis, S., Karpouzi, V.S., and Kapantagakis, A. 2008. Trends in trawl and purse seine catch rates in the north-eastern Mediterranean. Medit. Mar. Sci. 9(1): 49-65

Mackinson, S., Nottestad, L., Guenette, S., Pitcher, T., Misund, O.A., and Ferno, A. 1999. Cross-scale observations on distribution and behavioural dynamics of ocean feeding Norwegian spring-spawning herring (*Clupea harengus* L.). ICES J. Mar. Sci. 56 (5):613-626

Marini, M., Jones, B.H., Campanelli, A., Grilli, F., and Lee, C.M. 2008. Seasonal variability and Po River plume influence on biochemical properties along western Adriatic coast. J. Geophys. Res. 113, C05S90, doi:10.1029/2007JC004370

Millot, C. 1990. The Gulf of Lions' hydrodynamics. Cont. Shelf. Res. 10(Suppl. 9-11)**:** 885-894

Millot, C. 1999. Circulation in the Western Mediterranean Sea. J. Mar. Systems 20: 423–442

Morello, E.B., and Arneri, E. 2009. Anchovy and sardine in the Adriatic Sea – An Ecological Review. Oceanogr. Mar. Biol. Annu. Rev. 47:209-256

Niermann, U., Bingel, E., Gorban, A., Gordina, A. D., Gucu, A. C., Kideys, A. E., Konsulov, A., Radu, G., Subbotin, A. A., and Zaika, V, E, 1994. Distribution of anchovy eggs and larvae (*Engraulis encrasicolus* Cuv.) in the Black Sea in 1991–1992. ICES J. Mar. Sci. 51: 395–406

Olivar, M.P., Salat, J., and Palomera, I. 2001. Comparative study of spatial distribution patterns of the early stages of anchovy and pilchard in the NW Mediterranean Sea. Mar. Ecol. Prog. Ser. 217:111–120

Osborne, P.E., and Suárez-Seoane, S. 2007. Identifying core areas in a species' range using temporal suitability analysis: an example using little bustards *Tetrax tetrax* L. in Spain. Biodivers. Conserv. 16:3505-3518

Palomera, I., Olivar, M.P., Salat, J., Sabatés, A., Coll, M., García, A., Morales-Nin, B. 2007. Small pelagic fish in the NW Mediterranean Sea: An ecological review. Progr. Oceanogr. 74 (2-3):377-396

Patti, B., Bonanno, A., Basilone, G., Goncharov, S., Mazzola, S., Buscaino, G., Cuttitta, A., García Lafuente, J., García, A., Palumbo, V., and Cosimi, G. 2004. Interannual fluctuations in acoustic biomass estimates and in landings of small pelagic fish populations in relation to hydrology in the Strait of Sicily. Chem. and Ecol. 20: 365–375

Patti, B., Cuttitta, A., Bonanno, A., Basilone, G., Buscaino, G., Patti, C., García Lafuente, J. García, A., and Mazzola, S. 2005. Coupling between the hydrographic circulation in the Strait of Sicily and the reproductive strategy of the European anchovy *Engraulis encrasicolus*: effects on distribution of spawning grounds. MedSudMed Technical Document 5: 19–2

Patti, B., Guisande, C., Bonanno, A., Basilone, G., Cuttitta, A., and Mazzola, S. 2010. Role of physical forcings and nutrient availability on the control of satellite-based chlorophyll a concentration in the coastal upwelling area of the Sicilian Channel. Sci. Mar. 74(3): 577-588, doi: 10.3989/scimar.2010.74n3577

Pauly, D., Christensen, V., and Walters, C. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J. Mar. Sci. 57:697-706

Petitgas, P., Beillois, P., Grellier, P., and Massé J. 2004. On the importance of adults in maintaining population habitat occupation of recruits as deduced from observed schooling behaviour of age-0 anchovy in the bay of Biscay ICES CM 2004/J:13

Planque, B., Bellier, E., and Lazure, P. 2007. Modelling potential spawning habitat of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) in the Bay of Biscay. Fish. Oceanogr 16:16–30

Pujol, M.I., and Larnicol, G. 2005 Mediterranean Sea eddy kinetic energy variability from 11 years of altimetric data. J. Mar. Systems 58: 121-142

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available online at: www.R-project.org

Regner, S. 1996. Effects of environmental changes on early stages and reproduction of anchovy in the Adriatic Sea. Sci. Mar. 60: 167–177

Russo, A., Coluccelli, A., Iermano, I., Falcieri, F., Ravaioli, M., Bortoluzzi, G., Focaccia, P., Stanghellini, G., Ferrari, C.R., Chiggiato, J., and Deserti, M. 2009. An operational system for forecasting hypoxic events in the northern Adriatic Sea. Geofizika 26:191–213

Sacau, M., Pierce, G.J., Wang, J., Arkhipkin, A.I., Portela, J., Brickle, P., Santos, M.B., Zuur, A.F., and Cardoso, X. 2005. The spatio-temporal pattern of Argentine shortfin squid *Illex argentinus* abundance in the southwest Atlantic. Aquat. Living Resour. 18:361–372

Schismenou, E., Giannoulaki, M., Valavanis, V.D., and Somarakis, S. 2008 Modeling and predicting potential 1spawning habitat of anchovy (*Engraulis encrasicolus*) and round sardinella (*Sardinella aurita*) based on satellite environmental information. Hydrobiologia 612 (1): 201-214

SGMED. 2009. Report of the SGMED-09-02 Working Group on the Mediterranean Part I. Scientific, Technical and Economic Committee for Fisheries (STECF), European Commission. In: Cardinale M, Cheilari A, Ratz HJ (eds), 8-10 June 2009, Villasimius, Sardinia, Italy

SGMED. 2010. Report of the SGMED-10-02 Working Group on the Mediterranean Part I. Scientific, Technical and Economic Committee for Fisheries (STECF), European Commission. In: Cardinale M, Cheilari A, Ratz HJ (eds), 31 May -4 June 2010, Iraklion, Crete, Greece

Simmonds, J., and MacLennan, D. 2005. Fisheries acoustics, theory and practice. 2nd edition, Blackwell Publishing, Oxford, 437pp

Smith, W.H.F., and Sandwell, D.T.S. 1997. Global sea floor topography from satellite altimetry and ship depth soundings. Science 277:1956–1962

Smith P.E. and Hewitt R.P. 1985. Anchovy egg dispersal and mortality as inferred from close – interval observations. Californian Cooperative Oceanic and Fisheries Investigations Report. 26, 97-110.

Somarakis, S., Drakopoulos, P., and Filippou, V. 2002. Distribution and abundance of larval fishes in the northern Aegean Sea -Eastern Mediterranean- in relation to early summer oceanographic conditions. J. Plankton Res. 24:339–357

Somarakis, S., Palomera, García, A., Quantanilla, L., Koutsikopoulos, C., and Motos, L. 2004. Daily egg production of anchovy in European waters. ICES J. Mar. Sci. 61: 944–958

Somarakis, S., 2005. Marked interannual differences in reproductive parameters and daily egg production of anchovy in the northern Aegean Sea. Belgian Journal of Zoology 134: 123–132

Somarakis, S., Tsianis, D. E., Machias, A., and Stergiou, K. I. 2006. An overview of biological data related to anchovy and sardine stocks in Greek waters. In Palomares, M. L. D., K. I. Stergiou and D. Pauly (eds), Fishes in Databases and Ecosystems. Fisheries Centre Research Reports 14. Fisheries Centre, University of British Columbia: 56–64

Somarakis, S., Machias, A., Giannoulaki, M., Schismenou, E., Tsagarakis, K., Siapatis, A., Stamataki, C., Torre, M., Anastasopoulou, A., Vassilopoulou, V., Kalianiotis, A., and Papaconstantinou, C. 2007. Ichthyoplanktonic and acoustic biomass estimates of anchovy in the Aegean Sea (June 2003, 2004, 2005 and 2006). General Fisheries Commission for the Mediterranean, Scientific Advisory Committee, Sub-Committee for Stock Assessment, Working Group on Small Pelagic Species, Athens: 29

Somarakis, S., and Nikolioudakis, N. 2007. Oceanographic habitat, growth and mortality of larval anchovy (*Engraulis encrasicolus*) in the northern Aegean Sea (eastern Mediterranean). Mar. Biol. 152:1143–1158

Stergiou, K.I., Christou, E.D., Georgopoulos, D., Zenetos, A., Souvermezoglou, C. 1997. The Hellenic Seas: Physics, chemistry, biology and fisheries. Oceanogr. Mar. Biol. Annu. Rev. 35:415–538

Tičina, V., Kačić, I., and Cetinić, P. 1999. Two-boat mid-water trawling on the northern Adriatic Sea. Proceedings of the International Symposium on Responsible Fisheries and Fishing Techniques, IŃSKO – POLAND, 16-19 June: 267-274

Tičina, V., Katavić, I., Dadić, V., Marasović, I., Kršinić, F., Grbec, B., Kušpilić, B., Cetinić, P., Ninčević, Ž., Matić Skoko, S., Franičević, M., Soldo, A., Vidjak, O., Emrić Tičina, V., Bojanić, D., Marinov, S., Matić, F. 2006. Acoustic estimates of small pelagic fish stocks in the eastern part of Adriatic Sea. Biologia Marina Mediterranea 13 (3) part 2: 124-136

Turan, K., Erguden, D., Gurlek, M., Basusta, N., and Turan, F. 2004. Morphometric structuring of the Anchovy (*Engraulis encrasicolus* L.) in the Black, Aegean and

Northeastern Mediterranean Seas. Turkish Journal of Veterinary and Animal Sciences 28: 865–871

Valavanis, V.D., Georgakarakos, S., Kapantagakis, A., Palialexis, A., and Katara, I. 2004. A GIS environmental modeling approach to Essential Fish Habitat designation. Ecol. Model. 178:417–427

Wassef, E., Ezzat, A., Hashem, T., and Faltas, S. 1985. Sardine fishery by purse-seine on the Egyptian Mediterranean coast. Mar. Ecol. Prog. Ser. 26: 11–18

Weber, E.D., and McClatchie, S. 2010. Predictive models of northern anchovy *Engraulis mordax* and Pacific sardine *Sardinops sagax* spawning habitat in the California Current. Mar. Ecol. Prog. Ser. 406: 251-263

Woillez, M., Rivoirard, J., and Petitgas, P. 2009. Notes on survey-based spatial indicators for monitoring fish populations. Aquat. Living Resour. 22:155-164

Wood, S.N. 2006. Generalized Additive Models. An Introduction with R. Chapman & Hall, London

Zarrad, R., Missaoui, H., Alemany, F., Salah, R, M., García, A., Ridhah, M., Othman, J., and Amor, E, 2006. Spawning areas and larval distributions of anchovy *Engraulis encrasicolus* in relation to environmental conditions in the Gulf of Tunis (Central Mediterranean Sea). Sci. Mar. 70: 137–146

Zervakis., V., and Georgopoulos, D. 2002. Hydrology and circulation in the Northern Aegean Sea throughout 1997 and 1998. Medit. Mar. Sci. 3:5–19

Table 1. Environmental satellite parameters and their characteristics.

PARAMETER	ABBREVIATION	SENSOR/MODEL	RESOLUTION	SOURCE
Sea Surface Chlorophyll-a	CHLA	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. Surveys summary description. Avg No Pelagic Hauls: Average number of pelagic haul per survey in an annual basis, Avg No Ichthyoplankton Stations: Average number of Ichthyoplankton Stations in an annual basis

Life stage	Area	Month	Period	No Transects	Avg No Pelagic Hauls	Avg No Ichthyoplankton Stations
Adults	North Aegean Sea	June	2004-2008	70	30	
	Sicily Channel	June	2004-2008	40	18	
	Western Adriatic	September	2004-2008	50	28	
	Eastern Adriatic	September	2004-2008	30	25	
Juveniles	Spanish Mediterranean waters	mid November- mid December	2003-2008	128	50	
	Gulf of Lions	mid November- mid December	2007	9	18	
	Western Adriatic	mid November- mid December	2007	13	20	
	North Aegean Sea	mid November- mid December	2007	18	17	
	Gulf of Lions	Mid January- mid February	2009	11	35	
	Western Adriatic	Mid January- mid February	2009	13	20	
	North Aegean Sea	Mid January- mid February	2009	18	19	
Eggs	North Aegean Sea	June	2003-2008			204
	Sicily Channel	July	2003-2008			180

Table 3. GAM model construction for anchovy adults: analysis of deviance for GAM covariates and their interactions of the final models fitted. The N. Aegean Sea model has been previously published in Giannoulaki *et al.,* 2008.

Parameter	Res. Df	Res. Deviance	Deviance explained %	AIC	P-value
N. Aegean Sea model (June)					
Null model	2126.00	2321.67		2323.67	
s(Depth)	2120.93	1652.66	28.80%	1664.79	<<0.000
s(Depth)+s(PAR)	2119.27	1616.15	30.40%	1631.60	<<0.000
s(Depth)+s(PAR)+s(SLA)	2066.18	1499.55	33.00%	1531.18	<<0.000
s(Depth)+s(PAR)+s(SLA)+s(SST)	2061.24	1487.18	33.60%	1528.70	<<0.000
s(SST, SLA)+s(PAR)+s(Depth)	2059.25	1456.72	35.56%	1502.22	<<0.000
Total variation % explained			35.56%		
Adriatic Sea model (September)					
Null model	9936.00	13621.22		13623.22	
s(Depth)	9932.00	11058.09	18.8%	11068.08	<<0.000
s(Depth)+s(CHLA)	9928.06	10954.57	19.6%	10972.45	<<0.000
s(Depth)+s(SLA)+s(CHLA)	9924.12	10569.88	22.4%	10595.65	<<0.000
s(Depth)+s(SLA,CHLA)	9904.04	9990.6	26.7%	10056.53	<<0.000
Total variation % explained			26.7%		

Table 4. GAM model construction for anchovy juveniles: analysis of deviance for GAM covariates and their interactions of the final models fitted.

Parameter	**Res. Df**	**Res. Deviance**	**Deviance explained %**	**AIC**	**P-value**
Spanish waters (mid November to mid December)					
Null model	4997.00	6792.89		6794.89	
s(Depth)	4988.59	6047.43	11.0%	6066.25	<<0.000
s(Depth)+s(CHLA)	4953.25	5769.90	14.6%	5805.40	<<0.000
s(Depth)+s(CHLA)+s(SLA)	4877.19	5183.99	22.3%	5235.62	<<0.000
s(Depth)+s(CHLA)+s(SLA)+s(SST)	4782.65	4939.21	24.5%	5007.92	<<0.000
s(Depth, SLA)+s(CHLA,SST)	4761.71	4708.38	28.1%	4818.97	<<0.000
Total variation % explained			28.1%		
Pooled Adriatic Sea, Gulf of Lions and N. Aegean Sea model (midJanuary-midFebruary)					
Null model	750.00	1041.09		1043.09	
s(SST)+factor(month)	745.80	766.98	26.3%	777.38	<<0.000
s(SST)+s(CHLA)+factor(month)	741.46	734.84	29.4%	753.93	<<0.000
s(SST)+s(CHLA)+s(DEPTH)+factor(month)	740.20	732.40	29.7%	754.00	<<0.000
s(Depth,SST)+s(CHLA)+factor(month)	721.28	672.05	35.5%	731.50	<<0.000
Total variation % explained			35.5%		

Table 5. GAM model construction for anchovy eggs: analysis of deviance for GAM covariates and their interactions of the final models fitted. The N. Aegean Sea model has been previously published in Schismenou *et al.,* 2008.

Parameter	Res. Df	Res. Deviance	Deviance explained %	AIC	P-value
N. Aegean Sea model (June)					
Null model	549.00	760.42			
s(Depth)	516.60	494.02	27.70%	504.81	<<0.000
s(SST)+s(Depth)	515.75	472.10	30.90%	484.61	<<0.000
s(SST)+s(Depth)+s(CHLA)	507.36	422.09	38.20%	451.38	<<0.000
s(Depth, CHLA)+s(SST)	510.03	420.34	41.90%	444.28	<<0.000
Total variation % explained			41.90%		
Sicily Channel (July)					
Null model	658.00	821.81		823.81	
s(Depth)	654.12	683.01	16.9%	692.76	<<0.000
s(Depth)+s(CHLA)	644.34	633.41	22.3%	646.74	<<0.000
s(Depth)+s(SST)+s(CHLA)	640.98	617.15	24.1%	631.19	<<0.000
s(Depth,SST)+s(CHLA)	632.83	611.85	24.8%	642.19	<<0.000
Total variation % explained			24.7%		

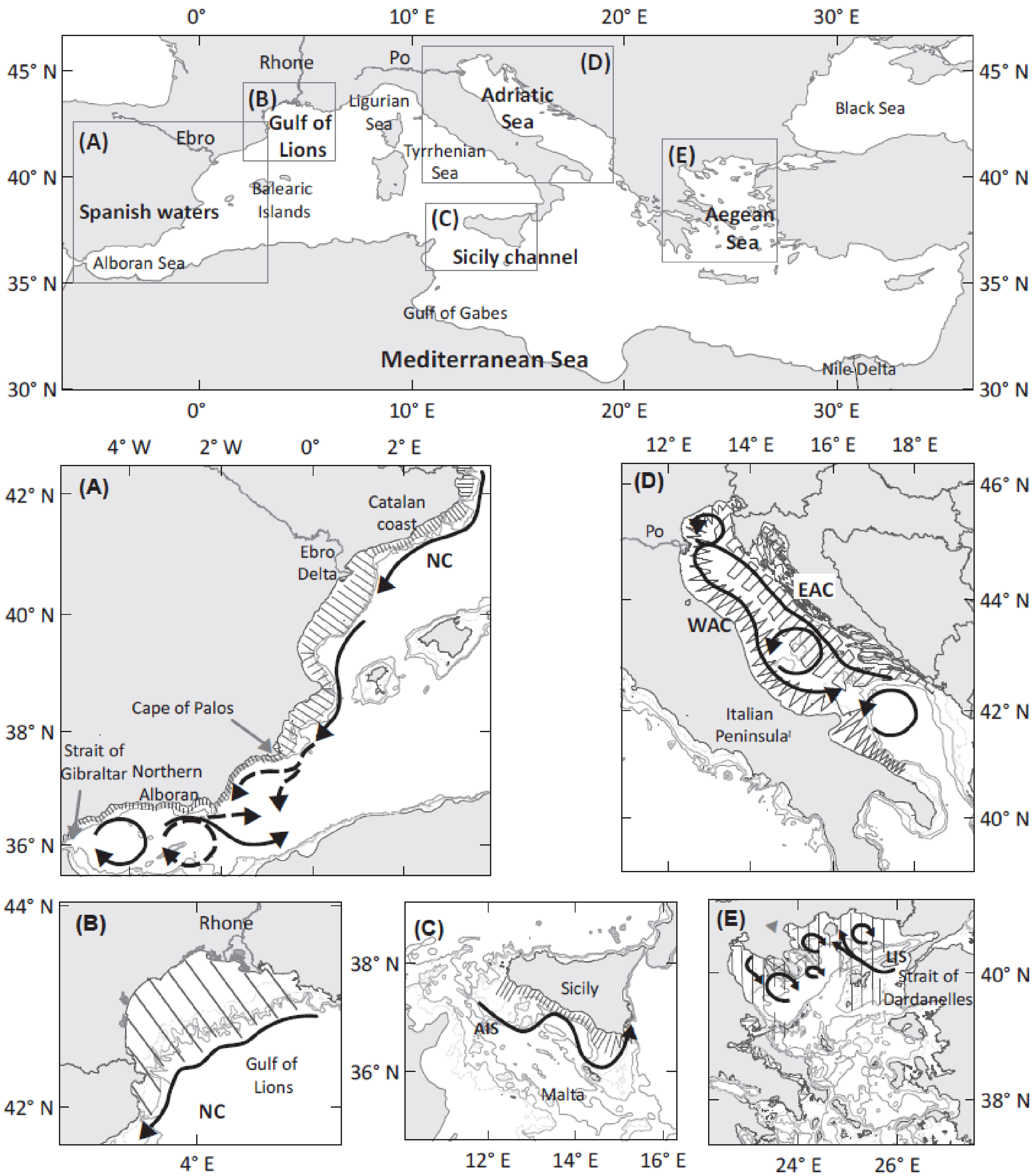

Fig. 1 Map of the study areas where also transects of acoustic sampling are shown. Water circulation is also shown. Arrows indicate the presence of fronts and gyres (redrawn from Millot, 1990; Somarakis *et al.*, 2002; Artegiani, 1997; Patti *et al.,* 2004). LIS: Limnos–Imvros Stream, NC; Northern Current, 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.

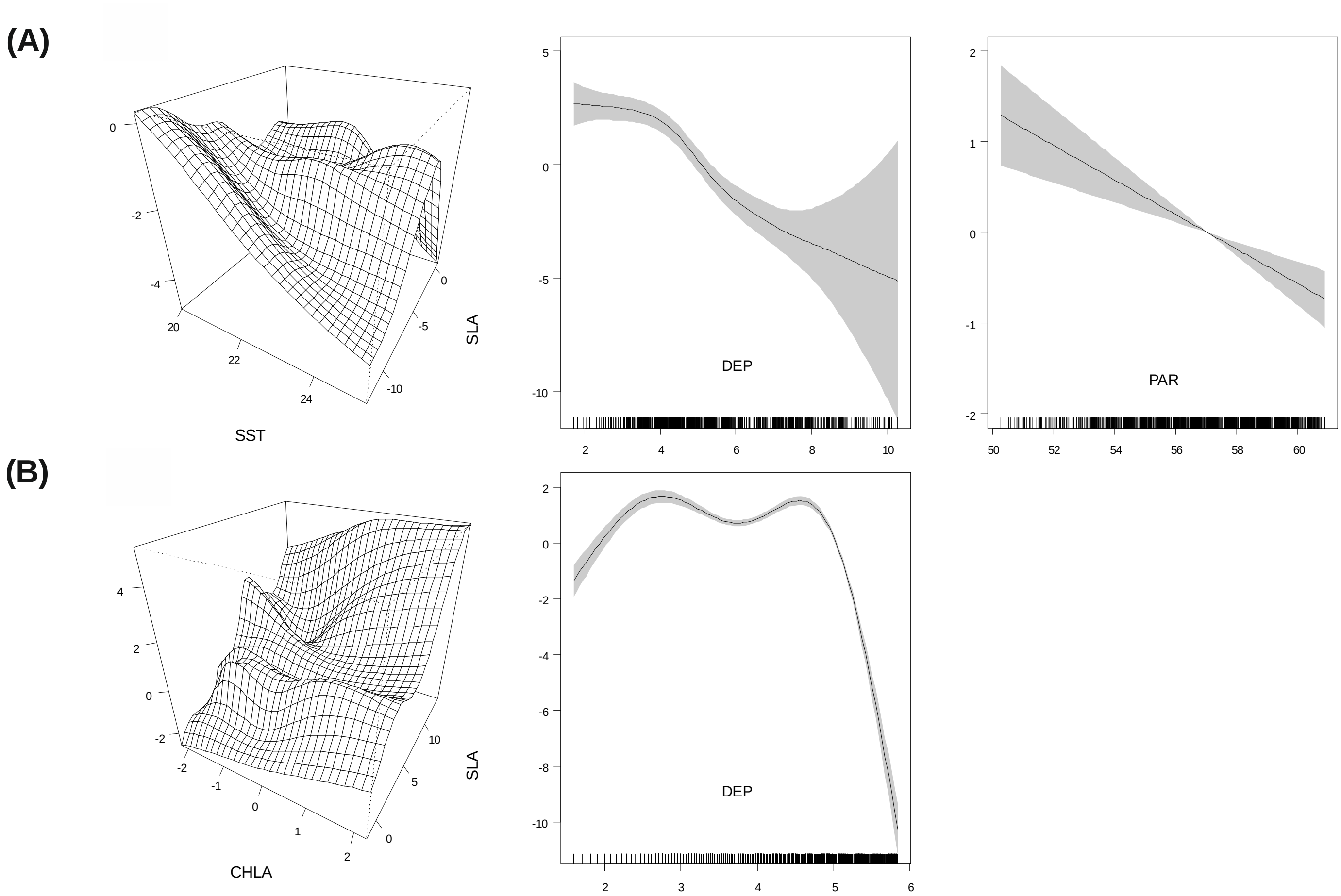

Fig. 2. Coefficients of the Generalized Additive Models (GAMs) concerning anchovy adults' (A) Summer model (B) Early autumn model. The interaction plots are also shown. Black thick lines indicate the value of GAMs coefficient, grey shadows represent the confidence intervals at $p = 0.05$.

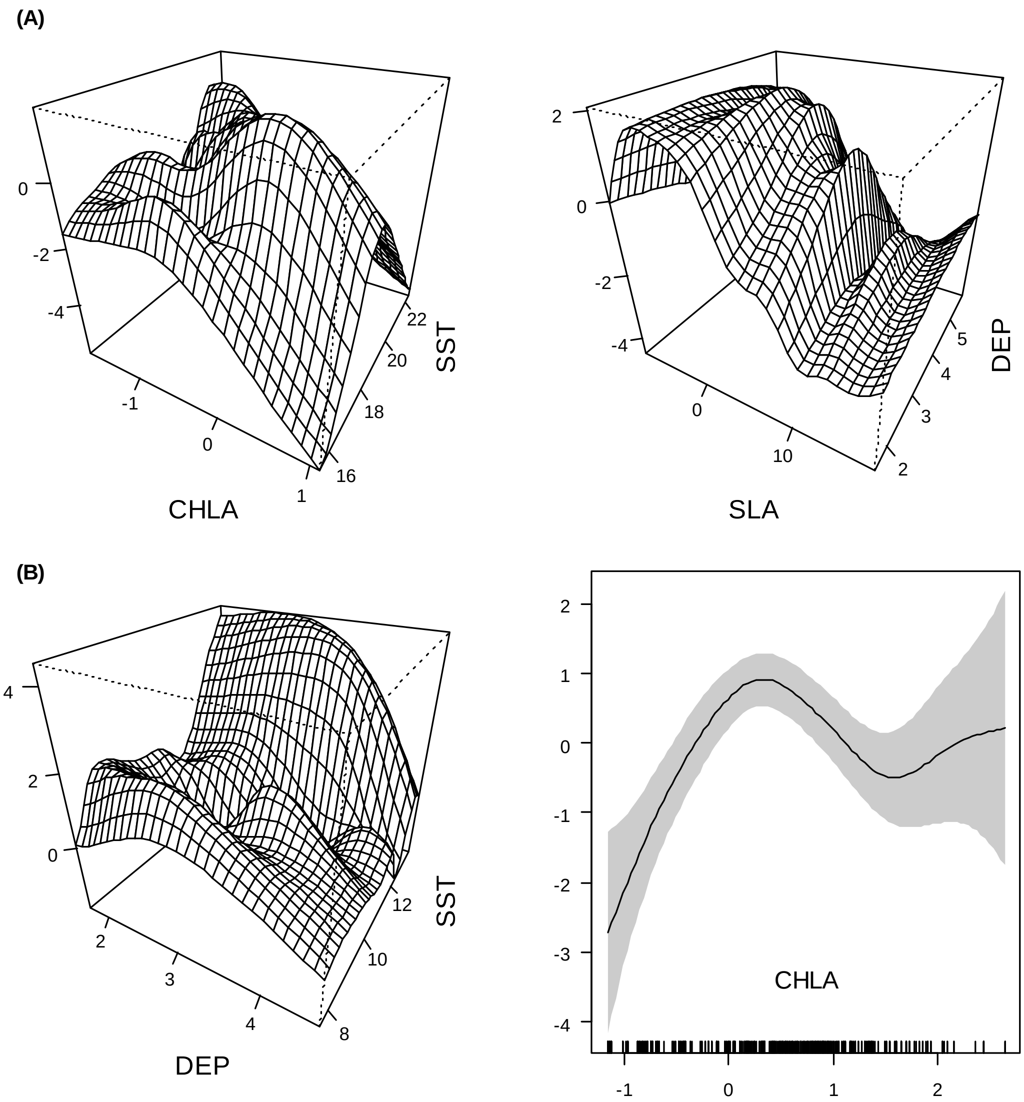

Fig. 3. Coefficients of the Generalized Additive Models (GAMs) concerning anchovy juveniles (A) Late autumn model (B) Winter model. The interaction plots are also shown. Black thick lines indicate the value of GAMs coefficient, grey shadows represent the confidence intervals at p = 0.05.

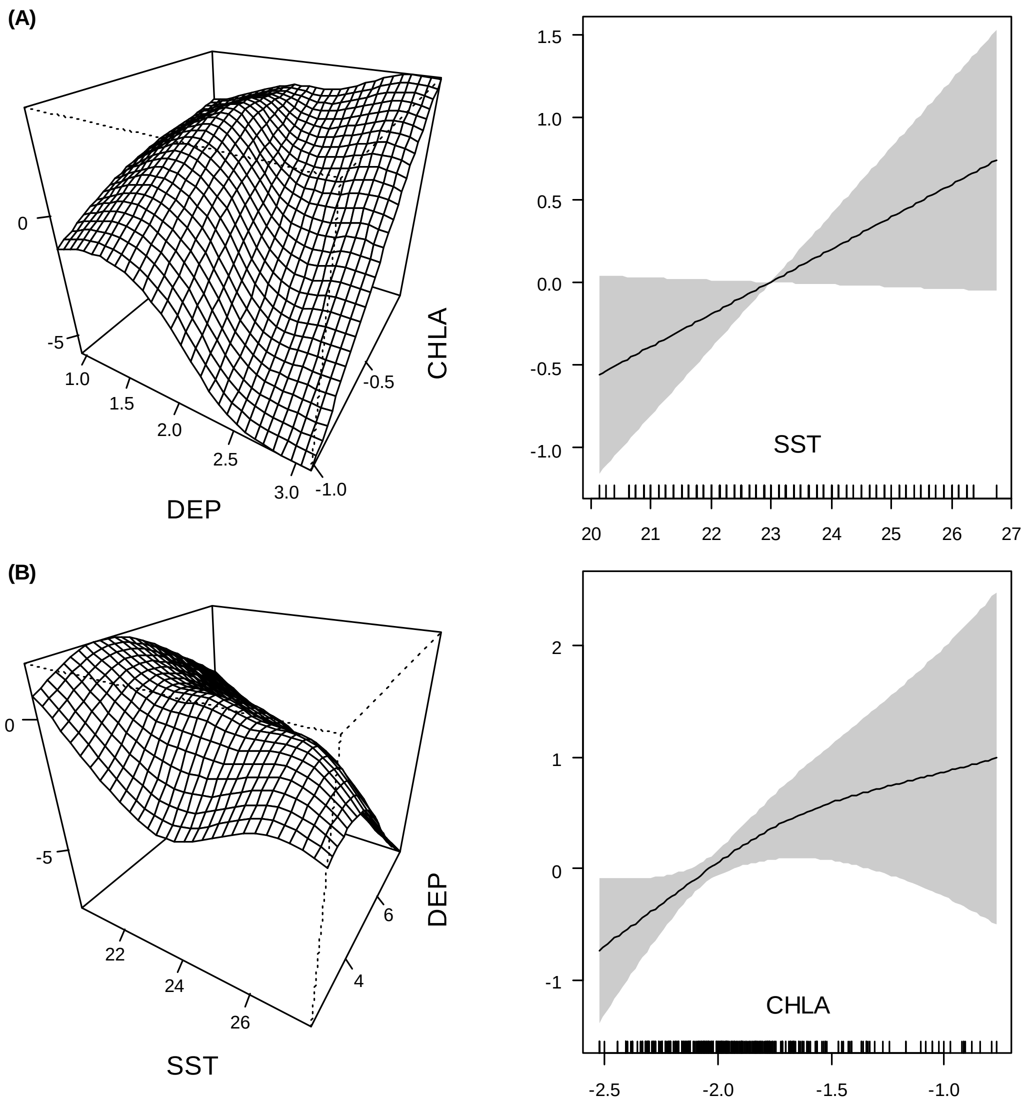

Fig. 4. Coefficients of the Generalized Additive Models (GAMs) concerning anchovy eggs (A) June model (B) July model. The interaction plots are also shown. Black thick lines indicate the value of GAMs coefficient, grey shadows represent the confidence intervals at p = 0.05.

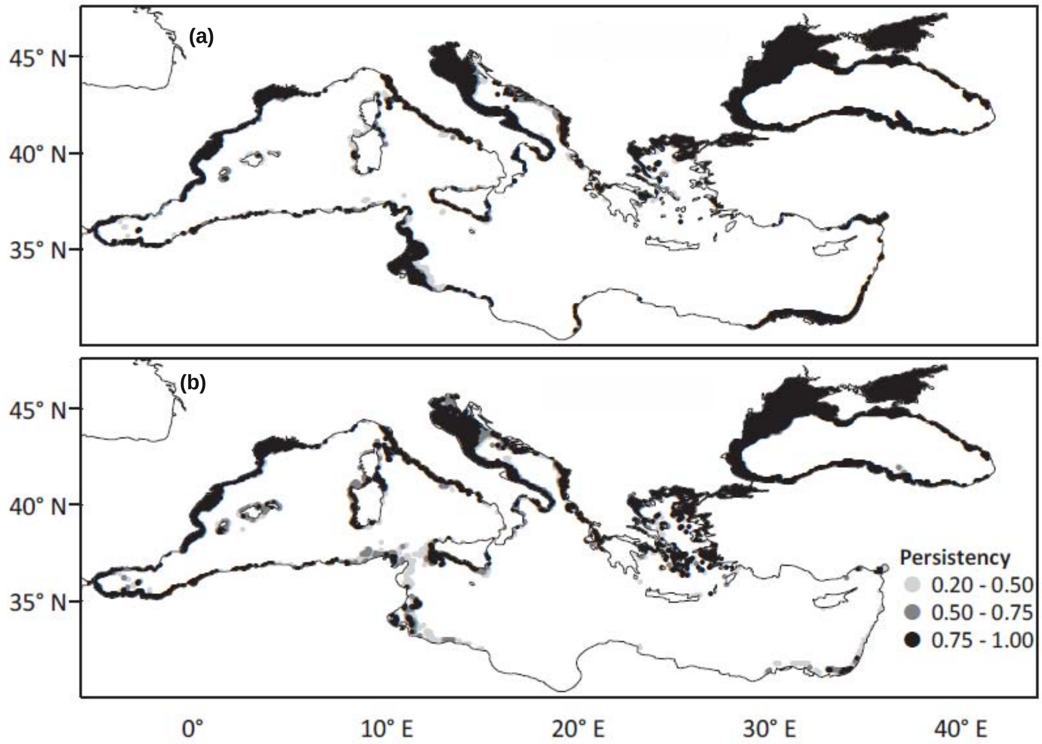

Fig 5. Potential spawning habitat persistency maps based on anchovy eggs data, in the Mediterranean Sea during (a) June and (b) July. Areas with low (PI: 0.20 to 0.50), medium (PI: 0.50 to 0.75) and high persistency (PI: >0.75) are shown in all cases.

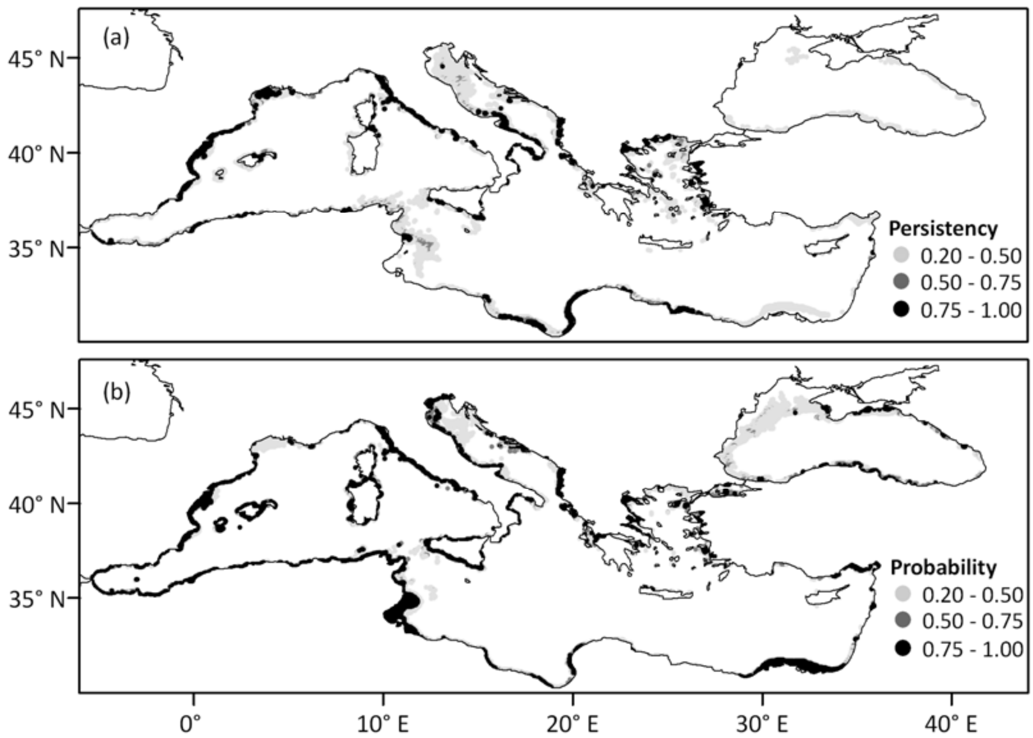

Fig 6. (a) Potential juveniles' habitat persistency maps for anchovy in the Mediterranean Sea during late autumn. Areas with low (PI: 0.20 to 0.50), medium (PI: 0.50 to 0.75) and high persistency (PI: >0.75) are shown in all cases.

(b) Habitat suitability maps indicating the probability of anchovy juveniles' presence in the Mediterranean Sea based on the estimated GAM model in winter (mid January-mid February 2009). Spatial resolution used for prediction was 4 km of mean monthly satellite values from the respective period. The scale indicates probability ranges.

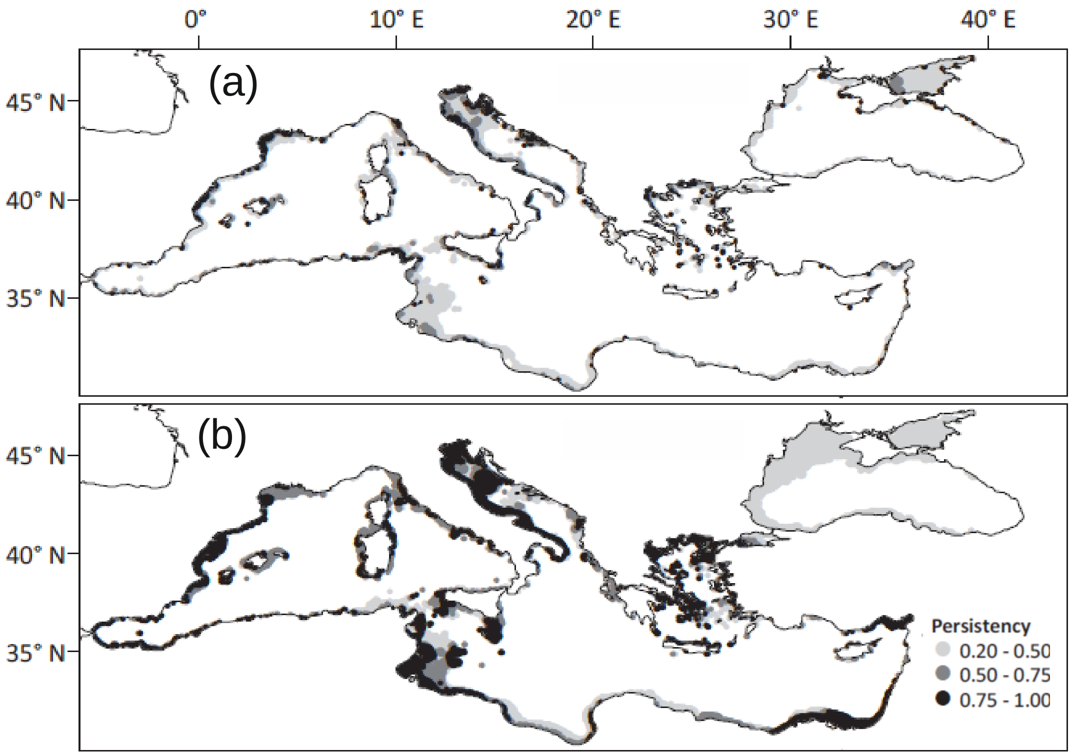

Fig 7. Potential habitat persistency maps for anchovy adults in the Mediterranean Sea during (a) summer (June) and (b) early autumn (September). Areas with low (PI: 0.20 to 0.50), medium (PI: 0.50 to 0.75) and high persistency (PI: >0.75) are shown in all cases.