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Characterizing the potential habitat of European anchovy *Engraulis encrasicolus* in the Mediterranean Sea, at different life stages

M. GIANNOULAKI[1,*], M. IGLESIAS[2], M. P. TUGORES[2], A. BONANNO[3], B. PATTI[3], A. DE FELICE[4], I. LEONORI[4], J. L. BIGOT[5], V. TIČINA[6], M. M. PYROUNAKI[1], K. TSAGARAKIS[1], A. MACHIAS[1], S. SOMARAKIS[1], E. SCHISMENOU[1], E. QUINCI[3], G. BASILONE[7], A. CUTTITTA[3], F. CAMPANELLA[4], J. MIQUEL[2], D. OÑATE[2], D. ROOS[5] AND V. VALAVANIS[1]

[1] *Hellenic Centre for Marine Research, Institute of Marine Biological Resources, PO Box 2214, GR 71003, Iraklion, Greece*

[2] *Instituto Español de Oceanografia, Centro Oceanográfico de Baleares, Muelle de Poniente s/n, 07015 Palma de Mallorca, Baleares, Spain*

[3] *Istituto per l'Ambiente Marino Costiero, Consiglio Nazionale delle Ricerche, Capo Granitola, 91021, Campobello di Mazara (TP), Italy*

[4] *Istituto di Scienze Marine, CNR, Largo Fiera della Pesca, 60125 Ancona, Italy*

[5] *IFREMER, Boulevard Jean Monnet, B.P. 171 34203, Sète Cedex, France*

[6] *Institute of Oceanography and Fisheries, Šet. I. Meštrovića 63 21000, Split, Croatia*

[7] *Istituto per l'Ambiente Marino Costiero, Consiglio Nazionale delle Ricerche, Mazara, 91026, Mazara del Vallo (TP), Italy*

ABSTRACT

Identification of the potential habitat of European anchovy (*Engraulis encrasicolus*) at different life stages in relation to environmental conditions is an interesting subject from both ecological and management points of view. For this purpose, acoustic data from different seasons and different parts of the Mediterranean Sea along with satellite environmental and bathymetry data were modelled using generalized additive models. Similarly, egg distribution data from summer ichthyoplankton surveys were used to model potential spawning habitat. Selected models were used to produce maps presenting the probability of anchovy presence (adults, juveniles and eggs) in the entire Mediterranean basin, as a measure of habitat adequacy. Bottom depth and sea surface chlorophyll concentration were the variables found important in all models. Potential anchovy habitats were located over the continental shelf for all life stages examined. An expansion of the potential habitat from the peak spawning (early summer) to the late spawning season (early autumn) was observed. However, the most suitable areas for the presence of anchovy spawners seem to maintain the same size between seasons. Potential juvenile habitats were associated with highly productive inshore waters, being less extended and closer to coast during winter than late autumn. Potential spawning habitat in June and July based on ichthyoplankton surveys overlapped but were wider in extent compared with adult potential habitat from acoustics in the same season. Similarities and dissimilarities between the anchovy habitats as well as comparisons with sardine habitats in the oligotrophic Mediterranean Sea and other ecosystems with higher productivity are discussed.

Key words: anchovy, anchovy potential nurseries, habitat suitability modelling, Mediterranean Sea, small pelagics

INTRODUCTION

Small pelagic fish 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 populations strongly dependent on the environment. European anchovy (*Engraulis encrasicolus*) along with European sardine (*Sardina pilchardus*) make up the bulk of small pelagic fish catches in the Mediterranean Sea (Lleonart and Maynou, 2003). The effects of

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[*] *Correspondence. e-mail: marianna@hcmr.gr*

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large-scale, environmentally driven changes in the distribution and abundance of small pelagic fish populations have been a major concern for fisheries scientists and managers during the last decades (Checkley *et al.*, 2009).

Anchovy in the Mediterranean is mainly fished by purse seiners, although midwater pelagic trawls also operate in the Adriatic Sea, the Strait of Sicily and the French coastal waters (Tičina *et al.*, 1999; Lleonart and Maynou, 2003; Basilone *et al.*, 2006). Both fishing techniques are based on the detection of major anchovy and/or sardine aggregations using acoustics. Anchovy stocks are highly variable in terms of their recruitment, abundance and distribution, whereas in many areas of the Mediterranean, the anchovy fishery suffers from a high degree of exploitation, with most stocks exhibiting declining trends in terms of abundance (Study Group on Mediterranean Fisheries, SGMED 2010). Thus, determining the relationship between species spatial distribution and environmental conditions can provide essential information to support the needs of effective management.

The Mediterranean Sea is highly heterogeneous in terms of hydrography, bathymetry and productivity. It contains different kinds of ecosystems, including areas with strong upwelling (e.g., the Alboran Sea and the Strait of Sicily), closed basins with shallow waters and high productivity (e.g., the Adriatic Sea), coastal areas influenced by the outflow from large rivers (e.g., the Northwestern Mediterranean), and less productive areas (e.g., the Aegean Sea), which receives waters originating from the Black Sea. This variety of ecosystems makes the Mediterranean Sea an appealing area for habitat modelling studies.

The increasing focus on climate change effects on fish and fisheries has inspired studies on habitat suitability modelling (e.g., Guisan and Zimmermann, 2000; 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, assessing the combination of these environmental conditions that are suitable for the survival of the species (Planque *et al.*, 2007; Zwolinski *et al.*, 2011) in the absence of explicit biotic interactions (such as competition or predation). Quantifying the distribution of a species along environmental gradients can provide habitat maps presenting geographic areas where environmental variables are considered suitable for the presence of a particular species.

The majority of published habitat modelling work concerning anchovy has either addressed non-Mediterranean areas (e.g., Bellier *et al.*, 2007; Planque *et al.*, 2007; Reiss *et al.*, 2008; Weber and McClatchie, 2010) or, within the Mediterranean, regional-scale studies focussing on a particular time of year or life stage (e.g., Basilone *et al.*, 2006; Bellido *et al.*, 2008; Giannoulaki *et al.*, 2008; Schismenou *et al.*, 2008). The present study takes advantage of acoustic and ichthyoplankton studies that have been carried out routinely in most European Mediterranean areas, mainly for the purposes of stock assessment, to map the habitat of anchovy at different stages and in different seasons.

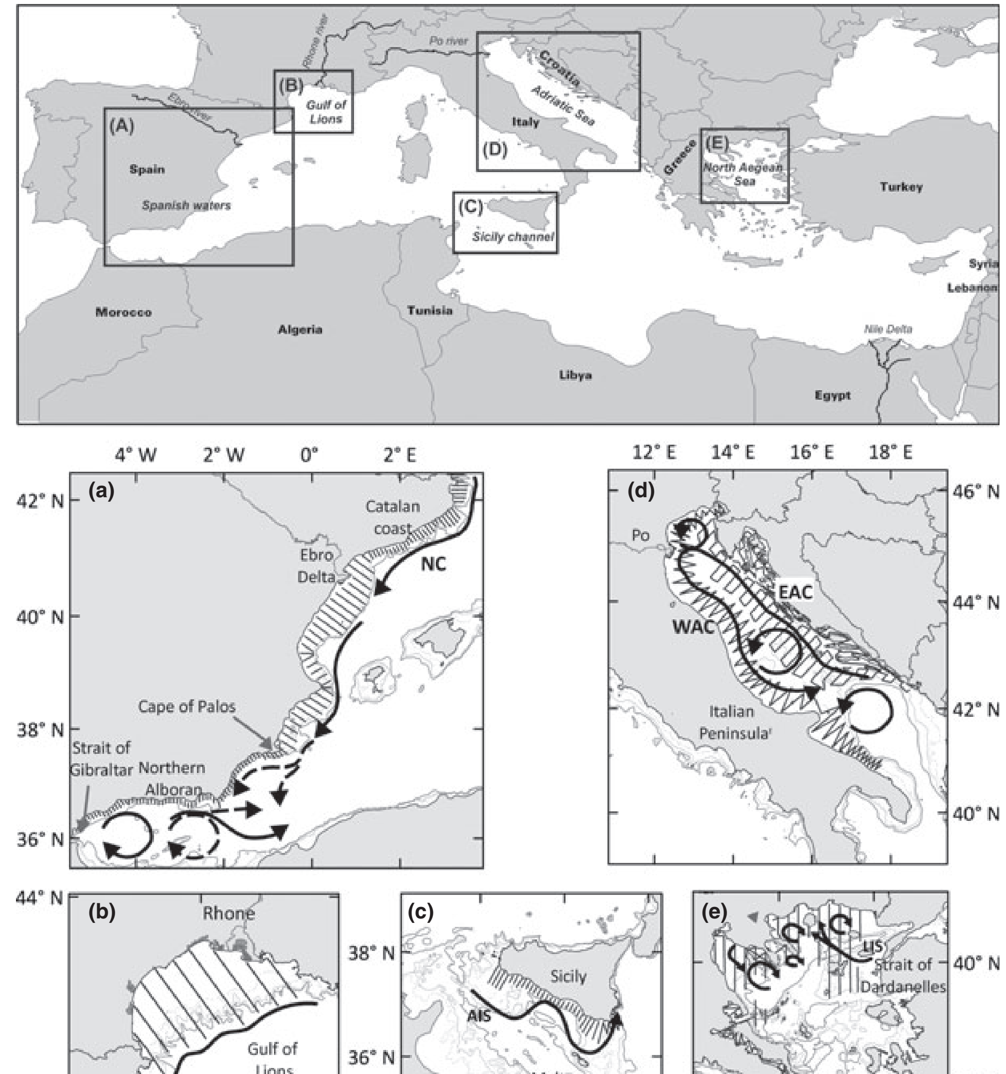
The spawning period of anchovy in the Mediterranean Sea lasts from spring to autumn with a peak in June/July (Somarakis *et al.*, 2004; Palomera *et al.*, 2007). Therefore, during early summer, anchovy stocks are dominated by spawning adults, whereas in late autumn/winter they encompass a large number of juvenile fish. In the present work, satellite environmental data were used because they allow predictions for different years and regions, operating as proxies or surrogates to causal factors (Giannoulaki *et al.*, 2011; Tugores *et al.*, 2011). The potential habitat of anchovy for the entire Mediterranean basin was assessed over survey seasons and years in order to evaluate those areas with persistently high probability of anchovy presence as well as the seasonal and annual variability of this probability. Results were evaluated in the framework of existing information from surveys and landings, as well as the hydrographic and productivity patterns of the study areas. Since the persistence of suitable characteristics in an area is a basic prerequisite for its selection as 'habitat', the interannual persistence of a high probability of anchovy presence was also examined (Colloca *et al.*, 2009). Finally, preferential and occasional anchovy habitat areas were defined based on probability, variability and persistence maps (Bellier *et al.*, 2007; Giannoulaki *et al.*, 2011) obtained for the examined periods.

Extended migrations between juvenile habitat and spawning grounds have been reported for anchovy in large upwelling ecosystems such as the Benguela and the California Current Systems (Checkley *et al.*, 2009). Therefore, to examine whether a similar pattern exists in the Mediterranean Sea and extent to which there are consistent locations for anchovy habitat all year-round, we examined the spatial overlap of potential adult and juvenile habitats within the studied period.

Study areas

In the Spanish Mediterranean waters (Fig. 1a), the continental shelf is generally narrow, being wider near the Ebro River. The circulation is dominated by the

Figure 1. Map of the study areas. Transects of acoustic sampling and major water circulation patterns are shown. Arrows indicate the presence of fronts and gyres (redrawn from Millot, 1990; Artegiani *et al.*, 1997; Patti *et al.*, 2005; Somarakis and Nikolioudakis, 2007). LIS, Limnos–Imvros Stream; NC, Northern Current; AIS, Atlantic Ionian Stream; WAC, West Adriatic Current; EAC, East Adriatic Current. Positions of the main rivers and bathymetry are indicated. Toponyms mentioned in the text are also shown. (A) Spanish Mediterranean waters (B) Gulf of Lions (C) Strait of Sicily (D) Adriatic Sea (E) North Aegean Sea.



inflow of less saline Atlantic waters through the Strait of Gibraltar, which generates upwelling and a local enrichment with nutrients and enhanced primary production in the Alboran Sea. The North Current (NC), a cyclonic along-slope front flowing southwards and the outflow of fresh water from large rivers, (i.e., the Rhone and the Ebro) characterize these north-western Mediterranean waters.

The Gulf of Lions (Fig. 1b) is one of the most productive zones in the western Mediterranean Sea owing to a number of hydrographic features, such as the existence of a wide continental shelf, river runoff and strong vertical mixing during winter. Occasionally, coastal upwelling is generated by local wind systems and complex orographic effects (Millot, 1990).

The Strait of Sicily connects the western and the eastern Mediterranean basins. It has a fairly narrow (15 nm) continental shelf in the middle of the southern coast but it widens in both its eastern and western parts (Fig. 1c). The surface circulation is largely determined by the Atlantic-Ionian Stream (AIS; Fig. 1c). The interannual variability of the AIS has a large impact on upwelling extent and the formation of frontal structures (Cuttitta *et al.*, 2003). The upwelling is further reinforced by wind-induced events (Patti *et al.*, 2010).

The Adriatic Sea is an elongated basin located in the Central Mediterranean (Fig. 1d). Its northern section is very shallow, gently sloping, with an average bottom depth of about 35 m and a large number of rivers discharging into it. The main fresh water input is due to the Po River in the north causing high nutrient concentrations along the coast. In contrast, the eastern coastal waters exhibit moderate production. The general circulation is cyclonic, with a northwest flow along the eastern coast (East Adriatic Current) and a return southeast flow (West Adriatic Current) along the western coast (Artegiani *et al.*, 1997).

The North Aegean Sea is characterized by high hydrological complexity mostly related to the Black Sea water (BSW) that enters the Aegean Sea through the Dardanelles strait (Fig. 1e). Most of the BSW moves to the northwest, forming the so-called the Limnos-Imvros stream (LIS) (Zervakis and Georgopoulos, 2002). The outflow of BSW enhances local productivity and its advection in the Aegean Sea induces high hydrological and biological complexity. This is further enhanced by the presence of a series of large rivers that flow out into semi-closed gulfs (Somarakis and Nikolioudakis, 2007).

MATERIALS AND METHODS

Acoustic sampling

Acoustic sampling was performed by means of scientific split-beam echosounders (Simrad EK500, Simrad EK60 and Biosonic DT-X depending on the area) working at 38 kHz and calibrated following standard techniques (Foote *et al.*, 1987). Acoustic data were recorded at a 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 1 nautical mile (nmi, 1.852 km). We considered as anchovy presence any school or echo assigned to anchovy either by echo trace classification or based on the catch composition of identification hauls (Simmonds and MacLennan, 2005). Midwater pelagic trawl sampling was carried out to identify and verify anchovy echo traces (see Table 1 for details). Acoustic data analysis was done using the MYRIAX ECHOVIEW software, except in the case of the Eastern Adriatic and the Gulf of Lions, where BI60 SIMRAD and MOVIES+ software were used, respectively. Further details on acoustic sampling per survey area are described below.

Reproductive period (June and September)

In the Northwestern Adriatic Sea, acoustic data were collected on board the R/V *Dallaporta* during September from 2004 to 2008. Acoustic sampling was carried out along predetermined zigzag transects from

Table 1. Summarized information on acoustic and ichthyoplankton surveys.

Life stage	Area	Month	Period	No. of transects	Avg. No. pelagic hauls	Avg. No. ichthyoplankton stations
Adults	North Aegean Sea	June	2004–2008	70	30	
	Strait of Sicily	June	2004–2008	40	18	
	Western Adriatic	September	2004–2008	50	40	
	Eastern Adriatic	September	2004–2008	30	28	
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
	Strait of Sicily	July	2003–2008			180

Avg. No. Pelagic Hauls, average number of pelagic haul per survey in an annual basis; Avg. No. Ichthyoplankton Stations, average number of ichthyoplankton stations per survey in an annual basis.

2004 to 2007 (Fig. 1d; Leonori *et al.*, 2007) and along predetermined parallel transects perpendicular to the coastline with 8–10 nm inter-transect distance in 2008.

In the Eastern Adriatic Sea, acoustic data were collected on board the R/V *BIOS* during September 2004–2008. Acoustic sampling was carried out along predetermined parallel transects with 10 nmi inter-transect distance (Fig. 1d). In the inner part (i.e., between the Croatian islands) transects were positioned in respect to the topographic features of these areas. Details of the sampling methodology and data collected are described elsewhere (Tičina *et al.*, 2006).

In the Strait of Sicily, acoustic data were collected on board the R/V *Dallaporta* during June 2003–2008. Sampling design consisted of parallel equidistant transects, perpendicular to the coastline with an inter-transect distance of 5–8 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 sampling was carried out along predetermined parallel transects with 10 nmi inter-transect distance in open areas and zigzag transects were used inside gulfs (Fig. 1e). Details of the surveys, sampling methodology and data collected are described elsewhere (Giannoulaki *et al.*, 2008).

Recruitment period

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 juveniles surveys held in the Gulf of Lions, the Adriatic Sea and the North Aegean Sea in 2007 and 2009. The Spanish surveys were carried out 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 identification hauls, held within the framework of the acoustic surveys (Table 1). The age structure of the catches verified that the majority of anchovy were age 0 (unpublished data of the Instituto Español de Oceanografía). Data from the acoustic surveys of targeted juveniles in the Adriatic Sea, the Gulf of Lions and the North Aegean Sea obtained from mid-November to mid-December 2007 were used for validation purposes of the late autumn model that was based on the Spanish data. Furthermore, acoustic data from targeted juvenile surveys in the Adriatic Sea, the Gulf of Lions and the North Aegean Sea obtained from mid-January 2009 to mid-February 2009 were also used to model the anchovy juveniles habitat during the winter period. During the targeted juvenile surveys, the minimum sampling depth was set at 10 m.

Echo discrimination of anchovy juveniles was based on the characteristic echogram shape of the schools and the catch composition of concurrent pelagic trawls (Table 1) (Simmonds and MacLennan, 2005). Anchovy smaller than 105 mm (Aegean Sea, Gulf of Lions and Adriatic Sea) were considered to be juveniles, based on the estimated approximate length at first maturity (Somarakis *et al.*, 2006; Morello and Arneri, 2009).

Egg sampling

Egg data were collected from Daily Egg Production Method (DEPM) surveys carried out in the North Aegean Sea in June 2003–2006 and 2008 (Somarakis *et al.*, 2012). A 10 × 5 nmi grid of stations was sampled by vertical plankton hauls (Table 1) using a WP2 sampler (mouth opening, 0.255 m^2; mesh size, 0.200 mm). More details are provided in Schismenou *et al.* (2008).

Similarly, egg data were collected in the Strait of Sicily during ichthyoplankton surveys carried out on board the R/V *Urania* in the Strait of Sicily in July 2003–2008. Plankton was sampled on the continental shelf of the southern Sicilian coast over a station grid of 4 × 4 nmi close to the coasts and 12 × 12 nmi in off-shore areas (Table 1). Bongo-net oblique hauls were carried out at each station using nets of 0.200 mm mesh size. Nets were towed from the bottom to the surface or from 100 m to the surface where depth was more than 100 m, with a speed of 2 nmi h^{-1} (Cuttitta *et al.*, 2003). Samples were preserved in 4% buffered formaldehyde solution for later analysis and enumeration of anchovy eggs in the laboratory.

Environmental data

Satellite environmental data as well as bottom depth 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 (summarized in Table 2). Specifically, sea surface temperature (SST in °C), sea surface chlorophyll concentration (CHLA in mg m^{-3}), photosynthetically active radiation [PAR in Einstein m^{-2} day^{-1}, 1

Table 2. Environmental satellite parameters and their characteristics.

Variable	Abbreviation	Sensor/model	Resolution	Source
Sea surface Chlorophyll-a	CHLA	MODISA	4 km	http://www.oceancolor.gsfc.nasa.gov
Sea surface Temperature	SST	AVHRR	1.5 km	http://www.eoweb.dlr.de:8080
Photosynthetically active radiation	PAR	SeaWiFS	9 km	http://www.oceancolor.gsfc.nasa.gov
Sea Level Anomaly	SLA	Merged Jason-1, Envisat, ERS-2, GFO, T/P	0.25° (interpolated to 1.5 km using ArcInfo topogrid)	http://www.jason.oceanobs.com

Einstein (Ein) = 1 mole of photons], and sea level anomaly (SLA in cm) were downloaded from respective databases (see Table 2) and used. These environmental variables are considered important either as a direct influence on the distribution of anchovy (e.g., SST, CHLA) or as proxies for causal factors. For example, SLA varies with ocean processes such as gyres, meanders and eddies (Pujol and Larnicol, 2005), which enhance productivity and often function as physical barriers affecting the distribution of species or their life stages. Similarly, satellite-measured SeaWiFS PAR is the photosynthetically active radiation (integrated over the spectral range 400–700 nm) reaching the sea surface over a 24-h period (Frouin *et al.*, 2003). It is indicative of the solar energy available for photosynthesis, controlling the growth of phytoplankton and thus critical also for fisheries and carbon dynamics. Bathymetry, as an indirect factor, was 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). Such topographic variables have the potential to summarize important surrogate predictor variables that are not captured by the available satellite variables. All monthly averaged satellite images from daily measurements were processed as regular grids in a GIS (geographic information system) environment using ARCINFO GRID software (ESRI, 1994). Satellite variables were mostly used at their best available resolution provided by the online satellite data distribution archives (Table 2) to obtain environmental characteristics for each sampling point. This results in an average spatial resolution of 1.5 km (Valavanis *et al.*, 2008), adequately defining environmental spatial heterogeneity in relation to both the applied EDSU (1.852 km) of acoustic data and the best available resolution of the explanatory environmental variables.

Data analysis

Generalized additive models (GAMs; Hastie and Tibshirani, 1990) were applied to define the set of environmental factors that describe anchovy distribution in the study areas. The selection of the GAM smoothing predictors was done using the MGCV library in the R statistical software (R Development Core Team, 2012). In each model fit, a double penalty was applied to the penalized regression solved by MGCV, which allows variables to be solved out of the model entirely (Marra and Wood, 2011), being more robust to identify important features. The degree of smoothing was chosen based on the observed data and the restricted maximum likelihood (REML) estimation that outperforms the generalized cross validation (GCV) smoothing parameter selection, as suggested by Marra and Wood (2011).

Autocorrelation was evident in the spatial structure of acoustic data in the study areas. Spatial autocorrelation is known to inflate the perceived ability of models to make realistic predictions favouring autocorrelated variables (Segurado *et al.*, 2006), although GAMs are not as much influenced by the effect of autocorrelation compared with other methodologies like GLMs (Segurado *et al.*, 2006). However, to avoid this effect, we adjusted to Type I error rate by setting the accepted significance level for each term at the more conservative value of 1%, rather than the usual 5% (Fortin and Dale, 2005).

For each case, a final model was built by testing all variables that were considered biologically meaningful, starting from a simple initial model with one explanatory variable. The best model was selected based on the minimization of the the Akaike's information criterion (AIC) and the level of deviance explained (0–100%; the higher the percentage, the more deviance explained), also taking into account the model's predictive ability. Specifically, as response variable (y), we used the presence/absence of anchovy echo or anchovy eggs. Only datasets presenting at least a percentage of 20% of anchovy presence were used for modelling to ensure the credibility of the selected model. As independent variables (x covariates), we used the cube 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), SST, SLA and PAR.

The binomial error distribution with the logit link function was used and the natural cubic spline smoother (Hastie and Tibshirani, 1990) was applied for smoothing the independent variables and GAM fitting. Following the selection of the main effects of the model, all first-order interactions of the main effects were tested. To avoid over-fitting and to simplify the interpretation of the results, the REML method was applied and the maximum degrees of freedom (measured as number of knots k) allowed to the smoothing functions were limited to the main effects at $k = 4$ and, for the first-order interaction effects, at $k = 20$.

Validation graphs (e.g., residuals versus fitted values, QQ-plots and residuals versus the original explanatory variables) were plotted to detect the existence of any pattern and possible model misspecification. Residuals were also checked for autocorrelation. The output of the final selected GAMs is presented as plots of the best-fitting smooths. Interaction effects are shown as a perspective plot without error bounds. In each case the following models were constructed.

Model selection for potential adult habitat in the spawning period

Two models were selected concerning anchovy adult habitat and validated based on acoustic data derived from: (i) the North Aegean Sea in summer (June 2004–2008), and (ii) the Adriatic Sea (both eastern and western parts) in early autumn (September 2004–2008). In the case of the North Aegean Sea, an already published model (Giannoulaki *et al.*, 2008) was re-evaluated based on additional years of data. 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.

Model selection for potential juvenile habitat

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

Model selection for potential spawning habitat

Two models were selected concerning the anchovy spawning habitat and validated using egg presence/absence data derived from the summer ichthyoplankton surveys in (i) the North Aegean Sea (June 2003–2008) and (ii) the Strait of Sicily (July 2003–2008). In the case of the North Aegean Sea, a published model was used (Schismenou *et al.*, 2008) and re-evaluated based on the REML method and the double penalized regression approach.

Model validation. In a subsequent step, each final model was tested and evaluated for its predictive performance for areas and periods not included in model selection. For this purpose, we estimated the receiver operating characteristic curve (ROC) and the area under the curve (AUC) metric (Guisan and Zimmermann, 2000). AUC is a threshold-independent metric, widely used in the species distribution modelling literature. Moreover, sensitivity (i.e., the proportion of observed positives that are correctly predicted) and specificity values (i.e., the proportion of observed negatives that are correctly predicted) were used for model evaluation (Lobo *et al.*, 2008). They were measured in relation to two threshold criteria: (i) the maximization of the specificity-sensitivity sum (MDT) and (ii) the prevalence values (Jiménez-Valverde *et al.*, 2008; Lobo *et al.*, 2008).

Areas and periods used for model validation concerning the potential habitat of adults were (i) the North Aegean Sea in June 2008, (ii) the Strait of Sicily in June 2003, 2005 and 2006, and (iii) the western Adriatic Sea for September 2006 and 2008. The GAM for the potential juvenile habitat in mid-November – mid-December was validated using data from the Gulf of Lions, the Adriatic Sea and the North Aegean Sea for the same period in 2007. The GAM for the potential juvenile habitat in mid-January to mid-February was validated using data from the same areas and period used for modelling due to the absence of any additional data. The GAMs for the potential spawning habitat were validated using data from (i) the North Aegean Sea in 2008 (not included in the published model) and (ii) the Strait of Sicily in July 2006. Mean monthly satellite values, estimated for each sampled coordinate, were used for this purpose. A specific probability of habitat adequacy for anchovy adults, juveniles and spawners was estimated for each sampled coordinate. All metrics estimation was performed using the 'Presence/Absence' library of R statistical language.

Mapping. Based on validation results, the selected single month models were applied in a predictive mode to provide probability estimates and habitat adequacy over a grid of mean monthly satellite values at a GIS resolution of 4 km, covering the entire Mediterranean basin (i.e., practically indicating areas where a specific set of values concerning satellite variables occur). Although the model was fitted and validated at a finer resolution (1.5 km) it was re-predicted and mapped at a coarser grid (about 2.5 times coarser). The error was considered minimum since the available satellite data were derived from a single optimum resolution (see Table 2) that minimizes the interpolation error and provides similar values for the variables at any point in space for the two grids. This was considered a reasonable trade-off between the patterns identified by the model and the required computer power to map the resultant probabilities at the scale of the Mediterranean Sea.

Subsequently, annual habitat suitability maps were constructed. GIS techniques were used to estimate the mean of these annual maps, summarising the mean average probability estimates at each grid point. Similarly, the variability map, representing the inter-annual variability in potential adult and juvenile habitats and spawning grounds, was also produced by estimating the standard deviation of the annual maps. Additionally, maps indicating areas that persistently exhibited adult, juvenile and spawning preference within the study period (i.e., with >50% probability of presence) were drawn. For this purpose, for each grid cell (i.e., 4 × 4 km based on the satellite data grid) in the entire Mediterranean Sea, we calculated an Index of Persistence (I_i), measuring the relative persistence of the cell i as an annual anchovy habitat (Colloca *et al.*, 2009). Let $\delta_{ik} = 1$ if the grid cell i is included in anchovy habitat in year k, and $\delta_{ik} = 0$ if the grid cell is not included. We computed I_i as follows:

$$I_i = \frac{1}{n}\sum_{k=1}^{n}\delta_{ik} \qquad (1)$$

where n is the number of years considered. I_i ranges between 0 (cell i never included in an annual anchovy potential habitat) and 1 (cell i always included in an annual anchovy potential habitat) for each cell in the study area.

Subsequently, preferential and occasional adult, juvenile and spawning grounds were defined based on average probability, variability and persistence maps (Bellier *et al.*, 2007). Based on Bellier *et al.* (2007) a habitat allocation map was created indicating: (i) recurrent adult, juvenile and spawning sites: areas with high mean probability, low standard deviation values and high persistence index, (ii) occasional adult, juvenile and spawning sites – areas with high mean probability and high standard deviation values (i.e., where anchovy or anchovy eggs are present indicating high probability in some years but not in others) and (c) rare adult, juvenile and spawning sites – areas with low mean and low standard deviation values (anchovy or anchovy eggs are rarely present in these areas). SURFER v8.0 of Golden Software Inc. software (Golden, CO, USA) was used for mapping.

Spatial overlapping between adult and juvenile potential habitat. In the current work available data allowed us to study both the juvenile and spawning grounds of anchovy. As previously stated anchovy spawning in the Mediterranean Sea occurs from late April till late September. Thus going a step further, we examined the spatial overlap between the potential juvenile (late autumn) and spawning adult habitat (early summer) trying to define to what extent there are consistent locations that serve both as juveniles and spawning habitat in the Mediterranean basin. ArcGIS tools were used to examine the spatial overlap between early summer (adult spawning grounds) to late autumn (juvenile grounds) of the same year as well as from late autumn (juvenile grounds) to early summer (adult spawning grounds) of the next year for the entire Mediterranean Sea and areas with a) >50 and >75% probabilities of anchovy presence.

RESULTS

Habitat modelling

Anchovy adults in the spawning period (early summer and early autumn). For early summer, the model included as main effects: Depth (cube root transformed), PAR and the interactive effect of SLA with SST (Table 3). Depth was the variable that initially entered the model explaining most of the total variation. The results of this model indicated a higher probability of finding anchovy present in waters <100 m and PAR values <57 Ein m^{-2} day^{-1}. The interaction plot between SLA and SST indicated higher probability of finding anchovy present at SST<22°C (Fig. 2a) when combined with −12 to −6 cm SLA (i.e., implying lifting of isopycnals and the presence of mesoscale cyclonic eddies or upwelling conditions) and at SST 24–25°C when combined with −6 to −2 cm SLA. Within the present work, this model was validated with presence/absence data derived from the acoustic surveys held in the North Aegean Sea in 2008 and in the Strait of Sicily in 2003, 2005 and 2006. Results indicated moderate model performance (Table 4).

The early autumn selected GAM (Table 3) included as main effects: Depth (cube-root transformed) and the interactive effect of SLA with CHLA (log-transformed). Depth was the variable explaining most

Table 3. GAM model selection for anchovy adults, juveniles and eggs: analysis of deviance for GAM covariates and their interactions of the final fitted models.

	Period	Model	Res. Df	Res. deviance	Deviance explained %	AIC	REML	P-value
Adults	Early summer	N. Aegean Sea model						
		s(SST, SLA) + s(PAR) + s(Depth)	2061.1	1459.7	34.8	1501.6	768	≪0.000
	Early autumn	Adriatic Sea model						
		s(Depth) + s(SLA, CHLA)	9408.7	9401.6	26.1	9462.1	4226	≪0.000
Juveniles	Late autumn	Spanish Mediterranean						
		s(Depth, SLA) + s(CHLA, SST)	4764.9	4715.3	28.0	4819.4	2474	≪0.000
	Winter	Pooled Adriatic Sea, Gulf of Lions and N. Aegean Sea model						
		s(Depth, SST) + s(CHLA) + factor(month)	736.2	718.9	30.9	748.5	381	≪0.000
Eggs	June	N. Aegean Sea model						
		s(Depth, CHLA) + s(SST)	509.0	418.1	42.2	444.1	228	≪0.000
	July	Strait of Sicily						
		s(Depth, SST) + s(CHLA)	634.2	615.5	24.3	643.1	329	≪0.000

The North Aegean Sea models for adults and eggs have been published in Giannoulaki *et al.* (2008) and Schismenou *et al.* (2008), respectively.

of the total variation. Model results indicated higher probability of finding anchovy in waters <180 m depth and at SLA of 5–12 cm (i.e., implying preference for anticyclonic mesoscale eddies or downwelling conditions) when co-existing with CHLA of 0.5–7.4 mg m^{-3} (Fig. 2b). In addition to the areas and periods that were included in model estimation, the model was validated with data derived from acoustic surveys held in the western Adriatic during September 2006 and 2008. Results indicated moderate model performance (Table 4).

The average probability, persistence and habitat allocation maps for the Mediterranean Sea within the study periods identified specific locations that were quite persistent as adult habitat during early summer (Fig. 3) and early autumn (Fig. 4). These areas included the gulfs and coastal areas of the North Aegean Sea. Similarly, in the Adriatic Sea, 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. In the Western Mediterranean potential habitat areas were mainly identified in the coastal waters, being wider in extent in the proximity of the Rhone and the Ebro Rivers as well as in the Balearic Islands plateau. The coastal waters of the northern part of the Strait of Sicily generally contain occasional habitat for adult anchovy, whereas the persistent areas are in the plateau between Sicily and Malta.

Anchovy juveniles (late autumn and winter). In late autumn, the selected GAM included as main effects: Depth (cube root transformed) and the interactive effect of SLA with CHLA (log-transformed). Depth was the variable explaining most of the total variation (Table 3). Model results indicated higher probability of finding anchovy present in waters <150 m combined with SLA of −5 to 5 cm, SST of 17–19°C and CHLA values of 0.36–2 mg m^{-3} (Fig. 5a). In addition to data from Spanish Mediterranean waters that were included in the model estimation, the model was also validated with presence/absence data from juvenile surveys in the North Aegean Sea, the Adriatic Sea and the Gulf of Lions held in the mid-November to mid-December 2007. Results indicated moderate to high model performance (Table 4).

For winter, the selected GAM included the effect of CHLA (log-transformed) as well as the interactive effect of the SST with Depth (cube root transformed). SST was the variable that explained most of the total variation (Table 3). Model results indicated higher probability of finding anchovy in waters of 15 m to 60 m depth combined with SST of 8–10, 12–14°C and at CHLA of 0.9–5.4 mg m^{-3} (Fig. 5b). Due to the lack of adequate numbers of data, the model was validated only for those areas and periods that were included in the model estimation. Validation results indicated good model performance (Table 4). The average, persistence and habitat allocation maps for the Mediterranean Sea within the study period for late autumn,

Figure 2. Coefficients of the generalized additive models (GAMs) for anchovy adults in (a) early summer (June), (b) early autumn (September). CHLA, log-transformed surface chlorophyll concentration (in mg m^{-3}); SST, sea surface temperature (°C); SLA, sea level anomaly (in cm); Depth, cube root-transformed bottom depth (in m); PAR, photosynthetically active radiation (in Einsteins m^{-2} day^{-1}). The interaction plots are also shown. Black thick lines indicate the value of GAMs coefficient. Shadowed areas represent the confidence intervals at P = 0.01. The rug under the single variable effects plots indicates the density of points for different variable values.

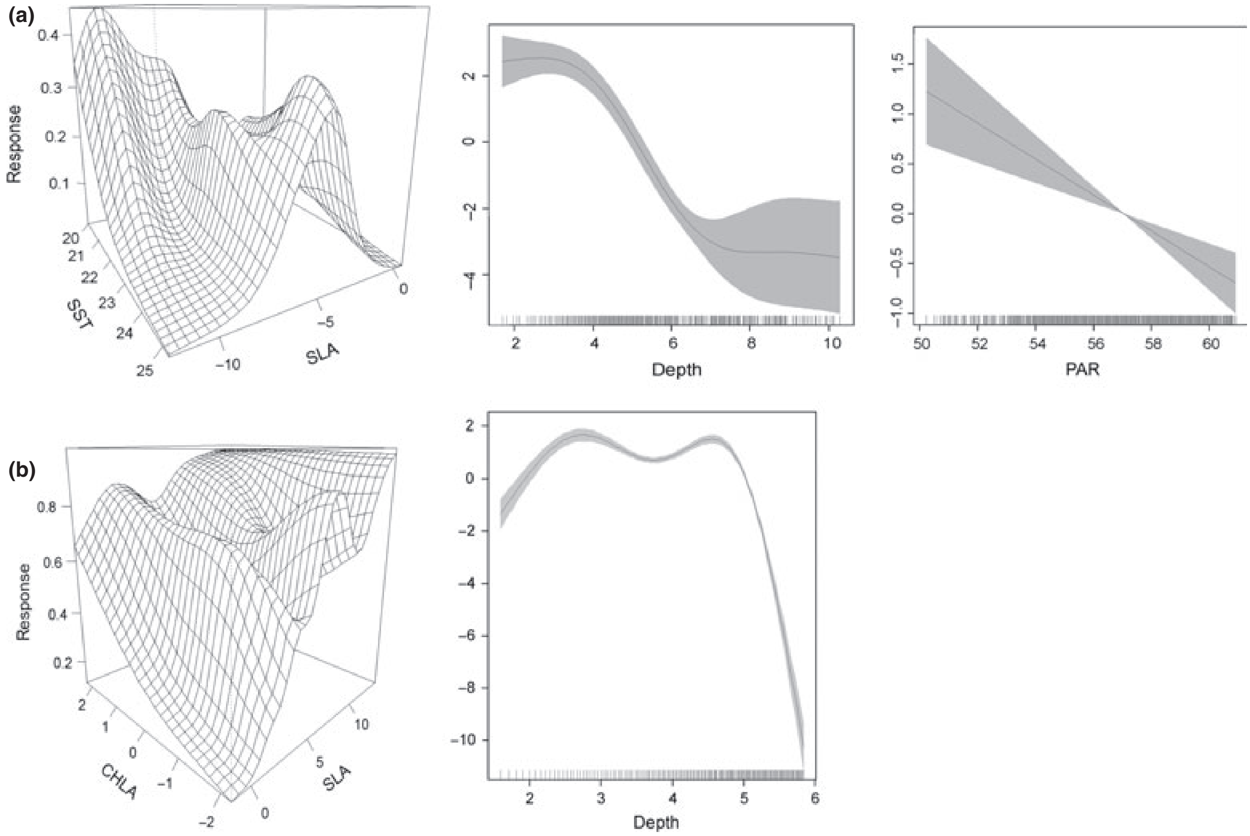


Table 4. Mean values of sensitivity and specificity accuracy measures ± standard error (SE) for two threshold criteria: MDT (maximize the specificity–sensitivity sum) and prevalence values.

	Model	AUC	MDT sensitivity	MDT specificity	Prevalence sensitivity	Prevalence specificity
Adults	Early summer	0.71 ± 0.02	0.82 ± 0.09	0.51 ± 0.09	0.50 ± 0.13	0.74 ± 0.13
	Early autumn	0.68 ± 0.05	0.39 ± 0.40	0.79 ± 0.14	0.76 ± 0.01	0.30 ± 0.16
Juveniles	Late autumn	0.80 ± 0.14	0.79 ± 0.07	0.79 ± 0.12	0.77 ± 0.14	0.81 ± 0.10
	Winter	0.72 ± 0.04	0.64 ± 0.19	0.68 ± 0.19	0.72 ± 0.08	0.50 ± 0.03
Eggs	June	0.79	0.54	0.89	0.77	0.64
	July	0.77	0.84	0.62	0.80	0.66

The estimated area under the ROC curve (AUC) for each model is also indicated. In the case of egg models, only one area and 1 year not included in model selection was used for validation.

as well as the annual habitat suitability maps for anchovy juveniles in late autumn and winter 2009, are shown in Figure 6.

Areas with high probability as anchovy nurseries were similar in both seasons, differing mostly in areal extent. In the Western Mediterranean, potential nursery areas were identified to be in association with the outflow of the Rhone river in the Gulf of Lions and the Ebro river south in the Spanish waters. In the Adriatic Sea, potential nurseries were located in the inner part of the continental shelf in the coastal part of the basin. They were closely associated with the Po

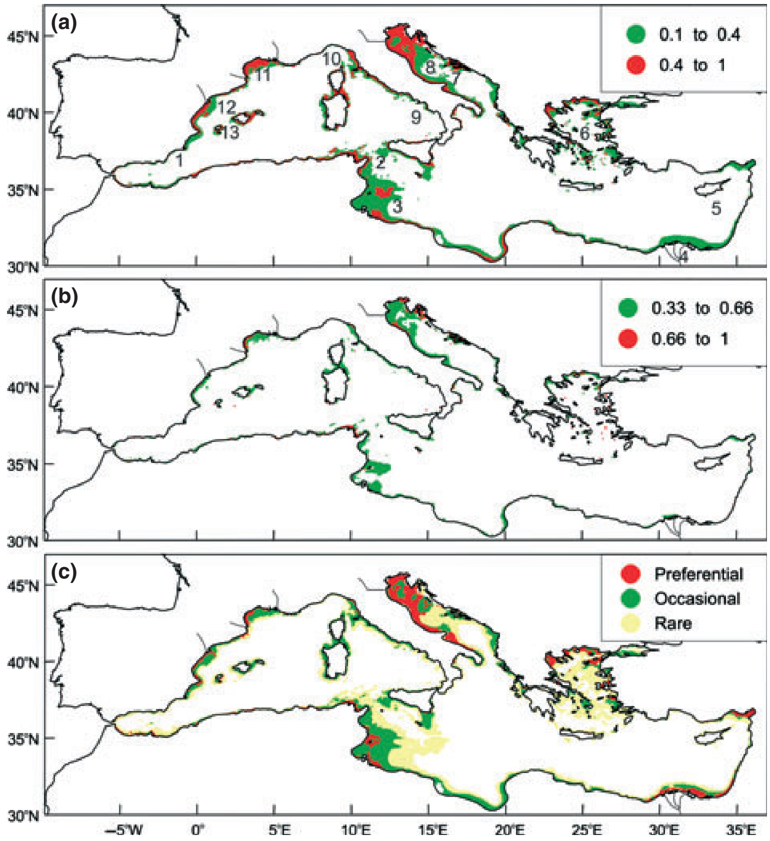


Figure 3. Early summer: habitat suitability maps for adult anchovy in the Mediterranean Sea for the period 2003–2008. (a) Mean probability map. (b) Persistence map. (c) Habitat allocation map. Numbers indicate toponyms mentioned in the text. 1 – Alboran Sea, 2 – Sicily Strait, 3 – Gabes Gulf, 4 – Nile Delta, 5 – Levantine basin, 6 – Aegean Sea, 7 – Dalmatian islands, 8 – Adriatic Sea, 9 – Tyrrhenian Sea, 10 – Ligurian Sea, 11 – Gulf of Lions, 12 – Catalan Sea, 13 – Baleares Islands.

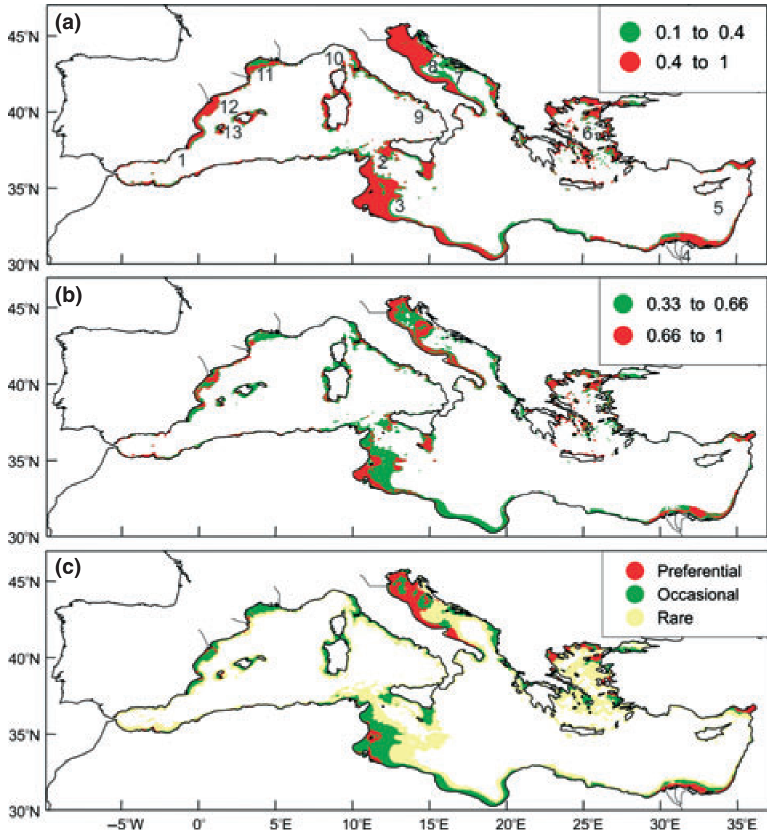


Figure 4. Early autumn: habitat suitability maps for adult anchovy in the Mediterranean Sea for the period 2003–2008. (a) Mean probability map. (b) Persistence map. (c) Habitat allocation map. Numbers indicate toponyms mentioned in the text. Locations as in Fig. 3.

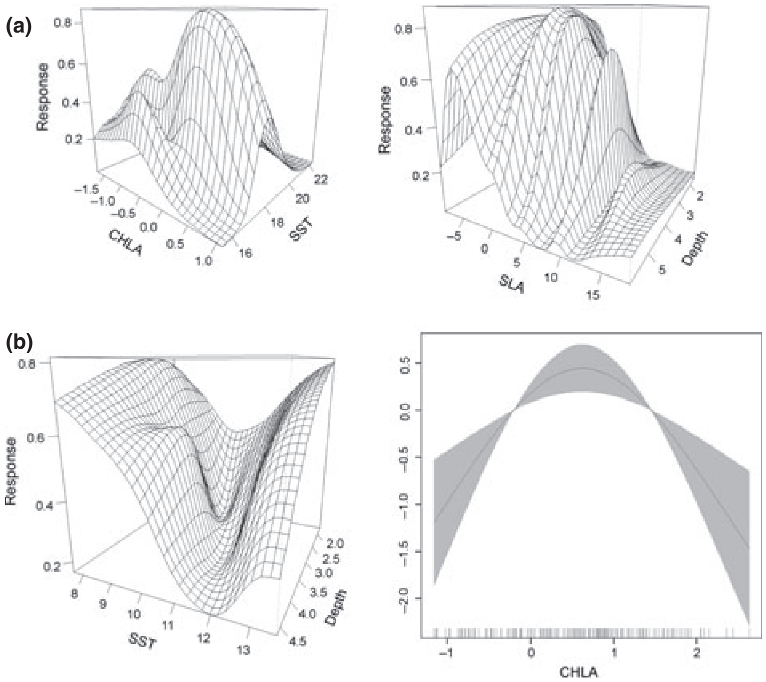


Figure 5. Coefficients of the generalized additive models (GAMs) for anchovy juveniles in (a) late autumn (mid-November–mid-December), (b) winter (mid-January–mid-February). Variables as in Fig. 2. The interaction plots are also shown. Black thick lines indicate the value of GAMs coefficient. Shadowed areas represent the confidence intervals at P = 0.01. The rug under the single variable effects plots indicates the density of points for different variable values.

river outflow, also extending south along the coasts of the western and the eastern part of the Adriatic Sea. Suitable areas in the Strait of Sicily were also located in coastal waters being wider in the north and south part where the continental shelf is wider.

Anchovy eggs (June and July). The GAM for anchovy eggs in June was based on a previously published model for the North Aegean Sea estimated for June 2004–2006 (Schismenou *et al.*, 2008) but smoothing was adjusted for consistency with the other models. This model included as main effects: SST and the interactive effect of Depth (cube root transformed) with CHLA (log-transformed) (Table 3). Model results indicated a higher probability of finding eggs with increasing SST. The interaction plot of Depth and CHLA indicated increasing probability of spawning with increasing values of CHLA in the 40–150 m bathymetric range (Fig. 7a). Additionally to the areas included in model estimation, the model was also validated in the current paper with presence/absence data derived from the Aegean DEPM survey in June 2008 (Somarakis *et al.*, 2012). Validation results indicated good model performance (Table 4).

The GAM for anchovy eggs in July included as main effects Depth (cube-root transformed), CHLA (log-transformed) and SST. Depth was the variable that explained most of the total variation (Table 3). Model results indicated higher probability of anchovy spawning with increasing values of CHLA, at waters of 40–160 m depth but at lower values of SST (Fig. 7b). Additionally to surveys used for modelling, the model was also validated with presence/absence data derived from an ichthyoplankton survey held in the Strait of Sicily in July 2006. Validation results indicated good model performance (Table 4).

Persistence and habitat allocation maps of anchovy spawning habitat showed similar favourable areas in both June and July (Figs 8 and 9). In the Aegean Sea, besides the northern part and the coastal areas within gulfs that are known spawning grounds for anchovy (Somarakis *et al.*, 2006), spots with high probability of anchovy eggs were also identified in the coastal areas of the Turkish part of Aegean Sea (e.g., Izmir Bay) where information is largely missing. Nevertheless, these areas are reported as anchovy fishing areas (Turan *et al.*, 2004). In the Adriatic Sea areas with higher probability of anchovy spawning were consistently found in the northern and the western part of the basin as well as around the coastal waters of the mid-Dalmatian islands in the eastern part (Figs 8 and 9).

Spatial overlapping between adult and juvenile potential habitat

Habitat suitability maps indicated that a certain number of grid cells spatially overlapped between the potential adult and juvenile habitat. The percentage of grid cells with more than 50% probability of anchovy presence that spatially overlapped among early summer (adult habitat) and late autumn (juvenile

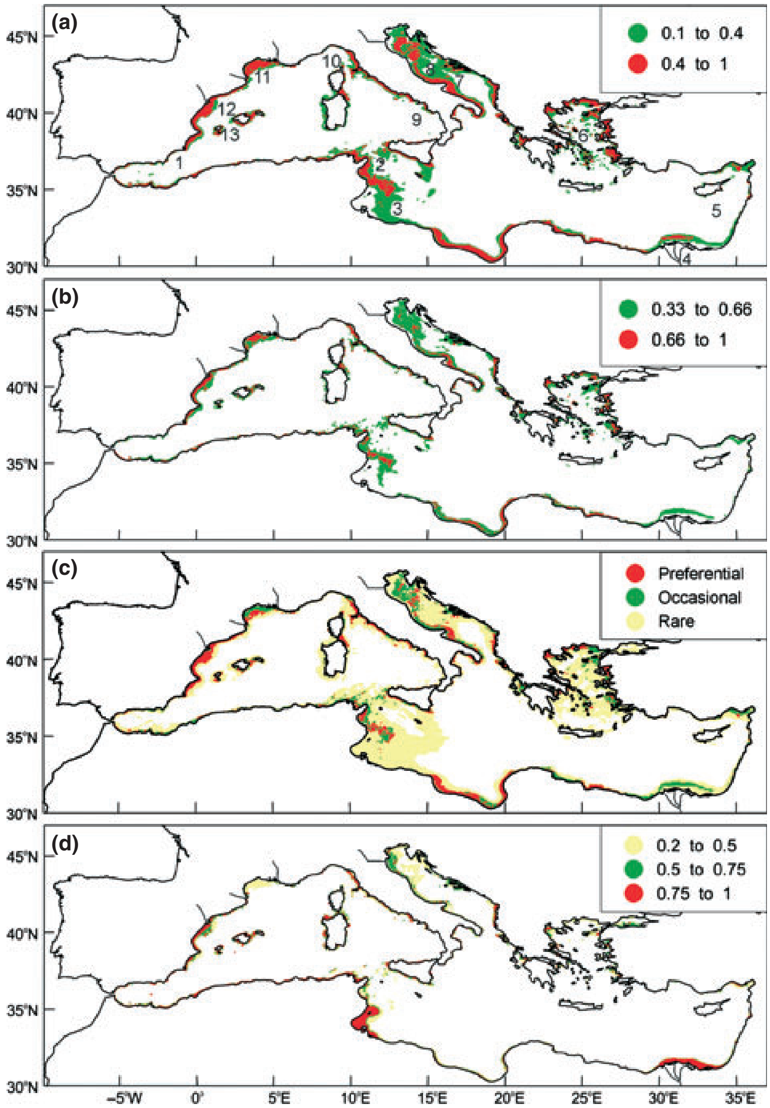


Figure 6. Habitat suitability maps for juvenile anchovy in the Mediterranean Sea. (a) Mean probability map during late autumn for 2003–2008. (b) Persistence map during late autumn, 2003–2008. (c) Habitat allocation map for late autumn, 2003–2008. (d) Annual probability map in winter 2009. Numbers indicate toponyms mentioned in the text. Locations as in Figure 3.

habitat) of the same year was 21% (~28 000 km^2, Table 5). Similarly, 20% (~30 500 km^2, Table 5) overlap was estimated among late autumn and early summer of the following year.

The percentage of the grid cells that corresponded to hot spot areas (i.e., more than 75% probability of anchovy presence) and showed spatial overlap between early summer (adult habitat) and late autumn (juvenile habitat) of the same year was only 2.7% (~1267 km^2). 2.5% (~2028 km^2) overlap was estimated between late autumn and early summer of the following year (Table 5).

DISCUSSION

The objective of the present work was to estimate the potential habitat of European anchovy in the Mediterranean Sea during different life stages and different periods within the year. Our aim was to improve our knowledge on the spatial distribution of anchovy resources in the Mediterranean Sea. Acoustic and ichthyoplankton data from the Western, Central and Eastern part of the Mediterranean collected in different seasons (i.e., early summer, early autumn, late autumn and winter) within the year were used for the first time in an integrated way to serve this purpose.

Potential adult habitat

Bottom depth and SLA were the variables that were found important in both early summer and early autumn models implying that bathymetry and currents are the primary abiotic factors controlling anchovy adult habitat, practically operating as proxies for the presence of favourable conditions related to food

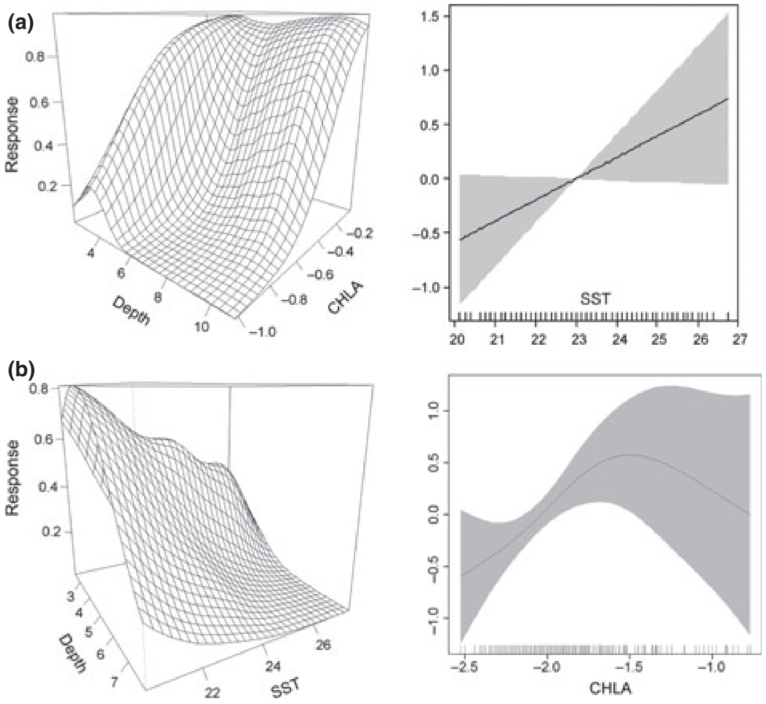


Figure 7. Coefficients of the generalized additive models (GAMs) for anchovy eggs in (a) June and (b) July. Variables as in Figure 2. The interaction plots are also shown. Black thick lines indicate the value of GAMs coefficient. Shadowed areas represent the confidence intervals at P = 0.01. The rug under the single variable effects plots indicates the density of points for different variable values.

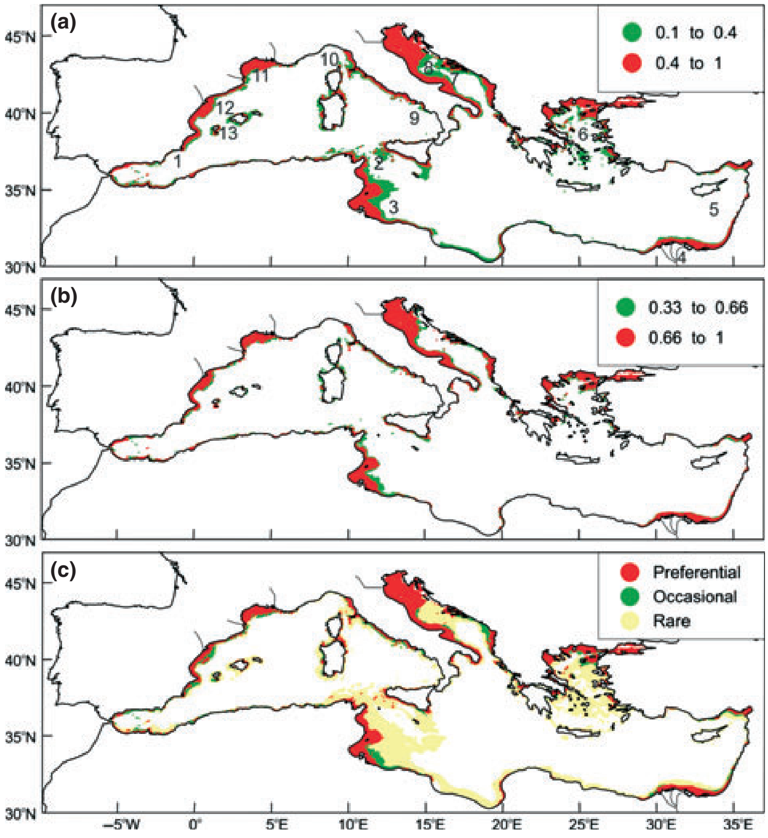


Figure 8. June: potential spawning (egg) habitat for anchovy in the Mediterranean Sea for the period 2003–2008. (a) Mean probability map. (b) Persistence map. (c) Habitat allocation map. Numbers indicate toponyms mentioned in the text. Locations as in Figure 3.

availability (i.e., zooplankton aggregations). This might sound simplified, nevertheless it is in agreement with findings concerning anchovy habitat in large upwelling ecosystems like the California and the Humboldt Currents (Checkley *et al.*, 2009 and references therein) or the Bay of Biscay in northeast

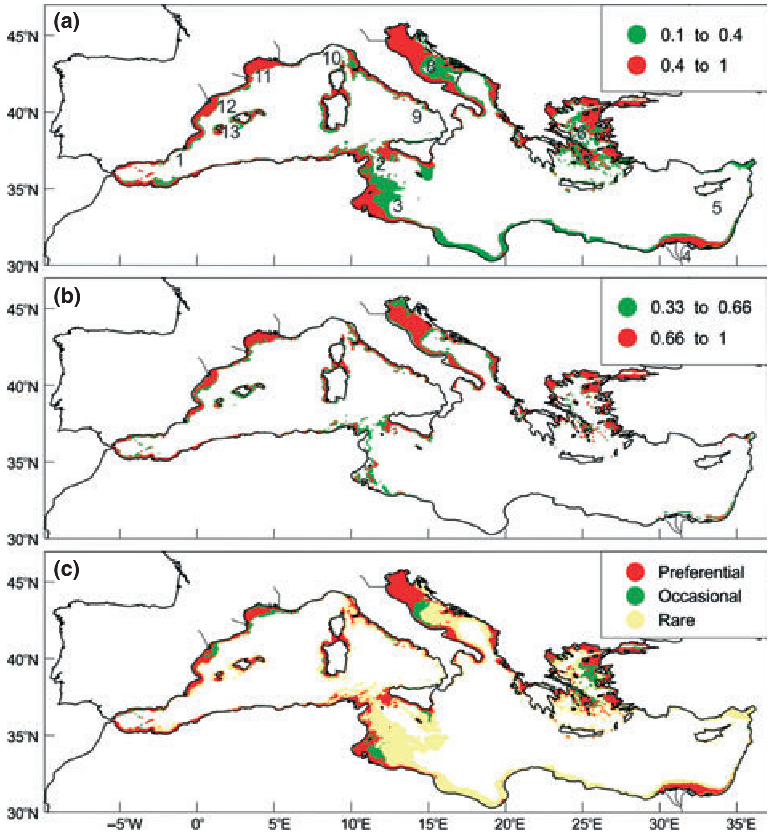


Figure 9. July: potential spawning (egg) habitat for anchovy in the Mediterranean Sea for the period 2003–2008. (a) Mean probability map. (b) Persistence map. (c) Habitat allocation map. Numbers indicate toponyms mentioned in the text. Locations as in Figure 3.

Atlantic (e.g., Bellier *et al.*, 2007). Following the common rule, anchovy habitat in the Mediterranean lies on the continental shelf (Checkley *et al.*, 2009 and references therein), but opposed to large upwelling systems, it extends more offshore compared to the potential habitat of European sardine *Sardina pilchardus* (Tugores *et al.*, 2011).

The temporal (interannual) variability of suitable areas for adult anchovy was assessed through the estimation of the mean probability, variability and persistence maps for both seasons within the study period. Locations with high variability for anchovy habitat were the coastal waters of the North Alboran Sea and the western part of the Italian Peninsula (i.e., the Ligurian and the Tyrrhenian Sea), shelf areas in the central/southern Aegean, and areas along the coastline of the Levantine Sea. Therefore, these areas seem to represent suitable habitat for anchovy only occasionally depending on the interannual variability of environmental conditions. Similarly, the coastal waters of the northern part of the Strait of Sicily seem to support occasional habitat for anchovy, presenting large dependence on the interannual variability of the environmental conditions mainly related to the AIS (Atlantic Ionian Stream) and its subsequent impact on the upwelling extent. Persistent habitat areas are also supported by past surveys in Greek waters (Giannoulaki *et al.*, 2005), the Strait of Sicily (e.g., Bonanno *et al.*, 2005; Patti *et al.*, 2005), the Adriatic Sea (e.g., Tičina *et al.*, 2006; Leonori *et al.*, 2007, 2009) and the Spanish Mediterranean waters (e.g., Giráldez and Alemany, 2002; Iglesias *et al.*, 2006).

The present study provides for the first time a picture of the potential adult anchovy habitat over the entire Mediterranean Sea during early autumn (September), which corresponds to the late phase of the reproductive period. Information on the spatial distribution of adult anchovy during this period is generally lacking in the Mediterranean Sea, since acoustic surveys are limited to the Adriatic Sea during this season. The mean probability maps indicated an expansion of anchovy adult habitat from early summer to early autumn, with higher probability of finding anchovy at <100 m depth during June but reaching deeper waters, up to 180 m depth, during September. Especially in the Adriatic Sea, the anchovy's potential habitat seems to expand southward compared to the summer period, covering most of the continental shelf. In the central part of the Adriatic, anchovy favourable areas were identified along the coastal waters of the Italian pen-

Table 5. Habitat area annual estimates (in km^2) for anchovy in early summer and late autumn in the Mediterranean Sea for the study period (2004–2008).

	Year	Early summer habitat	Late autumn habitat	Overlap habitat between early summer and late autumn (%)
A050	2004	73 568	111 920	18 272 (0.16)
	2005	112 320	224 384	53 984 (0.24)
	2006	103 040	128 464	40 624 (0.32)
	2007	81 120	112 112	13 296 (0.12)
	2008	51 728	74 704	14 544 (0.19)
	Average	84 355	13 0317	28 144 (0.21)
A075	2004	810	42 144	624 (0.02)
	2005	954	131 232	1584 (0.01)
	2006	22 704	50 800	2336 (0.05)
	2007	26 128	37 936	256 (0.01)
	2008	16 240	26 000	1536 (0.06)
	Average	13 367	57 622	1267 (0.03)

The spatial overlap between early summer (spawning adult) and late autumn (juvenile) potential habitat is also shown. A050, area with >50% probability; A075, area with >75% probability of anchovy presence.

insula, as well as in the eastern part, along the Slovenian and Croatian coastal zone, also extending offshore over the shelf of the mid-Dalmatian islands. In North Aegean Sea and the Western Mediterranean, the potential habitat expanded over the continental shelf compared to early summer suitable areas.

This indicates that occasional habitats and to a lesser degree preferential habitats of adult spawning anchovy tend to change size between seasons, expanding from early summer to early autumn. Similarly in upwelling areas, an expansion of anchovy preferable habitat from summer to autumn has also been described for Peruvian anchoveta (*Engraulis ringens*) in the Humbold Current system (Checkley *et al.*, 2009 and references therein). In contrast to the California Current, the adult anchovy habitat in the Mediterranean Sea seems to present less temporal and interannual variation (Checkley *et al.*, 2009 and references therein). The latter could be attributed to the oligotrophic character of the Mediterranean Sea and the high spatial heterogeneity in productivity that limit the location and extent of recurrent ‘hotspots’ i.e., areas associated with point sources of nutrient and local enrichment over continental shelf areas. Indeed, the European anchovy in the Mediterranean Sea does not exhibit the marked density-dependent expansions/contractions of spawning habitats characteristic of many stocks in upwelling areas and the Bay of Biscay (Somarakis *et al.*, 2012). Instead, spawners tend to maintain position in the spatially restricted areas of higher productivity exhibiting density dependent daily specific fecundity (Somarakis *et al.*, 2012).

Outside the surveyed areas, suitable habitats for adult anchovy were also indicated in the Ligurian Sea, along the North African coast, the extended continental shelf of the Gulf of Gabes in Tunisia and the Nile Delta region. Information for these areas is very scant. However, scattered survey and/or landings information indicate the presence of anchovy along the Moroccan and the Algerian coasts (Djabali *et al.*, 1991), the Tunisian and Libyan coastal waters as well as the Nile Delta region (El Haweet, 2001; Ben Abdallah and Gaamour, 2005). Further east, in the Levantine basin, information on the distribution grounds of anchovy and local landings composition (Bariche *et al.*, 2006) supports model results in the Lebanese waters. Adding data from more years and areas from the North Africa region is necessary to improve the accuracy and the performance of anchovy habitat models especially when addressing transitional seasons like autumn and spring.

Potential juvenile habitat

In the Mediterranean Sea anchovy spawns from spring to autumn with a peak in June/July (e.g., Somarakis *et al.*, 2004; Palomera *et al.*, 2007). Therefore, late autumn and winter are periods that juveniles are found in the populations in high percentages. In the present study, the potential juvenile habitat of anchovy during late autumn (mid-November to mid-December) and winter (mid-January to mid-February) was mapped for the first time throughout the Mediterranean basin. Although the winter model was built on 1 year of data, both model results and habitat suitability maps indicated that anchovy juvenile habitats were located in high productivity waters over the continental shelf. These habitats were more extensive in late autumn (i.e., up to 150 m depth) than later in the season (15–60 m depth). Bathymetry and SST along with productivity were the variables that largely defined anchovy juvenile habitat. Selection was for shallower/more coastal waters as the season progressed from autumn to winter. The coastal, warmer waters are likely to serve as refuges richer in food as weather conditions become worse. Moreover, as seasons progress, a part of the young-of-the-year has grown enough to be recruited to the adult stock; therefore juvenile behaviour with respect to environmental conditions can change accordingly (Petitgas *et al.*, 2004). Potential juvenile habitat presented higher interannual variability compared with adult habitat during early and late summer, implying the vulnerability of potential nurseries to changing environmental conditions. Potential nurseries were also indicated along the North Africa coast in association with productive areas such as the Gulf of Gabes in Tunisia and the Nile Delta region.

Unlike the Bay of Biscay (e.g., Petitgas *et al.*, 2004; Irigoien *et al.*, 2008), the California (e.g., Reiss *et al.*, 2008; Checkley *et al.*, 2009) and the Benguela Current systems (e.g., Checkley *et al.*, 2009 and references therein), no extended, off-shelf anchovy juvenile grounds seems to occur in the Mediterranean Sea. This can be explained either in terms of restricted offshore advection of early life stages (e.g., Somarakis and Nikolioudakis, 2007) or by avoidance of the oligotrophic offshore waters by juveniles. Suitable juvenile grounds were mainly located over the continental shelf, at sites with enrichment processes such as areas in the vicinity of river mouths. Juvenile grounds in open water, but still over the continental shelf, were indicated in specific regions such as the Gulf of Lions and the Gulf of Gabes (Fig. 7a). Later in winter, suitable juvenile grounds appeared to shift towards more coastal areas, which are presumably more suitable for overwintering.

Potential spawning habitat

Concerning the potential spawning habitat of anchovy, two different models were constructed using egg data to address the peak of the spawning season (i.e., June and July). Depth, SST and CHLA were the variables important in both cases. A consistent preference was for 40–150 m bathymetric range and more productive waters. SST preference is most likely related to the available range of values in each area that is associated with more productive waters. Habitat adequacy maps produced from each model presented a high degree of overlap, generally indicating the same areas, which reasonably well depict the species' spawning grounds as known from past studies and publications (reviewed in Schismenou *et al.*, 2008). Potential spawning grounds in June and July, as estimated from egg data, closely match the potential adult grounds in early summer, for acoustic data, although the former are more extensive. This is explainable in terms of egg dispersal: egg development can last several days during which eggs can be advected away from original spawning sites (e.g., Ospina-Alvarez *et al.*, 2012).

Although recent information from ichthyoplankton surveys is largely missing from the Adriatic, the indicated areas are in agreement with the results of past ichthyoplankton surveys conducted mainly during the 1980s and 1990s (Morello and Arneri, 2009 and references therein). In the western Mediterranean, suitable spawning areas were located in the Gulf of Lions and off the Catalan coast, the Alboran Sea and, to a lesser extent, the Italian coasts of the Ligurian and Tyrrhenian Seas. Past information from this part of the basin is consistent with the indicated preferable spawning sites in the present study (e.g., García and Palomera, 1996; Palomera *et al.*, 2007). Similar to adult maps, our habitat adequacy maps for eggs also indicated potential spawning grounds for anchovy in the Gulf of Gabes in Tunisia, which agrees with the limited anchovy ichthyoplankton research in this area (e.g., Zarrad *et al.*, 2006) as well as the coasts of Egypt (e.g., El Haweet, 2001) and the northeastern corner of the Levantine Basin (e.g., Bariche *et al.*, 2006).

In upwelling areas (i.e., California Current, Benguela Current) anchovies are known to present extended seasonal migrations for spawning purposes, largely in relation to wind-driven coastal upwelling or river runoff, forming water masses that can maintain enhanced nutrient supply and water column stability (Checkley *et al.*, 2009 and references therein). In the Bay of Biscay (Bellier *et al.*, 2007), spawning is strongly related to river plumes, shelf edge fronts and oceanic eddies, whereas coastal and oceanic regions are utilized by different age groups of the spawning population (Uriarte *et al.*, 1996; Vaz and Petitgas, 2002). The question of whether different age groups of anchovy segregate their spawning habitats in the Mediterranean remains to be explored. Nevertheless, there is no sign of extended migrations off the shelf for spawning in the Mediterranean Sea, since suitable spawning grounds generally occurred within the 160-m isobath.

Summarizing, bathymetry (preference for continental shelf waters) was the major factor in all habitat models, but CHLA (high productivity) was also important in characterizing juvenile and egg habitats. SST was most important for the juvenile model in winter, showing a preference for warmer waters, presumably associated with higher growth rate. Potential anchovy habitat in the Mediterranean changes over the annual cycle while sustained on the shelf, expanding from the peak spawning season (early summer) to late spawning (early autumn), to the juvenile habitat in late autumn, and subsequently contracting towards inshore waters in the winter. Nevertheless, anchovy inhabits a small percentage of certain preferable areas (~12 to 30%) and highly suitable areas (~1 to 6%) all year-round. Oceanographic characteristics, especially along the north coast of the Mediterranean Sea, generate a mosaic of small- to meso-scale habitats suitable for anchovy.

Therefore, preferred spawning grounds tend to be localized, mostly associated with point sources of nutrient enrichment that enhance productivity, such as river runoff or local upwelling. The spatially restricted areas of high productivity, along with topographic peculiarities (i.e., complex coastlines and bathymetric heterogeneity) of the Mediterranean Sea, result in a low degree of mixing between different anchovy stocks (Somarakis *et al*., 2004) and prevent long-distance migrations between spawning, feeding and juvenile grounds, such as those observed in some large upwelling ecosystems (Checkley *et al*., 2009 and references therein). As discussed in Somarakis *et al.* (2012) there is limited scope for moving away from the spatially restricted continental shelf areas of higher productivity when adjacent areas are deep and extremely oligotrophic.

Comparison between anchovy and sardine potential habitat

Although in the Mediterranean anchovy and sardine spawn in different periods of the year (i.e., summer and winter, respectively), their suitable spawning sites largely seem to overlap, being located mainly over extended continental shelves with river outflows and upwelling features (current paper; Tugores *et al*., 2011). However, the potential spawning habitat of anchovy shows less interannual spatial variability compared with sardine, and persistent spawning locations are more extensive. This might indicate that spawning during the winter mixing period in the Mediterranean is less predictable than the summer stratification period with subsequent implications for recruitment dynamics. In addition, the high dependence of sardine spawning on SST (Tugores *et al*., 2011), compared with anchovy, given global warming, could partly explain the decline in sardine populations throughout the northern part of the Mediterranean Sea over the last decade (SGMED 2010).

Adult sardine shows higher probability of being present in shallow waters (<65 m depth) during summer, expanding its potential habitat to deeper waters of up to 100 m in late autumn. This habitat expansion is more pronounced for the species' preferred habitat sites (Tugores *et al*., 2011). Similarly, in the case of adult anchovy, an expansion in species potential habitat is observed from early summer (i.e., peak of spawning season) to early autumn (i.e., late spawning period), from a bottom depth of 100–180 m, respectively. However, in contrast to sardine, habitat expansion for anchovy is more pronounced for occasional habitat sites. This might imply the existence of processes that bring together spawning anchovy in certain spatially restricted areas of higher productivity to promote spawning in the peak season (summer). As the season progresses, the population expands over wider areas in search of resources. In contrast to sardine, for which SST seems to drive spawning habitat, in the case of anchovy spawning habitat seems to be driven largely by depth, SLA and CHLA, implying that circulation and food-related processes are of major importance.

Finally, looking at the potential juvenile habitat of both species (summer and winter for sardine and anchovy, respectively), it is noted that both species potentially can occur at similar suitable locations over the continental shelf (present study, Giannoulaki *et al*., 2011). Depth is the dominant factor for both species, followed by CHLA in the case of sardine, indicating the suitability of shallow, more productive waters for juveniles during summer. Depth and SST along with productivity were the variables that largely defined anchovy juvenile habitat, indicating a selection for shallower/more coastal waters as the season progresses from autumn to winter. In this case, the coastal, warmer waters are likely to serve as rich food refuges as weather conditions become worse.

Nevertheless, the common habitats of the two species were characterized as preferential sites for anchovy, whereas they are occasional sites for sardine (Giannoulaki *et al*., 2011). This is more apparent in the northwestern Mediterranean and the Aegean Sea, indicating higher interannual variability and implying higher dependence of juvenile sardine on environmental conditions, at least for the study period in question. Similarly,the potential juvenile habitat of anchovy presented higher interannual variability compared with adult habitat during early and late summer, also indicating a vulnerability of potential nurseries to changing environmental conditions.

Habitat suitability models used in the present work are defined only in terms of hydrographic and other variables, and ignore factors such as population or predator abundance. However, they are still of special interest from an ecological perspective as they can be combined with climate change scenarios to assess potential changes in anchovy life cycle patterns. Regime shifts are known to occur, with associated fluctuations in the relative abundance of small pelagic species (Cury and Shannon, 2004). Habitat suitability maps like the ones in the present study may help to detect such shifts by observing the shrinkage and expansion of species suitable habitat.

Large-scale conservation planning requires the identification of sensitive or priority areas in which species present a high likelihood of long-term persistence, defining areas of particular importance for the maintenance of the stock. Therefore, the spatially explicit information of habitat maps can be essential input for operational systems required to apply ecology-based planning and management.

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