Hydrobiologia (2008) 612:201–214
DOI 10.1007/s10750-008-9502-1

FISH HABITAT MAPPING

Modeling and predicting potential spawning habitat of anchovy (*Engraulis encrasicolus*) and round sardinella (*Sardinella aurita*) based on satellite environmental information

Eudoxia Schismenou · Marianna Giannoulaki · Vasilis D. Valavanis · Stylianos Somarakis

Abstract Anchovy and round sardinella are two important small pelagic species in the Mediterranean that spawn during the summer period. This is a first attempt to model and predict the two species' potential spawning habitats in this area. Generalized additive models (GAMs) were constructed based on satellite environmental variables and presence/absence egg data, available from ichthyoplankton surveys conducted in the North Aegean Sea during early summer (June 2003–2006). These models were subsequently used to predict the probability of anchovy and round sardinella spawning in the Greek Seas as well as the entire Mediterranean and Black Sea during the same month of the year. The interaction of bottom depth and chlorophyll explained most of the deviance in the presence/absence GAMs of both species, indicating spawning over continental shelf areas with increased surface chlorophyll values. Round sardinella spawned closer to coast than anchovy. Predicted potential spawning areas for anchovy and round sardinella in unsampled areas of the Greek Seas and the entire Mediterranean and Black Sea were in good agreement with existing information on the distribution and extent of the spawning grounds, especially for anchovy. Modeling the species' reproductive activity in relation to easily accessible environmental information and applying the models in a predictive way could be an initial, low-cost step to designate potential spawning fish habitats.

Keywords Anchovy · Sardinella · Potential spawning habitat · GAMs · Satellite data

Introduction

European anchovy (*Engraulis encrasicolus*) and round sardinella (*Sardinella aurita*) are two of the most important (together with sardine, *Sardina pilchardus,* and sprat, *Sprattus sprattus*) small pelagic species in the Mediterranean in terms of commercial interest (Lleonart & Maynou, 2003). Anchovy is abundant in the northern Mediterranean basins, whereas round sardinella is most important in the southern part of this Sea (Pawson & Giama, 1985;

Guest editor: V. D. Valavanis
Essential Fish Habitat Mapping in the Mediterranean

E. Schismenou · S. Somarakis (✉)
Department of Biology, University of Crete, Vassilika
Vouton, P.O. Box 2208, 71409 Heraklion Crete, Greece
e-mail: somarak@her.hcmr.gr

E. Schismenou · M. Giannoulaki · S. Somarakis
Institute of Marine Biological Resources,
Hellenic Centre for Marine Research,
Thalassocosmos, 71003 Heraklion Crete, Greece

V. D. Valavanis
Marine GIS Laboratory, Institute of Marine Biological
Resources, Hellenic Centre for Marine Research,
Thalassocosmos, 71003 Heraklion Crete, Greece

Wassef et al., 1985; Stergiou et al., 1997; Lleonart & Maynou, 2003; Palomera et al., 2007).

Both species spawn during the summer period (Pawson & Giama, 1985; Wassef et al., 1985; Palomera & Sabates, 1990; Giraldez & Abad, 1995; Garcia & Palomera, 1996; Lisovenko & Andrianov, 1996; Somarakis et al., 2004; Gaamour et al., 2005; Tsikliras & Antonopoulou, 2006; Palomera et al., 2007). Eggs and larvae can be found in the plankton from spring to autumn (Palomera & Sabates, 1990; Sabates, 1990; Garcia & Palomera, 1996; Regner, 1996). Anchovy mainly spawns over continental shelf areas characterized by waters of low salinity and high primary and secondary production (Garcia & Palomera, 1996; Regner, 1996; Kideys et al., 1999; Somarakis et al., 2004; Somarakis et al., 2007; Palomera et al., 2007). Its spawning is usually associated with hydrographic structures (e.g., jets, gyres, eddies) that favor the advection of eggs and larvae within appropriate habitats (Salat, 1996; Agostini & Bakun, 2002; Garcia Lafuente et al., 2002; Cuttitta et al., 2003; Sabates et al., 2007; Somarakis & Nikolioudakis, 2007). The spawning of round sardinella is strongly associated with warm surface temperatures (Palomera & Sabates, 1990; Sabates et al., 2006; Tsikliras & Antonopoulou, 2006; Palomera et al., 2007) probably due to the species subtropical origin. However, in recent years, a number of studies have reported the occurrence and/or spawning of round sardinella in northern parts of the Mediterranean Sea (northern Aegean: Tsikliras & Antonopoulou, 2006; northern Adriatic: Dulcic & Grbec, 2000; Sinovcic et al., 2004; Gulf of Lions: Francour et al., 1994).

In recent years, predictive habitat distribution models have been gaining high popularity in ecology. This is mainly due to the introduction of new powerful statistical techniques and GIS (Geographic Information System) tools (Guisan & Zimmermann, 2000). Satellite environmental data have become largely available through international databases and provide promptly accessible and low-cost environmental variables to be used in habitat modeling.

In this paper, an attempt is made to model and predict the potential spawning habitat of anchovy and round sardinella in the Greek Seas, the entire Mediterranean basin, and the Black Sea. The term "potential spawning habitat," (PSH) has been recently defined by Planque et al. (2007). It is used to describe the areas where the environmental conditions are suitable for spawning, i.e., the broad geographical area that could support the spawning activity of a species, defined by environmental conditions and the preferred ranges for spawning. The PSH can change spatially and temporally according to changes in climate and the environment and includes the actual 'realized spawning habitat', i.e., the area where "spawning actually occurs" (Planque et al., 2007).

To predict the PSH for anchovy and round sardinella, we modeled presence/absence egg data from DEPM (Daily Egg Production Method) surveys in the North Aegean Sea (June 2003–2006, Somarakis et al., 2007) and satellite environmental data using Generalized Additive Models (GAMs). Spawning probability was subsequently predicted for non-sampled areas (including other areas of the Greek Seas and the entire Mediterranean and Black Seas) and compared with published information on the distribution and characteristics of spawning grounds of the two species.

Materials and methods

The egg data were used to fit the GAM models derived from four DEPM surveys for estimation of the spawning stock biomass of the North Aegean anchovy stock (Somarakis et al., 2007). The ichthyoplankton surveys were carried out during June of the years 2003–2006. The sampling scheme was based on transects spaced approximately ten nautical miles apart and stations located at five-nautical-mile intervals on each transect (Fig. 1). 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 and round sardinella eggs and larvae were counted. The presence/absence data were used in the GAM models.

The environmental data analyzed here originated from satellite monitoring of the area. Sea surface temperature distribution (SST in °C) was downloaded from the German Aerospace Agency's (DLR) satellite data archive and sea surface chlorophyll

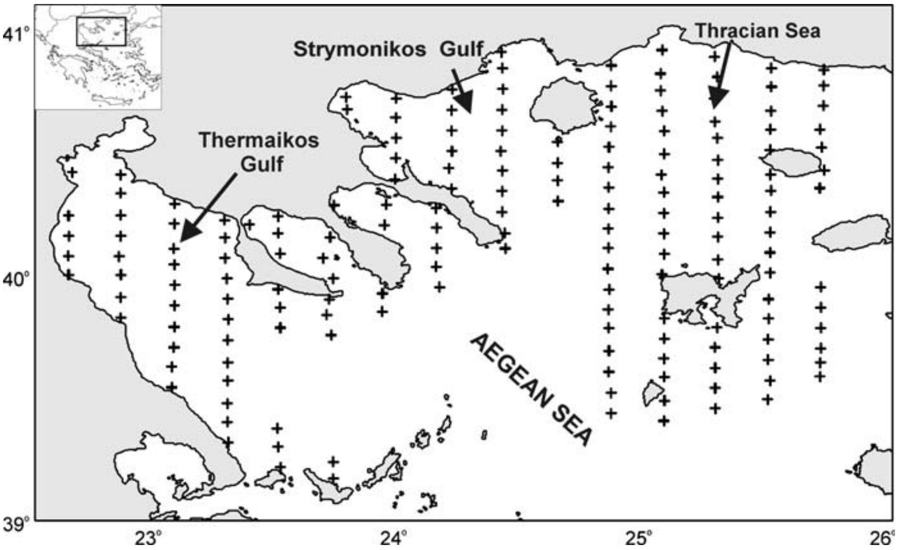

Fig. 1 Map of the North Aegean Sea showing the location of sampling sites used to derive the egg presence/absence data for anchovy and round sardinella. (+) Vertical tow stations

concentration (CHLO in mg/m^3) was provided through NASA's Distributed Active Archive Center. Sea surface salinity (SSS) was downloaded from the Mediterranean Oceanic Database as a decadal climatological product (Brasseur et al., 1996). Bathymetry was 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). Sea level anomaly (SLA in cm) was provided from the AVISO website using their Live Access Server. Photosynthetically active radiation (PAR in Ein/m^2/day) is defined as the quantum energy flux from the sun in the spectral range 400–700 nm and it is available through Oceancolor web, NASA's online Distributed Active Archive Center. The mean monthly values of satellite imagery were estimated for all these variables (Valavanis et al., 2004).

Anchovy and round sardinella egg presence/absence data and satellite environmental data were used to fit a GAM model in order to define the set of parameters that describe the PSH of the two species. For the selection of the GAMs smoothing predictors we applied the methodology proposed by Wood and Augustin (2002), using the "mgcv" library in the R statistical software (R Development Core Team, 2004). GAMs produced smoothed fits for each environmental predictor. The individual models could not be tested for significance based on the *P*-values from the "mgcv" library output, since it was not possible to define the true number of degrees of freedom. The true number of degrees of freedom is probably much smaller than the one used to calculate the *P*-value because of strong spatial autocorrelation in the data (Planque et al., 2007). Thus, each fit was analyzed on the level of deviance explained (0–100%; the higher the better), the Akaike 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 selected based on the observed data and the Generalized Cross Validation method suggested by Wood (2006) and available in the "mgcv" library. According to the above criteria, the environmental predictors were ranked and the best model for anchovy and round sardinella was selected based on a stepwise forward selection method. The presence/absence of anchovy and round sardinella eggs were used as a response variable (y). The predictor variables (x) that we examined were the decadic logarithm of the bottom depth (DEP), the decadic logarithm of the chlorophyll (CHL), the SST, the SLA, and the PAR. The parameters bottom depth and chlorophyll were transformed in order to stabilize the variance (Venables & Dichmont, 2004). To ensure a good prediction of anchovy and round sardinella PSH, applicable over larger areas, data collected from a wide range of environmental conditions should be applied to fit the model (Planque et al., 2007). Thus, we used pooled data from all four years (2003–2006). The total number of positive (egg presence) stations for anchovy and round sardinella was 335 and 216, respectively. The data were modeled using a binomial error distribution and a logit link. All first-order interactions of the parameters included in the final model were tested.

To evaluate the predictive performance of the final models we used the Receiver Operating Characteristic (ROC)-plots (Fieldings & Bell, 1997; Guisan & Zimmerman, 2000) and the area under the Receiver Operating Characteristic curve (AUC) for each examined year. AUC measures the ability of a model to discriminate between those sites where a species is present and those where it is absent and has been broadly used in the species' distribution modeling literature (Hanley & McNeil, 1982). AUC values range from 0 to 1, with 1 standing for perfect discrimination, 0.5 for predictive discrimination that is no better than a random guess, and values <0.5 indicate performance worse than random (Boyce et al., 2002; Elith et al., 2006). For the estimation of ROC and AUC the presence/absence library of the R statistical software was applied.

Finally, the GAM models were used to predict areas that could serve as PSHs of anchovy and round sardinella in larger grids: the Greek Seas and the Mediterranean Sea with the adjacent Black Sea at a GIS resolution of 4 and 8 km, respectively. The 4-km GIS resolution was the best resolution available for chlorophyll (which had the less dense grid of all parameters), while the 8-km GIS resolution was chosen to reduce the volume of the dataset to a size that could be processed. These prediction grids included mean monthly satellite data of the environmental parameters that were selected in the final models concerning June 2003, 2004, 2005, and 2006. It must be pointed out here that predicted PSHs included those located in areas with environmental parameters of the range encountered during the Aegean Sea research surveys (i.e., the ranges of parameters used to develop the GAMs). For mapping we used the Surfer v8.0 of the Golden Software Inc. software.

Results

The distribution and abundance of anchovy and round sardinella eggs are presented in Figs. 2 and 3,

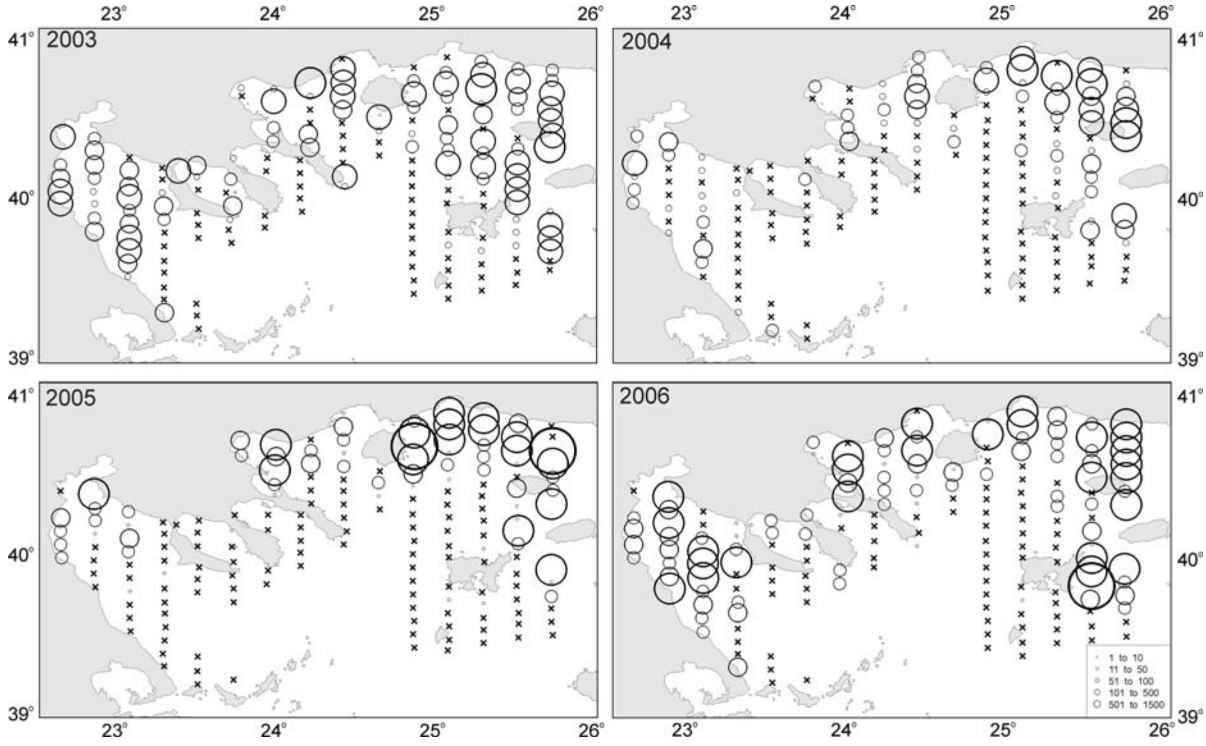

Fig. 2 Distribution and abundance of anchovy eggs (eggs m^{-2}) in June 2003–2006. The symbol (x) denotes negative station

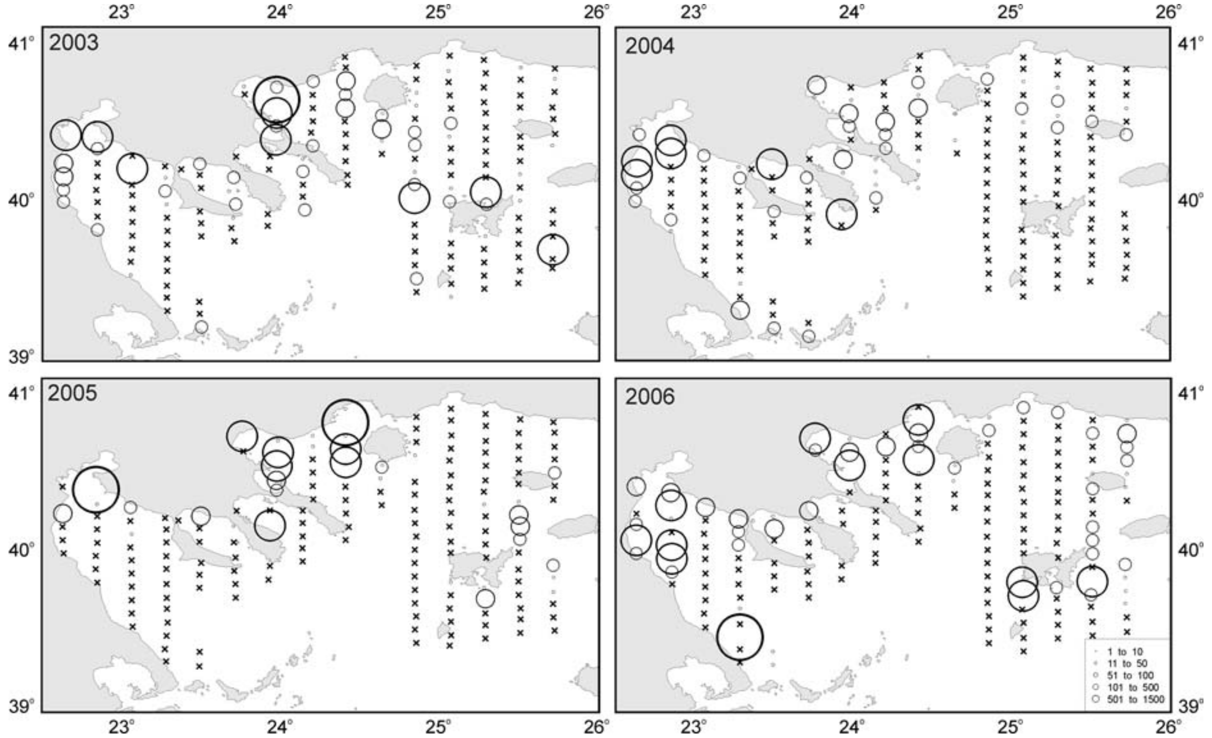

Fig. 3 Distribution and abundance of round sardinella eggs (eggs m^{-2}) in June 2003–2006. The symbol (x) denotes negative station

respectively. Anchovy eggs were occurring frequently and with higher abundance in the Thracian Sea, the Strymonikos Gulf, and the Thermaikos Gulf, except in 2004 and 2005 when spawning was less intense in the latter two gulfs. On the other hand, round sardinella eggs were consistently present and more abundant in the Strymonikos Gulf and the inner part of the Thermaikos Gulf.

The final model selected for anchovy eggs' presence/absence data (total deviance explained: about 41%) included SST as a main effect and the interaction of depth (DEP) and chlorophyll (CHL) (Table 1). All parameters in the final model were statistically significant.

In Fig. 4, results of the final GAM model are presented as plots of the best-fitting smooths for the effect of the environmental variables on anchovy egg presence. The 95% confidence intervals are also plotted around the best-fitting smooths for the main effect. The interactive effect is shown as perspective plot without error bounds. The relative importance of each environmental variable of the model is presented in x- and y-axes. In the z-axis, the interactive effect of both variables is presented (Fig. 4b). The rug under the single variable effects plot indicates the density of points for different variable values (Fig. 4a). The effect of each variable is the conditional effect, i.e., the effect that this variable has, given that the other variables are included in the model. For anchovy, the SST plot indicated increasing probability of spawning with increasing temperature (Fig. 4a). The interaction plot of DEP and CHL indicated increasing probability of spawning with increasing values of CHL and intermediate available values of DEP (Fig. 4b).

The final model for round sardinella included Sea Level Anomaly (SLA) and the interaction of DEP and CHL (Table 1) and explained a low percentage of the deviance (about 20%). All parameters in the final model were statistically significant. In Fig. 5, results of the final GAM model are also presented as plots of the best-fitting smooths for the effect of the environmental variables on sardinella egg presence. For round sardinella, the SLA plot revealed increasing probability of spawning for values between −8 and −4 cm (Fig. 5a). The interaction plot of DEP and CHL indicated increasing probability of finding sardinella eggs with increasing values of CHL and in smaller depths (Fig. 5b).

Table 1 Analysis of deviance for GAM covariates and their interactions of the final model fitted for anchovy and round sardinella

	Parameter	Res. Df	Residual deviance	Deviance explained (%)	AIC	*P*-value
Anchovy	Null model	549	760.42			
	s(SST)	541.91	725.62	4.58	741.81	0.026
	s(SST) + s(DEP : CHL)	536.71	450.34	40.80	476.92	$\ll$0.000
Round sardinella	Null model	531	626.52			
	s(SLA)	522.94	589.29	5.94	607.42	0.002
	s(SLA) + s(DEP : CHL)	509.10	500.41	20.10	546.21	$\ll$0.000

Level of significance was set to 0.05. The (:) sign denotes interaction. Res. d.f. = residual degrees of freedom.; AIC = Akaike Information Criterion value

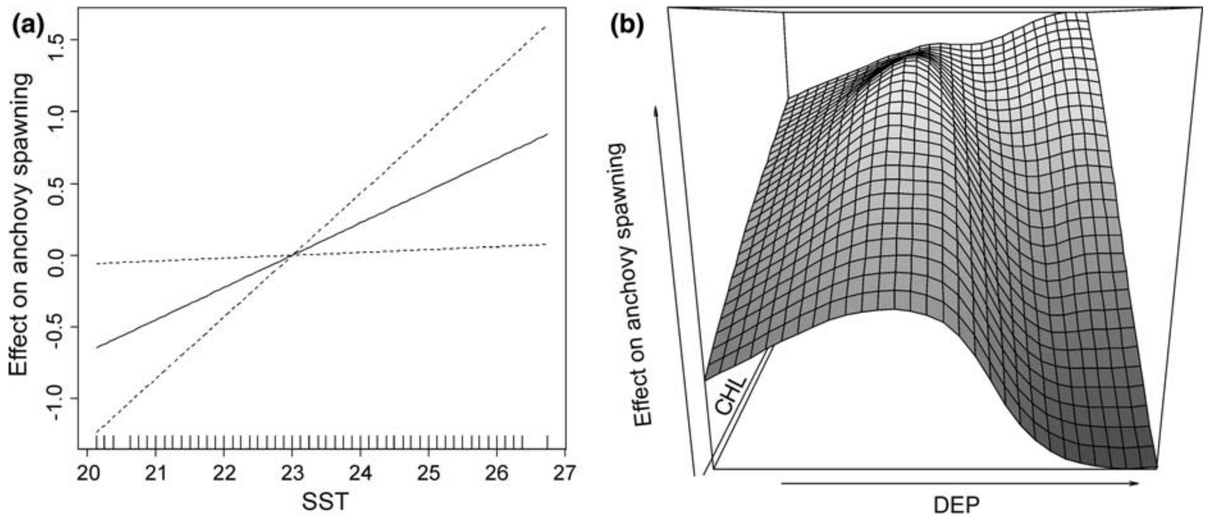

Fig. 4 Plots of the smoothing response of the Generalized Additive Model for anchovy spawning against (**a**) SST and (**b**) the interaction of DEP and CHL. Black thick line indicates the value of the GAM smoothing response and dotted lines represent the 95% confidence intervals

Model validation indicated good discrimination ability for both models as in most cases the estimated values of AUC exceeded 0.80 (Elith et al., 2006). More specifically, AUC values ranged between 0.87 and 0.91 for anchovy and between 0.81 and 0.87 for round sardinella, with the exception of 2003 when the AUC value for sardinella was lower (0.65).

The models for the two species were applied in a predictive way for the Greek Seas as well as for the entire Mediterranean and adjacent Black Sea. The resultant maps are presented in Figs. 6–9. For anchovy, the model indicated that the northern Aegean Sea is the major potential spawning ground (Fig. 6), while in the Mediterranean Sea, potential sites of increased spawning probability were mainly predicted in the Alboran Sea, the Gulf of Lions and the Catalan coast, the eastern part of the Adriatic Sea, the Gulf of Gabes, the northern Aegean Sea, and the entire Black Sea (Fig. 8). For round sardinella, the model also indicated the northern Aegean Sea as the major potential spawning ground (Fig. 7). In the Mediterranean Sea, round sardinella potential spawning grounds were consistently predicted in the Gulf of Lions, the Gulf of Gabes, the northern and eastern Adriatic, the northern Aegean, and the coastal waters of Egypt (Fig. 9).

Discussion

The application of the northern Aegean Sea GAM models to larger areas of similar environmental ranges

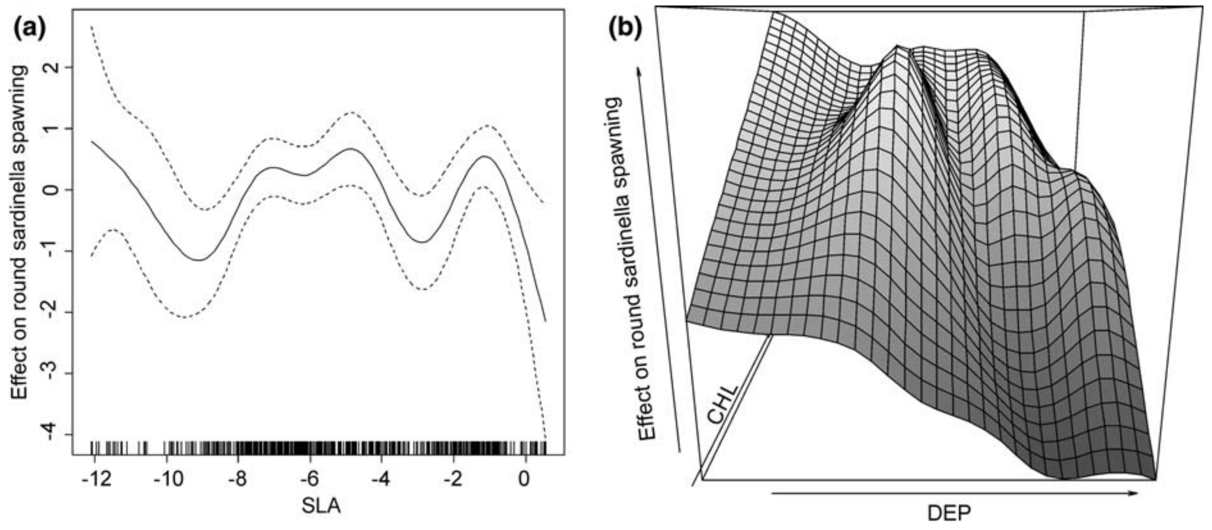

Fig. 5 Plots of the smoothing response of the Generalized Additive Model for round sardinella spawning against (**a**) SLA and (**b**) the interaction of DEP and CHL. Black thick line indicates the value of the GAMs smoothing response and dotted lines represent the 95% confidence intervals

in order to predict PSHs of anchovy and round sardinella seemed to depict reasonably well the two species' spawning grounds as known from past studies and publications. More specifically, in the Greek Seas the main spawning areas for anchovy were predicted in the North Aegean Sea (Fig. 6), which is in agreement with the observed distribution patterns of eggs (Fig. 2) and data from previous surveys (Somarakis et al., 2004; Somarakis, 2005; Somarakis et al., 2006). The North Aegean Sea is largely influenced by the Black Sea Water and river runoffs exhibiting characteristics that are favorable for anchovy spawning (Agostini & Bakun, 2002; Somarakis et al., 2002a; Isari et al., 2006; Somarakis & Nikolioudakis, 2007). Other smaller spawning grounds were also predicted by the model in the central Ionian and Aegean Seas, which match well survey results of July 1998 and June 1999 in this area (Somarakis et al., 2002b; Somarakis et al., 2006). Certain recurring spots have also been identified in 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).

The main spawning areas of round sardinella in the Greek Seas were also predicted to be located in the North Aegean Sea (Fig. 7), as observed in the June 2003–2006 surveys (Fig. 3) and published elsewhere (Somarakis et al., 2002a; Tsikliras & Antonopoulou, 2006). Potential spawning sites were also identified in specific coastal sites of central Greece and Turkey.

The anchovy model predictions for the entire Mediterranean and Black Sea indicated areas that corresponded well to already known spawning grounds (Fig. 8). Namely, the model indicated that the Black Sea is a major anchovy spawning ground. Indeed, anchovy is the most abundant species in the Black Sea and spawns all over the basin (Niermann et al., 1994; Kideys et al., 1999).

In the Adriatic Sea, anchovy was predicted to spawn with a high probability in the northern and the western part of the basin (Fig. 8). This Sea is characterized by major river outflows and increased primary production, especially in its shallow northern part, and anchovies are known to spawn mainly along the western part of the basin (Regner, 1996). This is in good agreement with the predictions of our GAM model.

In the western Mediterranean, potential anchovy spawning grounds were found in the Gulf of Lions and the Catalan Sea, the Alboran Sea, and, to a lesser extent, along the Italian coasts of the Ligurian and Tyrrhenian Seas. Indeed, these are the main anchovy spawning areas in the western Mediterranean as indicated in all published reviews (Garcia & Palomera, 1996; Palomera et al., 2007).

Anchovy spawning was further predicted along the south Sicilian coasts, the Gulf of Gabes, the coasts of Egypt and the northeastern corner of the Levantine Basin (Iskenderum Bay). Although the Sicilian channel is known to be inhabited by a small, highly

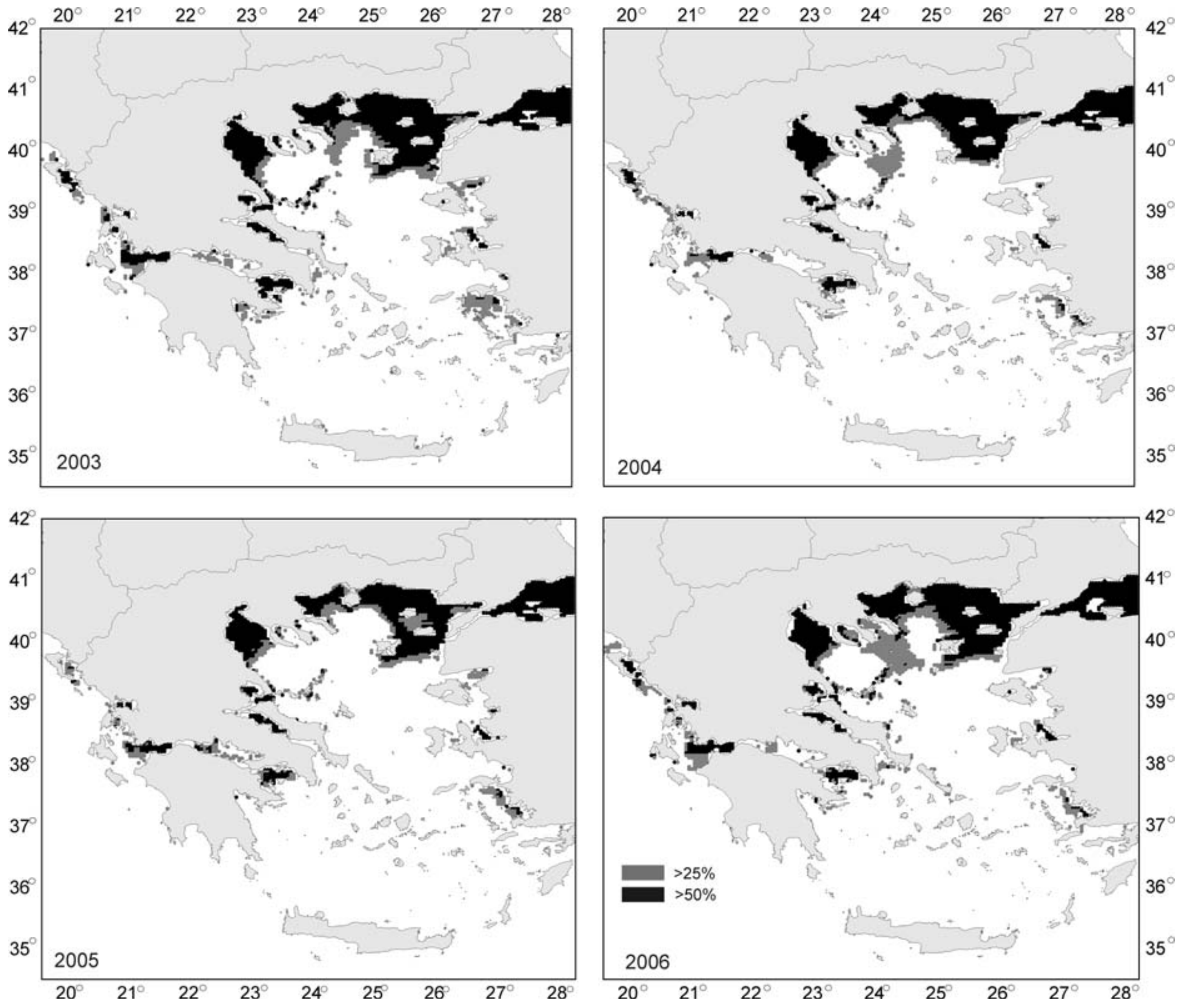

Fig. 6 Map of areas representing anchovy potential spawning habitat in Greek waters based on the GAM model from the North Aegean Sea. Gray color: >25%; black color: >50% probability of spawning

fluctuating anchovy stock (Cuttitta et al., 2003; Somarakis et al. 2004), very few are known about anchovy spawning in the remaining areas (e.g., Zarrad et al., 2006). However, anchovy constitutes a significant proportion of the pelagic fish catch in Tunis (Gaamour et al., 2005), Egypt (Wassef et al., 1985) and the Iskenderum Bay (Turan et al., 2004).

Except the Greek Seas, potential spawning grounds for round sardinella in the eastern Mediterranean (Fig. 9) were mainly predicted along the coasts of Egypt where round sardinella is the most important of the exploited species (Wassef et al., 1985). The prediction of potential spawning for sardinella in the Black Sea for June 2003 is not supported by existing knowledge, although there are records of round sardinella presence in the area (Bauchot, 1987).

In the central Mediterranean, round sardinella potential grounds were consistently predicted in the Adriatic Sea and the Gulf of Gabes. Although relevant information is scant, there are several reports of spawning of this species in the Adriatic (Gamulin & Hure, 1983; Sinovcic et al., 2004) and its abundance has been increasing during recent years (Dulcic & Grbec, 2000). In the Tunisian waters there are also several reports for round sardinella reproductive activity and spawning (Gaamour et al., 2005; Zarrad et al., 2007). The round sardinella is an important

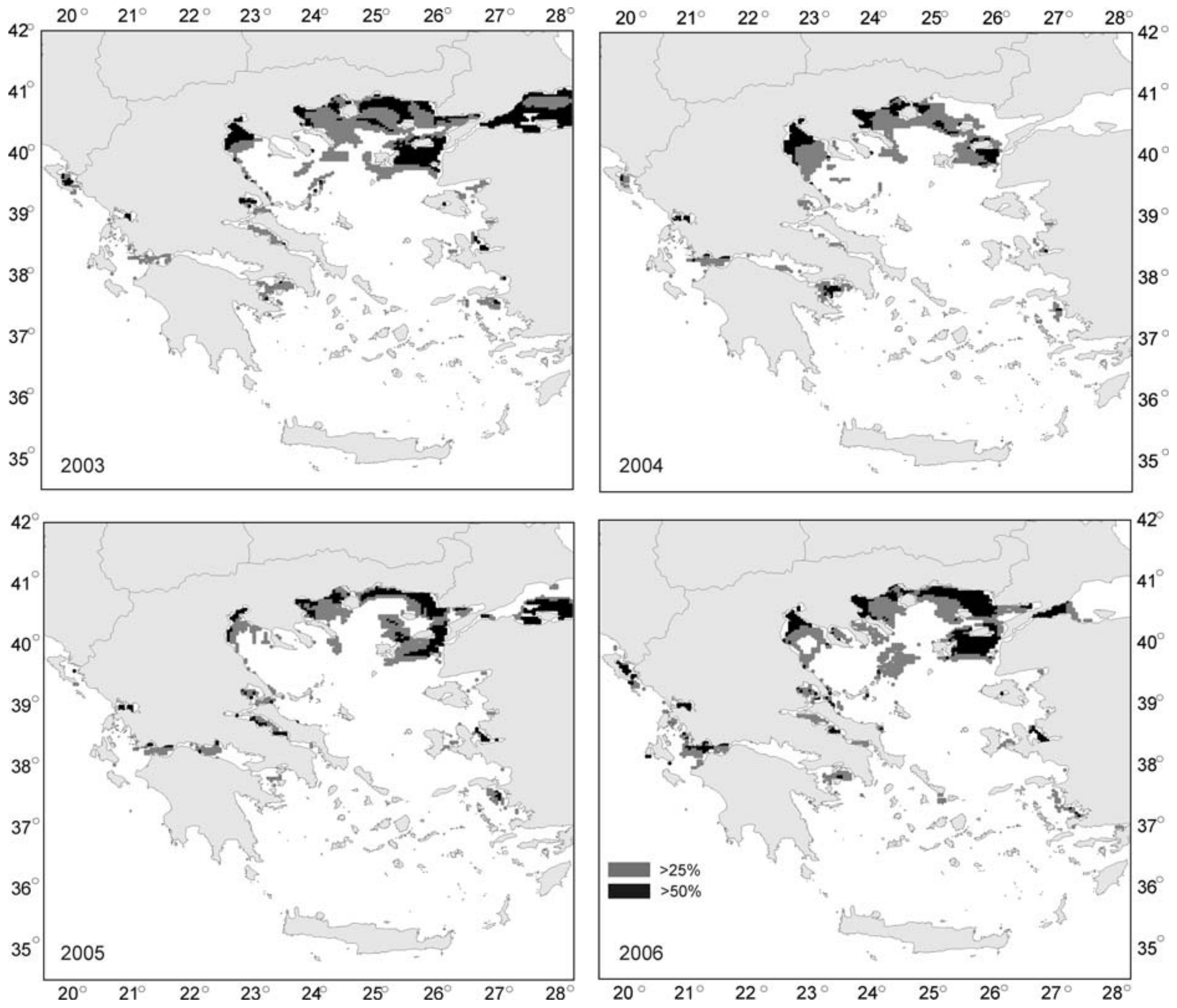

Fig. 7 Map of areas representing round sardinella potential spawning habitat in Greek waters based on the GAM model from the North Aegean Sea. Gray color: >25%; black color: >50% probability of spawning

catch of the Tunisian pelagic fishery (Gaamour et al., 2005).

In the western Mediterranean, potential spawning sites for round sardinella were mainly predicted in the Gulf of Lions and the Catalan coasts in accordance with known spawning grounds (Palomera & Sabates, 1990; Sabates et al., 2006; Palomera et al., 2007).

In this study, egg presence data of anchovy and round sardinella were modeled with satellite environmental data. The data do not represent the actual environmental conditions that the populations experience in the water column. They rather reflect the sea surface conditions. However, the predictions for anchovy and round sardinella potential spawning areas corresponded well with our knowledge of the distribution and extent of the spawning grounds. Especially for anchovy, the model was quite effective explaining almost 41% of the deviance and predicted well the main spawning grounds of the species in the Mediterranean Sea (northern Aegean, western Adriatic, Gulf of Lions and Catalan coast, Alboran Sea). The deviance explained by the sardinella model was low (about 20%) and this could be partially attributed to the limited number of positive stations used to estimate the general additive model.

Further development of such models with larger datasets covering numerous spawning sites in

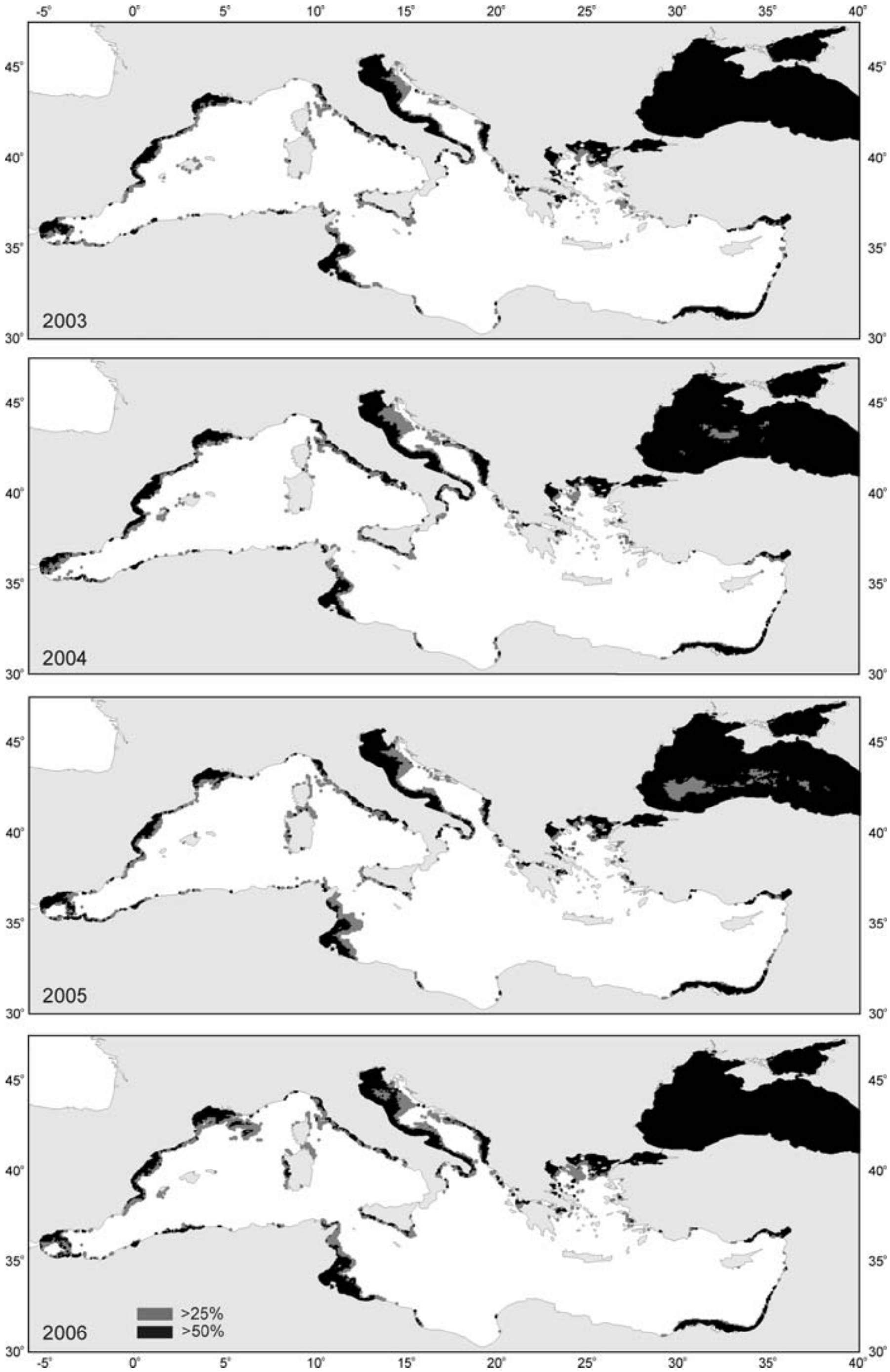

Fig. 8 Mediterranean Sea. Map of areas representing anchovy potential spawning habitat based on the GAM model from the North Aegean Sea. Gray color: >25%; black color: >50% probability of spawning

different seasons and years (i.e., taking into account a wider range of environmental conditions) would be expected to significantly increase the effectiveness of the method and the predicting capacities of spawning habitats (Twatwa et al., 2005). Predicting PSHs using parameters that represent layers of the water column other than the surface would evidently improve our understanding of species spawning habitats. For example, Planque et al. (2007) found that anchovy potential spawning in the Bay of Biscay was primarily related to bottom temperature followed by surface temperature and the mixed-layer depth.

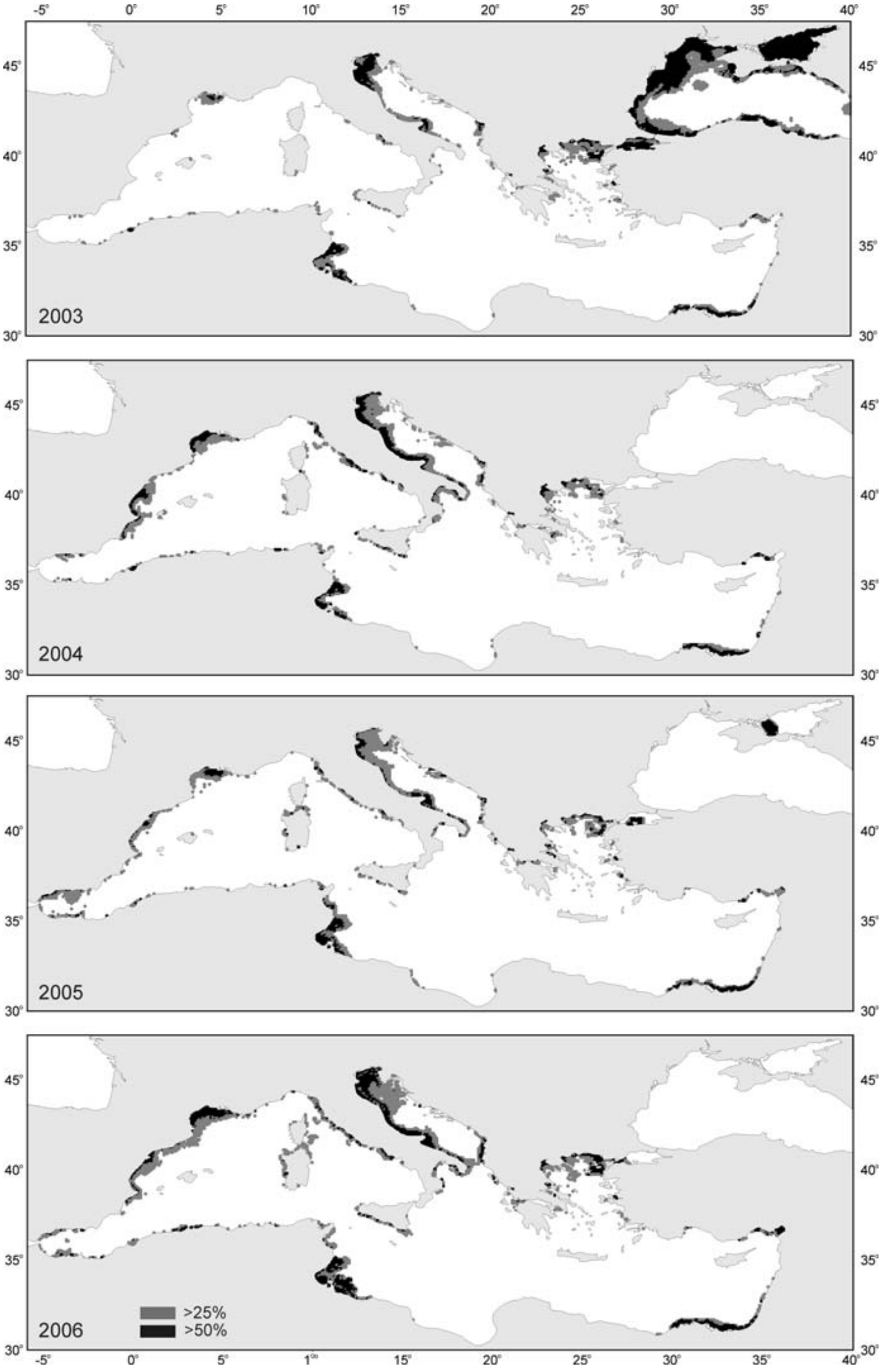

Fig. 9 Mediterranean Sea. Map of areas representing round sardinella potential spawning habitat based on the GAM model from the North Aegean Sea. Gray color: >25%; black color: >50% probability of spawning

Our models for both anchovy and round sardinella incorporated the interaction term of depth and chlorophyll. This term explained the larger part of deviance, especially in the anchovy model. Both species seem to have a preference for relatively high values of chlorophyll, i.e., high primary productivity. However, they are both coastal species seeking for particular depth ranges. This can explain the significance of the depth-chlorophyll interaction, i.e., the two species spawn in the more productive areas within their preferred depth ranges over the continental shelf.

The observed patterns of egg distribution and predicted spawning habitats indicate that there might be significant overlap between the spawning areas of the two species in both the Greek Seas and the Mediterranean basin. Spawning habitats are mainly located over continental shelf waters (<200 m); however, the spawning areas of round sardinella seem to be located more closely to the coast compared to those of anchovy, which is evident in this study if we consider the >50% probability of spawning (Figs. 6–9). Consequently, although the spawning periods of the two species largely coincide, a degree of spatial segregation seems to exist. These observations are consistent with published studies from the NW Mediterranean (Palomera & Sabates, 1990; Palomera et al., 2007).

In the anchovy model, there was a linear positive relationship with temperature. The association of anchovy eggs and larvae with areas of higher surface temperature has recently been demonstrated in Somarakis & Nikolioudakis (2007). In the northern Aegean Sea, such areas are mainly those characterized by anticyclonic circulation, which are rich in zooplankton and likely to constitute important areas for the retention of ichthyoplankton (Somarakis & Nikolioudakis, 2007).

The GAM model for round sardinella did not include the SST but this may again be attributed to poor model definition due to the limited positive egg data available for this species. Temperature is well known to play a major role in controlling the distribution and spawning of round sardinella in the Mediterranean Sea (Sabates et al., 2006). In recent years, there have been an increasing number of studies reporting the incidence of the warm-water round sardinella in northern areas of the Mediterranean basin. This has been attributed to climate change and sea warming (Francour et al. 1994; Dulcic & Gbrec, 2000; Sabates et al. 2006; Tsikliras & Antonopoulou, 2006). An increase of the species' population sizes in the northern Mediterranean could result in the expansion of its spawning grounds. Based on the potential spawning grounds maps produced in this study such an expansion is likely to cause major spatial overlap, increasing interspecific competition of the two species.

Finally, in the round sardinella model, the SLA was included as a main effect. The three peaks of SLA seemed to correspond to different ranges of the parameter prevailing in different years. However, it is hard to evaluate at this stage the full ecological significance of this parameter.

Information on and prediction of potential spawning as well as habitats of other important life history phases (e.g., nursery habitats) could be of use in fisheries management for the design of appropriate actions to protect the exploited stocks. For example, the implementation of measures such as closed areas and seasons requires good knowledge of the spatial/temporal distribution of sensitive habitats based on the collection and synthesis of fisheries-independent information on species requirements. Modeling the species' biological activities (e.g., spawning) in relation to easily accessible environmental information and applying the models in a predictive way could be an initial, low-cost step to designate potential habitats.

Acknowledgments The present study was partly supported by the DEPM and acoustic cruises of the National Program for Fisheries Data collection (2002–2006). The authors would like to thank the captain and the crew of R/V 'PHILIA' as well as Mr. A. Siapatis and Mrs. C. Stamataki for their help in sample collection and analysis.

References

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

Bauchot, M. L., 1987. Poissons osseux. In Fisher, W., M. Schneider & M. L. Bauchot (eds), Fishes FAO d'identification des especes pour les besoins de la peche: Mediterranee et mer Noire, Zone de peche 37, Vertebres: 861–1422.

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

Brasseur, P., J. M. Brankart, R. Schoenauen & J. M. Beckers, 1996. Seasonal temperature and salinity fields in the Mediterranean Sea: climatological analyses of an historical data set. Deep-Sea Research 43: 159–192.

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

Dulcic, J. & B. Grbec, 2000. Climate change and Adriatic ichthyofauna. Fisheries Oceanography 9: 187–191.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudık, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick,

A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. McC, A. T. Overton, S. J. Peterson, K. S. Phillips, R. Richardson, R. E. Scachetti-Pereira, J. Schapire, S. Soberon, M. S. Williams, N. E. Wisz & Zimmermann, 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129–151.

Fieldings, A. H. & J. F. Bell, 1997. A review of methods for the assessment of prediction errors in conservation presence: absence models. Environmental Conservation 24: 38–49.

Francour, P., C. F. Boudouresque, J. G. Harmelin, M. L. Harmelin-Vivien & J. P. Quignard, 1994. Are the Mediterranean waters becoming warmer? Information from biological indicators. Marine Pollution Bulletin 28: 523–526.

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

Gamulin, T. & J. Hure, 1983. The spawning and spawning areas of pelagic fishes (*Sardina plichardus, Engraulis encrasicolus, Scomber scombrus, Sardinella aurita* and *Sprattus sprattus sprattus*) in the Adriatic Sea. Acta Adriatica 24: 97–131.

Garcia, A. & I. Palomera, 1996. Anchovy early life history and its relation to its surrounding environment in the Western Mediterranean basin. Scientia Marina 60: 155–166.

Garcia Lafuente, J., A. Garcia, S. Mazzola, L. Quintanilla, J. Delgado, A. Cuttita & B. Patti, 2002. Hydrographic phenomena influencing early life stages of the Sicilian Channel anchovy. Fisheries Oceanography 11: 31–44.

Giraldez, A. & R. Abad, 1995. Aspects on the reproductive biology of the Western Mediterranean anchovy from the coasts of Malaga (Alboran Sea). Scientia Marina 59: 15–23.

Guisan, A. & N. E. Zimmermann, 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135: 147–186.

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

Isari, S., A. Ramfos, S. Somarakis, C. Koutsikopoulos, A. Kallianiotis & N. Fragopoulu, 2006. Mesozooplankton distribution in relation to hydrology of the Northeastern Aegean Sea, Eastern Mediterranean. Journal of Plankton Research 28: 241–255.

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

Lisovenko, L. A. & D. P. Andrianov, 1996. Reproductive biology of anchovy (*Engraulis encrasicolus ponticus* Alexandrov 1927) in the Black Sea. Scientia Marina 60: 209–218.

Lleonart, J. & F. Maynou, 2003. Fish stock assessments in the Mediterranean: state of the art. Scientia Marina 67: 37–49.

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

Palomera, I. & A. Sabates, 1990. Co-occurrence of *Engraulis encrasicolus* and *Sardinella aurita* eggs and larvae in the northwestern Mediterranean. Scientia Marina 54: 61–67.

Palomera, I., M. P. Olivar, J. Salat, A. Sabates, M. Coll, A. Garcia & B. Morales-Nin, 2007. Small pelagic in the NW Mediterranean Sea: An ecological review. Progress in Oceanography 74: 377–396.

Pawson, M. G. & M. S. Giama, 1985. A biological sampling problem illustrated by the population structure and growth patterns of *Sardinella aurita* at Tripoli, Libya. Environmental Biology of Fishes 12: 143–154.

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

R Development Core Team, 2004. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

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

Sabates, A., 1990. Distribution pattern of larval fish populations in the Northwestern Mediterranean. Marine Ecology Progress Series 59: 75–82.

Sabates, A., P. Martin, J. Lloret & V. Raya, 2006. Sea warming and fish distribution: the case of the small pelagic fish *Sardinella aurita*, in the western Mediterranean. Global Change Biology 12: 2209–2219.

Sabates, A., M. P. Olivar, J. Salat, I. Palomera & F. Alemany, 2007. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. Progress in Oceanography 74: 355–376.

Salat, J., 1996. Review of hydrographic environmental factors that may influence anchovy habitats in northwestern Mediterranean. Scientia Marina 60: 21–32.

Sinovcic, G., M. Franicevic & V. Cikes-Kec, 2004. Unusual occurrence and some aspects of biology of juvenile gilt sardine (*Sardinella aurita* Valenciennes, 1847) in the Zrmanja River estuary (eastern Adriatic). Journal of Applied Ichthyology 20: 53–57.

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

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., P. Drakopoulos & V. Filippou, 2002a. Distribution and abundance of larval fish in the northern Aegean Sea -eastern Mediterranean- in relation to early summer oceanographic conditions. Journal of Plankton Research 24: 339–357.

Somarakis, S., C. Koutsikopoulos, A. Machias & N. Tsimenides, 2002b. Applying the daily egg production method (DEPM) to small stocks in highly heterogenous seas. Fisheries Research 55: 193–204.

Somarakis, S., A. Machias, M. Giannoulaki, E. Schismenou, K. Tsagarakis, A. Siapatis, C. Stamataki, M. Torre, A. Anastasopoulou, V. Vassilopoulou, A. Kalianiotis & C. Papaconstantinou, 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. & N. Nikolioudakis, 2007. Oceanographic habitat, growth and mortality of larval anchovy (*Engraulis encrasicolus*) in the northern Aegean Sea (eastern Mediterranean). Marine Biology 152: 1143–1158.

Somarakis, S., I. Palomera, A. Garcia, L. Quantanilla, C. Koutsikopoulos & L. Motos, 2004. Daily egg production of anchovy in European waters. ICES Journal of Marine Science 61: 944–958.

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

Stergiou, K. I., E. D. Christou, D. Georgopoulos, A. Zenetos & C. Souvermezoglou, 1997. The Hellenic Seas: Physics, chemistry, biology and fisheries. Oceanography and Marine Biology 35: 415–538.

Tsikliras, A. C. & E. Antonopoulou, 2006. Reproductive biology of round sardinella (*Sardinella aurita*) in the north-eastern Mediterranean. Scientia Marina 70: 281–290.

Turan, K., D. Erguden, M. Gurlek, N. Basusta & F. Turan, 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.

Twatwa, N. M., C. D. van der Lingen, L. Drapeau, C. L. Moloney & J. G. Field, 2005. Characterising and comparing the spawning habitats of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguella upwelling ecosystem. African Journal of Marine Science 27: 487–499.

Valavanis, V. D., S. Georgakarakos, A. Kapantagakis, A. Palialexis & I. Katara, 2004. A GIS environmental modeling approach to Essential Fish Habitat Designation. Ecological Modeling 178: 417–427.

Venables, W. N. & C. M. Dichmont, 2004. GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. Fisheries Research 70: 319–337.

Wassef, E., A. Ezzat, T. Hashem & S. Faltas, 1985. Sardine fishery by purse-seine on the Egyptian Mediterranean coast. Marine Ecology Progress Series 26: 11–18.

Wood, S. N., 2006. Generalized Additive Models. An Introduction with R. Chapman & Hall/CRC, Boca Raton.

Wood, S. N. & N. H. Augustin, 2002. GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. Ecological Modelling 157: 157–177.

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

Zarrad, R., H. Missaoui, M. S. Romdhane, O. Jarboui & R. M'Rabet, 2007. *Sardinella aurita* egg and larval distributions and sea temperature in the Tunis Gulf. Rapporte de la Communaute Internationale de la Mer Mediterranee 38: 640.