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FISH HABITAT MAPPING

Identification of hake distribution pattern and nursery grounds in the Hellenic seas by means of generalized additive models

George Tserpes · Chrissi-Yianna Politou · Panagiota Peristeraki · Argyris Kallianiotis · Costas Papaconstantinou

Abstract A time series of hake abundance data obtained from the "MEDITS" experimental surveys carried out in the Greek seas from 1996 to 2006 have been modeled by means of Generalized Additive Models (GAMs), as functions of spatial and temporal variables, including sampling position (latitude–longitude interaction), depth, and year. All variables were highly significant but most of the variation was explained by the sampling position and the depth. Total abundance was higher in the 100–450 m depth zone, while juveniles showed preference for shallower waters, being more abundant from 100 to 320 m. Model predictions were used to generate density distributions maps, which revealed that total abundance is relatively higher in the western part of the Aegean Sea and in the eastern part of the Cretan Sea, while its maximum values are expected in the Saronikos Gulf. Nursery grounds are restricted in specific regions with the most important of them being in the Saronikos Gulf and its surrounding area.

Keywords Hake · Mediterranean · Distribution · Nursery · Generalized Additive Models

Introduction

European hake, *Merluccius merluccius* L., 1758, is a demersal fish species distributed throughout the Mediterranean Sea and in the eastern Atlantic from the Barents Sea to the Mauritanian coast (Whitehead et al., 1984). In the Mediterranean, hake is a species of high economic importance as it is one of the main target species of most bottom-trawl fisheries (Papaconstantinou & Farrugio, 2000).

Genetic studies have shown that a clear genetic difference exists between the Atlantic and the Mediterranean hake (Pla et al., 1991; Roldan et al., 1998). Morphometric studies and preliminary findings of genetic studies support the hypothesis that differences also exist among western, central, and eastern Mediterranean hakes (Inada, 1981; Lo Brutto et al., 1998).

Studies on the bathymetric distribution of the species in the Mediterranean indicated that hake inhabits a wide depth range from 20 to 1,000 m,

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depending on the area and the size of the fish (Oliver & Massutí, 1995; Papaconstantinou & Stergiou, 1995). Information, however, on the spatial distribution pattern of the species in relation to its biological cycle is limited to a few studies carried out mostly in the central and western Mediterranean, which have indicated the existence of nursery grounds in certain areas such as the Ligurian Sea and the Gulf of Lions (Orsi Relini et al., 1989; Campillo et al., 1991; Recasens et al., 1998; Orsi Relini et al., 2002). In the eastern Mediterranean, information from various local surveys has suggested the existence of hake nursery grounds in specific region of the Aegean and Ionian seas (Tsimenides et al., 1978; Papaconstantinou & Stergiou 1995; Maravelias & Papaconstantinou, 2006; Maravelias et al., 2007). However, not any quantitative estimate has been provided.

In the present work, we attempt to model bottom-trawl survey abundance data as functions of spatial and temporal variables, in order to identify spatiotemporal trends and built abundance density maps demonstrating on a quantitative basis the hake distribution in the Aegean and Ionian seas. The data we are using are coming from the Mediterranean International Trawl Survey (MEDITS) carried out in several parts of the Mediterranean Sea since 1994 (Bertrand et al., 2000, 2002). Abundances were modeled by means of Generalized Additive models (GAM) techniques (Hastie & Tibshirani, 1990), as functions of longitude, latitude, sampling year, and water depth.

Materials and methods

Within the frames of the "MEDITS" project, a series of annual bottom trawl surveys are performed in various areas of the Mediterranean Sea since 1994. The surveys, which mainly aimed to obtain estimates of abundance indices and length frequency distributions for a series of target species, were accomplished from late spring to middle summer and included sampling at predefined stations. Further details on the sampling protocol can be found elsewhere (Bertrand et al., 2000, 2002). Since 1996, the sampling scheme of the Greek MEDITS survey is consistent covering annually (with the exception of 2002, when the survey was not accomplished) a total of about 180 stations distributed all over the Aegean and Ionian seas (Fig. 1).

In the present study, we analyzed hake abundance data by station from the surveys carried out in the 1996–2006 period. The examined abundance indices considered the total hake biomass and the number of juveniles. Abundance indices were expressed in terms of kg and number, respectively, per square km of swept area (kg/km^2, n/km^2). As juveniles, were conventionally considered all immature virgin

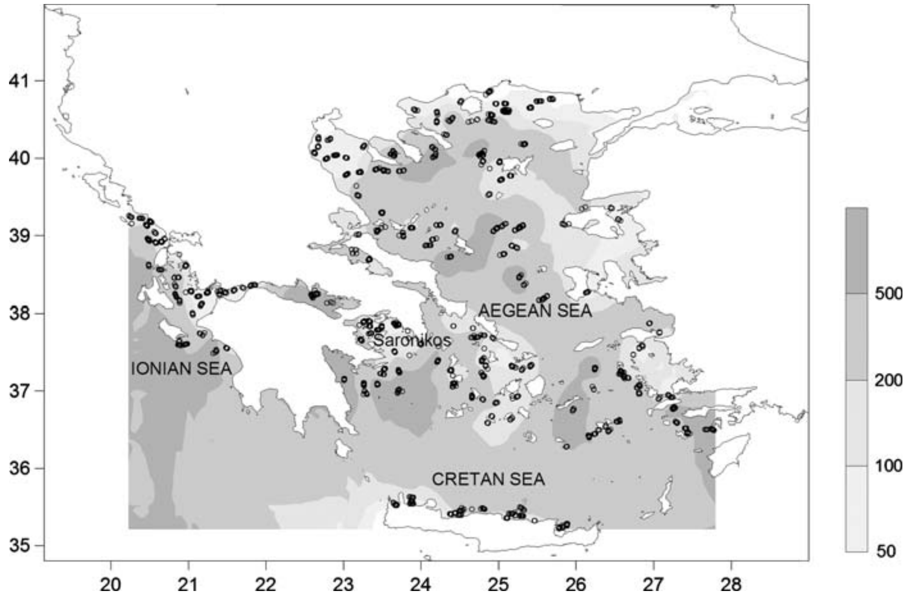


Fig. 1 Distribution of the sampling stations over the 50–100, 100–200, 200–500 and 500–800 bathymetric zones

individuals (gonads belonging to stage 0 and 1 according to MEDITS scale for maturity).

The effects of the station position and depth on both, the total and juvenile abundances were examined by means of GAMs. The latter, which are able to deal with non-linear relationships between a dependent variable and multiple predictors in the same model, are nonparametric generalizations of multiple linear regression that are less restrictive in assumptions about the underlying distribution of data (Hastie & Tibshirani, 1990). In GAMs, a predefined link function is related to predictor variables by scatterplot smoothers in lieu of least-squares fits.

In the present case, our nonlinear components were fitted with a locally weighted regression scatterplot smoother (*loess* smoother, Cleveland & Devlin, 1988) by means of the S-PLUS software package, in the way described by Venables & Ripley (1997). Apart from the trawling position and the depth, the year parameter was also modeled as a categorical variable. Hence, the following variables were included in the analysis: Year, Position (entered as the latitude–longitude interaction) and Depth. The general GAM model was of the form:

$$\begin{aligned}\text{Abundance} = a + \text{Year} + \text{lo}_1(\text{Position}) \\ + \text{lo}_2(\text{Depth}) + e,\end{aligned}$$

where a is a constant, lo_i is the *loess* smoother function of the corresponding independent variable and e is a random error term.

Based on the diagnostic residual plots of preliminary runs we assumed a Poisson distribution accompanied by its canonical log-link function for the analysis of the total abundance.

In the case of the juvenile abundance, due to the high frequency of zero values in the data set, a Delta-X error-model was employed, which makes possible to treat separately the question of whether an abundance rate is zero or not, and the size of a rate given that it is non-zero (Vignaux, 1996). For the purposes of this analysis, the Bernoulli-type 0/1 measurements for each abundance index were recorded by assigning the value 0 in stations not having juveniles and the value 1 to the positive ones. The obtained measurements were assumed to follow a binomial distribution, where the estimated probability is a linear function of the predictor variables. The logit function was used as a link between the linear factor component and the binomial error. In this way the probability of having juveniles was estimated for the different combinations of predictor variables. Since the data are 0/1 measurements, the deviance follows a χ^2-distribution; hence a χ^2 statistic was used to test for the significance of the predictor variables (Ye et al., 2001).

The choice of the most appropriate link function and error distribution for the analysis of the nonzero juvenile abundance rates was made on the basis of residual plots. A poisson model accompanied by a log link function was found to be adequate in this case.

After obtaining model predicted values for the sampled stations for: (a) the probability, P, of nonzero rate, and (b) for the expected rate, μ, conditional on it being positive, the unconditional abundance of each station is given by $P\mu$ (Ye et al., 2001).

In all GAMs, variable selection proceeded by a stepwise forward entry and the Akaike Information Criterion (AIC) was used to detect the relative importance of each variable in explaining variations and determine the order of those that should be included in the final model. The AIC statistic accounts simultaneously for the degrees of freedom used and the goodness of fit, whereas a smaller AIC statistic corresponds to a better model in the sense of smaller residual deviance penalized by the number of parameters that are estimated in fitting the model. At each stage of the forward entry, the AIC was computed for every candidate predictor not yet entered. The variable resulting in the highest AIC decrease was entered into the model. Forward entry continued until additional variables no longer yielded reductions in the AIC statistic. Significant levels for the added predictors were estimated by means of the chi-square test and the level of significance was set at 95%.

The predicted abundance indices from the GAM analysis were used to construct density distribution maps for the total and juvenile abundance, respectively. Maps were generated using the SURFER software (Golden Software, 2002) and interpolation was made by means of the "inverse distance to a power" gridding method, adjusting properly the R parameter to avoid predictions in areas not covered by the survey (Davis, 1986).

Results

Data from 1,714 trawling operations were analyzed (Fig. 1). The three stepwise GAMs explained 36–53%

Table 1 Analysis of deviance for the GAM models fitted to the hake abundance data

Explanatory variable	Residual d.f.	Residual deviance	Cumulative variance explained in CPUE
Total abundance			
Mean	1,713	180,021	
Position	1695.28	136,594	24.12
Depth	1689.11	118,243	34.32
Year	1680.11	113,803	36.78
Juvenile presence (binomial model)			
Mean	1,713	2,165	
Depth	1707.01	1,824	15.75
Position	1688.95	1,643	24.14
Year	1679.95	1,597	26.24
Juvenile abundance (positive values)			
Mean	1,151	3,832,741	
Position	1132.33	2,211,842	42.29
Depth	1126.01	1,936,595	49.47
Year	1116.98	1,782,956	53.48

of the total variation (Table 1) and all variables were highly significant ($P < 0.0001$). The sampling position had the highest explanatory power both, for the total and juvenile abundance, explaining 24.12% and 42.29%, respectively. Depth was the most important explanatory variable in the case of the juvenile presence binomial GAM, explaining as much as 15.75% of the total variance.

The effect (loess plot) of the predictors on abundance, or probability of juvenile presence in the case of the binomial model, is shown on the *y*-axis (*z*-axis, in the case of “position”) for different values of the predictor (*x*-axis) (Figs. 2–4). The zero line indicates mean model estimates, while the *y* (or *z*)-axis is a relative scale where the effect of different values of the predictors on the response variable is shown. Hence,

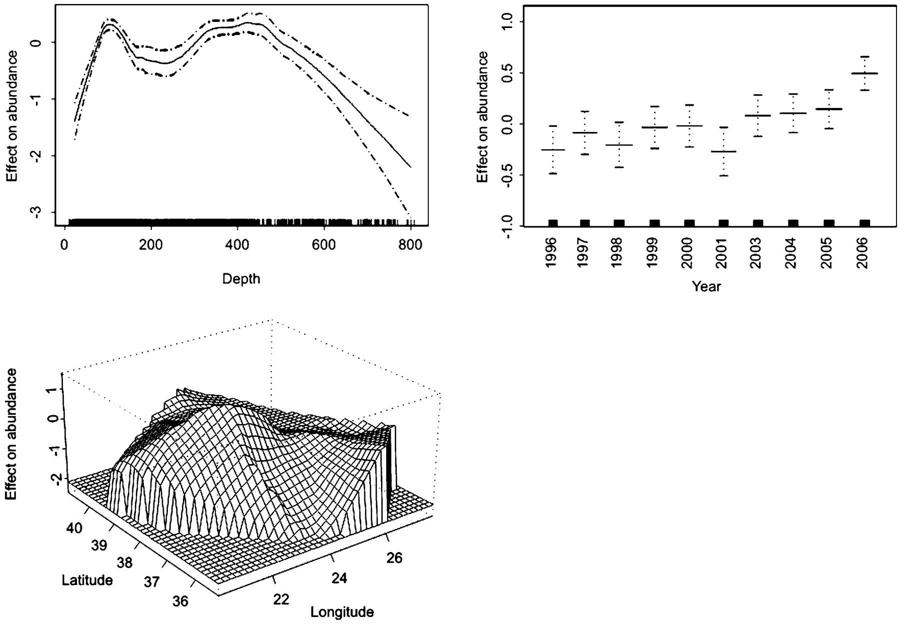


Fig. 2 GAM derived effects on the total hake abundance index. Each plot represents the contribution of the corresponding variable to the fitted predictor. The fitted values are adjusted to average zero and the broken lines indicate two standard errors. The relative density of data points is shown by the “rug” on the *x*-axis

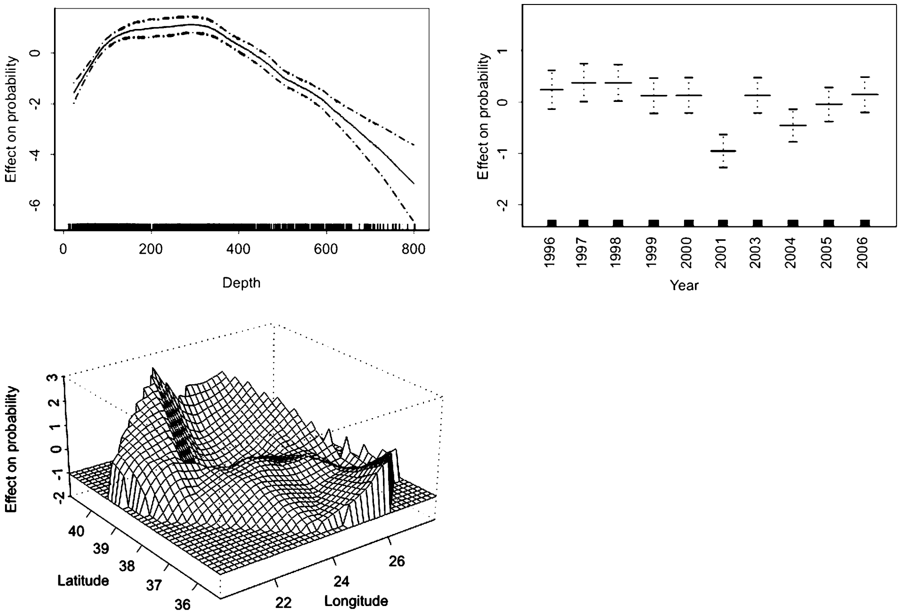


Fig. 3 GAM derived effects on the probability of presence of juvenile hake. Each plot represents the contribution of the corresponding variable to the fitted predictor. The fitted values are adjusted to average zero and the broken lines indicate two standard errors. The relative density of data points is shown by the "rug" on the *x*-axis

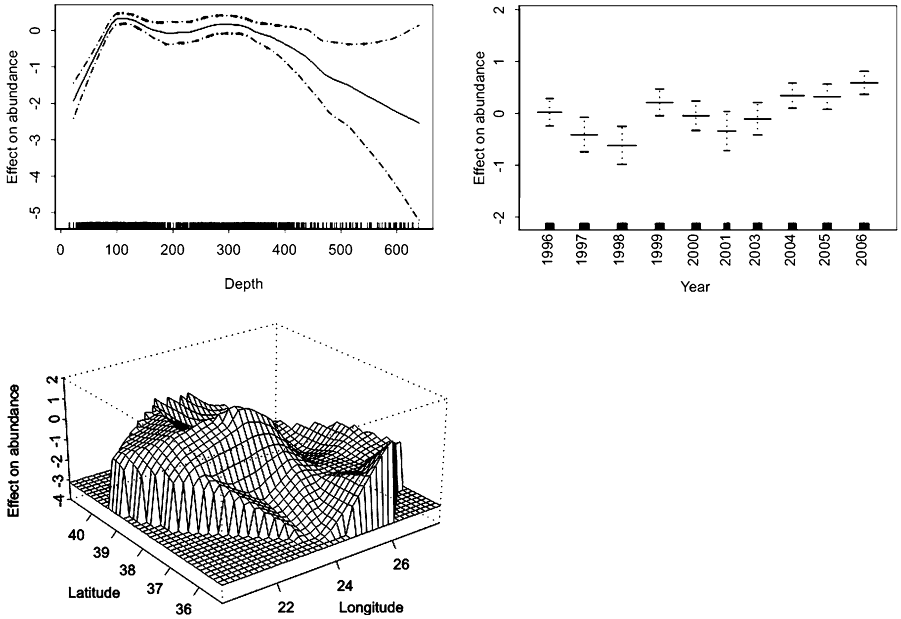


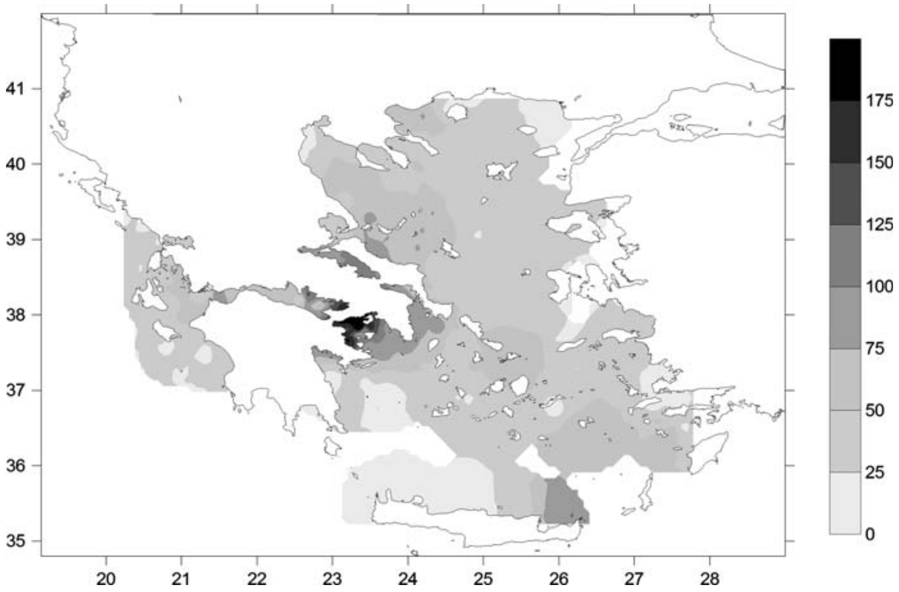
Fig. 4 GAM derived effects on the juvenile abundance index. Each plot represents the contribution of the corresponding variable to the fitted predictor. The fitted values are adjusted to average zero and the broken lines indicate two standard errors. The relative density of data points is shown by the "rug" on the *x*-axis

negative values on the *y* (or *z*)-axis indicate that at the corresponding levels of the predictor (*x*-axis), the model estimates abundance/probability that is lower than the mean, while the opposite holds for positive values on the *y* (or *z*)-axis.

In that sense, loess plots revealed that total abundance drops drastically after about 450 m while both, juvenile abundance and probability of finding juveniles drop after about 320 m. Total abundance is higher in the 100–450 m bathymetric zone, having two major peaks around 100 and 400 m, respectively. The major peak regarding juvenile abundance was around to 100 m. All indices and the probability of finding juveniles were increasing with depth, up to 100 m.

The "year" loess plots suggest the existence of an increasing trend for both, the total and juvenile abundances from 2001 onwards. The corresponding

Fig. 5 Map of the total hake distribution. Abundance is expressed in terms of kg/km^2

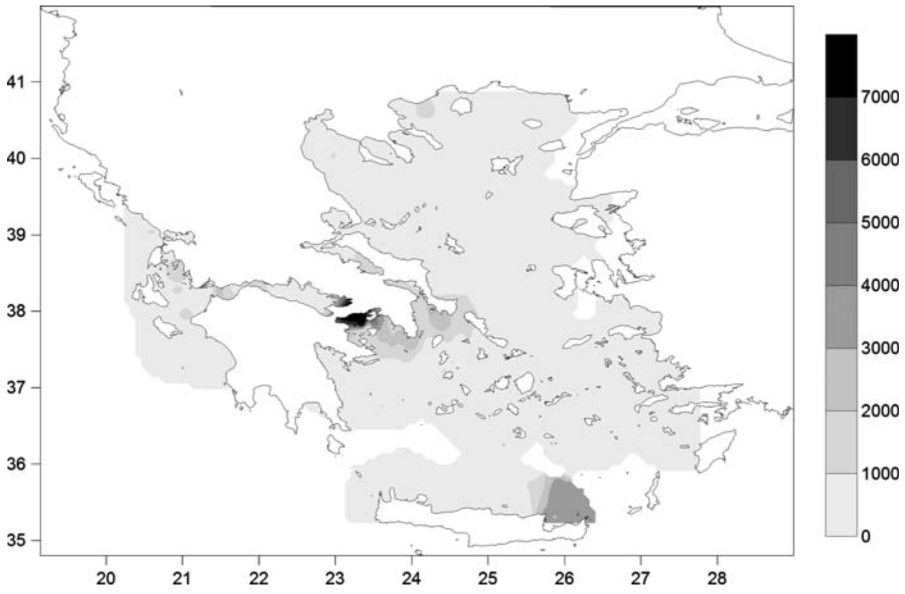


latitude-longitude loess plots have quite similar patterns suggesting the presence of certain local maxima with the highest one being around 23–24° E and 38–39° N. The latitude–longitude loess plot of the binomial model, suggest that the probability of finding juveniles is higher in the northern part of the examined area.

The density distribution maps that were built based on the GAM estimates, indicate that total hake abundance is relatively higher in the western part of the Aegean Sea and in the eastern part of the Cretan Sea, with the maximum values expected in the Saronikos Gulf (Fig. 5).

The juvenile abundance map suggested the presence of certain major nursery grounds in specific regions. The most important of them is located in the Saronikos Gulf and its surrounding area, while relatively high juvenile abundances are estimated for an area off the eastern part of the Cretan coast. A few other nurseries of much less importance are found in the northern part of the Aegean and in the Ionian seas (Fig. 6).

Fig. 6 Map of the juvenile hake distribution. Abundance is expressed in terms of *n*/km



Discussion

The present study gives a global picture of the hake distribution in the Greek seas based on a time series of data obtained through the "MEDITS" experimental survey, which is carried out on a regular basis following the same sampling protocol. Such standardized surveys are able to provide estimates that are independent of factors, as for instance the behavior of the fisheries, which may bias commercial data.

The use of GAM techniques for the examination of population abundance indices in relation to environmental and spatiotemporal variables is gaining popularity among fisheries scientists over the last years, (e.g., Bigelow et al., 1999; Daskalov, 1999; Walsh & Kleiber, 2001; Maravelias & Papaconstantinou, 2003). In the current study, GAMs explained a relatively high percentage of the abundance variations confirming their suitability in addressing non-linear trends that cannot be easily captured through linear models (Borchers et al., 1997). This methodological approach permitted direct spatiotemporal comparisons as it removed effects that could bias nominal indices and provided a quantitative basis for the study of hake distribution in the Greek seas. Certainly, the analysis did not fully consider the complex geomorphology of the examined area (e.g., enclosures and islands), but the depth parameter included in the models, incorporates certain geomorphological features.

Our analysis revealed that hake is generally more abundant in the 100–450 m bathymetric zone. This is in agreement with the findings of previous studies in different Mediterranean areas, such as the Gulf of Lions (Campillo et al., 1991; Recasens et al., 1998), the Ionian (Vassilopoulou & Papaconstantinou, 1987), the Adriatic (Zupanovic & Jardas, 1986) and the Ligurian seas (Orsi Relini et al., 1989). Although the presence of juveniles affects the total abundance estimates, the fact that the corresponding distribution maps and GAM graphs do not show similar patterns, suggests that total abundance is not largely driven by the abundance of juveniles.

Juveniles seem to prefer somehow shallower waters than adults, being more abundant from 100 to 320 m and having their major abundance peak around 100 m. Most probably, the first total abundance peak, occurring around to 100 m (Fig. 2), is due to the high presence of juveniles in that depth. In general, juveniles seem to be mostly distributed over the continental shelf (depths up to 200–300 m) as it happens all over the Mediterranean (Orsi Relini et al., 2002). Similarly to our results, Orsi Relini et al. (1989), has reported that the main concentration of juveniles in the Ligurian Sea is around to 100 m.

Our analysis indicated the presence of an increasing trend in the examined abundance indices over the last five years and this finding is in agreement with the reported total catch levels of hake of the Greek fisheries that show a similar trend (Tserpes et al., 2007). A previous analysis based on MEDITS survey data from the south Aegean Sea covering the 1994–2000 period did not reveal the presence of any abundance trend over time (Tserpes & Peristeraki, 2002).

In general, the Mediterranean demersal stocks are considered to be over-exploited (Papaconstantinou & Farrugio, 2000). A recent assessment of hake in the Greek seas suggested that the current stock biomass levels are about 30–40% lower than the optimum ones (B_{msy}), although an increasing stock biomass trend was observed over the 1999–2003 period (Tserpes et al., 2007). The progressive reduction of the total Greek fleet capacity, accompanied by the increase of the trawl-net mesh size over the past 10 years, may have resulted in stock level increases that are reflected in the MEDITS survey abundance indices. Environmental changes such as water temperature increase due to global warming may have also favored hake recruitment, and consequently stock size increase. Studies in the Adriatic support this hypothesis as they have shown a positive relationship among sea surface temperature during spring, and hake larval abundance (Zupanovic & Jardas, 1986). However, this hypothesis cannot be confirmed in the current case due to lack of relevant data.

The density maps revealed that hake is widely distributed over the examined area, but it is relatively more abundant in the western part of the Aegean Sea and in the eastern part of the Cretan Sea. They have also indicated quantitatively the location of the most important nursery grounds.

Papaconstantinou & Stergiou (1995) suggested specific areas of the Aegean and Ionian seas as hake nursery grounds, without, however, providing any quantitative estimate. In general, their suggestions agree with our findings apart from the area off the Cretan coast that they did not mention at all, probably due to lack of relevant data. Our study, however, has shown that the identified nursery grounds are not all of the same importance and that the Saronikos Gulf is by far the most significant one. It seems that the prevailing abiotic and/or biotic factors in Saronikos Gulf, an area of high fishing activity, favor the hake distribution in the area. Certain fishery closures that are locally applied may be also in favor of hake juvenile survival.

Considering that the Mediterranean demersal stocks are managed through control effort regimes, spatio-temporal closures and technical measures, our findings can provide useful information for spatial management purposes. The present results, however, are based on surveys carried out in a specific season; hence they do not take into account possible seasonal migrations. In case that hake in the Greek seas undertake seasonal migrations, as it has been suggested by Zupanovic & Jardas (1986) for the Adriatic and Recasens et al., 1998 for the Gulf of Lions, further studies are needed to confirm the consistency of the currently suggested distribution pattern throughout the year.

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