FISH HABITAT MAPPING

Distribution of swordfish in the eastern Mediterranean, in relation to environmental factors and the species biology

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Abstract Swordfish catch per unit effort (CPUE) data from the Greek commercial fisheries operating in the eastern Mediterranean have been modeled on a seasonal basis as functions of environmental spatial, and temporal variables, including Sea Surface Temperature (SST), Chlorophyll-a (Chl-a), Mean Sea Level Anomaly (MSLA), Latitude, Longitude and Year. All variables were highly significant but most of the CPUE variation was explained by the spatial factors. Model predictions were used to generate swordfish density distributions maps, which revealed that swordfish migrates toward the eastern Levantine for spawning and suggested the existence of a major spawning ground in a region between the islands of Cyprus and Rhodes surrounded by persistent eddies and the Rhodes gyre. During periods other than the time of spawning migration, swordfish distribution is

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Marine GIS Laboratory, Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Thalassocosmos, 71003 Heraklion, Crete, Greece much broader with relatively higher concentrations occurring in areas with important prey potential.

Keywords Swordfish · Mediterranean · Environmental parameters · Migration · Reproduction · Distribution

Introduction

The swordfish, *Xiphias gladius* (Linnaeus, 1758), is a commercially important highly migratory fish, globally distributed between the latitudes 45° N and 45° S (Palko et al., 1981). Mediterranean swordfish populations constitute a unique stock having different growth and maturity characteristics from the adjacent Atlantic ones (Cavallaro et al., 1991; Ehrhardt, 1992; Kotoulas et al., 1995, 2003; Tserpes & Tsimenides, 1995).

The swordfish fisheries in the Mediterranean are characterized by relatively high catch levels and the annual reported catches (on average 14,500 t from 1984 to 2002) are similar to those observed for larger marine areas, such as the North Atlantic (Anonymous, 2003).

The Greek swordfish fishery started developing in the early 1980s and Greek fleets currently exploit a large part of the E. Mediterranean basin extending their activities from the east Ionian to the Levantine Seas (Tserpes et al., 2003a, b). Fishing is carried out by means of two different drifting longline types: the traditional and the so-called American, owing its name to its similarity to the longline used by the USA fishery in the Atlantic. Detailed descriptions of the Greek swordfish fishery have been presented elsewhere (Tserpes et al., 2003a, b; Tserpes & Peristeraki, 2004). Recent ICCAT catch records indicate that Greece together with Italy, Spain and Morroco are the most important swordfish producers in the Mediterranean (Anonymous, 2006).

Although certain aspects of the biology and fisheries of the Mediterranean swordfish, such as age, growth, maturity and fishing tactics, have been examined (e.g., Cavallaro et al., 1991; Orsi-Relini et al., 1995; Tserpes & Tsimenides, 1995; De La Serna et al., 1996; Tserpes et al., 2001a, b, 2003a, b, 2006; Stergiou et al., 2003; Tserpes & Peristeraki, 2007), studies on the distribution of the fish in relation to biological and environmental parameters are limited and very little information has been provided on the species migration pattern (Tserpes et al., 2001b; Damalas et al., 2007; Peristeraki et al., 2007).

In the present work, we attempted to model seasonal spatial trends in swordfish abundance in the eastern Mediterranean as functions of environmental spatial and temporal variables. Those variables were: Sea Surface Temperature (SST), Chlorophyll-a (Chl-a), Mean Sea Level Anomaly (MSLA), Latitude, Longitude and Year. As swordfish has a near-surface distribution, at least during the night (Carey & Robison, 1981), we expected that SST will be important either as a direct influence on distribution or as a proxy for other factors (e.g., prey abundance). Chl-a level provides information on the primary production of an area, while MSLA is an indicator of possible oceanographic activities such as gyres and eddies. There may be spatial trends in abundance due to other reasons (e.g., topography of the area) than oceanographic parameters. Consequently, we included longitude and latitude as possible predictors. Finally, year was included as a predictor variable to account for abundance trends due to annual recruitment variations.

Abundance variations were modeled by means of Generalized Additive models (GAM) techniques (Hastie, 1990) commonly used for examining fisheries data in relation to environmental and spatiotemporal variables (e.g., Bigelow et al., 1999; Daskalov, 1999; Walsh & Kleiber, 2001; Maravelias & Papaconstantinou, 2003). Apart from exploratory purposes, GAM analysis was utilized in a predictive way, as the model estimates were used to construct density distribution maps of the swordfish in the studied area.

Materials and methods

CPUE and oceanographic data

A series of catch and effort data from the main Greek longline fleets exploiting the eastern Mediterranean basin have been gathered, past projects which sought to monitor the Greek large pelagic fisheries and since 2002, through the National Fisheries Data Collection Program established in accordance with 1639/2001 EU Regulation. Data were obtained from trained technicians located at the main landing ports or through onboard observations. Further details on the sampling scheme that has been followed are provided in Tserpes et al. (2003a).

In the present study, we used only datasets available on a trip basis and for which the fishing location could be identified on a fairly accurate basis, i.e., within a circle of 50 Km diameter, taking into account the length of the longline and its drifting potential. Catch per unit effort (CPUE) that was calculated from the available catch-effort data and expressed in terms of kg/1,000 hooks, was assumed to represent the local abundance index. As already mentioned, the Greek fishermen use two types of longlines that differ in catchability. For the needs of the current analysis, the CPUE series from the different gear-types were harmonized through the application of a multiplication factor previously identified from a large dataset (Tserpes & Peristeraki, 2004). Considering that gears have not changed in the last years, it was assumed that the already estimated catchability differences remain constant throughout the examined years.

The analyzed CPUE records were collected from 1998 to 2006. Based on the species biology and the fisheries characteristics, data were divided into three sets, representing different fishing periods: (a) the peak of the spawning period, i.e., June and July (Tserpes et al., 2001b), (b) two months before and after the spawning peak, when the fleets migrate toward and off the spawning grounds following the migration patterns of the fish, and (c) the rest months, representing the fish presence in the winter feeding grounds (Stergiou et al., 2003).

The oceanographic data used to characterize fish habitats included satellite-derived estimates of monthly averages of SST, Chl-a and MSLA for the corresponding fishing locations. AVHRR-SST (Advanced Very High Resolution Radiometer-Sea Surface Temperature) data were downloaded through DLR's (Deutsches Zentrum fur Luftund Raumfahrt) EOWEB Server (http://eoweb. dlr.de:8080/) as monthly averaged image products and were processed as ArcGIS grids.

Data analysis

The effects of environmental conditions, and fishing location on CPUE in the three aforementioned fishing periods were examined by means of Generalized Additive models (GAMs). GAMs, which are able to deal with nonlinear 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 pre-defined link function is related to predictor variables by scatter-plot 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). The span of the smoother, which determines the fraction of data used for smoothing at each point, was set at 0.2. Preliminary trials showed that this was the most suitable choice, as smaller span sizes were resulting in unrealistically bumpy and complex responses.

Based on the diagnostic residual plots of preliminary runs, we assumed a Poisson distribution accompanied by its canonical log-link function. Apart from the environmental parameters and the fishing location, the year parameter was also modeled as a categorical variable. Hence, six variables were included in the analysis: Year, Latitude (Lat), Longitude (Lon), SST, Chlorophyll (Chl-a) and MSLA. The GAM model was of the form:

$$CPUE = a + Year + lo_1(Lat) + lo_2(Lon) + lo_3(SST) + lo_4(Chl-a) + lo_5(MSLA) + e,$$

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

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 CPUE values from the GAM analysis were used to construct density distribution maps of the swordfish in the examined area. Maps were generated using the SURFER software (Golden Software, 2002) and interpolation was made by means of the "natural neighbor" griding method, which is considered to produce good contours for irregularly spaced data (Sibson, 1981). The method does not generate data in areas without data and contouring is based on an algorithm that creates different size polygons from the existing dataset. For this reason, the produced contours may not match exactly the sampled area.

Results

A total of 1,647 longline sets broadly distributed from $20-35^{\circ}$ E to $34-39^{\circ}$ N were analyzed (Fig. 1). Data covered 10,056 fishing days of 63 commercial boats. The three stepwise GAMs explained 46–59% of the total variation (Table 1) and all variables were highly significant (P < 0.0001). Spatial covariates (longitude, latitude) and the "year" accounted for a large part of the variance (40–48%), while MSLA had a relatively high explanatory power (16.30%) during the feeding period. Latitude provided the largest reduction in residual deviance in the migration and feeding periods, while longitude was the most important variable in terms of explanatory power during the peak spawning.

The effect (loess plot) of the spatial and environmental predictors that explained at least 2% of the total variation on CPUE is shown on the y-axis for





 Table 1
 Analysis of deviance for the GAM models fitted to the swordfish CPUE data by fishing period

Explanatory variable	Residual d.f.	Residual deviance	Cumulative variance explained in CPUE
Spawning			
Mean	480.00	82635.42	
Longitude	468.84	64217.27	22.29
Year	460.83	53404.53	35.37
Latitude	450.48	50273.84	39.16
MSLA	440.18	47665.50	42.32
SST	429.57	45872.56	44.49
Chl-a	418.06	44406.80	46.26
Migration			
Mean	826.00	165225.00	
Latitude	816.00	109900.10	33.48
Longitude	805.73	93979.90	43.12
Year	797.68	84744.10	48.71
SST	787.83	79358.20	51.97
Chl-a	777.36	77679.50	52.99
MSLA	767.25	76284.20	53.83
Winter feeding			
Mean	338.00	154697.50	
Latitude	327.38	114474.70	26.00
MSLA	316.47	89255.90	42.30
Year	309.38	75132.70	51.43
Longitude	298.70	67414.50	56.42
SST	287.41	64710.40	58.17
Chl-a	275.76	63024.60	59.26

different values of the predictor (*x*-axis) (Figs. 2–4). The zero line indicates mean CPUE estimated by the model, while the *y*-axis is a relative scale where the effect of different values of the predictors on the response variable is shown. Hence, negative values on the *y*-axis indicate that at the corresponding levels of the predictor (*x*-axis), the model estimates CPUE that is lower than the mean, while the opposite holds for positive values on the *y*-axis.

During the peak spawning period, catch rates showed their maximum between longitudes ca. 30 and 32° E and latitudes ca. $35-36^{\circ}$ N. Concerning SST, the maximum catch rate was around 22.5° C. MSLAs had a positive effect on catch rates only in a narrow range of values (2–3) although variations were rather small for values higher than -4(Fig. 2).

During the migration (transitional) period the loess plot of latitude exhibited a negative effect on catch rates from ca. 35° N northward. The effect was stronger beyond 39° N. Considering longitude, its effect was positive from ca. 27° E eastward. The most prominent feature of the loess plot of SST was its sharp decline after ca. 26° C (Fig. 3).

In the winter feeding period, there was a positive relationship between latitude and catch rate from 36° N up to ca. 39° N. Beyond 39° N, catch rates seem to decline. Catch rates were higher at the MSLA range of -2 to 2. In general, catch rate was increasing as the negative MSLA values were

Fig. 2 GAM derived effects on swordfish CPUE during the peak spawning period. 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





approaching zero. Longitude was positively related with catch rate from ca. 24° E eastward (Fig. 4).

The density distribution maps indicated that during the peak spawning period the highest swordfish biomass density is expected in the eastern Levantine basin in the region around 30° E and 35.5° N. In general, higher densities are expected from ca. 28° E eastward to 36° N southward. With some local exceptions, densities in the region north of 36° N are considerably lower (Fig. 5).

In the migration period, densities are also higher in the south-eastern region from ca. 30° E eastward to 36° N southward but maximum density is expected further east than during the peak spawning. Relatively lower but homogeneous density is observed in the rest area (Fig. 6). **Fig. 4** GAM derived effects on swordfish CPUE during the winter feeding period. 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

Effect on CPUE

Effect on CPUE

42

40

38

36

34

32

30

20

22

24

26

28

30

Longitude (East)

32

Latitude (North)

c

7



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The most prominent feature of the winter feeding period is the relatively high fish density north of 36° N. On the contrary, density is very low in the region which is south of ca. 36° N and west of ca. 27° E (Fig. 7).

Discussion

Our results indicated that in all seasons, the spatial and temporal variables played an important role in explaining swordfish abundance variations. Past authors who have studied the effects of spatial and environmental variables on swordfish abundance in various areas have also reported that spatial variables are of greater importance in explaining abundance variations (Bigelow et al., 1999; Damalas et al., 2007).

34

36

38

200

100

In general, in agreement with previous findings (Damalas et al., 2007), swordfish abundance was found to be higher in the eastern Levantine. In the present case, however, the use of the GAM predictions for constructing density maps enabled us to detect seasonal differences in the spatial distribution pattern. Such differences seem to be related, at least partly, to the species biological cycle.

Fig. 6 Map of swordfish distribution during the migration period, based on the GAM predictions. Abundance is expressed in terms of kg/1,000 hooks. Observations are depicted on the small map on the upper right corner; the diameter of the circles is proportional to the CPUE value



Fig. 7 Map of swordfish distribution during the winter feeding period based on the GAM predictions. Abundance is expressed in terms of kg/1,000 hooks. Observations are depicted on the small map on the upper right corner; the diameter of the circles is proportional to the CPUE value

The high swordfish density during the peak of spawning season between the islands of Cyprus and Rhodes provides indirect evidence for the presence of a major spawning ground in that region. This hypothesis is supported by the fact that the highest abundance rates are expected for SST ca. 22.5°C, which is within a preferred narrow temperature range during spawning (Palko et al., 1981). Results of a regional plankton survey, carried out in the Levantine Sea in July 2000 seem to support this hypothesis as it was found a small number of fertilized swordfish eggs in the samples (Tserpes et al., 2001a, b).

The available information on the reproductive activity of the Mediterranean swordfish is rather limited. Spawning occurs in the summer months and since the beginning of the twentieth century it is known the presence of a spawning ground in the Straits of Sicily (Palko et al., 1981; Cavallaro et al., 1991). Rey (1988), based on the capture of few young specimens along the Spanish Mediterranean coast, has also speculated the presence of a spawning ground in the area. Large-scale ichtyoplankton surveys for large pelagic species are lacking in the eastern Mediterranean and the fact that large pelagic larvae are able to avoid the typical plankton samplers (Doherty, 1987) makes difficult the identification of spawning grounds through general plankton surveys.

Mejuto et al. (1995, 1998) who revised literature information on spatiotemporal variation of swordfish sex ratio in commercial catches from the Atlantic and the Indian oceans suggested that a male biased sex ratio, in certain size ranges, is typical for several spawning areas. Tserpes et al. (2001a, b) have also reported a similar male biased sex ratio, regarding individuals of lower jaw fork length greater than 120 cm, in commercial catches of the eastern Levantine basin during the spawning period and suggested the possible existence of a major spawning ground in the broader area. The current approach has provided more specific information on the location of the spawning ground which seems to be located near the Anaximander seamounts, at an area between the Anaximander eddy, the Antalya eddy and the Rhodes Gyre, which is one of the most distinct features of the Levantine basin (Ozsoy et al., 1993; Zervakis et al., 2005). According to Bakun (2006), zones situated near eddies outer edges often produce outbursts in biological productivity and in some cases support spawning of highly migrating fishes.

Although, the effect of environmental variables was always significant, their explanatory power was relatively lower, with the exception of MSLA during the winter feeding period, when it explained about 16% of the total variance. Further examination of the MSLA values in the studied area revealed that the MSLA range which corresponds to high swordfish density values in the feeding period is found in areas surrounding eddies. These zones are often characterized by high productivity (Bakun, 2006) and it is likely that high concentrations of swordfish prey occur in such areas, supporting the hypothesis that swordfish abundance variations are closely related to prey availability during the winter feeding period. It is notable that in the above period, swordfish appear in relatively high densities in the northern part of the Aegean Sea (north of 36° N), where their presence is infrequent in the rest of the year.

Our analysis suggest that swordfish in the eastern Mediterranean migrates toward the eastern Levantine for spawning, concentrating in specific areas during the peak of the spawning season. During the migration period (i.e., the months before and after the reproduction peak) high abundance indices are observed only in the wider area of the proposed spawning ground providing further support on the hypothesis of existence of a major spawning ground in the Levantine basin. In the rest of the year, swordfish spatial distribution is much broader with relatively higher concentrations occurring in areas with important prey potential.

As fisheries management in the Mediterranean is mainly realized through technical measures and effort control regimes, distribution studies can provide useful background information regarding the potential establishment of fisheries limitations on certain essential habitats. The present study has provided information on swordfish distribution in a region of high fishing activity. Such information could be utilized for the rational management of the resource. In particular, this study may become of major importance if recent inferences based on genetics findings (Kotoulas, Hellenic Centre for Marine Research, personal communication) that swordfish in the eastern Mediterranean form a unique substock are corroborated.

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