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Dimitrios Damalas[a][b] & Persefoni Megalofonou[b]

[a] European Commission, Joint Research Center, Institute for the Protection and Security of the Citizen (IPSC), Maritime Affairs Unit, FISHREG, Scientific Support to Fisheries, Ispra (VA), Italy

[b] Faculty of Biology, Department of Zoology-Marine Biology, University of Athens, Panepistimiopolis, Ilissia, Athens, Greece

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DIMITRIOS DAMALAS[1,2] and PERSEFONI MEGALOFONOU[2]

[1]European Commission, Joint Research Center, Institute for the Protection and Security of the Citizen (IPSC), Maritime Affairs Unit, FISHREG, Scientific Support to Fisheries, Ispra (VA), Italy
[2]Faculty of Biology, Department of Zoology-Marine Biology, University of Athens, Panepistimiopolis, Ilissia, Athens, Greece

Based on fisheries data from the 1990s and 2000s in the eastern Mediterranean Sea, generalized additive models were applied to investigate the relative influence of environmental factors on swordfish catch rates. (1) Young-of-the-year swordfish and (2) the remaining "adult" swordfish were modeled separately. Results suggested that the two stock components differentiated significantly: adults were more abundant to the south-east (Levantine basin), at the open seas, showing a clear relationship to cooler water masses. In contrast, juveniles were more frequently observed to the north-west (Ionian Sea), close to the coast, in warmer waters. Seasonally, juvenile swordfish were more abundant during the start and end of the fishing period, and during years of elevated water temperature. Lunar disc illumination affected positively all year classes; maximum catches observed around full-moon. The proportion of large swordfish decreased significantly throughout the study period, indicating a change in size-structure of the population or availability to the fishing gear. There were strong indications that the Ionian and Levantine may actually constitute favorable spawning grounds. Based on the models suggested associations, an indirect identification of the swordfish potential habitats was obtained. It was further considered how size-dependent habitat delineation could form the basis for a more realistic management approach, through the introduction of spatio-temporal closures of fishing activities.

Keywords swordfish, Mediterranean, GAM, habitat, environmental, management

1. INTRODUCTION

Broadbill swordfish, *Xiphias gladius* (Linnaeus, 1758), is a large pelagic oceanic species, with a high market value. To date at least 27 countries participate in the swordfish catch and the annual global take is estimated to be about 80,000 tons (t). Mediterranean production fluctuated between 12,000–16,000 t during the past decade, with the main producers in 2008 being Italy (4549 t), Spain (2095 t), Morocco (1957 t), Tunisia (1011 t) and Greece (962 t) (ICCAT, 2011).

In the eastern Mediterranean, swordfish are predominantly caught (as target) by surface drifting long-lines (ICCAT, 2011); this fishery is probably the most spatially extensive economic activity in this region, making it ideal for a large scale study. The fishery has been operating mainly by the Italian and Greek long-line fleets, since the late 1960s, at depths from the surface down to about 50 m (De Metrio et al., 1988; Tserpes et al., 1993; Ward et al., 2000; Megalofonou et al., 2005).

Address correspondence to Dimitrios Damalas, European Commission, Joint Research Center, Institute for the Protection and Security of the Citizen (IPSC), Maritime Affairs Unit, FISHREG, Scientific Support to Fisheries, TP 051, I-21027 Ispra (VA), Italy. E-mail: shark@hcmr.gr; dimitrios.damalas@jrc.ec.europa.eu

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Since 1996, North Atlantic swordfish has been listed as endangered in International Union for Conservation of Nature (IUCN) "Red Data List" of threatened animals. This estimation was attributed to poor management that was ineffective in preventing over-fishing. Management actions have more or less reversed this negative trend during the recent years and currently the Atlantic populations are considered to be in a recovery phase (Neilson et al., 2013). However, in the Mediterranean, estimates of the swordfish stock status indicated a 40% reduction in spawning stock level over the past 20 years. This very low level, combined with the very high fishing mortality rates is giving rise to "non-negligible" risks of rapid future declines in the stock (ICCAT, 2008, 2011). Despite the enforcement of a minimum landing size (MLS) for all swordfish caught by the EU member state fleets (120 cm lower jaw fork length; EC, 1994), which was in action till recently (EC, 2006), still 50 to 70% of the Mediterranean landings consisted of immature fish that have never spawned (Ward et al., 2000; De Metrio et al., 2001).

Recently, it was suggested that instead of applying an ineffective maze of technical measures, a more simple/radical management alternative would be to establish a series of Marine Protected Areas (MPAs; Tudela, 2004; Stergiou et al., 2009; UNEP-MAP-RAC/SPA, 2010). However, demarcating such no-fishing zones for habitat conservation requires identification of areas where marine life flourishes. More specifically, the essential fish habitats (EFH) of pelagic species may be defined by oceanographic features, such as productive areas associated with upwelling. In the Mediterranean UNEP-MAP-RAC/SPA (2010) has indicated that spawning areas and migratory routes of bluefin tuna, swordfish, and albacore should be considered of high conservation interest.

The main goal of this study was to deliver an indirect identification of the swordfish potential habitat in the eastern Mediterranean region, by investigating the influence of certain environmental, spatial, temporal, and operational parameters on the catch rates of juvenile and adult swordfish. To reach this objective commercial swordfish fishery catches from the 1990s and 2000s were analyzed on a monthly basis.

2. MATERIALS AND METHODS

2.1. Study Area—Fishery

The Mediterranean is a temperate semi-enclosed sea with increased salinity and pronounced oligotrophy due to small amounts of discharge from land. There is a marked nutrient gradient, decreasing to the southeast, attributed to the incoming nutrient flow from the Black Sea, eastern Atlantic, and the European rivers (Caddy, 1998; Wurtz, 2010). The easternmost part comprises three large areas: Ionian Sea, Aegean Sea, and the Levantine (Figure 1). The Levantine is considered one of the most oligotrophic regions of the world oceans (Stergiou et al., 1997).

Swordfish longlining is conducted in Greece and Cyprus by almost 300 vessels, most of them involved occasionally,

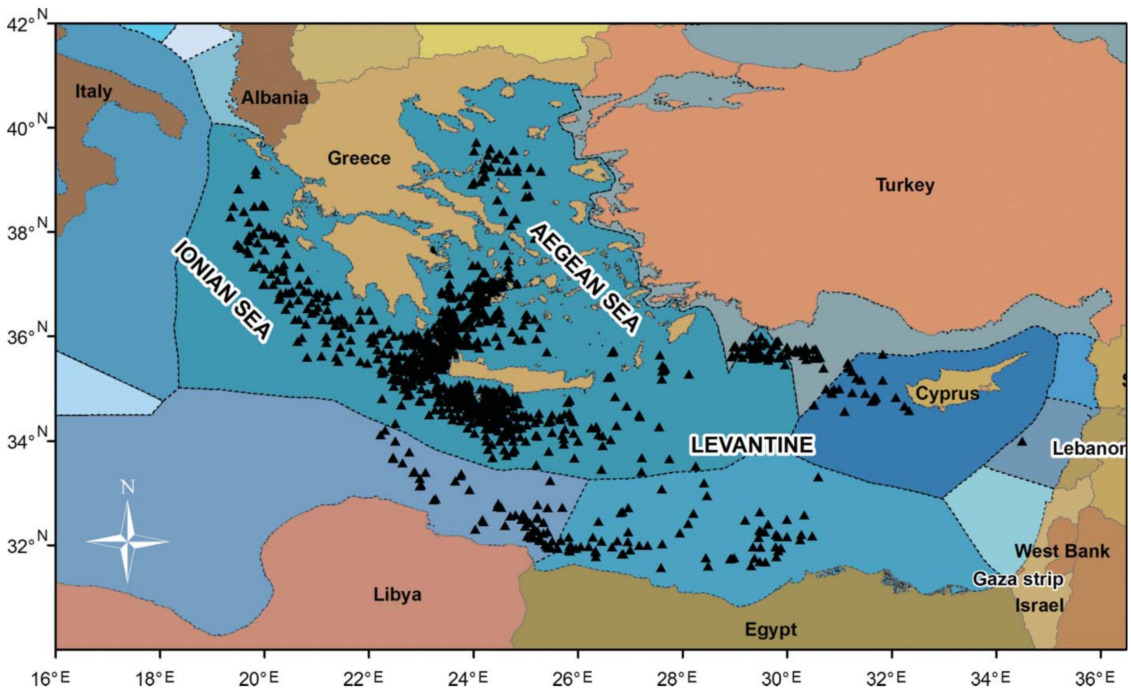

Figure 1 Map of the study area in the south-eastern Mediterranean Sea. Fishing locations are indicated by black solid triangles. Shaded marine regions designate potential Exclusive Economic Zones (EEZ) as provided by Flanders Marine Institute (VLIZ). Available from http://www.vliz.be/vmdcdata/marbound/. (To date, very few Mediterranean countries have claimed an EEZ.)

during the summer months (ICCAT, 2011). During 1998 and 2005, data were collected from a subset of the Greek and Cypriot commercial fleets targeting large pelagic fish in the eastern Mediterranean Sea (Ionian Sea, Aegean Sea, and Levantine basin—Figure 1). Two fishing gears were in use by the fleets at the time, all of them classified as surface drifting longlines: (i) traditional swordfish longline (SWO-LL) and, (ii) "American" type swordfish longline (SWO-LL Amer.). Detailed information regarding gear configuration, as well as hauling and retrieving tactics, can be found in Megalofonou et al. (2005). Data were obtained on board the vessels, as well as at their landing ports. Samplings were conducted on a monthly basis throughout the fishing period (March–September). In total, 38 fishing boats operating from 22 major fishing ports were monitored (Table 1).

Observers monitored fishing and operational data by: recording spatial and temporal variables (name of fishing boat, gear used, fishing sets per trip, date, and exact geographical coordinates of each fishing set—as determined by GPS, fishing effort for each fishing set—number of hooks), and identifying and measuring fish kept or discarded (in number and weight of fish per fishing set by species). Bottom depth, wind speed, distance from coast, lunar index, sea surface temperature (SST), SST frontal energy (SST gradient), and chlorophyll-a data were assigned to all sets based on the exact date and coordinates (Table 2).

Relative abundance of swordfish was approximated by the nominal catch-per-unit-effort (CPUE), which is a fishery performance index representing the success of fishing from commercial fishery statistics. The following explicit assumptions were made: (i) fishery performance can approximate, reasonably, the relative abundance at sea (Marr, 1951), and (ii) commercial fishery statistics is a fishery performance index (Ricker, 1975). CPUE values were calculated as number of fish/1000 hooks deployed. Fishing (soaking) time was assumed to be roughly constant; the gear was usually deployed at dusk and retrieved before sunrise.

2.2. *Statistical Analyses—Modeling*

The functional relationships between population density of marine species and environmental variables are neither linear nor monotonic (e.g., Bigelow et al., 1999). Assuming an inherent non-linearity, generalized additive models (GAMs; Hastie and Tibshirani, 1990) were applied to identify influential variables, reveal the form of the relationships, and quantify their effect on the relative index of abundance (CPUE). The selected models may serve as a preference indicator for the studied environmental variables (Kupschus, 2003) and can be associated to the underlying ecological processes (Austin, 2007). Implementation was done in R v.3.0.3 (R Core Team, 2014) using the package mgcv (Wood, 2000, 2006), according to the general formulation:

$$f(E[CUE_i]) = LP_i = c + \sum_m s_m(Z_{mi}),$$

where f is the link function, LP is the linear predictor, c is the intercept, $s_m()$ is the one-dimensional smooth function of covariate Zm, and Zm_i is the value of covariate m for the ith observation (Wood, 2006). The smooth function $s_m()$ was represented using penalized regression splines (cubic splines with basis dimension $q = 10$), estimated by penalized iterative least squares (Wood, 2006). Identification of the underlying probability distribution for the errors in the dependent variable (CPUE) was performed using the Akaike information criterion (AIC-Akaike, 1973). After selecting the appropriate error distribution family, an information theoretic approach was followed (Burnham and Anderson, 2002) to discriminate among the best model including the most influential parameters affecting catches. A set of pre-defined candidate models (see Table S.1 in the Supplemental Material) were investigated, and the optimum one was selected on the basis of its GCV score (generalized cross validation criterion; Wood, 2006). Year, month, and gear were forced to be present in all models, as potentially significant predictor variables of relative population density (Nakamura, 1969). No statistically significant correlation ($p < 0.05$) was evident between any pair of variables included in the candidate models.

Mediterranean swordfish is a fast growing species in the first year of its life when it can grow up to 100 cm in lower jaw fork length; in the following years growth rate decelerates markedly (Megalofonou et al., 1995; Tserpes and Tsimenides, 1995; Ward et al., 2000). Additionally, at this age the first mature individuals occur, although the size at which at least

Table 1 Number of ports, vessels, fishing sets, hooks deployed and swordfish caught by fishing gear in the eastern Mediterranean Sea surface drifting long-line fishery, during 1998–2005 (ports and vessels overlap between fishing gears)

Fishing gear	Nb ports	Nb vessels	Fishing sets	Average hooks per set	Nb young-of-the-year caught	Young-of-the-year as % of total catch	Nb adults caught	Adults as % of total catch	Total Nb swordfish caught
$SWO\text{-}LL_T$	12	12	283	1021.6	249	19.1	1052	80.9	1301
$SWO\text{-}LL_A$	16	32	978	505.7	398	7.2	5161	92.8	5559
Total	22	38	1261	621.5	647	9.4	6213	90.6	6860

Nb: number; $SWO\text{-}LL_T$: traditional swordfish long-line; $SWO\text{-}LL_A$: American type swordfish long-line.

Table 2 Summary of environmental parameters specifications included in the analyses

Parameter	Source	Raw data format	Units	Temporal resolution	Spatial resolution	Processed using
SST	NOAA[a] and GISIS-DLR[b]	Binary data	ºC	Daily	1.1 km	MATLAB[c]
SST gradient	NOAA[a] and GISIS-DLR[b]	Binary data	°C/km	Daily	1.1 km	MATLAB
Salinity	IRI Climate library[d]	Binary data	psu	Daily	0.5 degrees	MATLAB
Lunar index	RAJE software	Binary data	0–1 (0 = new moon 1 = full moon)	Daily	—	"Focus on Today"[e]
Bathymetry	NOAA Lab for satellite altimetry	Binary data	meters (below ocean surface)	—	1.5 km	MATLAB
Distance from coast[f]	NOAA Lab for satellite altimetry	Binary data	Nautical miles	—	1.5 km	MATLAB
Wind speed	CERSAT/IFREMER[g]	Binary data	m/sec (horizontal and vertical constituents)	Weekly	0.5 degrees	MATLAB
Chl-a	NASA SeaWiFS[h]	Binary data	mg/m^3	Daily	0.08 degrees	MATLAB

[a]NOAA (National Oceanic and Atmospheric Administration). SST gradient was calculated as the value of the gradient function in each fishing location taking into account the SST values of the surrounding area. Since we had binary data, it was preferred over the most commonly used "Sobel" operator, which is an image-detecting algorithm.
[b]GISIS-DLR (Graphical Interface to the Intelligence Satellite data Information System—Deutsches Zentrum für Luft und Raumfährt e.V.)
[c]MATLAB is a registered software of Mathworks Inc. Version 5.2.0 was used.
[d]IRI (International Research Institute) Climate library is a cooperative agreement between NOAA's Climate Program Office and Columbia University.
[e]"Focus on Today" is a freely available software by RAJE Software.
[f]Distance from coast was estimated locating the nearest land pixel (bottom depth > 0) based on the bathymetry data and calculated the straight line between the two points in nautical miles (after corrections due to the earth's spheroid shape).
[g]Centre ERS d'Archivage et de Traitement - IFREMER (French Research Institute for Exploitation of the Sea).
[h]SeaWiFS (Sea-viewing Wide Field-of-view Sensor) NASA OceanColor Web.

50% of the population is expected to be mature is estimated to 110 cm for males and 142 cm for females (SIDS, 2002; ICCAT, 2008). Obviously the maturation of animals has a dramatic effect on physiology and hence their behavior (e.g., commence of annual migrations). Consequently, swordfish resource abundance was investigated by separately modeling the catches of: (1) young-of-the-year juvenile fraction of the population (Lower Jaw Fork Length ≤ 100 cm) and (2) the remaining "adult" part of the population (Lower Jaw Fork Length > 100 cm). The term "adult" will be used throughout the text to indicate all swordfish with LJFL > 100 cm.

Following the methodology recently applied on Mediterranean bluefin tuna (Damalas and Megalofonou, 2012) and based on the GAM selected models, spatial estimations of catch rates were derived in the form of gridded matrices for the whole study area. The eastern Mediterranean marine region (31°–41° North, 18°–35° East) was gridded in a spatial resolution of 1/10 × 1/10 of a degree, concluding to a total of 11,471 grid cells (land excluded). Each one of these cells was assigned the corresponding values for each of the model parameters. Implementation was done using *predict.gam()* function of the mgcv package (Wood, 2006). Predicted values were accompanied by the corresponding standard errors (SE), serving as indications of the uncertainty around the estimate. For each prediction, the Relative Standard Error (RSE; SE expressed as a fraction of the estimate, in percentage) was calculated, as well as the number of prediction cells in a prediction matrix with an RSE of 25% or greater. Such predictions, with high RSE, are subject to high sampling error and should be dealt with caution (Efron, 1981). For facilitating the predictive procedure, lunar index was transformed from a continuous variable to a four level categorical factor (0.00 → 0.25 new moon; 0.25 → 0.75 first and last quarters; 0.75 → 1.00 full moon). Taking into account the different levels of the four categorical factors, a series of 392 different combinations were drawn (2 gears × 7 years × 7 months × 4 lunar phases). Each one of these prediction matrices included estimates of both young-of-the-year and adult swordfish, for a certain combination of gear, year, month, and lunar phase. With the intention to visualize the results, these matrices of gridded spatial predictions, were stored as Geographical Information System (GIS) raster datasets and mapped using ESRI's ArcMap desktop GIS software. Finally, trends in body size of swordfish captured were identified by examining the annual trend in the lengths of the large fish and specifically the average 90th percentile of the length distribution (average length of the large fish making up less than 10% of the sample). The annual rate of change was expressed by the slope of a linear regression when the average 90th percentiles of lengths were regressed upon year (least squares method; Zar, 1996).

3. *RESULTS*

3.1. *Nominal CPUE*

A total of 1261 fishing sets (123 on board, 1137 at landing locations) were monitored during the seven-year period of this study. Observers reported a total of 6860 swordfish, 647 young-of-the-year, and 6213 adults, comprising an impressive 91% of total catch, confirming the high selective nature of the surface drifting longlines targeting swordfish. By-catch species mostly comprised of bluefin tunas, oilfish, and large pelagic sharks. Monthly nominal CPUE values ranged from 0.4 to 1.6 swordfish/1000 hooks for young-of-the-year and from 1.8 up to 12.8 swordfish/1000 hooks for adult swordfish, depending on the fishing gear (Table 3).

3.2. *Young-of-the-Year Swordfish (LJFL ≤ 100 cm)*

Investigating different error distributions for the "full" model (all variables included), AIC's supported the use of a Gamma distribution with a log link function. Assuming a Gamma(log) distribution for the underlying dataset, a series of candidate models (Table S.2) was examined and analysis based on GCV scores revealed that a model including eleven variables, was the best to describe the data (Table 4):

f (E[CPUE]) = c + a_1Fishing gear type + a_2Year + a_3Month + s_4(Longitude:Latitude) + s_5(Distance from coast) + s_6(SST) + s_7(SSTgradient) + s_8(Lunar index) + s_9(Chl-a) + s_{10}(Salinity).

In total, the derived model explained 29.3% of the variance in juvenile swordfish CPUE. The temporal factors (year and month) had the predominant effect on relative resource abundance. Monthly effect on CPUE, revealed a U-shaped form, with peaks during the start and end of the fishing period (Figure 2, bottom left). The annual effect demonstrated a rapid decline during the three first years and then became more or less stable (Figure 2, mid left). SST plot dictated that catches were more common in warmer surface waters (Figure 2, mid top). Distance from coast, embracing both spatial and environmental properties as an explanatory variable, showed a positive trend in favor of coastal areas: more young-of-the-year swordfish were more likely to be detected in the vicinity of land (Figure 2, mid middle). Young swordfish also exhibited a tendency to avoid regions with high Chl-a concentration and showed a preference for more saline water masses (Figure 2, bottom middle and right). Lunar index had a minor influence in the model, however the probability of elevated swordfish densities increased monotonically with lunar light intensity (Figure 2, mid right). The effect of SST gradient (thermal fronts) was not statistically significant, although the fitted values plot gave indications of considerable association (Figure 2, top right). Geographical location played an important role; interaction of Longitude with Latitude indicated a strong spatial gradient in the presence of young-of-the-year swordfish, the probability increasing to the northwest (Ionian Sea) (Figure 2, extreme right).

3.3. *"Adult" Swordfish (LJFL > 100 cm)*

As with the young-of-the-year swordfish dataset, a Gamma (log) distribution was selected, and the following model was suggested as the most suitable (Table S.3 and Table 4):

f (E[CPUE>0]) = c + a_1Fishing gear type + a_2Year + a_3Month + s_4(Longitude:Latitude) + s_5(Distance from coast) + s_6(Lunar.index) + s_7(SST:Year).

Table 3 Effort (Nb of hooks), fish captured, and nominal CPUE values (number of fish/1000 hooks) by fishing gear and month for swordfish caught in the eastern Mediterranean Sea surface drifting long-line fishery, during the period 1998–2005

	Month							
Fishing gear	Mar	Apr	May	Jun	Jul	Aug	Sep	Total
SWO-LL$_T$								
Nb hooks (×1000)	8.8	8.0	55.8	46.3	46.0	54.7	69.7	289.1
Nb young-of-the-year swordfish	12	4	70	72	28	33	30	249
CPUE (Nb/1000 hooks) young-of-the-year swordfish	1.4	0.5	1.3	1.6	0.6	0.6	0.4	0.9
Nb adult swordfish	38	24	172	84	163	244	327	1052
CPUE (Nb/1000 hooks) adult swordfish	4.3	3.0	3.1	1.8	3.5	4.5	4.7	3.6
SWO-LL$_A$								
Nb hooks (×1000)	34.3	34.2	81.2	92.4	108.5	61.1	77.0	488.6
Nb young-of-the-year swordfish	21	9	44	65	96	71	92	398
CPUE (Nb/1000 hooks) young-of-the-year swordfish	0.6	0.3	0.5	0.7	0.9	1.2	1.2	0.8
Nb adult swordfish	369	320	753	847	1212	677	983	5161
CPUE (Nb/1000 hooks) adult swordfish	10.8	9.4	9.3	9.2	11.2	11.1	12.8	10.6
Total								
Nb hooks (×1000)	43.0	42.1	136.9	138.7	154.5	115.8	146.7	777.7
Nb young-of-the-year swordfish	33	13	114	137	124	104	122	647
CPUE (Nb/1000 hooks) young-of-the-year swordfish	0.8	0.3	0.8	1.0	0.8	0.9	0.8	0.8
Nb adult swordfish	407	344	925	931	1375	921	1310	6213
CPUE (Nb/1000 hooks) adult swordfish	9.5	8.2	6.8	6.7	8.9	8.0	8.9	8.0

SWO-LL$_T$: traditional swordfish long-line; SWO-LL$_A$: American type swordfish; CPUE: Catch per unit of effort.

Table 4 Summarized results of the best models selected for the swordfish caught in the swordfish long-line fishery of the eastern Mediterranean Sea. (Pr(*F*) refers to the p-values from an ANOVA F-ratio test; Edf are the estimated degrees of freedom). An upwards arrow indicates that the dependent variable increases as the independent one increases. A downwards arrow indicates that the dependent variable decreases as the independent one increases.

Young-of-the-year swordfish (≤100 cm LJFL)				“Adult” swordfish (>100 cm LJFL)			
	Error distribution	Gamma	Trend		Error distribution	Gamma	Trend
Link function	log			Link function	log		
Edf	37.9			Edf	18.2		
% of Deviance explained	29.3			% of Deviance explained	48.9		
Pr(*F*)	Gear	0.025	no obvious difference	Pr(*F*)	Gear	<0.001	$SWO\text{-}LL_A > SWO\text{-}LL_T$
	Year	<0.001	↓		Year	<0.001	unclear
	Month	<0.001	U shaped		Month	<0.001	autumn peak
	Long:Lat	<0.001	peak in the Northwest (Ionian Sea)		Long:Lat	<0.001	peak in the Southeast (Levantine)
	Distance from coast	0.017	↓		Distance from coast	0.049	↑
	SST	<0.001	↑		Lunar.index	0.010	↑
	SST.gradient	0.069	↑ (n.s.)		SST:Year	<0.001	peak in cooler waters, most of the years
	Lunar.index	0.041	↑				
	Chl-a	<0.001	↓				
	Salinity	0.005	↑				

n.s.: non significant; $SWO\text{-}LL_T$: traditional swordfish long-line; $SWO\text{-}LL_A$: American type swordfish.

The model explained 48.9% of the variance in adult swordfish CPUE (Table 4); most influential parameters being: Gear, Month, SST:Year interaction, and Long:Lat interaction. Fishing gear-type effect was the most significant variable affecting the catch rates of adult swordfish. The American type swordfish long-line displayed superiority in catching large swordfish (Figure 3, top left); large specimen exhibited a noticeable vulnerability to this gear. Large swordfish abundance by month, showed a seasonal peak in early autumn (Figure 3, bottom left). The year effect, although contributing significantly to the model convergence, demonstrated an unclear fluctuating trend (Figure 3, mid left). However, its interaction with SST revealed a clear relationship with cooler water masses, in some years more conspicuous than others (Figure 3, top right). Spatial interaction (Longitude : Latitude) was highly significant and the response surface in the three-dimensional XYZ space (X = longitude, Y = latitude, Z = response) gave evidence of increased probability for large numbers in the south-easternmost regions (Figure 3, top middle). Distance from coast, showed a positive trend in favor of open sea waters: larger swordfish were more likely to be detected far from land (Figure 3, bottom right). The likelihood of coming across a larger swordfish exhibited a periodicity analogous to the lunar cycle, reaching higher values during full moon (Lunar index 75–100%) (Figure 3, bottom mid).

The combined plot of GAM standardized catch rates values, for both adults and young-of-the-year swordfish, indicated an association between them; a strong year class of juveniles was followed by an increased abundance of larger swordfish during the succeeding year (Figure 4).

Finally, investigating the presence of large individuals in the catches, it was clear that the proportion of large swordfish declined significantly throughout the study period. The slope of the linear regression relating the average 90th percentile of the length distribution with year was negative and highly significant ($p < 0.01$) (Figure 5).

3.4. Mapping of Potential Habitat

By averaging over all years studied (1998–2005) a series of monthly maps was delivered (Figures 6 and 7 show predictions referring to a lunar index of 0.5 and American type swordfish long-line fishing gear, averaged over 1985–2005). The visualized predictions accuracy was assessed on the basis of RSEs (Table 5). March was usually the month for which a

Table 5 Proportions of relative standard errors (RSE) above 25% for the monthly prediction matrices

	% of prediction cells with RSE > 25%	
Month	Young-of-the-year swordfish (LJFL ≤ 100 cm)	‘Adult’ swordfish (LJFL > 100 cm)
March	7.90%	0.02%
April	3.59%	<0.01%
May	2.33%	<0.01%
June	1.76%	<0.01%
July	1.62%	<0.01%
August	0.73%	<0.01%
September	0.71%	<0.01%

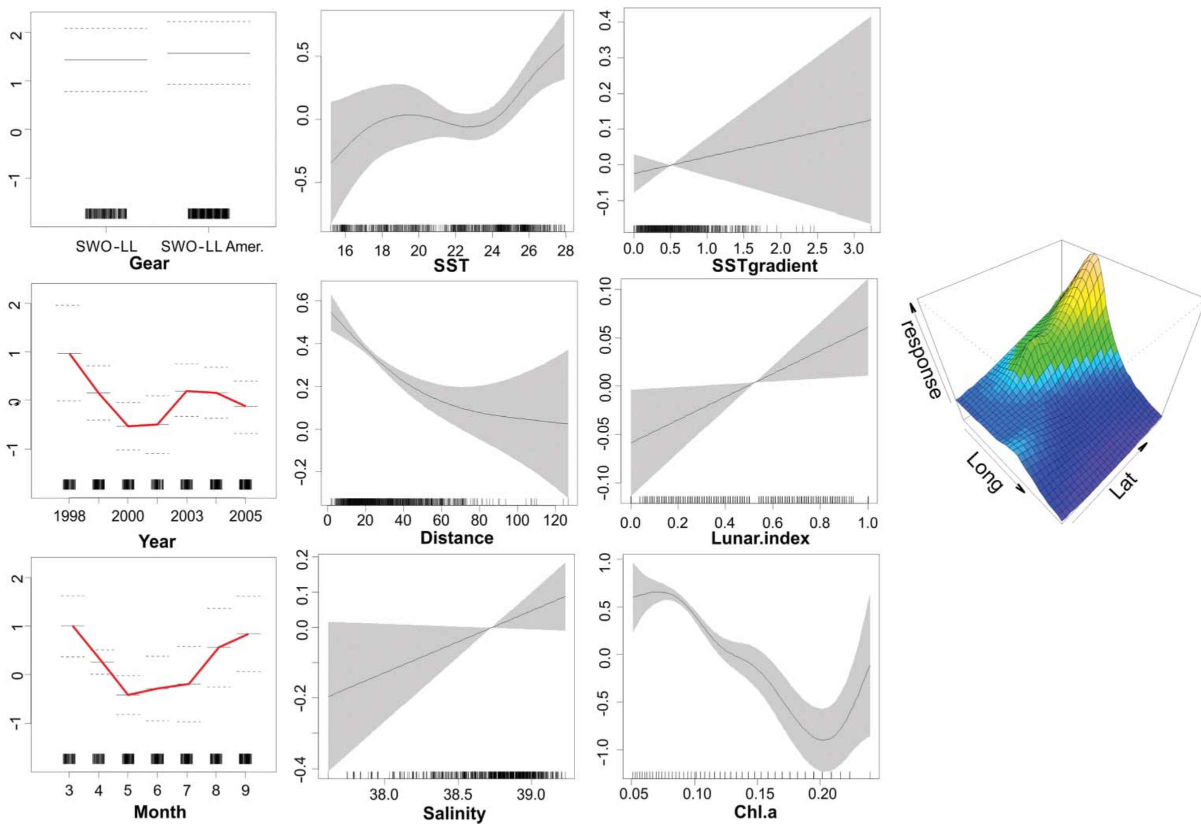

Figure 2 Generalized additive model (GAM) derived effects of the investigated parameters on the young-of-the-year swordfish catch rates. Upper-lower brackets and shaded areas indicate two standard errors above and below the estimates. Relative density of data points is shown by the "rug" on the X-axis.

part of the predictions was associated with a great deal of uncertainty. This approach was recently applied to map the potential habitat of bluefin tuna in the eastern Mediterranean (Damalas and Megalofonou, 2012). These prediction maps represent a potential or suitable habitat, as indicated by the linkage between oceanic features and commercial fishing success at specific locations and for fixed lunar phases and fishing gear types. The maps, more or less, illustrate visually the trends identified in the best models (Table 4). Young-of-the-year swordfish catch rates estimates demonstrated an elevated presence during the start of the fishing period (March), associated however by large standard errors (Figure 6). In general, catch rates values for young-of-the-year peaked around August–September with a persistent presence to the west (Ionian Sea). Elevated values in the N. Aegean region were not statistically significant. Unfortunately, the winter closure of the fishery did not allow for observing swordfish abundance in its full annual cycle. Strong presence of adults to the southeast was consistent throughout the fishing period, with a peak around the summer months (Figure 7). Obviously, large swordfish were more frequently observed in the Levantine than any other marine region.

Furthermore, the maps delineate regions of low model predictive power. Elevated standard errors (or RSEs) were consistently noticed in certain marine regions: in the easternmost areas (off the Middle East coast) and seasonally in the north Aegean and Sea of Marmara (Figures 6 and 7). One obvious reason was the low number of observations available in these areas (Figure 1), making model predictions imprecise.

4. DISCUSSION

To protect species and conserve stocks, managers require information on the resource distribution, which will enable them to identify the areas of most suitable habitat (Rubec et al., 1999; EC 2008). Knowledge on the spatial dynamics of species is vital for management, since marine spatial planning is based on the definition of management units, stocks, and boundaries (Fromentin and Powers, 2005). Commercial fishery-dependent surveys, like the one undertaken herein, can be useful in identifying (indirectly) the potential habitat, by associating environmental preferences and catch rates, providing an early habitat proxy defined from the available data. Actual habitat selection is based on more complex aspects such as behavioral characteristics, physiological tolerances, and predator-prey interactions (Planque et al., 2010).

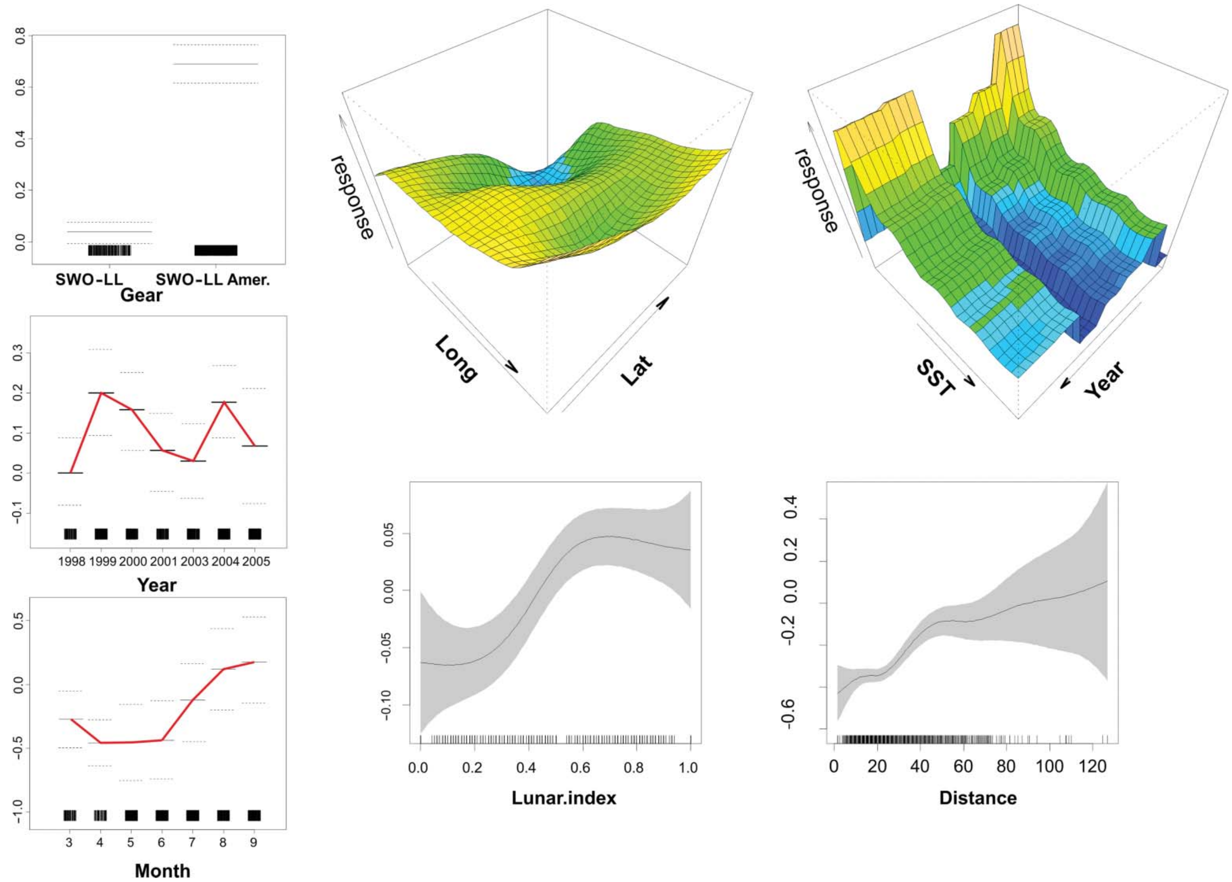

Figure 3 Generalized additive model (GAM) derived effects of the investigated parameters on the adult swordfish catch rates. Upper-lower brackets and shaded areas indicate two standard errors above and below the estimates. Relative density of data points is shown by the "rug" on the X-axis.

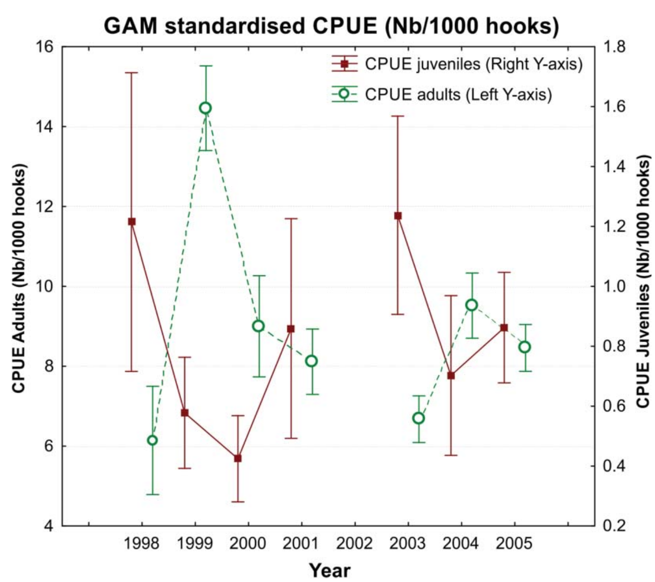

Figure 4 Annual GAM standardized mean catch rates (Nb fish/1000 hooks +/– 95% confidence intervals) for young-of-the-year (right Y-axis) and adult swordfish (left Y-axis) in the eastern Mediterranean Sea.

4.1. Catch Rates

Values of relative abundance (CPUE) observed in the present study fell within the range reported by similar studies in the world's oceans. ICCAT (2008), in the Atlantic, between 1981 and 2005, cites rates of 3–17 fish per 1000 hooks with a mean value of 6 fish per 1000 hooks. Bigelow et al. (1999) in the North Pacific refer to values between 5 and 20 swordfish per 1000 hooks, while Guyomard et al. (2004) in the Indian Ocean mention an average value of 9 fish/1000 hooks. In the Mediterranean, published values vary between areas: in the W. Mediterranean values range from 3–25 fish per 1000 hooks (Buencuerpo et al., 1998; Megalofonou et al., 2000; Ortiz de Urbina et al., 2004); in the central Mediterranean catch rates observed go from 2 up to 25 fish/1000 hooks (Megalogonou et al., 2000; De Metrio et al., 2001; Orsi-Relini et al., 2008); in the eastern regions CPUE ranged from 3 to 16 fish/1000 hooks (De Metrio et al., 2001) and 49–156 kg/1000 hooks (Tserpes and Peristeraki, 2003). It is impressive that Mediterranean swordfish catch levels are comparable to those of the North Atlantic (averaging ∼12,000 t annually), despite the Mediterranean being a much smaller water body (Ward et al., 2000).

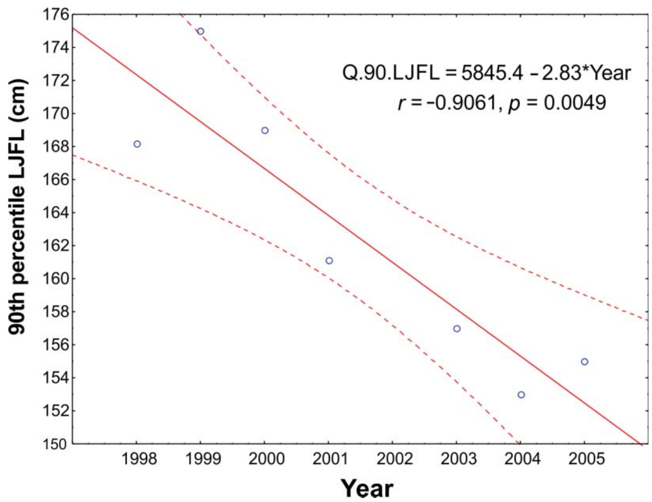

Figure 5 Annual trend of large fish size (0.90 quantiles of LJFL) as inferred from the slope of a linear regression of the 90th percentiles of LJFL upon year. Open circles depict the average 90th percentile of the length distribution. Dashed lines indicate centered 95% confidence intervals.

4.2. Young-of-the-Year Swordfish (LJFL ≤ 100 cm)

The high values of CPUE in late summer-early autumn should be considered as the result of a large numbers of juveniles entering the recruitment phase. The peak of spawning season in the Mediterranean usually includes the month of June and July (De Metrio et al., 1988; Megalofonou et al., 1990; Tserpes et al., 2001). As mentioned before, swordfish is a fast growing species, especially in its first year of life. It is therefore reasonable for young individuals to be quite abundant in the last quarter of the year. Tserpes et al. (2004) have concluded to similar results studying swordfish relative abundance in the Ionian and Aegean Sea from 1987 to 2001. Increased presence of juveniles becomes even more conspicuous during the winter months (De Metrio & Megalofonou, 1987; Megalofonou et al., 2001).

Annual fluctuations of estimated abundance illustrated strong recruitment classes during 1998 and 2003. Similar patterns were observed throughout the Mediterranean during the same years (ICCAT, 2008). In fact the aforementioned years were the warmest ones during the period of this study. Such periodic cycles of 3–4 years have been observed in the captures of the Spanish, Italian and Greek fleets during the period 1987 to 2001 (ICCAT, 2008).

Numerous studies confirm that swordfish can withstand extremely large temperature fluctuations and thermal habitat choice may actually be linked to other factors such as light levels or food availability (Carey and Robison, 1981; Holts et al., 1994; Sedberry and Loefer, 2001; Takahashi et al., 2003). Official records of ICCAT point out 1998 as an exceptional year, with the strongest recorded "recruitment" of young individuals (ICCAT, 2008). It is no coincidence that 1998 was the warmest year in the timeline of this study. According to Peristeraki et al. (2007) it seems that the role of temperature is extremely important for successful recruitment. Sudden outbreaks of young individuals in certain years are positively correlated to elevated ambient water temperatures. The plausible causes could be that lower temperatures: (i) delay the spawning period and (ii) reduce the growth rate of juveniles.

Spatiotemporally, the models suggested that the Ionian Sea is a region of high concentration for young individuals (year round), with seasonal peaks during the opening and end of the fishing season. It is still not clear if young-of-the-year swordfish remain in the spawning areas where they hatched, and if so until what age. Southern Italian waters, with the core located around the Strait of Messina, have been confirmed to be a spawning area for Mediterranean swordfish (Nakamura, 1985; De Metrio et al., 1988). Other areas, such as the Balearic Islands (Rey, 1988), the Tyrrhenian and Ionian Seas (ICCAT, 2008), and the Levantine (Tserpes et al., 2008), have been proposed as spawning areas. The observed increased presence of individuals < 100 cm of LJFL throughout the Ionian Sea, could be corroborated by the common hypothesis that the Ionian is actually a significant spawning ground, and assuming that juvenile swordfish do not leave these grounds during the first year of their life.

Finally, the most convincing parameter affecting young-of-the-year swordfish distribution was distance from the coast. A clear preference for coastal areas was evident throughout the year. Analogous patterns have been observed in the northwest Atlantic as well as the Mediterranean, being more prominent during the winter months (Beckett, 1974; De Metrio & Megalofonou, 1987; Megalofonou et al., 2001).

4.3. "Adult" Swordfish (LJFL > 100 cm)

By investigating variations in the estimated annual abundance, what becomes noticeable is the distinctive association between the abundance of juveniles in year X and adults in year X + 1. This serves as a confirmation of how successful recruitment has a positive impact on the future population and how sensitive is the population density to environmental fluctuations. In the North Atlantic, swordfish adjust, on an annual basis, their spatial and temporal distribution according to their physiological needs, largely influenced by the annual latitudinal position of the path of the Gulf Stream, which in turn has been associated with temperature changes and abundant zooplankton (Mejuto, 2003). Bigelow et al. (1999) in the North Pacific, as well as Osipov (1968) in the NW Indian Ocean, have reached similar conclusions: annual and seasonal trends, observed in swordfish distribution and abundance, were related to environmental conditions or turbulent patterns in large oceanographic features.

It is generally acknowledged that the spatial distribution of swordfish is obscured, characterized by multidirectional annual periodic movements, and the species is considered to

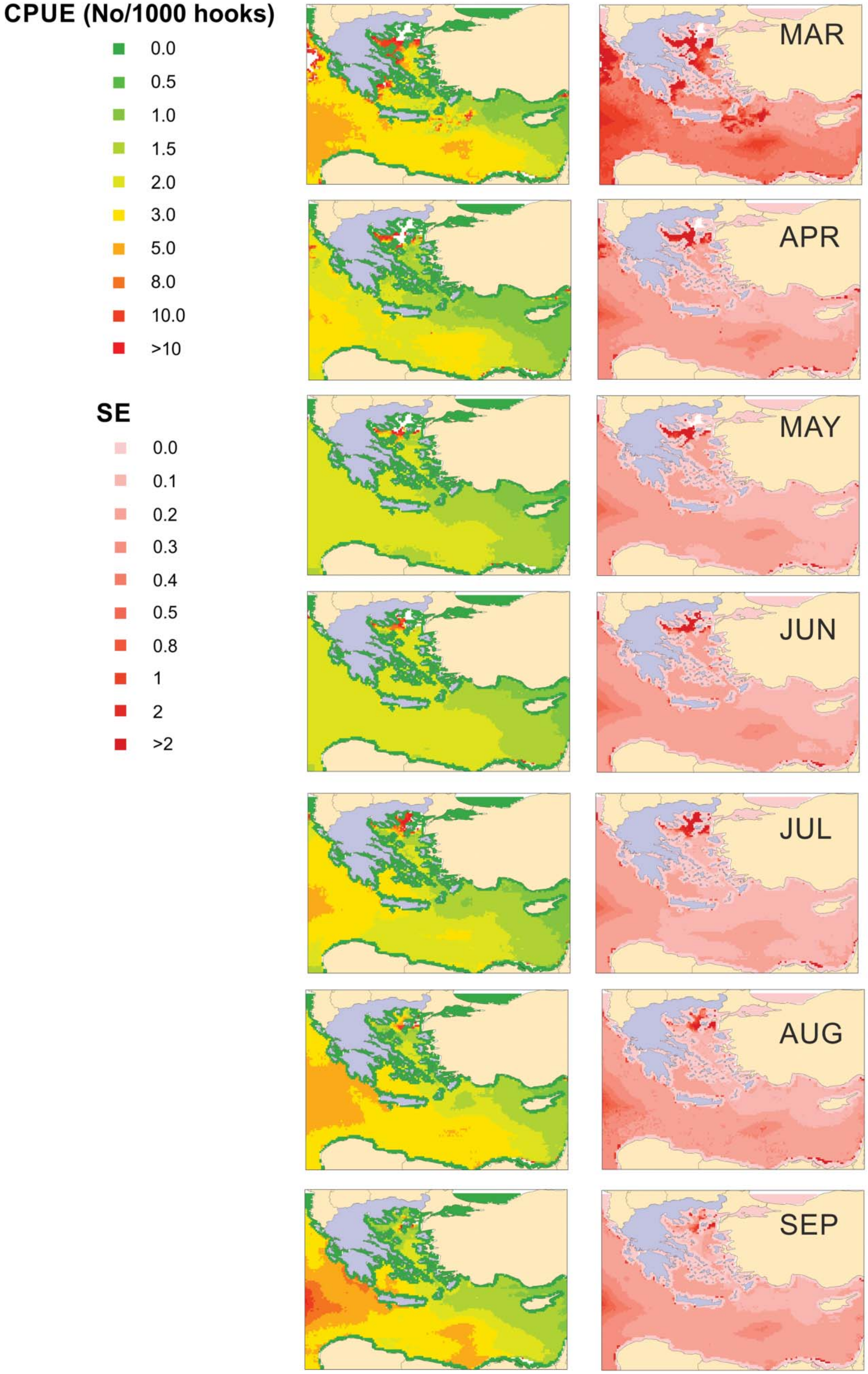

Figure 6 Predicted monthly relative abundance (Number of fish/1000 hooks—left column) and corresponding standard errors (right column) for young-of-the-year swordfish in the eastern Mediterranean Sea during 1998–2005. (Predictions refer to a lunar index of 0.5 and American type swordfish long-line fishing gear.)

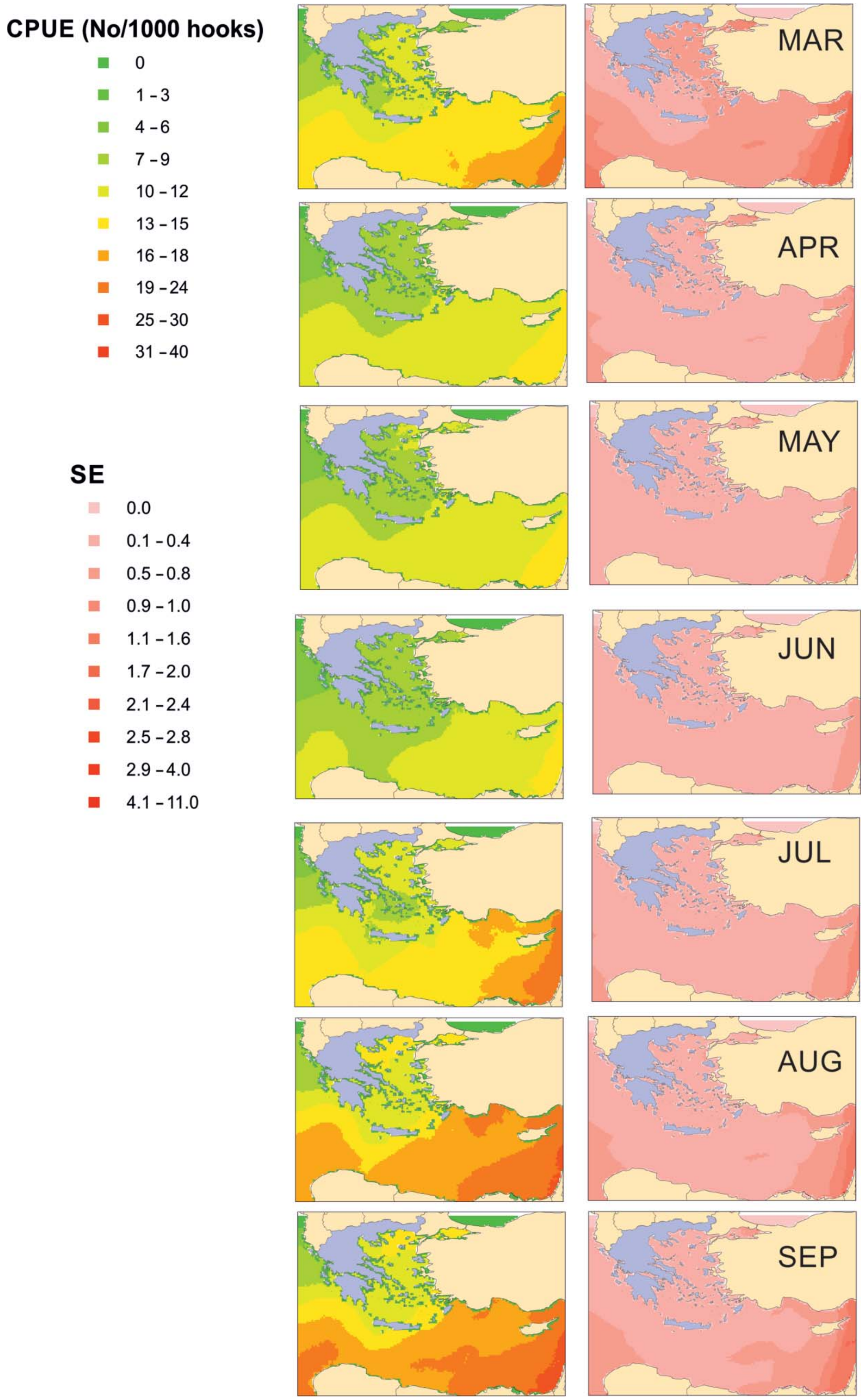

Figure 7 Predicted monthly relative abundance (Number of fish/1000 hooks—left column) and corresponding standard errors (right column) for adult swordfish in the eastern Mediterranean Sea during 1998–2005. (Predictions refer to a lunar index of 0.5 and American type swordfish long-line fishing gear.)

have the most complex behavior of all large pelagic fish (Palko et al., 1981). The main driver dictating locally increased concentrations is the seasonal movement to spawning areas. It has been observed that swordfish have different geographic and seasonal distributions depending on their size (Atlantic: Tibbo et. al., 1961; Guitart-Manday, 1964; Beckett, 1974; Mejuto et al., 1998; Ortiz et al., 2000—Pacific: Kume and Joseph, 1969; Ehrhardt, 1999—Mediterranean: Tserpes et al., 2001; Damalas et al.., 2007; Wang and Nishida, 2009). The almost continuous strong presence of large swordfish in the Levantine Basin, with some seasonal outbreaks, could be attributed to: (i) the specific oceanographic features of the area; although generally considered oligotrophic, local productivity hot-spots have been identified (Rhodes cyclonic gyre: Souvermezoglou and Krasakopoulou, 2005) and (ii) increased food availability; the open sea of the Levantine basin was never a traditional fishing ground and marine resources have faced less fishing pressure than the rest of the Mediterranean. Consequently, stocks of many species serving as prey for swordfish may be in good status and in abundance. In the Pacific, there is evidence that the concentration of cephalopods in the vicinity of thermal fronts is the major factor responsible for the distribution of swordfish (Seki et al., 2002). Cephalopods consist most of swordfish diet (Peristeraki et al., 2005) and their availability in large numbers attracts predators in dense formations. Furthermore, Tserpes et al. (2008) speculate that in the Eastern Mediterranean, during the spawning season (June–July) adult swordfish accumulate in the region between Rhodes and Cyprus, while the remainder are scattered to a larger area. This coincides with the findings of this study, also giving indications of high adult concentrations in the east Levantine between July and August. This aggregation of spawners in the area could not be straightforwardly justified by solely investigating surface oceanographic variables; the surface waters of Levantine are, as a rule, extremely oligotrophic. However, in the sub-surface layers (20–90 m) there is a great potential for sustaining swordfish larvae as can be seen from a map of net primary production in the Mediterranean (Figure 8). It has been suggested that the adults gather in the area due to these optimal environmental conditions favoring early spawning (Tserpes and Peristeraki, 2000).

Annual abundance of large swordfish showed a significant connection to water temperature, with a clear preference for cooler water masses (<20°C). The lowest levels of estimated catch rates coincided with the warmest years of the study period (1998 and 2003). Observations from the northern hemisphere confirm such thermal preferences ranges (18–22°C—Nakamura, 1985; 15–18°C—Bigelow et al., 1999). However, this inclination alters during the spawning season, when swordfish tend to aggregate in areas with ambient water temperatures of around 24°C. This temperature range has been linked with increased abundance of swordfish larvae (23–25°C: Atlantic Ocean—Tibbo and Lauzier, 1969; 24°C: N. Atlantic—Nakamura, 1985; 24°C: Indian Ocean—Kondritskaya, 1970).

The obvious prevalence of larger individuals for the open sea may confirm the classification of the species under "pelagic-oceanic." Carey and Robison (1981) documented a daily periodic behavior in adult swordfish. During the day they remained at the sea-bottom of coastal areas at depths < 90 m preying upon benthic species, emerging occasionally to the surface every 2–2.5 hr. At night, covering great distances, they headed to the open sea ascending to the surface layers and feeding on cephalopods and pelagic species. Early in the

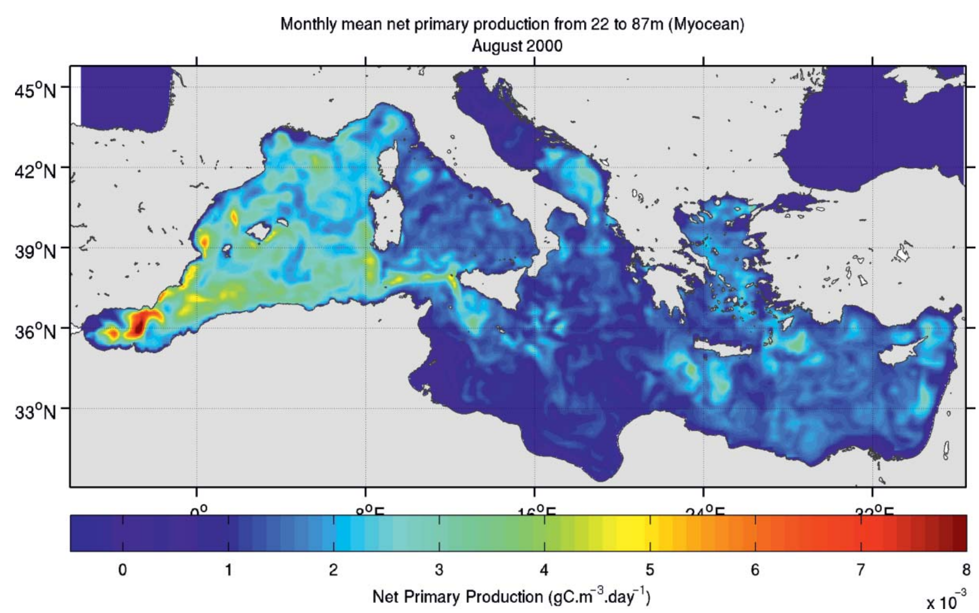

Figure 8 Map of the Mediterranean Sea depicting net primary production levels at the sub-surface layers (depth 22–87 m) during August 2000. Data source: *MyOcean Mediterranean Sea Biogeochemistry Reanalysis (http://www.myocean.eu/).*

morning, they returned once again in the coastal zone. However, classifying large swordfish as a true oceanic species may be more complicated. According to Ward and Elscot (2000), populations of swordfish do not demonstrate common behaviors, acting differently in different seas of the world. Thus, in areas where the continental shelf, the morphology of the seabed and sea-bottom elevations play the most important role in the distribution of swordfish, the population and the fishing grounds are characterized as "topographic." Conversely, areas where population density is linked to the existence of fronts and currents in the open sea, characterize the population as "convergent." The north-western coast of the Atlantic falls under the first category, while the open waters of the North Atlantic and Pacific under the second. It is quite difficult to classify the eastern Mediterranean population(s) under any of these two categories and reason on why the open sea hosts more large swordfish than the coastal areas. From the results of this study it is not clear if the increased relative abundance of large swordfish in remote sea regions is the result of circadian movements, or a constant preference for the open sea. It is more likely that due to these diurnal migrations between coastal and open-sea areas, adult swordfish become more vulnerable to surface gears in the open sea and this is translated to higher catch rates. Surface drifting longlining is a nocturnal activity taking place in the surface water layers. Fishermen, having accumulated decades of experience, are familiar with the behavior of swordfish and have adopted their fishing strategies so that to target the large individuals at the surface waters out in the open sea during night-time.

Swordfish catch rates, of all age classes, were positively correlated with the illumination of the lunar disc and this could be an indication of vision playing a dominant role in the behavior of swordfish during predation. Several authors provided similar findings investigating the influence of the moon on swordfish catches (Draganik and Cholyst, 1987; Bigelow et al., 1999; dos Santos and Garcia, 2005). Bluefin tuna and blue shark in the eastern Mediterranean exhibited analogous patterns associated with lunar activity (Damalas and Megalofonou, 2009, 2012). It is possible that nocturnal illumination of the upper sea layers may not affect the normal behavior of the fish, as it may affect the vulnerability to the fishing gear. During the luminous full moon nights the baited hooks can be easily detected by swordfish, increasing the likelihood of capture.

4.4. Management

Fisheries in the Mediterranean are managed by two major organizations: (i) the General Fisheries Council of the Mediterranean and, (ii) the International Commission for the Conservation of Atlantic Tunas (ICCAT). Northern Mediterranean waters are also regulated under the principles of the Common Fisheries Policy (CFP) of the European Union (EU). GFCM, ICCAT, and the EU coordinate efforts by governments to effectively manage fisheries at regional level following FAO's Code of Conduct for Responsible Fisheries and the CFP. However, it is acknowledged that ICCAT is the predominant authority in the region, playing a critical role when it comes to large pelagic fisheries governance. ICCAT, along with GFCM, cooperates making management recommendations and promotes data exchange between nations but, as a rule, they do not enforce regulations. As a result, most Mediterranean nations manage swordfish fisheries independently using ICCAT resolutions as an implementation guide. Implementation is carried on at the national level and management approaches among nations are diverse (Ward et al., 2000; Govender et al., 2003; ICCAT, 2008). European Union Mediterranean member states (Bulgaria, Romania, Cyprus, Greece, Slovenia, Croatia, Italy, Malta, France, and Spain) adopt recommendations agreed to by the European Council. Recent regulation 1967/2006 (EC, 2006) repealed the existing 1626/1994 (EC, 1994), which included a minimum landing size (MLS) for Mediterranean swordfish of 120 cm. A general ban for surface drifting nets targeting swordfish, tunas, and other large pelagics is in action since 2002 (EC, 1998). Greece has introduced, since 1987, a closed swordfish fishery season in the Greek Seas from October to January. In an analogous way, Cyprus closes its swordfish fishery from October to February and limits the number of boats to 60 per year. Italy, applies a state regulation of a MLS of 140 cm upper jaw fork length (UJFL) (Romeo et al., 2013). Spanish swordfish fishery is regulated by measures that pose certain technical characteristics for the longline gears and a MLS of 90 cm. Non-EU members, such as Tunisia, Turkey, and Croatia respect a minimum size limit of 120 cm, while Turkey has also implemented a closed fishing season between July and September and Tunisia between June and July. Morocco manages the fishery by controlling fishing effort, applying spatial and temporal closures, setting a minimum landing size limit of 125 cm and restricting driftnets to 2.5 km in length with mesh sizes greater than 40 cm. Japan limits its Mediterranean fleet to a maximum of 35 boats and disallows fishing by longliners larger than 24 m between June and July (Takeuchi, 1996; Ward et al., 2000; Govender et al., 2003; ICCAT, 2008).

Despite the aforementioned maze of management regulations, the most recent stock assessment session on Mediterranean swordfish concluded that all forms of multi-annual assessment conducted, gave a consistent view of a poor stock status (ICCAT, 2011). Current spawning stock biomass (SSB) levels are much lower than those in the early 80s, although no clear trend appears in the last 15 years. The stock can be considered to be in overfished condition and slight overfishing is taking place; current fishing mortality (F) is slightly higher than the estimated F needed to achieve maximum sustainable yield (MSY). Juveniles represented 50–70% of the total yearly catches in terms of numbers and 20–35% in terms of weight. It was suggested that a reduction of the volume of juvenile catches would be beneficial for the future of the stock, improving yield per recruit and spawning biomass per recruit levels. Moreover, the Mediterranean fisheries suffer—among others—from: (a) misreporting and incomplete monitoring of fishing effort and landings data, (b) absence of TAC restrictions and, (c) slack law enforcement.

Based on the results of this study (suggesting a significant spatio-temporal separation of young-of-the-year and adult swordfish habitat), a more realistic approach would be the introduction of a combined seasonal and spatial closure for the Mediterranean swordfish fishery. Seasonal closures are already in action for the swordfish fisheries of Greece, Cyprus, Turkey, Tunisia, and Morocco. In a recent work, Tserpes and Peristeraki (2007) simulated the effects of a plausible four-month seasonal closure, during the recruitment period (October–January), on all Mediterranean swordfish fisheries. They concluded that annual catch will increase by 6% in a period of five to six years after the closure. Moreover, catch reduction in juveniles will reach 18–23% of their total catch number. These are some impressive results, taking into account that fishing effort will be curtailed significantly. It is noted that a closure of less than four months will have undetectable effects on the population (Di Natale et al., 2002; Tserpes and Peristeraki, 2007). On the other hand, a closure during the spawning season will allow more mature specimens to spawn, and such a managerial strategy is practiced by the Turkish fleet (July to September). Why this approach hasn't been adopted by other Mediterranean countries is easy to envisage. The bulk of the fishing effort for swordfish is put forth during the summer months, mostly due to the favorable weather conditions and high market demand (De Metrio et al., 1999; Stergiou et al., 2003). Great difficulties start to arise for the managers, when socio-economic and biological requirements have to be met simultaneously.

Numerous Mediterranean marine regions are to date restricted to fishing activities, serving either as protected nursery grounds or marine reserves in general (Abdulla et al., 2008). Spatial closures explicitly enforced on swordfishing are known to exist only in the Moroccan waters (Govender et al., 2003). Increased abundance of young swordfish in the vicinity of land suggests that coastal areas should be a priority when protection of juveniles is an objective. The establishment of a restricted coastal zone would take away significant fishing pressure from the immature part of the population, while fishing activity would be trivially affected. Less than 10% of the fishing effort exerted during this survey took place inside the 6 nautical miles zone, verifying the open-sea nature of the fishery.

Currently, numerous Mediterranean fishing fleets (e.g., bottom trawlers and purse seiners) are regulated through such spatio-temporal restrictions (Cacaud, 2005). Seasonal and area closures are "inbuilt" in the culture of modern Mediterranean fisheries, making them a more plausible management strategy for swordfish than setting of various MLSs or TACs. This management harmonization of the swordfish fishery with most of the other fishing tactics, along with the introduction of vessel identifications systems (such as the VMS-Vessel Monitoring System or the AIS-Automatic Identification System) on all commercial boats, would facilitate control by the authorities and discourage illegal fishing practices. Establishing a network of Marine Protected Areas (MPA) could be the more unconventional management alternative, however, delineating such no-take zones, by identifying regions where marine life thrives can be achieved only by applying techniques similar to those employed in this study.

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SUPPLEMENTAL MATERIAL

Supplemental data for this article can be accessed on the publisher's website.

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