SCIENTIA MARINA 76(4)
December 2012, 691-704, Barcelona (Spain)
ISSN: 0214-8358
doi: 10.3989/scimar.03679.26A

Discovering where bluefin tuna, *Thunnus thynnus*, might go: using environmental and fishery data to map potential tuna habitat in the eastern Mediterranean Sea

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

[1] Department of Biology, Section of Zoology-Marine Biology, University of Athens, Panepistimiopolis, Ilissia, 15784, Athens, Greece. E-mail: shark@hcmr.gr; dimitrios.damalas@jrc.ec.europa.eu
[2] Maritime Affairs Unit, Institute for the Protection and Security of the Citizen (IPSC), Joint Research Centre (JRC), European Commission, via E. Fermi 2749, I-21027, Ispra (VA), Italy.

SUMMARY: Based on a dataset derived from commercial fisheries in the eastern Mediterranean Sea in 1998-2005, we applied generalized additive models (GAMs) to investigate the relative influence of a range of environmental factors on catch rates of Atlantic bluefin tuna (*Thunnus thynnus* Linnaeus, 1785). GAM analyses were conducted by separately modelling (1) the probability of making a catch (encountering a school), and (2) the positive catch rates (school size). Results suggested intra-annual variations in tuna distribution and revealed interesting associations with some environmental features, lunar periodicity being the most distinctive one. Probability of encountering a school peaked in late spring months, eastwards, at water temperatures above 22°C and around the full moon. Size of school was more likely to be larger in northeasternmost regions and in the vicinity of land in late spring, when the percentage of lunar disc illumination was higher. A moderate but continuous annual decline in the probability of encountering a bluefin tuna school was detected from the models' outputs. The models were used as an indication of preference or association for the selected environmental variables. Based on these associations, an indirect identification of the bluefin tuna potential habitat was obtained and used to map distributions in the eastern Mediterranean region.

Keywords: bluefin tuna, GAM, habitat, SST, lunar index, Mediterranean, management.

RESUMEN: DESCUBRIENDO A DONDE VAN LOS ATUNES ROJOS, *THUNNUS THYNNUS*: USO DE DATOS AMBIENTALES Y PESQUEROS EN MAPAS DEL HÁBITAT DEL ATÚN EN EL MEDITERRÁNEO ORIENTAL. – Se aplican modelos aditivos generalizados (GAMs) a la investigación de la influencia relativa de una serie de factores medioambientales en las tasas de captura de atún rojo Atlántico, mediante el uso de datos derivados de las capturas comerciales en el Mediterráneo oriental. Estos análisis se llevaron a cabo separadamente para: (1) la probabilidad de captura (encuentro con un banco) y (2) la tasa de captura (tamaño del banco). Ambos factores parecen variar a lo largo del año, y parecen estar asociados con algunos parámetros medioambientales, especialmente la fase lunar. La probabilidad de encontrar un banco de atún es mayor al final de la primavera, cuanto más al este, cuando la temperatura del agua supera los 22°C, y con luna llena. El tamaño del banco es probablemente mayor al final de la primavera, en la región noreste, cuando la luz del disco lunar es más intensa, y cerca de la costa. Los resultados muestran una disminución, moderada pero continua, de la probabilidad de encuentro con un banco de atún rojo. Ciertos modelos GAM se usaron como indicadores de la preferencia o asociación con ciertos factores ambientales. De acuerdo con estas asociaciones, se presenta una identificación indirecta del hábitat potencial del atún rojo, mostrando su distribución espacial en el Mediterraneo oriental.

Palabras clave: atún rojo, GAM, hábitat, TSM, indice lunar, Mediterráneo, manejo.

INTRODUCTION

Atlantic bluefin tuna (*Thunnus thynnus* Linnaeus, 1785) (Perciformes: Scombridae) occurs in tropical and temperate waters of the Atlantic Ocean and the Mediterranean Sea. It is a highly migratory species, oceanic but seasonally coming close to shore, and forming schools of more than 5000 individuals (Lutcavage and Kraus 1995). Praised for its high valued flesh, it has become one of the most important target species in fisheries worldwide (FAO 2005). It has been fished in eastern Mediterranean waters since at least the 7th millennium BC (Desse and Desse-Berset 1994). One of the earliest scientific references comes from Aristotle in his treatise *History of Animals*, written in 350 BC, describing the migratory and reproductive habits of tuna in the Aegean and Black Sea (D'Arcy Wentworth Thompson 1910). Aristotle's comments are based on fishermen who carefully observed tuna migrations in order to be able to trap them in the most efficient ways. In modern times, annual catches in the Mediterranean increased dramatically from less than 10000 t in the mid-1980s to more than 30000 t in the mid-1990s. Introduction of annual quota regulations by the International Commission for the Conservation of Atlantic Tunas (ICCAT) in 1998, which came into force in August 1999 levelled these numbers below 25000 t in subsequent years, reaching 12500 t in 2009 (ICCAT 2010).

In the eastern Mediterranean, bluefin tunas are caught (target or by-catch) using bluefin tuna purse seines, clupeoid purse seines, surface drifting longlines (targeting bluefin tuna, swordfish or albacore) and handlines. The bulk of catches are made by purse seiners targeting tuna (ICCAT 2011a). More specifically, in the eastern Mediterranean swordfish drifting longline fisheries, bluefin tuna accounts for a significant share of the catches (up to 13% in weight) being a significant by-catch in terms of both quantity and revenue (Megalofonou *et al*. 2000). Swordfish long-line fishing grounds cover large areas; this fishery is probably the most spatially extensive economic activity in this region, making it ideal for a large-scale study. In this vast region, a large pelagic fishery has been operated mainly by the Italian and Greek long-line fleets targeting primarily swordfish since the late 1960, fishing 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). Regarding Atlantic bluefin tuna stock status, the ICCAT assessment for the eastern Atlantic and Mediterranean area reported a strong decline in number and biomass of adult fish (spawning stock) since 1993 (ICCAT 2003). Establishing a maze of management regulations (total allowable catch [TAC], minimum landing size [MLS], spatio-temporal no-take zones) proved to be futile, mostly because of slack regulation compliance and low effort from the control authorities (ICCAT 2007). More recently (ICCAT 2010), after the establishment of a historical low TAC level at 12500 t for 2010, the Commission set up a framework to set future TACs at levels sufficient to rebuild the stock by 2023 with at least 60% probability. There is consensus (Juan-Jordá *et al*. 2011) that among 26 tuna populations worldwide, eastern Atlantic bluefin tuna can be attributed the lowest status, i.e. "ugly", "overexploited", "poorly managed", with F/F_{MSY}=2.90, B/B_{MSY}=0.35 (B/B_{MSY}, the ratio of the current adult biomass (B) relative to the adult biomass that would provide the maximum sustainable yield (MSY); F/F_{MSY}, the ratio of current fishing mortality (F) relative to the fishing mortality rate that maintains MSY). More radical management alternatives, such as Marine Protected Areas (MPA), are even suggested (Tudela 2004, Stergiou *et al*. 2009, UNEP-MAP-RAC/SPA 2010). However, delineating such no-take areas is far from straightforward; identification of areas where marine life thrives is required. More specifically, the essential habitats of pelagic species may be defined by oceanographic features, such as productive areas associated with upwelling. In the Mediterranean, such spawning areas and migratory routes of bluefin tuna, swordfish and albacore are of high conservation interest (UNEP-MAP-RAC/SPA 2010).

Since remote sensing data became available to the broad scientific community, incorporation of environmental data to analyse abundance trends has confirmed that bluefin tuna distribution is significantly affected by spatial and temporal variations of these parameters. During their seasonal migrations they follow changes in water temperature and currents, foraging along strong thermal fronts (Collette and Nauen 1983, Polovina 1996, Platonenko and de la Serna 1997, Block and Stevens 2001, Shick *et al*. 2004, Royer *et al*. 2005). Lately, approaches to standardizing tuna catch rates based on environmental factors have been applied by Okamoto *et al*. (2001), Rodriguez-Marin *et al*. (2003), Fromentin (2003) and Reglero *et al*. (2012). An attempt to associate fishery datasets with several plausible factors affecting bluefin tuna distribution and abundance was recently undertaken by Druon *et al*. (2011), providing potential feeding and spawning habitats in the Mediterranean Sea. However, the authors outlined that "the low number of observations in the eastern Mediterranean Sea remain the most prominent technical limitation of our current approach". In this paper, we aspire to fill part of this gap in our knowledge by applying an information theoretic generalized additive model (GAM) approach (Hastie and Tibshirani 1990, Burnham and Anderson 2002), studying the influence of certain environmental, spatial, temporal and operational parameters on the catch rates of bluefin tuna caught incidentally in the drifting surface longlines of the eastern Mediterranean. Based on the association with environmental variables, we have mapped the probability of occurrence as well as the relative abundance, delivering an indirect identification of the bluefin tuna potential habitat in the eastern Mediterranean region.

MATERIALS AND METHODS

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. It

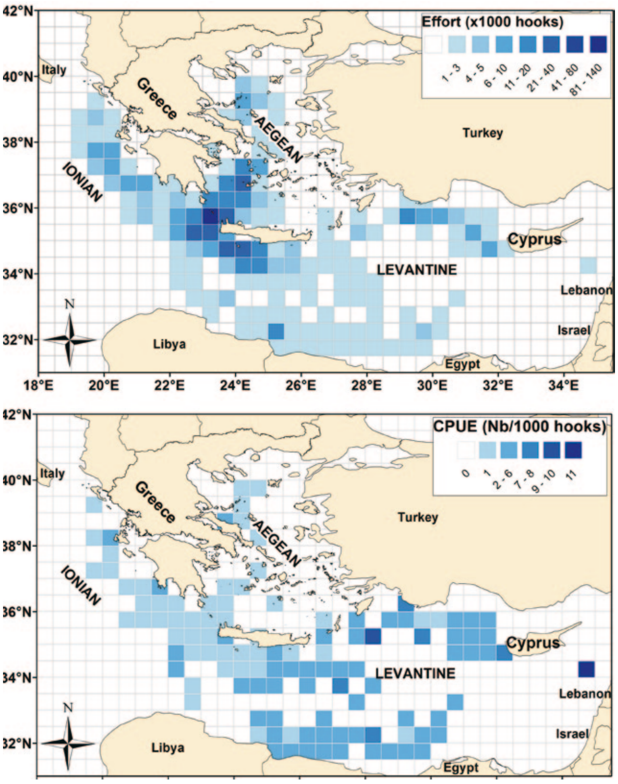

FIG. 1. – Map of the study area with spatial distribution of fishing effort (top) and nominal catch per unit of effort (bottom) in 1998–2005 in the eastern Mediterranean Sea. (Note: spatial resolution of fishing effort is 1/2 a degree; values refer to the whole study period and not individual fishing sets; Nb: number)

is characterized by decreasing nutrient gradients to the southeast, due to incoming nutrients from the adjacent more productive Black Sea and eastern Atlantic as well as the European rivers (Caddy 1998, Wurtz 2010). The easternmost part comprises three large areas: the Ionian Sea, the Aegean Sea and the Levantine Sea (Fig. 1). The Levantine Sea is considered one of the most oligotrophic regions of the world oceans (Stergiou *et al.* 1997).

The Greek and Cypriot swordfish long-line fleets comprise approximately 280 vessels, carrying out their activities from late February to September. Most of these vessels enter the fishery occasionally, mainly during the summer months (ICCAT 2011b). During the eight-year period 1998-2005, sampling was carried out throughout the eastern Mediterranean Sea using a network of fishing ports. Data were obtained from records taken by observers stationed either at fishing ports or on board commercial fishing vessels targeting the swordfish *Xiphias gladius* (Linnaeus 1758). In total, 38 fishing boats operating from 22 major fishing ports were monitored (Table 1). The types of fishing gear deployed were surface drifting long-lines targeting swordfish (SWO-LL$_T$: traditional swordfish long-line; SWO-LL$_A$: American-type swordfish long-line). The fishing period was March to September. Detailed information regarding gear configuration and hauling and retrieving tactics can be found in Megalofonou *et al.* (2005). Observers gathered fishing and operational data, identified and measured fish, and recorded spatial and temporal variables, including name of fishing boat, gear used, fishing sets per trip (each trip could last from 1 to 20 days; one fishing set per day), fishing effort for each fishing set (number of hooks), number and weight of fish caught per fishing set by species and discards, date, and exact geographical coordinates of each fishing set (determined by GPS). 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). Occurrence of tunas was assessed based on a presence/absence flag assigned to each fishing set, while resource abundance 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. CPUE values were calculated as number of fish per 1000 hooks deployed. Fishing time was assumed to be equal since soaking time was roughly constant, setting beginning at dusk and retrieving before sunrise.

Statistical analyses - modeling

Fishery performance (CPUE) was modeled by applying GAMs (Hastie and Tibshirani 1990, Maunder and Punt 2004), which were initially applied to identify the most significant factors affecting bluefin tuna occurrence or relative abundance, and afterwards to quantify their contribution to bluefin tuna distribution. Although our methodology does not resemble that of Druon *et al.* (2011), who developed habitat models based mostly on climatic variables (bioclimate envelopes), it is widely used to model species distribution (Guisan *et al.* 2002). GAM selected models can serve as an indication of preference or association for the

TABLE 1. – Number of ports, vessels, fishing sets, hooks deployed, bluefin tuna and swordfish caught by fishing gear in the eastern Mediterranean Sea swordfish long-line fishery, during 1998-2001 and 2003-2005 (ports and vessels overlap between fishing gears).

Fishing gear	ports	vessels	fishing sets	hooks deployed	average hooks per set	bluefin tunas caught	kg bluefin tunas caught	% of total catch (in Nb / in kg)	swordfish caught	% of total catch (in Nb)
SWO-LL$_T$	12	12	283	289110	1021.6	42	1902	2.8 / 7.0	1299	85.2
SWO-LL$_A$	16	32	978	494609	505.7	466	31118	6.6 / 16.5	5562	78.4
Total	22	38	1261	783720	621.5	508	33020	5.9 / 15.3	6861	79.6

Nb: number; kg: kilograms; SWO-LL$_T$: traditional swordfish long-line; SWO-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	ºC/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 (below ocean surface)	meters	-	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 by locating the nearest land pixel (bottom depth >0) based on the bathymetry data and calculating 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.

selected environmental variables (Kupschus 2003) and can be linked to the underlying ecological processes (Austin 2007). Implementation was done in R v.2.12.0 (R Development Core Team 2010) using the mgcv package (Wood 2000, 2006) according to the general formulation:

$$f\left(E\left[C\hat{P}UE_i\right]\right) = LP_i = c + \sum_m s_m(Z_{mi})$$

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 i-th 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). CPUE distributions were skewed, including many zero values and few large observations. This is quite common for catch distributions of non-targeted species (Caddy 1998, Guisan *et al*. 2002). To account for this variability, the Delta-model was applied with the general form:

$$Pr(Y=y) = \begin{cases} w, & y = 0 \\ (1-w)f(y) & \text{otherwise} \end{cases}$$

where w is the probability of a zero observation and $f(y)$ the error distribution of catch rates from positive catch sets (Pr, probability; y, response variable). It was assumed that the two sub-models refer to different processes. In the first sub-model (presence-absence), the probability of a zero catch is the probability of encountering a school. In the second sub-model (presence only), the distribution of the positive catch sets is the probability of the school size (Maunder and Punt 2004). Identification of the underlying probability distribution for the errors in the dependent variable (positive catches of bluefin tunas) was performed using the Akaike information criterion (AIC, Akaike 1973). After selecting the appropriate error distribution family, we followed an information theoretic approach (Burnham and Anderson 2002) to discriminate the best model, including the most influential parameters affecting catches. A set of pre-defined candidate models (Table 3) were investigated, and the optimum one was selected on the basis of its Generalized Cross Validation (GCV) score (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 strong correlation was evident between any pair of variables included in the candidate models.

Based on the selected models, spatial estimations of probability occurrence and positive catch rates were derived in the form of gridded matrices for the whole study area. The eastern Mediterranean marine region (31°-41°N, 18°-35°E) was gridded in a spatial resolution of 0.1×0.1 degrees, concluding to a total of 11471 grid cells (land excluded). Each of these cells was assigned the corresponding values for each of the model parameters. Implementation was done using the 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,

Table 3. – The set of candidate models. (":" denotes interaction between predictors).

Model	Linear predictor (LP)
mod_0	*c (Null model)*
mod_1	*c+Gear+Year+Month+s(Long)+s(Lat)+s(Distance)+s(SST)+s(SSTgradient)+s(Salinity)+s(Chl.a)+s(Lunar.index)+s(WS) (Full model)*
mod_2	*c+Gear+Year+Month*
mod_3	*c+Gear+Year+Month+s(Long)*
mod_4	*c+Gear+Year+Month+s(Lat)*
mod_5	*c+Gear+Year+Month+s(Long)+s(Lat)*
mod_6	*c+Gear+Year+Month+s(Long)+s(Lat)+s(Distance)*
mod_7	*c+Gear+Year+Month+s(Long)+s(Lat)+s(Distance)+s(SST)*
mod_8	*c+Gear+Year+Month+s(Long)+s(Lat)+s(Distance)+s(SST)+s(SSTgradient)*
mod_9	*c+Gear+Year+Month+s(Long)+s(Lat)+s(Distance)+s(SST)+s(SSTgradient)+s(Lunar.index)*
mod_{10}	*c+Gear+Year+Month+s(Long)+s(Lat)+s(Distance)+s(SST)+s(SSTgradient)+s(Lunar.index)+s(Chl.a)*
mod_{11}	*c+Gear+Year+Month+s(Long)+s(Lat)+s(Distance)+s(SST)+s(SSTgradient)+s(Lunar.index)+s(Chl.a)+s(Salinity)*
mod_{12}	*c+Gear+Year+Month+s(Long:Lat)*
mod_{13}	*c+Gear+Year+Month+s(Long:Lat)+s(Distance)*
mod_{14}	*c+Gear+Year+Month+s(Long:Lat)+s(Distance)+s(SST)*
mod_{15}	*c+Gear+Year+Month+s(Long:Lat)+s(Distance)+s(SST)+s(Lunar.index)*
mod_{16}	*c+Gear+Year+Month+s(Long:Lat)+s(Distance)+s(SST)+s(Lunar.index)+s(SSTgradient)*
mod_{17}	*c+Gear+Year+Month+s(Long:Lat)+s(Distance)+s(SST)+s(Lunar.index)+s(SSTgradient)+s(Chl.a)*
mod_{18}	*c+Gear+Year+Month+s(Long:Lat)+s(Distance)+s(SST)+s(Lunar.index)+s(SSTgradient)+s(Chl.a)+s(Salinity)*

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). In order 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.

RESULTS

Nominal CPUE

Between April 1998 and September 2005 the observers reported a total of 508 bluefin tuna as part of the swordfish long-line catch in 1261 fishing days of sampling, having a total weight of 33020 kg and averaging 65 kg per fish. Bluefin tuna was the second most abundant by-catch after the oilfish *Ruvettus pretiosus* (Cocco 1829), reaching an overall 5.9% of the total catch in number of fish and 15.3% in weight (Table 1). Monthly nominal CPUE values ranged from 0.00 to 0.34 bluefin tunas per 1000 hooks for the traditional swordfish long-line and from 0.18 up to 2.05 bluefin tunas per 1000 hooks for the American-type swordfish long-line (Table 4).

Encountering a school (presence-absence sub-model)

For the initial Delta sub-model, in view of the probability of obtaining a zero catch and the discrete nature of the data, we assumed by default a binomial error distribution with logit as the link function and we recoded bluefin tuna catches to the binary variable Presence, so it is assigned a value of 0 if no bluefin tunas were present in the catch, and 1 otherwise (Bernoulli-type 0/1 measurements). Analysis based on GCV revealed that model mod_1, including 12 variables, was the best to describe our data (Table 5):

$$\begin{gathered} f\,(E[\text{Presence}]) = c + a_1\text{Fishing gear type} + a_2\text{Year} + \\ + a_3\text{Month} + s_4(\text{Longitude}) + s_5(\text{Latitude}) + \\ + s_6(\text{Distance from coast}) + s_7(\text{SST}) + \\ + s_8(\text{SST.gradient}) + s_9(\text{Salinity}) + s_{10}(\text{Chl-a}) + \\ + s_{11}(\text{Lunar.index}) + s_{12}(\text{Wind speed}) \end{gathered}$$

In total, the derived model explained 29% of the variance in the probability of encountering a bluefin tuna school. The temporal factors (year and month) had the predominant effect on encountering a school. The fitted probability as a function of month, revealed a seasonal peak, with late spring-early summer being

Table 4. – Effort (Nb of hooks), fish captured, and nominal CPUE values (number of fish/1000 hooks) by fishing gear and month for bluefin tunas caught in the eastern Mediterranean Sea swordfish long-line fishery during the period 1998-2005.

Fishing gear		Month							
		Mar	Apr	May	Jun	Jul	Aug	Sep	Total
$SWO\text{-}LL_T$	Nb hooks(x1000)	8.8	8.0	55.8	46.3	46.0	54.7	69.7	289.1
	Nb bluefin tuna	3	0	18	4	8		9	42
	CPUE	0.34	0.00	0.32	0.09	0.17	0.00	0.13	0.15
$SWO\text{-}LL_A$	Nb hooks(x1000)	34.3	34.2	81.1	98.4	108.5	61.1	77.0	494.6
	Nb bluefin tuna	6	15	166	112	104	18	45	466
	CPUE	0.18	0.44	2.05	1.14	0.96	0.29	0.58	0.94
Total	Nb hooks(x1000)	43.0	42.1	136.9	144.7	154.5	115.8	146.7	783.7
	Nb bluefin tuna	9	15	184	116	112	18	54	508
	CPUE	0.21	0.36	1.34	0.80	0.73	0.16	0.37	0.65

$SWO\text{-}LL_T$: traditional swordfish long-line; $SWO\text{-}LL_A$: American-type swordfish long-line; CPUE: Catch per unit of effort.

TABLE 5. – Summarized results of the best models selected for the presence-absence and presence only sub-models data of bluefin tunas 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.

Data		Presence-absence sub-model	Trend	Presence only sub-model	Trend
Error distribution		Binomial		Gamma	
Link function		Logit		log	
Best model		mod_1		mod_{15}	
Edf		38.5		26.6	
% of deviance explained		29.0		52.4	
Pr(*F*)	Gear	0.073	n.s.	<0.001	$SWO\text{-}LL_A > SWO\text{-}LL_T$
	Year	<0.001	↓	<0.001	unclear
	Month	<0.001	late spring peak	0.016	late spring peak
	Long	<0.001	↑	<0.001	↑
	Lat	0.004	U-shaped		
	Distance from coast	0.539	n.s.	0.003	↓
	SST	0.015	↑	<0.001	unclear
	SST.gradient	0.691	n.s.	-	-
	Salinity	0.007	unclear	-	-
	Chl-a	0.179	n.s.	-	-
	Lunar.index	<0.001	↑	<0.001	↑
	WindSpeed	<0.001	unclear	-	-

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

the most favourable period (Fig. 2). The annual effect demonstrated a constant decline for the whole time period of the study (Fig. 2). Lunar index had the following influence on the model, probability increasing almost monotonically with lunar light intensity (Fig. 2) and giving the impression that bluefin tuna become more vulnerable to surface long-lining around the full moon phase. Geographical location played an important role, longitude being more influential than latitude. The effect of longitude (Fig. 2) indicated a strong gradient in the presence of bluefin tuna schools, the probability increasing in an easterly direction, while latitude plot was U-shaped, peaking in anti-diametrical locations (Fig. 2). SST was another parameter yielding a significant reduction in deviance, with a school being more likely to occur in warmer water masses (Fig. 2). The effects of salinity and wind speed were unclear and problematical to assess, while the remaining factors made a minor contribution to the overall variance explained by the model.

School size (presence only sub-model)

AICs among the "full" model versions, assuming different error distributions, supported the use of a Gamma distribution with a log link function. Assuming a Gamma(log) distribution for the underlying dataset, we examined a series of candidate models based on their GCV scores. Model mod_{15} was selected as the most suitable (Table 5):

$$f\,(E[CPUE>0]) = c + a_1\text{Fishing gear type} + a_2\text{Year} + a_3\text{Month} + s_4(\text{Longitude:Latitude}) + s_5(\text{Distance from coast}) + s_6(\text{SST}) + s_7(\text{Lunar.index})$$

The model explained a considerable 52.4% of the variance in the probability of positive bluefin tuna CPUE (Table 5). Fishing gear type effect was the most significant variable affecting the positive catch rates of bluefin tunas. The American-type swordfish long-line displayed superiority in catching tunas (Fig. 3); the species exhibited a noticeable vulnerability to this gear. The year effect contributed significantly to the model convergence, the plot for year demonstrating a trivial declining trend in catch rates between 1998 and 2004, followed by a slight rise in 2005 (Fig. 3). The modelled probability of the school size by month showed a seasonal peak in late spring analogous to the one of the previous sub-model (Delta-binomial presence-absence, encountering a school) (Figs 2 and 3). Spatial interaction (longitude : latitude) was significant and the response surface in the three dimensional XYZ space (X, longitude; Y, latitude; Z, response) gave evidence of increased probability for a large school size in the northeasternmost regions (Fig. 3). Distance from coast, embracing both spatial and environmental properties as an explanatory variable, showed a positive trend in favour of coastal areas: larger bluefin tuna schools were more likely to be detected in the vicinity of land (Fig. 3). The likelihood of coming across a larger bluefin tuna school exhibited a periodicity analogous to the lunar cycle, reaching higher values during full moon (Lunar index 75-100%) (Fig. 3). The SST effect was vague and no obvious thermal preference was detected.

Mapping of potential habitat

To facilitate 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 was drawn (2 gears × 7 years × 7 months × 4

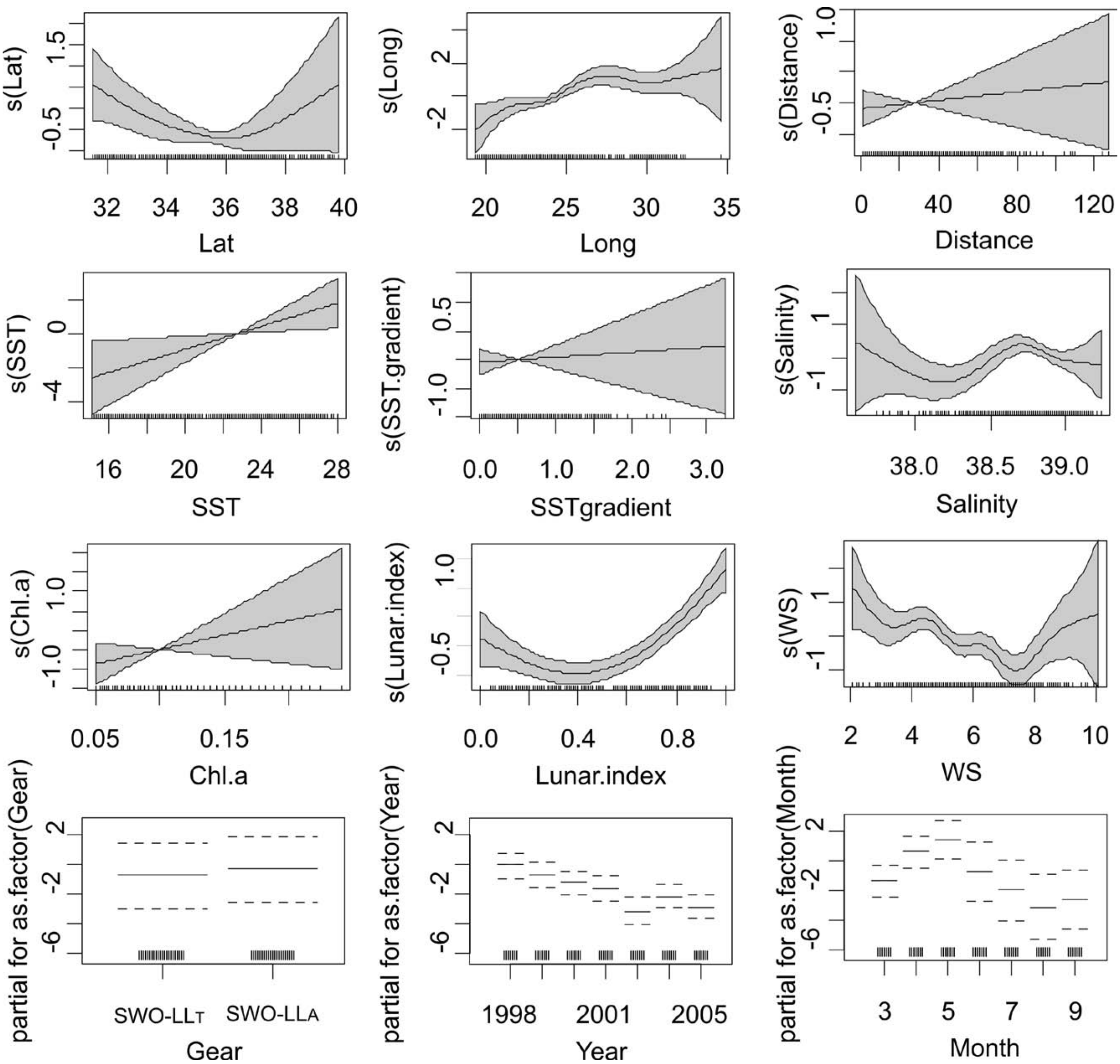

FIG. 2. – Generalized additive model (GAM) derived effects of the investigated parameters on the Delta-binomial probability of encountering a bluefin tuna school (presence-absence sub-model). Shaded areas indicate two standard errors above and below the estimates. Relative density of data points is shown by the 'rug' on the x-axis.

lunar phases). Each of these prediction matrices included estimates of both occurrence probability (presence-absence sub-model) and relative abundance (presence only sub-model) for a certain combination of gear, year, month and lunar phase. Averaging over all years studied (1998-2005) delivered a more comprehensive series of monthly maps (Figs 4 and 5). The visualized prediction accuracy was assessed on the basis of RSEs (Table 6). March was the only month for which a fairly large number of the predictions were associated with a great deal of uncertainty. 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 lu-

TABLE 6. – Proportions of relative standard errors (RSE) above 25% for the monthly prediction matrices.

Month	% of prediction cells with RSE >25%	
	Probability of occurrence Presence-absence sub-model	Relative abundance (CPUE>0) Presence only sub-model
March	22.17%	2.70%
April	2.57%	0.84%
May	0.22%	0.05%
June	0.24%	0.02%
July	0.34%	0.01%
August	1.46%	0.01%
September	0.72%	0.01%

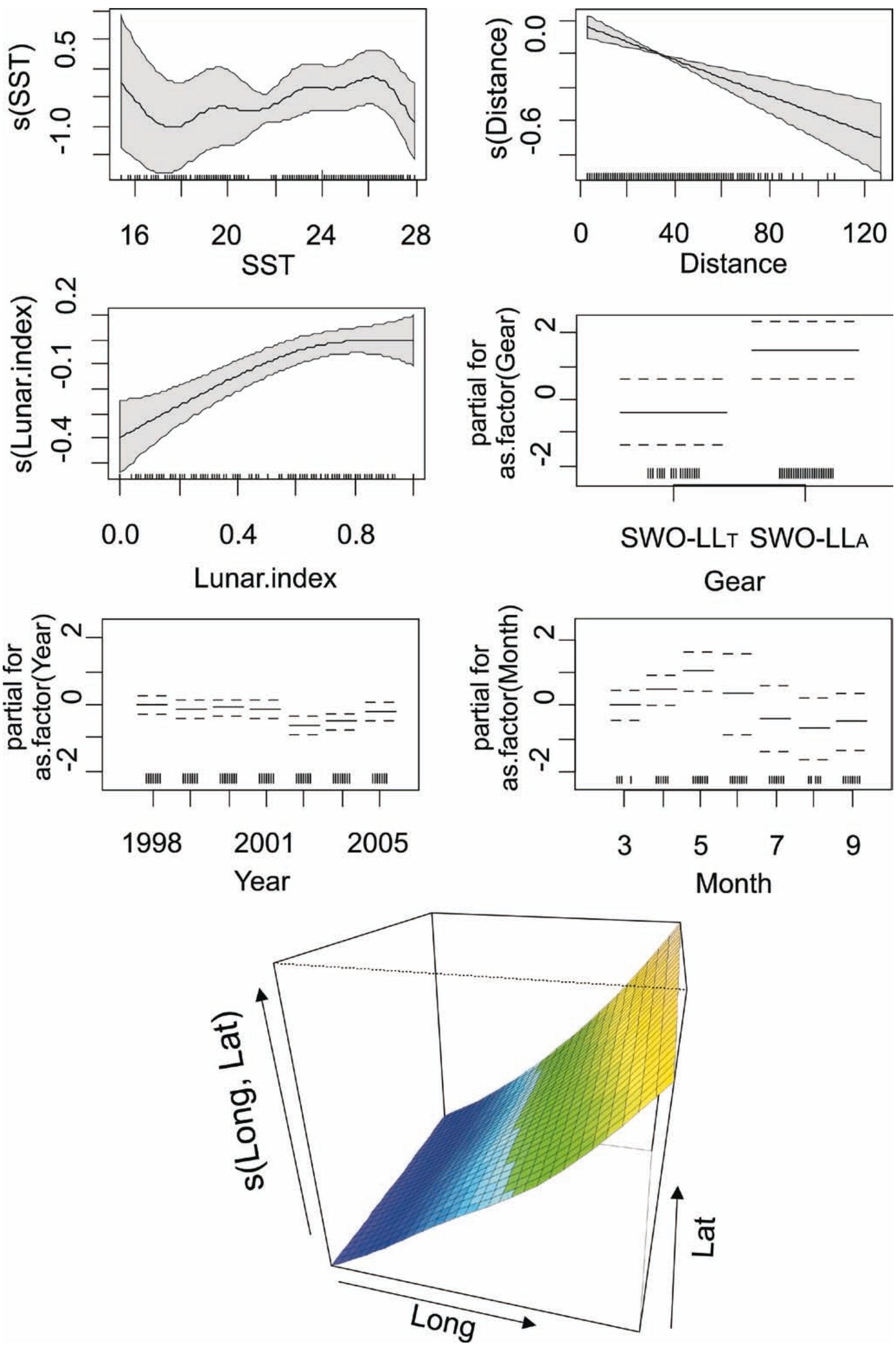

FIG. 3. – Generalized additive model (GAM) derived effects of the investigated parameters on the Delta-Gamma (log) probability of positive bluefin tuna catch rates (school size – presence-absence sub-model). Shaded areas indicate two standard errors above and below the estimates. Relative density of data points is shown by the 'rug' on the x-axis.

nar phases and fishing gear types. The maps, more or less illustrate visually the trends identified in the best models (Table 5). May to July was the period in which a school was more likely to be encountered, preferably in the Levantine basin and the north Aegean plateau (Fig. 4), while the school size likelihood demonstrated a northeast increasing gradient, peaking in the northern Aegean, the Sea of Marmara and the northeastern Levantine. Furthermore, the maps delineate regions of low model predictive power. Elevated standard errors

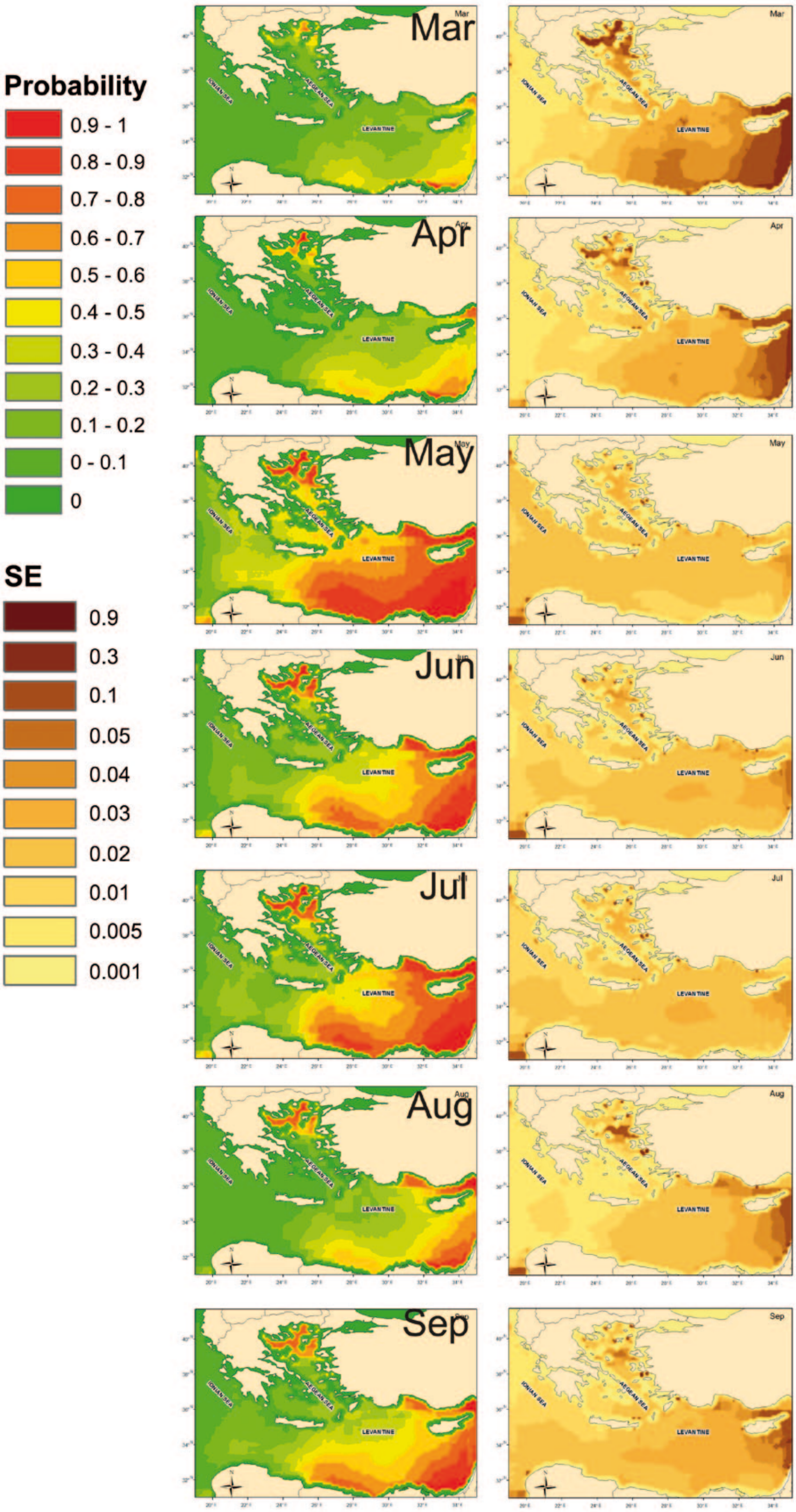

Fig. 4. – Predicted monthly probability of occurrence (presence-absence sub-model, left column) and corresponding standard errors (right column), for bluefin tunas in the eastern Mediterranean Sea in 1998-2005. (Predictions refer to a lunar index of 0.5 and American-type swordfish long-line fishing gear)

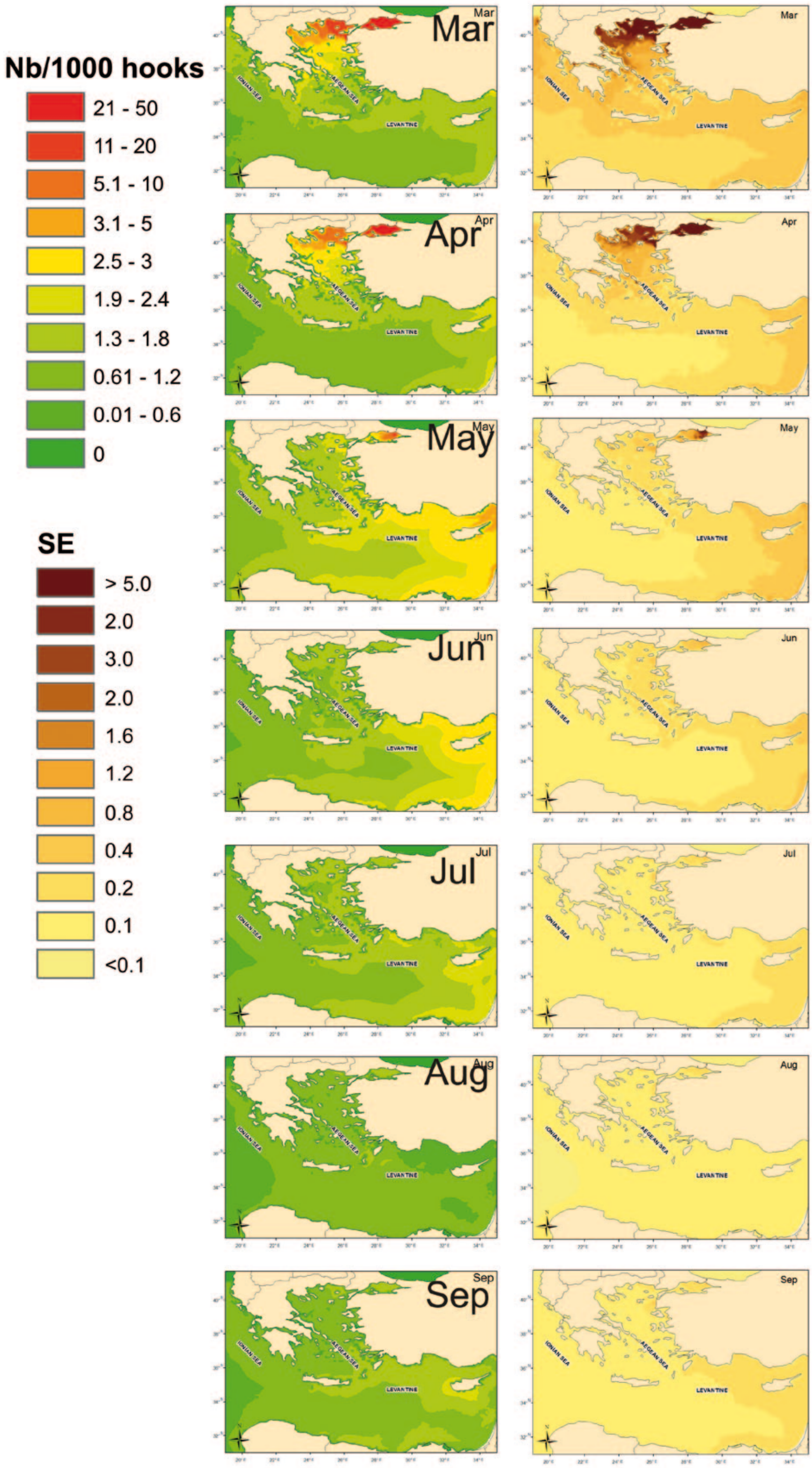

FIG. 5. – Predicted monthly relative abundance (presence only sub-model – number of fish/1000 hooks, left column) and corresponding standard errors (right column), for bluefin tunas in the eastern Mediterranean Sea in 1998-2005. (Predictions refer to a lunar index of 0.5 and American-type swordfish long-line fishing gear)

(or relative standard errors) 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 (Figs 4 and 5). One obvious reason was the low number of observations available in these areas (Fig. 1), which made model predictions imprecise.

DISCUSSION

Mediterranean bluefin tuna fisheries are among the world's fisheries that continue to produce lucrative revenues. However, the race for fish due to the constantly very high market value, coupled with the specific life history characteristics of the species, and the relatively poor monitoring, have occurred elsewhere in the past and have led several fish stocks to depletion (Hilborn *et al.* 2003). Moreover, Mediterranean bluefin tuna fisheries have evolved, in just a few decades, from traditional seasonal trap fisheries in designated areas to intensive industrial open sea fleets covering the whole Mediterranean marine region. In order 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). Understanding the dynamics and spatial distribution of species is crucial for management, as spatial variability governs the definition of management units, stocks, and boundaries (Fromentin and Powers 2005). One way of accomplishing such a task is through commercial fishery-dependent surveys like the one undertaken herein. An indirect identification of the potential habitat can be delivered, based on the associations between environmental preferences and catch rates, and the current results may provide an early habitat proxy defined from the available data. Actual habitat selection is based on more complex aspects such as behavioural characteristics, physiological tolerances and predator-prey interactions (Planque *et al.* 2010).

Temporal distribution of bluefin tuna catches indicated a higher probability of catching tunas during late spring–early summer. This period coincides with the species' spawning period in the region (Corriero *et al.* 2003, Karakulak *et al.* 2004, Heinisch *et al.* 2008). More recently, Druon *et al.* (2011) identified the potential bluefin tuna spawning season as occurring from mid-May to July, gradually building up from eastern to western Mediterranean waters. Kitagawa *et al.* (2004) described that during the spawning season (June) bluefin tunas stop undertaking repeated dives, limiting their movements to the surface layer. This behaviour was interpreted as behavioural thermoregulation. The use of fish attractant chemical light-sticks and thicker (more resilient) lines are reasonable explanations for the increased catches of the American-type swordfish long-line when compared with the traditional one. Moreover, depths where fishing takes place can affect catches as well. SWO-LL_A targets in much deeper waters, often below 50 metres (m), while SWO-LL_T depth ranges rarely exceed 20 m. We assumed that this variable reflected the vulnerability of bluefin tunas rather than their actual abundance.

The highly statistical significance of spatial predictors confirmed that bluefin tuna schools are not randomly encountered with the same likelihood; they tend to congregate in certain marine regions following a seasonal pattern. High probabilities of encountering a school increased to the southeast (Levantine), tunas showing a persisting presence mostly during the spring and summer. This finding is in accordance with Druon *et al.* (2011), suggesting that the region comprises a favourable spawning habitat as early as May, since surface water temperatures reach the desired thresholds much earlier than in the rest of Mediterranean areas. It is documented that the purse seine fleets are twice as efficient when fishing in spawning grounds rather than in feeding grounds (Druon 2010). The Levantine Sea is a relatively new fishing ground for Greek and Turkish fishermen (visited occasionally by the Italians), who have relocated their activities due to depletion or decline of catches in their traditional fishing grounds (Stergiou *et al.* 2003, Karakulak and Oray 2009). The most up to date statistical bulletin of the General Fisheries Commission for the Mediterranean (GFCM 2011) reports that 33 French purse seiners targeting bluefin tuna have started visiting the region (Geographic Sub-Areas: GSA 24, 25, 26, 27) during the spring-summer period in recent years. The supposition that the marine resources in the high seas of the Levantine basin may have been under-exploited, until recently, can be also supported by the fact that the average size of bluefin tunas caught in the area is among the largest in the eastern Mediterranean. In fact, bluefin tunas caught in the Levantine region had an average round weight of 76.1 kg, while in the Aegean and Ionian Sea their size was significantly smaller (Aegean 54.8 kg, Ionian 53.1 kg). Other pelagic fish, such as swordfish, are also larger on average and more abundant, compared with the rest of the Mediterranean areas (De Metrio *et al.* 2001, Megalofonou *et al.* 2001).

The likelihood of running into a large school was higher in early spring in the northernmost part of the study area (north Aegean Sea plateau, Sea of Marmara). Druon *et al.* (2011) identified the northern Aegean as a potential feeding habitat and drew attention to the fact that feeding and spawning habitats had little overlap. The northern Aegean Sea stands out as a region that hosts large aggregations of typical tuna prey (sardines, anchovies, mackerel); official statistics report very high landings for these species (Machias *et al.* 2007). Presumably, in the eastern Mediterranean Sea feeding occurs mainly in the northern, more productive waters in winter and early spring, while spawning takes place in the eastern part (Levantine Sea) in late spring-early summer. The thermal preference observed (warm waters >22°C) was apparent only for the probability of encountering a school. Our findings cannot be straightforwardly comparable with the outcomes of analogous research studies in recent years, since most of them were based on tagging experiments or satellite imagery analyses. Specifically, Brill *et al.* (2002) found that they spent most of their time in temperatures higher than 20°C, Itoh *et al.* (2003) defined their preference as between 14 and 20°C, and Schick *et al.* (2004) reported an average of 18.1°C. Finally, Wilson *et al.* (2005) reported that they tend to spend more than 50% of their time in ambient temperatures of 15°C to 23°C. Since our dataset was derived from a fishery-dependent survey, it was limited only to the fishing period (March to September). As such, the estimated temperature preferences cannot depict an overall year-round preference and bear more resemblance to the summer spawning season. Spawning in the Mediterranean Sea occurs in warm waters (>20°C) and most often in waters ranging from 22.5°C to 25.5°C (Schaefer 2001, Rooker *et al.* 2007).

The probability of catching a bluefin tuna exhibited a periodicity coincident with the lunar cycle, attaining higher values during the full moon phase (lunar index 75-100%). This finding may be an indication of vision playing an important role in predatory behaviour. Aristotle reasoned that "...tunnies are caught on nights of full moon, for the fishes are induced (by the warmth or the light) to emerge for a while from their lair in quest of food..." (D'Arcy Wentworth Thompson 1910). Marsac *et al.* (1996) suggested that yellowfin tuna habitat selection is influenced by the lunar phase and that fish swim in shallower water during nights of full moon. Blue sharks in the eastern Mediterranean exhibited analogous patterns associated with lunar activity (Damalas and Megalofonou 2009). All fishermen that took part in this study unanimously identified the phenomenon as an annual event, and referred to it as the full moon of May tunas. In fact, many of the sets deployed during this study around the full moon of May had more bluefin tunas in the catch than the target species (swordfish). Distance from land embracing both spatial and environmental properties as an explanatory variable was negatively correlated with catch rates (school size), suggesting that if a school is encountered, it is more likely to be a larger one in the shallow coastal areas. In general, coastal areas are characterized by high productivity, which in turn attracts large aggregations of pelagic fishes. Thus, our finding could be interpreted as reflecting foraging of bluefin tuna, as prey usually congregate near land or on seamounts and banks. Then again, Wilson *et al.* (2005) reported that the vertical behaviour of bluefin tuna differed among locations, with shallower swimming depths occurring when fish were in inshore waters and that night-time swimming depths were shallower than those at day. Therefore, if tunas tend to be at the surface layers whenever they are in the vicinity of land and especially during night hours, then they are more vulnerable to surface long-lining, which is mainly a nocturnal activity.

A moderate, but constant decline in the probability of encountering a bluefin tuna school was identified for the whole period of our study (1998-2005). These findings could be (1) linked to inter-annual environmentally-driven fluctuations of school distribution (2) linked to mal-apportioned fishing effort or (3) a sign that the population is under alarming fishing pressure. Druon *et al.* (2011) have detected significant environmentally based anomalies in the potential habitat of Mediterranean bluefin tunas. Regarding the status of bluefin tunas in the eastern Mediterranean Sea, because the time period of the existing data was too brief and projections are known to be impaired by various sources of uncertainties that have not yet been fully quantified, no reliable speculation could be made upon the annual trend in catches (declining, stable or increasing). Because of the small number of variables examined, it may be early to draw strong inferences regarding environmental effects on bluefin tuna distribution and abundance, above all because tunas were not the target species in our fishery-dependent dataset. However, the outcomes of this study supplement the recent study undertaken by Druon *et al.* (2011) on the potential habitats of Mediterranean bluefin tunas, which suffered from a verification of estimates in the eastern Mediterranean region. A better understanding of key ecological processes is needed, especially with regard to the habitat and spatial dynamics of this highly migratory species. Evidence shows that the effects of fishing in the Mediterranean go far beyond isolated impacts on overfished target species, vulnerable non-commercial groups or sensitive habitats. The ecosystem effects of fishing in the Mediterranean are also conspicuous at the systemic level, as highlighted by the massive ecological footprint of fishing or the marked effects on the food-web structure. A holistic approach, taking into account spatial dynamics of resource distribution, should therefore be adopted if the overall changes to the structure and the functioning of marine ecosystems caused by fishing are to be remedied.

ACKNOWLEDGEMENTS

We wish to thank all fishermen who assisted observers in data collection, both on board fishing boats and at landing locations. This study was performed with the finance of the Commission of the European Communities (Projects No: 97/050 and 97/074 DG XIV/C1), as well as within Operational Programme Education by the ESF (European Social Fund) and National Resources. Special thanks are due to Dr Iago Mosqueira (Joint Research Centre – European Commission) for providing valuable comments and the Spanish translation.

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Scient. ed.: J.J. Govoni.
Received June 6, 2012. Accepted September 27, 2012.
Published online November 26, 2012.