Spatiotemporal distribution and habitat use of commercial demersal species in the eastern Mediterranean Sea

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ABSTRACT

Generalized additive models (GAMs) were applied to investigate the influence of spatial (subarea), temporal (season) and environmental variables (substrate characteristics, depth, temperature and salinity) on the relative abundance of 27 demersal species of commercial importance in the Aegean Sea. Twelve species exhibited decreasing population density with increasing depth, whereas the abundance of the remaining species peaked at intermediate depths. Most of the species were mainly distributed on the continental shelf and upper continental slope. The dry weight percentage of sand in the sediment was included as an important predictor in the best models of all species with a lifecycle closely related to the substrate (flatfish, skates, gurnards, mullets, anglers, scorpionfish) and in most benthopelagic species (seven of 12). The weight percentage of carbonates in the sediment was also included in the best models of most species (19 of 27). Seasonal patterns in the relative abundance of species were observed, related in most cases to the seasonal differentiation of temperature and salinity gradients. During the period of water stratification (summer and autumn) the influence of temperature or salinity on fish abundance was always

greater than during the period of vertical mixing (winter). The present results are discussed in the light of fostering the current perception as to factors influencing the spatiotemporal distribution of fish, which is a prerequisite for the sustainable exploitation of commercial stocks.

INTRODUCTION

One of the objectives of the European Common Fisheries Policy Regulation of 2002 (EC, 2002) is the progressive implementation of an ecosystem approach to fisheries management (EC, 2008). Several steps have been taken in this direction, such as the protection of vulnerable habitats (EC, 1992), policy to reduce by-catches (EC, 2007), the progressive move to more long-term approaches in fisheries management, and the recently adopted MSY strategy (EC, 2006). Moreover, an ecosystem approach to fisheries management should also integrate the issue of impacts due to environmental and climate change, and responses to prevent and mitigate these impacts. The ecosystem approach should be based on current impacts and projections of expected impacts on the marine environment, and in particular its living marine resources, with the urgent view to prepare efficient climate change adaptation strategies. To this end, the prerequisite is a solid knowledge of species–environment relationships.

Marine fisheries have experienced dramatic growth in the last centuries, making the need for effective management greater than ever. However, management is greatly influenced by the behavior and dynamics of the fished stocks, specifically fluctuations in distribution and abundance, which in turn are affected not only by fisheries harvests but also by variations in the environment. Extrinsic factors influencing the spatial distribution of demersal fish are depth, which is often the main gradient along which faunal changes occur when analyzing shelf and upper slope assemblages (Bianchi, 1992; Fujita *et al.*, 1995; Moranta *et al.*, 1998; Demestre *et al.*, 2000;

Kallianiotis *et al.*, 2000), type of substratum (Mahon and Smith, 1989; Bianchi, 1992; McCormick, 1995; Gaertner *et al.*, 1999; Demestre *et al.*, 2000) and physical characteristics (such as temperature and salinity) of the water masses (Mahon and Smith, 1989; Maravelias *et al.*, 2007a,b,c). Intrinsic biotic interactions among assemblage members also affect the abundance of demersal species but seem to be of less importance (Mahon and Smith, 1989; Sale *et al.*, 1994).

The goal of the present work was to analyze the quantitative relationships between the relative abundance of the most important commercial species caught by trawlers in the Aegean Sea, and spatial, temporal and environmental variables (substrate characteristics, depth, temperature and salinity). Frequently used analytical tools (e.g., generalized linear models; McCullagh and Nelder, 1989) assume a linear relationship between relative abundance of marine species (or transformed relative abundance) and environmental variables. However, the dependence of population density on spatial and environmental parameters is anticipated to be more complex (e.g., Lehmann *et al.*, 2002; Katsanevakis, 2007), and thus there is a need for appropriate non-linear modeling techniques. Generalized additive models (GAM; Hastie and Tibshirani, 1990) are a modern non-parametric technique that frees the researcher from the limiting concept of a strict parametric shape and allows the fitting of statistical models that better agree with ecological theory and are not restricted by convenient mathematical formulas. GAMs are increasingly used in ecological studies to study spatial distribution and abundance of marine species (e.g., Maravelias and Reid, 1997; Daskalov, 1999; Lehmann *et al.*, 2002; Daskalov *et al.*, 2003; Katsanevakis, 2007; Maravelias *et al.*, 2007a,b,c), as the ecological interpretability of the non-parametric response curves and the flexibility of GAMs to fit the data closely are advantageous characteristics that make them a valuable tool in marine ecological studies.

MATERIALS AND METHODS

Study area

The Aegean Sea is characterized by an extended length of coastline (∼16 000 km), complex bathymetry, and many islands (more than 2500) (Fig. 1). Survey data in two subareas of the Aegean Sea were used in this study: the North Aegean Sea and the Central Aegean plateau (Cyclades plateau) (Fig. 1).

The North Aegean Sea comprises a wide continental shelf composed of shallow platforms. The North Aegean shelf represents the offshore continuation of the alluvial planes of northern Greece, which are drained by large rivers that feed the shelf with terrigenous clastic material (Sakellariou *et al.*, 2005). The North Aegean behaves as a dilution basin, i.e., as an exporter of light waters to the south-Central Aegean, due to the contribution of the light brackish
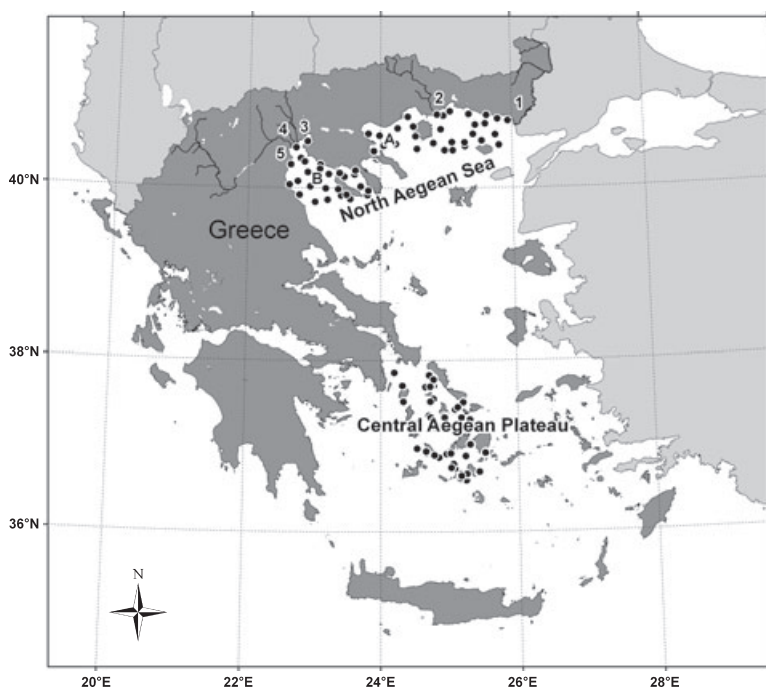

Figure 1. Map of the study area with the sampling stations indicated by black dots. (Rivers: 1 – Evros, 2 – Nestos, 3 – Axios, 4 – Loudias, 5 – Aliakmon; Gulfs: A – Strymonikos Gulf, B – Thermaikos Gulf).

waters of the Black Sea through the Dardanelles Strait (Zervakis *et al.*, 2005). In contrast, the south-Central Aegean Sea is classified as a concentration basin, where evaporation exceeds freshwater income. The Central Aegean plateau represents a shallow platform of about 200 m mean depth with numerous small islands. The trophic state of the North Aegean area is characterized as mesotrophic, whereas the Central Aegean plateau is considered an oligotrophic area (Gotsis-Skretas and Ignatiades, 2005; Siokou-Frangou *et al.*, 2005).

North Aegean bottom trawl landings exceeded those in the Central Aegean plateau by a factor of ~ 5.5 on average in the past decade (Fig. 2), although the two sub-areas have similar potentially trawlable surface area. This is not only attributed to the higher trophic potential of the region but also to the intense exploitation of marine resources, as >50% of the Greek otter trawl fleet operates in the North Aegean Sea, producing >57% of the total national demersal landings (NSSG, 2006).

Sampling – data collection

Sampling was performed on a seasonal basis in the two sub-areas of the Aegean Sea, between 1991 and 1996, by trawl surveys. A total of 342 hauls were conducted at depths ranging between 16 and 416 m. Sampling was random, stratified by depth, and took place only during daylight hours. The same vessel and the same type of gear were used in every case. The haul duration was 40 min on average, with a vessel speed of 2.9 knots. Trawl nets had a knot-to-knot cod-end mesh size of 16 mm. The average width of the trawl mouth opening was 13 m, as estimated with a SCANMAR catch control system.

The catch from each haul was sorted and identified to species, and specimens from each species were enumerated. Twenty-seven species were studied in the current context (Table 1). Catch per unit of effort (CPUE) was defined as the number of individuals caught per hour of trawling, and it was considered a relative measure of population density, although the constant of proportionality (i.e., catchability) is unknown and may vary by species. However, catchability for each species was assumed invariant by haul, as all hauls were carried out using the same vessel and gear configuration. Ambient water temperature and salinity at trawling depth were obtained using a Sea-Bird Electronics conductivity/temperature/depth (CTD) unit onboard the fishing boat.

The dataset of the grain-size (sand, silt and clay percentages) and the carbonate content (%) of surface sediments was based on the work of Karageorgis *et al.* (2005). This initial compilation had a total of 2878 records for grain-size data and 1779 for carbonate content, covering various sectors of the Greek territory, and all data were archived in OCEAN DATA VIEW (ODV) software (Schlitzer, 2008). However, this dataset had a relatively poor coverage of the Central Aegean plateau, and additional data were required to fit with the trawler tracks. Data mining revealed a number of HCMR reports that had not been archived digitally, and 136 new records were included in the new dataset. In addition, 36 records were obtained from Pehlivanoglou (2001). In all these compiled studies, grain-size data have been determined by separating the sand fraction (i.e., the percentage of material with grain sizes between 0.063 and 2 mm) by wet sieving according to Folk (1980). Carbonate content was determined with the carbonate bomb (Müller and Gastner, 1971).

The final dataset used in the present study provided a good coverage for grain-size and carbonate content data in the study area. To create gridded data for sand,
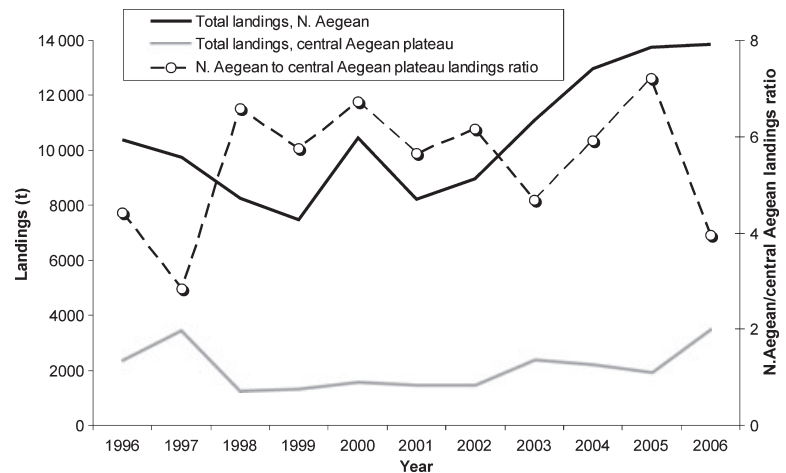

Figure 2. Total landings by bottom trawlers in the North Aegean and the Central Aegean plateau subareas, and the landings ratio between the two subareas.

Table 1. Number of individuals for each of the 27 species caught and percentage of their occurrence in the 342 hauls of the bottom trawl experimental surveys in the Aegean Sea are given.

Scientific name	Common name	Number caught	Occurrence in hauls (%)
Chelidonichthys lucernus	Tub gurnard	1451	29.1
Dentex maroccanus	Morocco dentex	6881	37.0
Diplodus annularis	Annular seabream	8796	30.0
Eutrigla gurnardus	Grey gurnard	1800	30.9
Lepidotrigla dieuzeidei	Spiny gurnard	3125	9.1
Leucoraja naevus	Cuckoo ray	144	16.4
Lophius budegassa	Black-bellied angler	4309	80.9
Macroramphosus scolopax	Longspine snipefish	6337	16.1
Merlangius merlangus euxinus	Whiting	3294	19.4
Merluccius merluccius	European hake	26 955	87.9
Microchirus variegatus	Thickback sole	601	19.4
Micromesistius poutassou	Blue whiting	18 680	14.2
Mullus barbatus	Red mullet	39 532	65.5
Mullus surmuletus	Striped red mullet	4460	34.5
Pagellus acarne	Axillary seabream	2255	19.7
Pagellus bogaraveo	Blackspot seabream	13 270	27.0
Pagellus erythrinus	Common pandora	1416	33.9
Phycis blennoides	Greater forkbeard	1063	28.5
Raja clavata	Thornback ray	1264	51.8
Raja miraletus	Brown ray	213	20.6
Scorpaena notata	Small red scorpionfish	4743	36.4
Solea solea	Common sole	590	22.7
Symphurus ligulatus	Elongate tonguesole	919	19.4
Symphurus nigrescens	Tonguesole	248	11.2
Trigloporus lastoviza	Streaked gurnard	1512	42.4
Trisopterus minutus capelanus	Poor cod	67 252	71.2
Zeus faber	John dory	698	52.7

silt, clay and carbonate content, and subsequently to correlate the substrate parameters with the trawl data, the following procedure was designed: (i) station and trawl coordinates were converted from latitude, longitude (in degrees) to x, y coordinates in Mercator projection (in meters); (ii) a 2000 × 2000 m grid was generated using SURFER® software and employing Kriging interpolation algorithm; and (iii) a custom interpolation subroutine was used to return z values (sand, silt, clay, carbonate content) from the grids, at the location of each haul. Kriging is a popular geostatistical gridding method that provides useful tools for the calculation of reliable gridding solutions (Davis, 1986 and references therein; Cressie, 1991). We used ordinary Kriging (no drift) with point Kriging type to generate the interpolated grids.

Modeling CPUE

The functional relationships between population density of marine species and environmental variables are very likely to be nonlinear (e.g., Bigelow *et al.*, 1999; Katsanevakis, 2007). Therefore, assuming an inherent non-linearity, we applied GAMs to identify variables influencing population density and to reveal the form of the relationships.

The expected values of CPUE in each haul were related to the spatial and environmental covariates, according to the general formulation

$$f(E[CPUE_i]) = LP_i = c + \sum_m s_m(z_{mi}) + \sum_r F_{ri} \quad (1)$$

where f is the link function, LP is the linear predictor, $s_m(\cdot)$ is the one-dimensional smooth function for covariate m, F_r are categorical predictors, and z_{mi} is the value of spatial covariate m for the ith haul. The smooth function $s_m(\cdot)$ was represented using penalized regression splines (cubic splines with basis dimension q = 5), estimated by penalized iterative least squares (Wood, 2006). The optimum degree of smoothing was defined by generalized cross validation (GCV), increasing the amount that the effective degree of freedom of each model counts, in the GCV score, by a factor $\gamma = 1.4$. The GCV method is known to have some tendency for occasional over-fitting, and it has been suggested that using $\gamma \approx 1.4$ can largely correct

this without compromising model fit (Kim and Gu, 2004). The model fitting was accomplished using the *mgcv* package (Wood, 2000, 2006) in R v.2.4.0 (R Development Core Team, 2006).

Seven predictor variables were used: (i) *Depth*; (ii) the dry weight percentage of sand in the sediment (*Sand*); (iii) the dry weight percentage of carbonate content in the sediment (*Carbonates*); (iv) *Season*, which was a categorical factor with four levels (1 – winter, 2 – spring, 3 – summer, 4 – autumn); (v) interaction of bottom temperature with season (*T:Season*); (vi) interaction of bottom salinity with season (*Sal:Season*); and (vii) subarea (*Area*), which was a categorical variable with two levels, one for the North Aegean subarea and the other for the Central Aegean plateau subarea. Temperature and salinity vary both spatially and temporally and if they had been included in the models on their own as predictor variables, it would have been difficult to interpret their effect on population density. A declining trend with temperature might be due to a preference for sites of lower temperatures (spatial interpretation) or due to a higher density during the cold season, e.g., because of recruitment (temporal interpretation). To avoid such issues, we included in the models the interactions of temperature and salinity with season, so that the temporal and the spatial effects would be separated. Texture (particle size distribution) is one of the fundamental mass properties of sediments, and is typically expressed as the weight percentage of sand and mud (material finer than 0.063 mm; silt plus clay). As the percentage of mud is linearly dependent on the percentage of sand (% sand + % mud = 100%), only the former was included as a predictor variable in the GAMs.

CPUE distributions are usually skewed and far from confronting the assumptions accompanying the normal (Gaussian) case. To identify the best underlying probability distribution (Gaussian, Lognormal, or Gamma) we followed an information theory approach, based on the Akaike Information Criterion (AIC) (Akaike, 1973; Burnham and Anderson, 2002). Comparisons among different error distributions were based on the full model, i.e., a model including all seven predictor variables.

After identifying the best probability distribution, the information theory approach was applied again for model selection among the set of candidate models. Specifically, the AIC criterion was used, and the AIC differences, $\Delta_i = AIC_i - AIC_{min}$, were computed over all candidate models g_i, where AIC_{min} is the minimum AIC corresponding to the 'best' model. All models with $\Delta_i < 2$ have substantial support from the data

(Burnham and Anderson, 2002) and were thus considered for inference.

Twenty-six different GAMs g_i, $i = 0$–25, were fitted, where g_0 was the reference model, i.e., a model with no predictor variable (Table 2). Depth was included in all candidate models, as it is the main gradient along which population density changes, and also because we wished to reveal the bathymetric distribution patterns of all studied species, which are of great importance for fisheries management and survey design. *Season* and each of the interactions *T:Season* or *Sal:Season* were not included together in the same model. This is because we wished to discriminate

Table 2. The set of candidate models of relative population density of commercial species in the Aegean Sea.

Model	Linear predictor (LP)
g_0	*c*
g_1	*c* + s(*Depth*)
g_2	*c* + s(*Depth*) + s(*Sand*)
g_3	*c* + s(*Depth*) + s(*Sand*) + s(*Carbonates*)
g_4	*c* + s(*Depth*) + *Season*
g_5	*c* + s(*Depth*) + s(*Sand*) + *Season*
g_6	*c* + s(*Depth*) + s(*Sand*) + s(*Carbonates*) + *Season*
g_7	*c* + s(*Depth*) + s(*T:Season*)
g_8	*c* + s(*Depth*) + s(*Sand*) + s(*T:Season*)
g_9	*c* + s(*Depth*) + s(*Sand*) + s(*Carbonates*) + s(*T:Season*)
g_{10}	*c* + s(*Depth*) + s(*Sal:Season*)
g_{11}	*c* + s(*Depth*) + s(*Sand*) + s(*Sal:Season*)
g_{12}	*c* + s(*Depth*) + s(*Sand*) + s(*Carbonates*) + s(*Sal:Season*)
g_{13}	*c* + s(*Depth*) + s(*T:Season*) + s(*Sal:Season*)
g_{14}	*c* + s(*Depth*) + s(*Sand*) + s(*T:Season*) + s(*Sal:Season*)
g_{15}	*c* + s(*Depth*) + s(*Sand*) + s(*Carbonates*) + s(*T:Season*) + s(*Sal:Season*)
g_{16}	*c* + s(*Depth*) + *Area*
g_{17}	*c* + s(*Depth*) + *Area* + s(*Sand*)
g_{18}	*c* + s(*Depth*) + *Area* + *Season*
g_{19}	*c* + s(*Depth*) + *Area* + s(*Sand*) + *Season*
g_{20}	*c* + s(*Depth*) + *Area* + s(*T:Season*)
g_{21}	*c* + s(*Depth*) + *Area* + s(*Sand*) + s(*T:Season*)
g_{22}	*c* + s(*Depth*) + *Area* + s(*Sal:Season*)
g_{23}	*c* + s(*Depth*) + *Area* + s(*Sand*) + s(*Sal:Season*)
g_{24}	*c* + s(*Depth*) + *Area* + s(*T:Season*) + s(*Sal:Season*)
g_{25}	*c* + s(*Depth*) + *Area* + s(*Sand*) + s(*T:Season*) + s(*Sal:Season*)

':' interaction between predictors.
g_0 : reference model.

between seasonal density differences unrelated to temperature or salinity variation (e.g., due to recruitment) and differences that were correlated with temperature or salinity patterns and might be related to migration in areas of preferred temperature or salinity, and at the same time avoid including correlated predictors. The two subareas were clearly differentiated by the weight percentage of carbonates in the sediment. *Carbonates* varied between 6 and 49% in the North Aegean subarea (mean = 19.7%) and between 40 and 91.7% in the Central Aegean plateau (mean = 69.6%) and were significantly different between the two subareas (*t*-test of the arcsine-transformed values, $P < 0.001$). Thus, *Area* and *Carbonates* were not included in the same model (except the full model) as they were largely redundant.
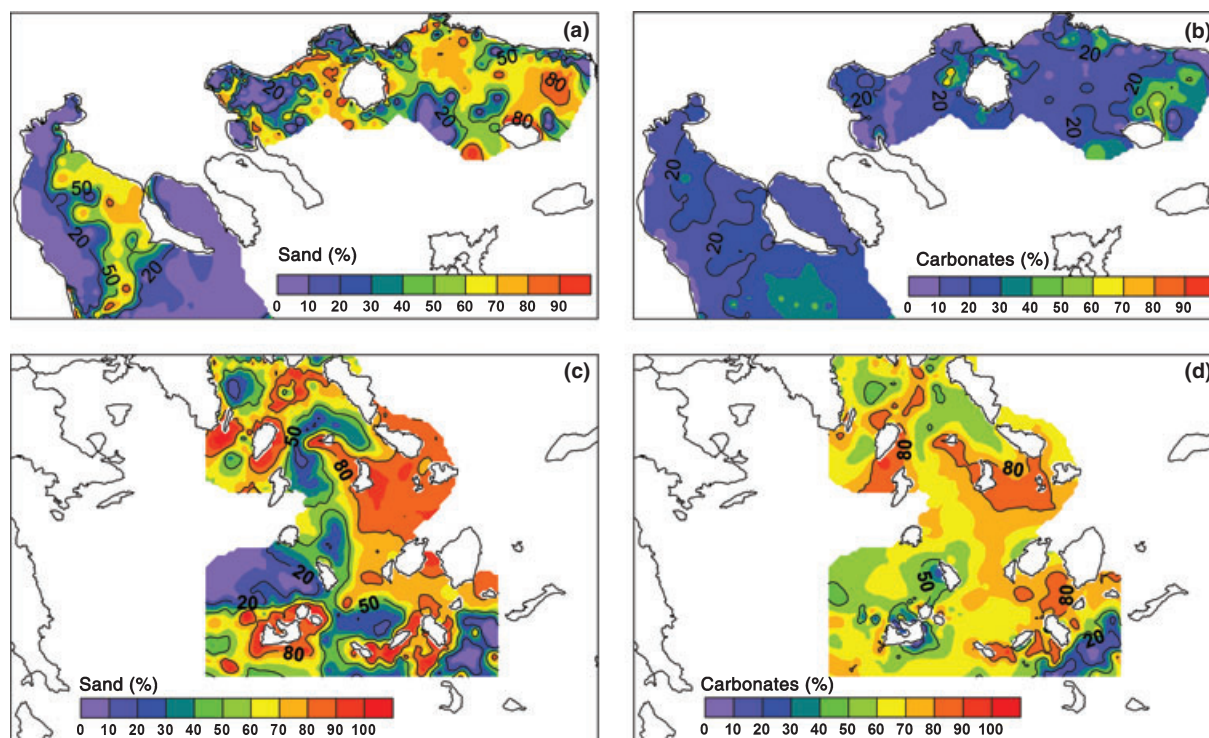
RESULTS

Raw data

More than 220 000 specimens of the 27 commercial species of this study were caught during the 342 bottom trawl hauls. Almost 60% of the commercial species catch (in numbers of fish) consisted of only

three species: poor cod (30%), red mullet (17%) and European hake (12%) (Table 1).

The substrate properties of the surface sediments were represented here by the spatial distribution of the sand and the carbonate contents (Fig. 3). In the North Aegean Sea, sand spatial distribution showed great patchiness (Fig. 3a). In more detail, the areas where the sand content was relatively small (<30%) were the north, western, and eastern sectors of the Thermaikos Gulf, the Strymonikos Gulf, the Nestos and Evros River deltas and some minor occurrences offshore. The majority of the area was dominated by sandy sediments (sand content >50%), with peaks of higher percentages in the central Thermaikos Gulf, and almost the entire continental shelf of the eastern part of the North Aegean sub-area. On the other hand, carbonate content exhibited much more homogeneous distribution (Fig. 3b). Generally, percentages <30% prevailed all over the study area.

In the Central Aegean plateau and the neighboring areas, sand was definitely the prevailing fraction, with values often exceeding 80% over large sectors (Fig. 3c). Patches of sediments with lower sand percentages (10–30%) were observed between the islands. In this case, most of the sand originated in biogenic

Figure 3. Spatial distribution of (a) sand (%) and (b) carbonate content (%) in the North Aegean Sea; (c) and (d) similarly for the central Aegean plateau.

calcareous shells and fragments of bivalves, foraminifera, gastropods, and fragments of hard calcareous crusts with an abundance of red algae. This texture was clearly represented in the carbonate content distribution, which largely followed the same patterns (Fig. 3d).

Overall modeling results

The Gamma probability distribution was selected as best among the candidate error distributions, based on AIC. Therefore, we assumed a Gamma error distribution for all candidate models, and 'log' as the corresponding natural link function. Model g_{15}, i.e., $\log(CPUE) = c + s(Depth) + s(Sand) + s(Carbonates) + s(T{:}Season) + s(Sal{:}Season)$, was the most frequently included in the set of substantially supported models (with $\Delta_i < 2$), in 13 of the 27 species (Table 3). The deviance explained by the best models varied between 29.5% for *Symphurus ligulatus* and 79.2% for *Lepidotrigla dieuzeidei*.

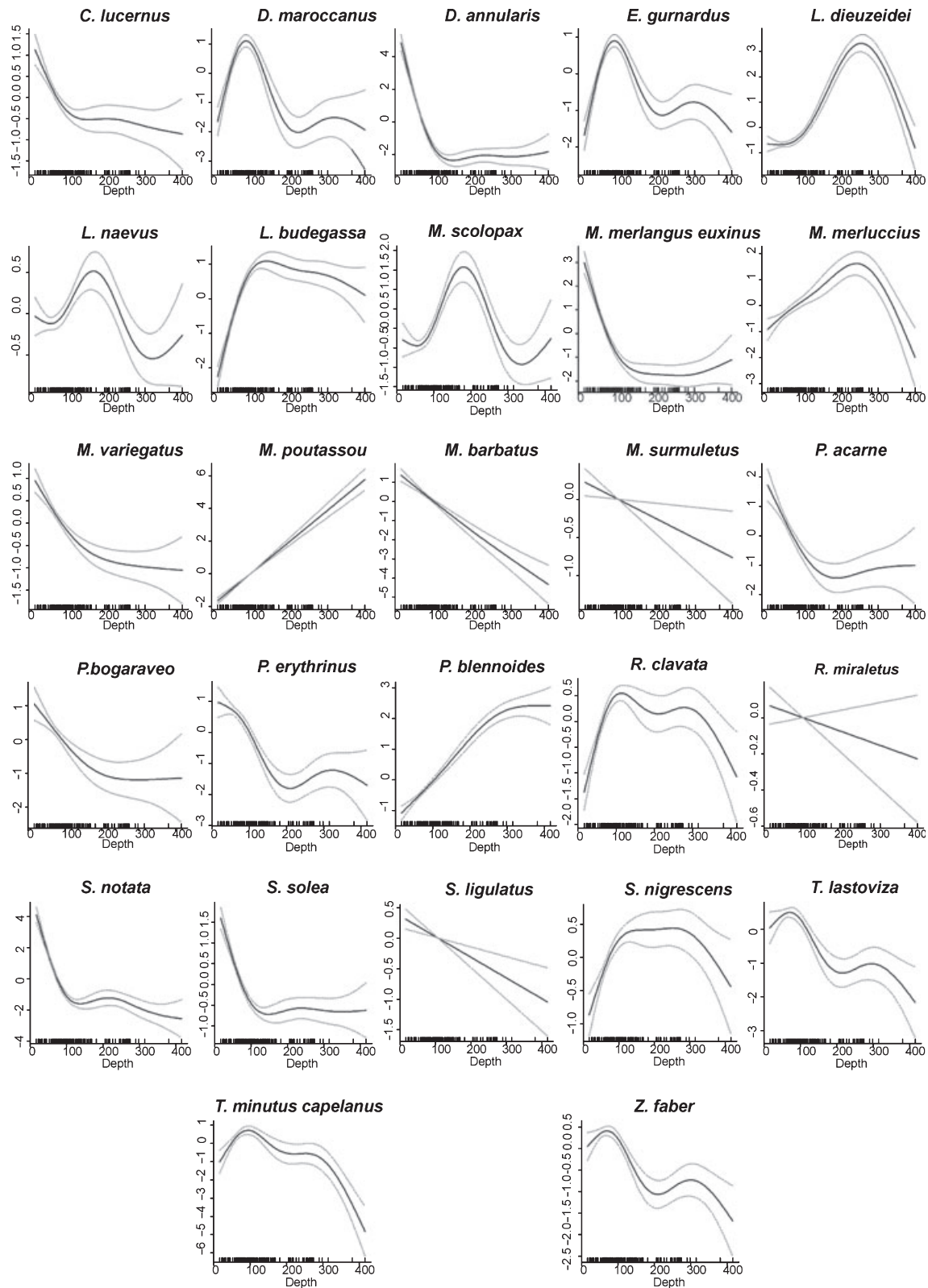*Patterns of bathymetric distribution*

The smooth term of depth was significant for all studied species, except for *Raja miraletus* (Table 3). This justifies our choice to *a priori* include depth as a predictor variable in all candidate models. A variety of patterns of the bathymetric distribution of the studied species was found (Fig. 4). Many species (*Chelidonichthys lucernus*, *Diplodus annularis*, *Merlangius merlangus euxinus*, *Microchirus variegatus*, *Mullus barbatus*, *Mullus surmuletus*, *Pagellus acarne*, *Pagellus bogaraveo*, *Pagellus erythrinus*, *Scorpaena notata*, *Solea*

Table 3. Summarized results for the 'best' model selected for the 27 commercial species caught in the bottom trawl experimental surveys of the Aegean Sea.

Species	Models with substantial support Δi <2	Edf	Pr(F) Depth	Area	Sand	Carbonates	Season	T:Season	Sal:Season	% of Deviance explained
C. lucernus	**g15**	13.8	<0.001		<0.001	<0.001		0.009	0.128	69.8
D. maroccanus	**g19**	12.6	<0.001	<0.001	<0.001		0.048			54.4
D. annularis	**g15**	14.5	<0.001		0.097	<0.001		<0.001	0.005	73.0
E. gurnardus	g15-**g12**	10.7	<0.001		0.152	<0.001			<0.001	52.1
L. dieuzeidei	**g5**-g19-g6	11.6	<0.001		<0.001		<0.001			79.2
L. naevus	g25-g14-**g6**	10.5	<0.001		<0.001	0.004	<0.001			30.6
L. budegassa	**g17**-g21-g23-g25	8.9	<0.001	<0.001	0.005					48.7
M. scolopax	g24-**g25**	10.5	<0.001	<0.001				0.004	0.116	78.6
M. merlangus euxinus	**g9**-g15	13.3	<0.001		<0.001	<0.001		<0.001		70.5
M. merluccius	**g6**	11.0	<0.001		<0.001	<0.001	0.028			32.2
M. variegatus	**g6**	12.4	<0.001		<0.001	<0.001	0.002			58.5
M. poutassou	**g5**	8.8	<0.001		<0.001		<0.001			71.3
M. barbatus	g15-**g9**	7.1	<0.001		<0.001	<0.001		0.012		41.3
M. surmuletus	**g25**	11.0	0.012	<0.001	<0.001			<0.001	0.061	72.3
P. acarne	**g9**-g15	15.5	<0.001		<0.001	<0.001		<0.001		49.2
P. bogaraveo	g21-**g20**	6.9	<0.001	<0.001				<0.001		50.1
P. erythrinus	g15-**g9**	12.3	<0.001		<0.001	<0.001		0.712		46.9
P. blennoides	**g12**-g15	12.6	<0.001		<0.001	0.016			0.011	74.1
R. clavata	**g6**-g9-g15	13.9	<0.001		0.002	<0.001	0.008			49.2
R. miraletus	**g6**-g21	10.4	0.191		<0.001	<0.001	0.006			43.4
S. notata	**g6**	15.5	<0.001		<0.001	<0.001	0.049			66.7
S. solea	**g6**	14.4	<0.001		<0.001	0.002	<0.001			74.0
S. ligulatus	g23-**g9**-g15	7.0	<0.001	<0.001	0.005				0.028	29.5
S. nigrescens	**g15**	17.0	<0.001		0.003	<0.001		<0.001	0.001	46.0
T. lastoviza	**g15**	14.6	<0.001		<0.001	0.006		<0.001	0.039	58.3
T. minutus capelanus	**g15**	15.5	<0.001		<0.001	<0.001		<0.001	0.124	53.1
Z. faber	**g6**	12.88	<0.001		0.079	<0.001	<0.001			33.7

Pr(F) refers to the *P*-values from an ANOVA *F*-ratio test. Edf are the estimated degrees of freedom. Among the models with substantial support the most parsimonious (in bold) was presented in Figs 4–10.

Figure 4. Estimated smooth terms of *Depth* in the selected best models of the relative abundance of demersal commercial fish species. The smooth terms (black lines) are given in the linear predictor scale. The corresponding 95% confidence intervals are given in gray. Rug on the horizontal axis represents density of datapoints.

solea, Symphurus ligulatus) exhibited decreasing population density with depth. Most of these species were mainly restricted to the continental shelf with highest densities in very shallow waters. For two species (*Micromesistius poutassou, Phycis blennoides*), an increasing trend of population density with depth was observed within the depth range of this study. Presumably, for these species there was a peak in population density deeper than the maximum depth surveyed. The remaining species had a peak in population density at intermediate depths. Among them, *Dentex maroccanus, Eutrigla gurnardus, Leucoraja naevus, Lophius budegassa, Macroramphosus scolopax, Trigloporus lastoviza, Trisopterus minutus capelanus, Zeus faber* exhibited a density peak on the continental shelf, while *Lepidotrigla dieuzeidei* and *Merluccius merluccius* had a density peak between the lower shelf and the upper continental slope. *Raja clavata* and *Symphurus nigrescens* had high densities in a wide depth range both on the continental shelf and on the upper continental slope.

Effect of substrate type

In all species except *M. scolopax* and *P. bogaraveo*, the dry weight percentage of sand in the sediment (*Sand*) was included in the selected model (Table 3). The dry weight percentage of carbonate content in the sediment was also included in the selected models of most species (19 of 27) (Table 3). For some species such as *L. naevus, R. clavata, R. miraletus, S. nigrescens, S. notata, S. ligulatus*, and *T. lastoviza* a clear preference for sandy bottoms was observed, with population density increasing with sand content (Fig. 5). The inverse trend was observed for some other species such as *D. annularis* and *M. merlangus euxinus*, whose densities decreased with sand content (Fig. 5). Other species such as *L. dieuzeidei, L. budegassa, M. merluccius, M. poutassou*, and *P. blennoides* exhibited a peak in relative density for specific values of sand content with declining densities at both lower and higher values (Fig. 5). In a few cases (*C. lucernus, M. variegatus*), a concave upward s(*Sand*) curve was observed with high relative densities at sites of both very low and very high sand content and low densities at intermediate values of *Sand* (Fig. 5).

For *C. lucernus, E. gurnardus, M. merluccius* and *M. barbatus*, relative density declined with carbonates, whereas the opposite was observed for *L. naevus, P. erythrinus, R. clavata, R. miraletus*, and *Z. faber* (Fig. 6). The other species exhibited either high density in an intermediate range of carbonate content or more complex patterns (Fig. 6).

Subarea differences

Subarea (North Aegean or the Central Aegean plateau) was included in the selected model for six of the 28 species. Half of these species (*L. budegassa, P. bogaraveo*, and *S. ligulatus*) had higher densities in the North Aegean subarea and the other half (*D. maroccanus, M. scolopax*, and *M. surmuletus*) in the Central Aegean plateau (Fig. 7).
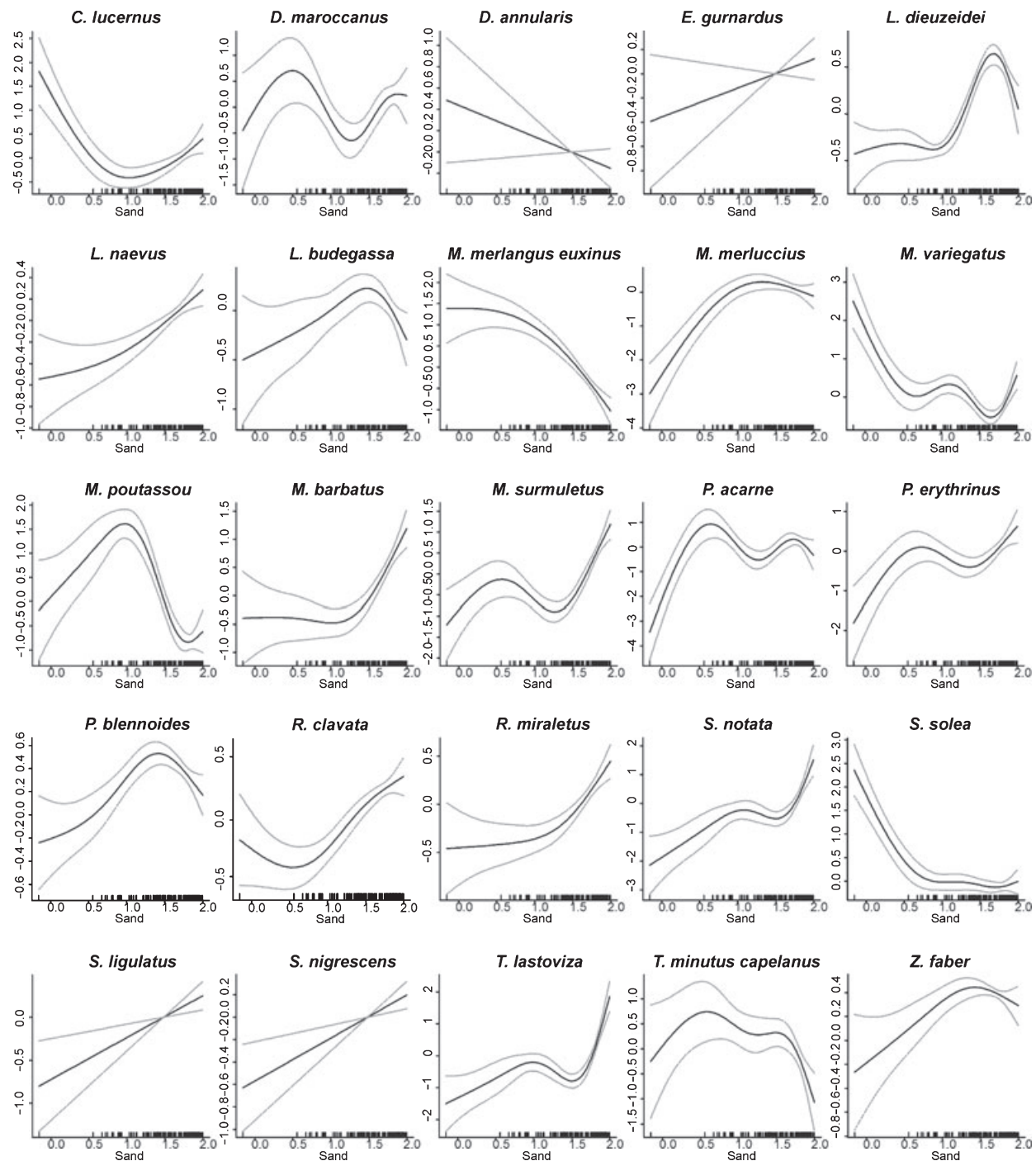
Seasonal patterns

Seasonal variation in the abundance of fish was apparent for 11 of the studied species (Fig. 8). Except for *S. solea*, which was found in higher densities during winter, and *D. marocannus*, which had marginally higher densities in winter and spring, all species were observed in higher densities during the 'warm' seasons (summer and fall). Hence, *M. variegatus, M. poutassou, R. miraletus* and *S. notata* had peaks in relative density during summer, and *L. dieuzeidei, L. naevus, M. merluccius, R. clavata* and *Z. faber* were observed in larger numbers during fall. The seasonal differences in relative abundance were most pronounced for *M. poutassou*, for which the relative density in summer was 7.7 times higher than the relative density in spring.

Temperature and salinity patterns

The *T:Season* interaction was included in the selected models of 12 species (Table 3; Fig. 9). Bottom temperature in the dataset varied between 7.5 and 25°C. In this temperature range three main patterns were observed: (i) population density increased with temperature (in *C. lucernus, D. annularis, M. barbatus, P. bogaraveo* and *T. lastoviza*); (ii) population density decreased with temperature, as in *S. nigrescens* and *P. erythrinus* (however, in *P. erythrinus* the trend is not statistically significant); (iii) population density was high in an intermediate range of temperatures and decreased at both higher and lower temperatures (in *M. merlangus euxinus, M. scolopax, M. surmuletus, P. acarne* and *T. minutus capelanus*). A common pattern in all cases was that the effect of temperature was pronounced in summer and autumn, when there is a marked thermocline, whereas it was much less intense in winter, when the thermocline has broken down.

The *S:Season* interaction was included in the best models of ten species (Table 3; Fig. 10). Bottom salinity in the dataset varied between 35.5 and 39.9. In this range of salinities four main patterns were observed: (i) population density increased with salinity (in *C. lucernus, D. annularis, P. blennoides* and *T. lastoviza*); (ii) population density generally decreased with salinity (in *M. scolopax, M. surmuletus,*
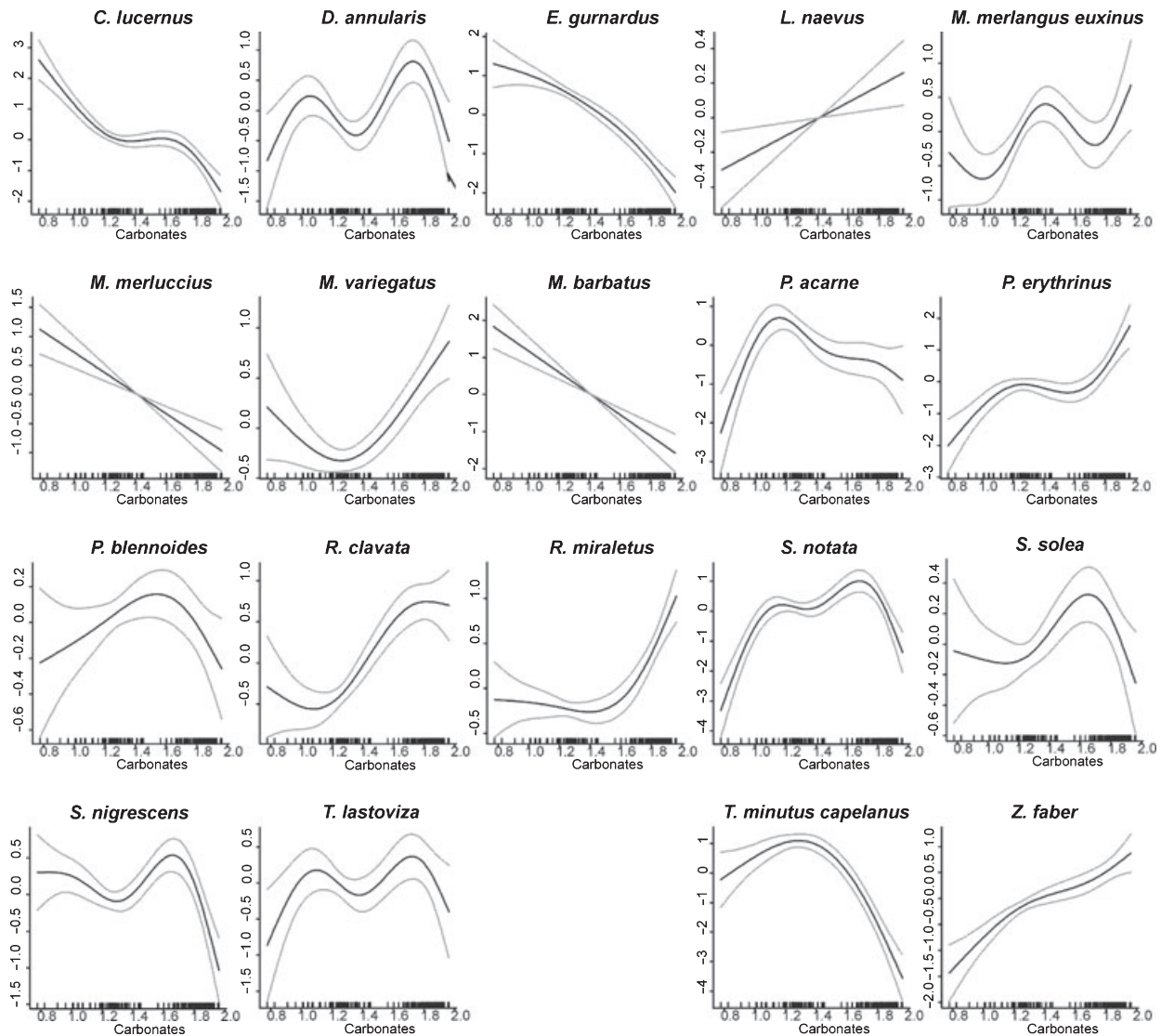
Figure 5. Estimated smooth terms of *Sand* in the selected best models of the relative abundance of demersal commercial fish species. The smooth terms (black lines) are given in the linear predictor scale. The corresponding 95% confidence intervals are given in gray. Rug on the horizontal axis represents density of datapoints.

S. ligulatus and *T. minutus capelanus*); (iii) population density was high in an intermediate range of salinities and decreased at both higher and lower salinities (in *S. nigrescens*); (iv) the curve of population density in relation to salinity was U-shaped, i.e., high densities were observed at both low and high salinities (in *E. gurnardus*). As in temperature patterns, the effect of salinity on population density was more

Figure 6. Estimated smooth terms of *Carbonates* in the selected best models of the relative abundance of demersal commercial fish species. The smooth terms (black lines) are given in the linear predictor scale. The corresponding 95% confidence intervals are given in gray. Rug on the horizontal axis represents density of datapoints.

intense during summer and autumn, and much less intense in winter.

DISCUSSION

Summarizing the similarities and the differences of the substrate properties of the North Aegean Sea and the Central Aegean plateau, it can be concluded that their grain-size characteristics are fairly similar, but that the latter area is clearly differentiated by its high carbonate content. Previous studies have documented that in North Aegean the sands represent relict sediments deposited during the last glacial lowstand, when the sea-level was ~120 m lower than its present level (Karageorgis and Anagnostou, 2001; Perissoratis and Conispoliatis, 2003). In the Central Aegean plateau, most of the sand is of biogenic origin, although there is a portion that is related to relict sediments deposited earlier (Karageorgis, 1992). Pehlivanoglou (2001) suggested that the influence of strong bottom currents in many areas of the Central Aegean plateau prevents the settling of finer particles and favours the growth of calcareous benthic organisms.

Due to the nature of the sampling, this paper dealt solely with species inhabiting soft bottoms or with species that may thrive both on soft bottoms and on

Figure 7. Estimated levels of the factor *Area* (black lines) in the selected best models of the relative abundance of demersal commercial fish species. The corresponding 95% confidence intervals are given in grey. (*Area* levels: 1 – North Aegean; 2 – Central Aegean plateau).
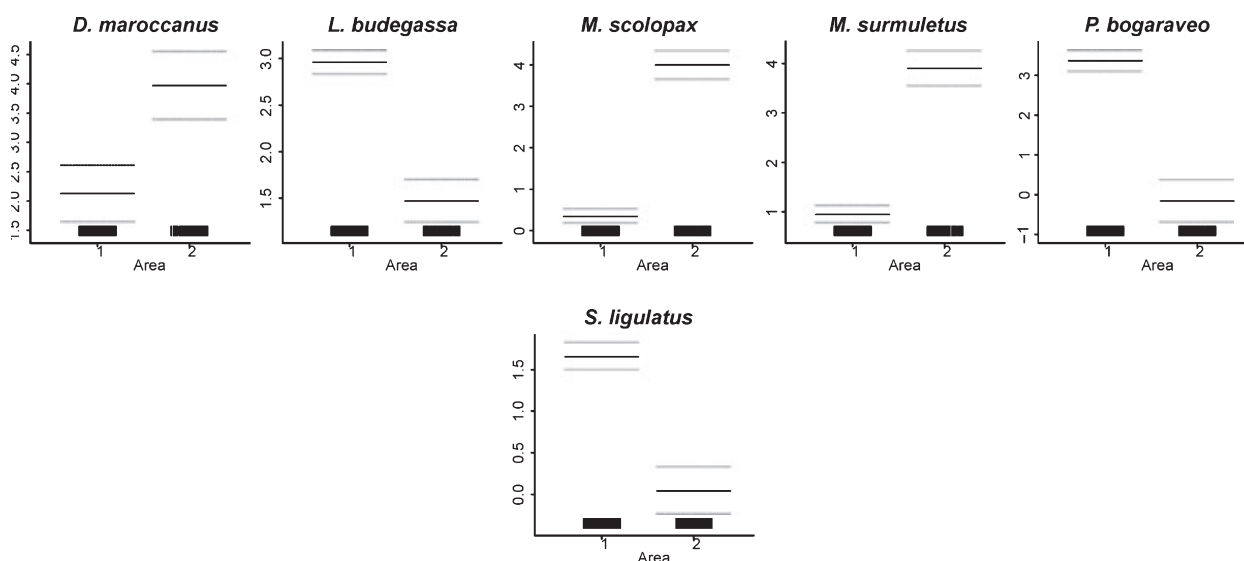

Figure 8. Estimated levels of the factor *Season* (black lines) in the selected best models of the relative abundance of demersal commercial fish species. The corresponding 95% confidence intervals are given in gray. (*Season* levels: 1 – winter; 2 – spring; 3 – summer; 4 – autumn).
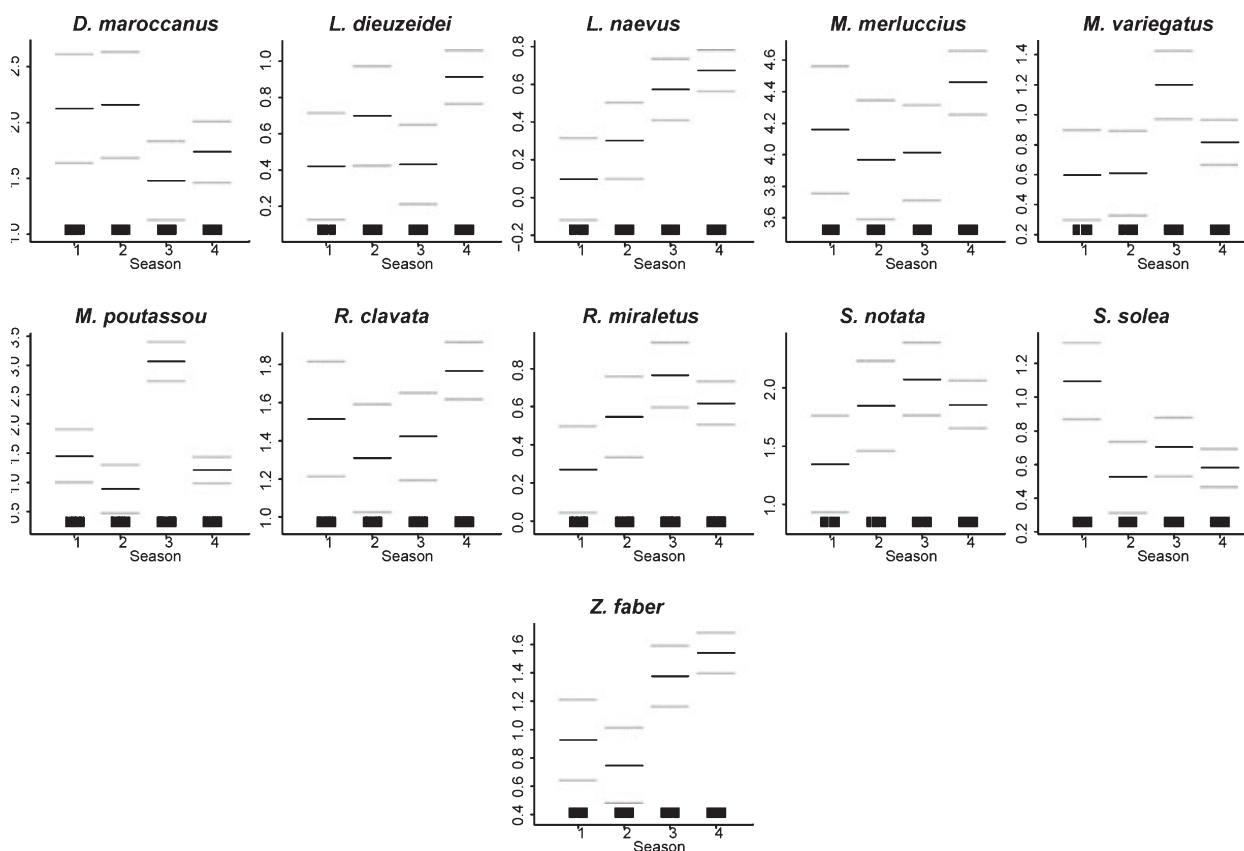
Figure 9. Estimated smooth terms of the interaction *T:Season* in the selected best models of the relative abundance of demersal commercial fish species, in the linear predictor scale. (*Season* levels: 1 – winter; 2 – spring; 3 – summer; 4 – autumn).

Figure 10. Estimated smooth terms of the interaction *Sal:Season* in the selected best models of the relative abundance of demersal commercial fish species, in the linear predictor scale. (*Season* levels: 1 – winter; 2 – spring; 3 – summer; 4 – autumn).
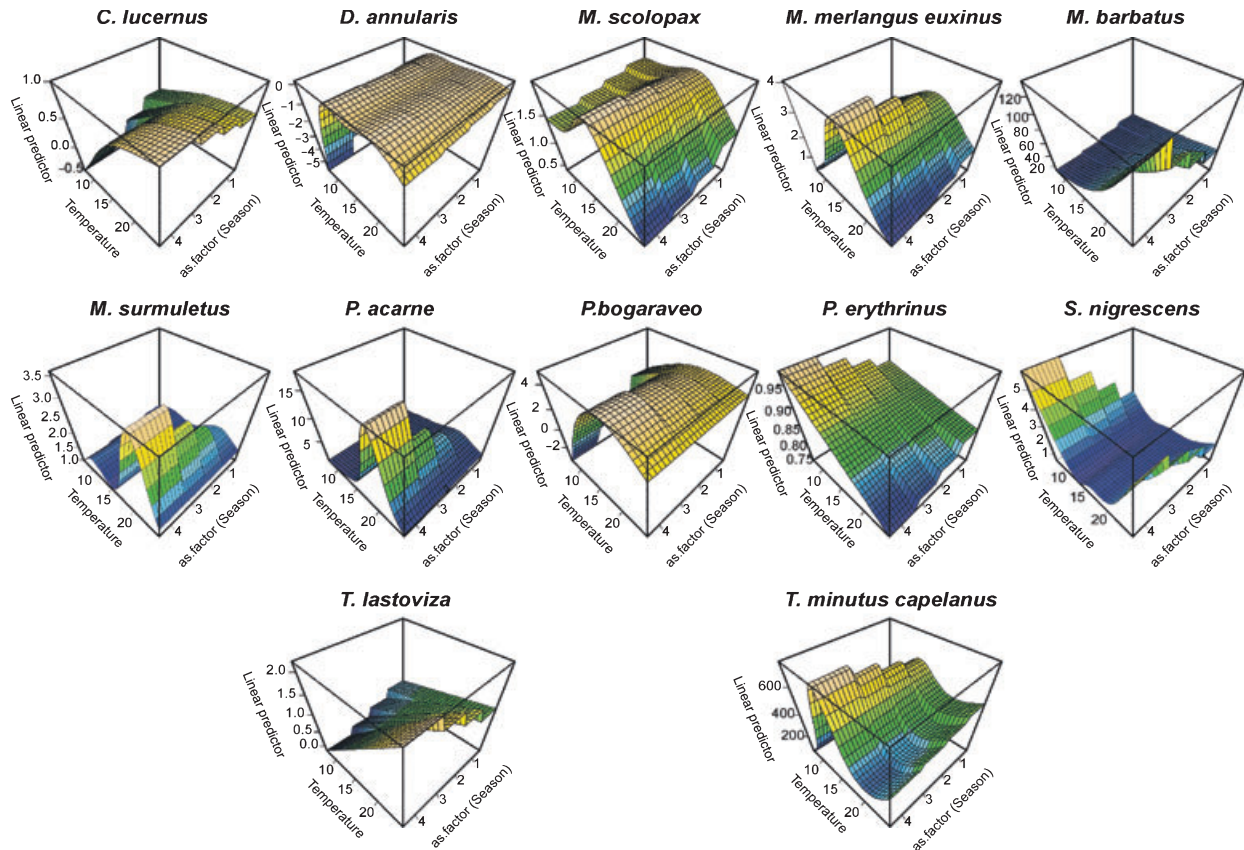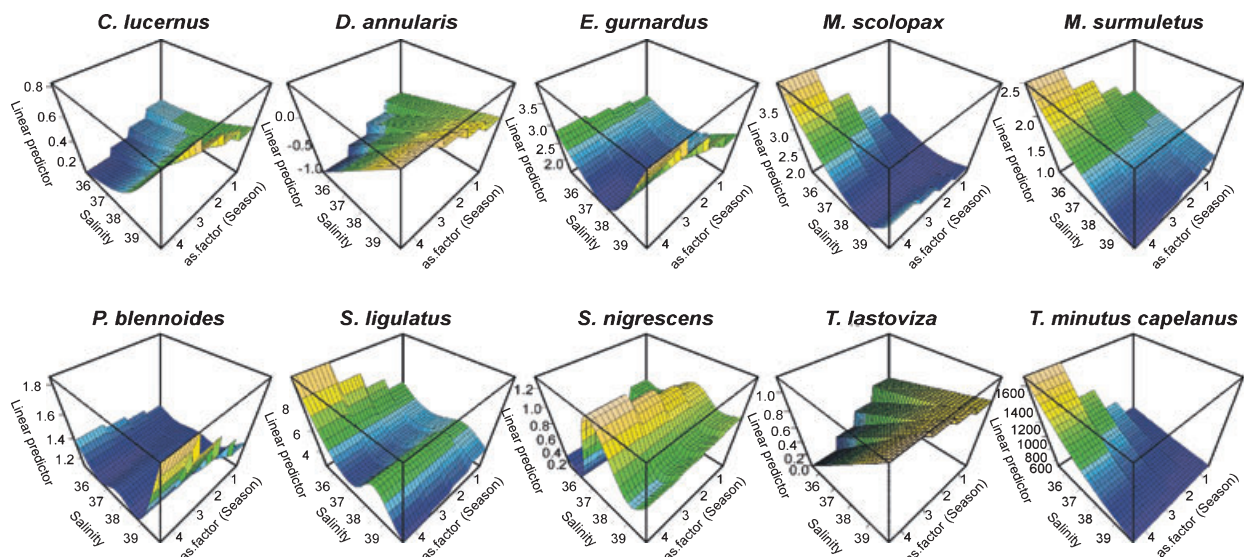

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other habitat types such as rocky substrates or seagrasses. For the latter species (such as most of the studied Sparidae and Scorpaenidae) the models presented in this paper refer to the portion of the population thriving on soft bottoms. Demersal fish may be split into two main groups regarding their relationship with the benthic macrofauna and the type of substratum, according to their ethology and diet habits (Gaertner *et al.*, 1999). In the first group (group A) belong groundfish species with very strong relations with benthic macrofauna that spend most of their lives lying on or in close contact to the substrate. In the second group (group B) belong the benthopelagic species that are more independent of the benthos and substratum, live in the water column near the sea bottom and feed both on benthic macrofauna and pelagic species. Among the study species of this study, 15 could be classified in group A and 12 in group B (Table 4). Sediment characteristics were included in the best models of all species of group A (*Sand* in all cases and *Carbonates* in 11 of the 15 cases) and in most species of group B (*Sand* in ten and *Carbonates* eight of the 12 cases). Only in two species of group B (*M. scolopax* and *P. bogaraveo*) was no sediment-related variable selected.

Sediment characteristics represent a major factor affecting distributional patterns of bottom fauna (Bacescu, 1972), and quite a few studies describe the effect of sediment characteristics on fish distribution (Mahon and Smith, 1989; Bianchi, 1992; McCormick, 1995; Gaertner *et al.*, 1999; Demestre *et al.*, 2000). In this study, it was confirmed that sediment characteristics are quite important in the patterns of spatial distribution of demersal species, especially those belonging to group A. The effect of sediment characteristics is mostly related to feeding and protection from predators. Many demersal fish feed on the benthic invertebrates that inhabit soft bottoms and many of them are specialist feeders targeting particular invertebrate groups or having a quite specific mode of foraging. The macrofaunal assemblages are quite dependent on the substrate type (Gray, 1974), and consequently the abundance of predators, especially of specialist feeders, will probably be higher on substrates suitable for their prey. Unlike fish of coral or rocky reefs that take advantage of physical structures (crevices, holes, etc.) for shelter, fish on sand flats have to seek other ways to protect themselves from predators. Some anti-predator adaptations in soft-bottom habitats include cryptic coloration, construction of permanent burrows, temporarily burying in the substrate, and sand-diving; all these adaptations depend on the type of the substrate (e.g.,

Tallmark and Evans, 1986; Gibson and Robb, 2000; Katsanevakis, 2005).

Quite often the substrate preference of a species changes during ontogeny. This could be the reason for the relatively high observed densities in *C. lucernus* in areas of both low and high sand content and lower densities between. In the northwestern Thermaikos Gulf (western part of the North Aegean subarea), a specific station was close to the mouth of three rivers (Axios, Loudias, and Aliakmon; Fig. 1). Due to the sediment discharge of the rivers, the most abundant grain-size fraction of the sediment in the region was silt (30–60%), followed by clay (20–40%), while the sand content was very low (Karageorgis *et al.*, 2005). In this specific station the sand content was 0.7%, i.e., very low in relation to all other stations of this study. Such areas near river mouths are usually very productive and many fish species may be attracted due to the availability of food. For some of the studied species (*C. lucernus*, *M. variegatus*, *M. barbatus*, *D. annularis*, *S. solea*) high relative densities were observed in this station during all seasonal samplings and largely affected the s(*Sand*) curves.

Examples of specialist feeders are the members of the Mullidae family (*M. barbatus* and *M. surmuletus* in this study). All Mullidae species use barbels to excavate the sediment and detect chemical cues associated with their prey. Most mullids are benthic microcarnivores feeding mainly on crustaceans, polychaetes, and molluscs inhabiting the sediment. The use of barbels is probably the reason of a restricted trophic diversity of the family (McCormick, 1995). The preference of *M. barbatus* and *M. surmuletus* for sediments with a high percentage of sand and the much higher densities in shallow waters probably reflect the distribution of preferred prey and the specialist feeding mode of the species.

Sediment characteristics were included in the best models of all flatfish (*M. variegatus*, *S. solea*, *S. ligulatus*, *S. nigrescens*), indicating that substrate type is an important factor determining their distribution. This is an anticipated outcome, as flatfish are uniquely adapted for a benthic lifestyle, and similar findings have been reported in other studies (Jager *et al.*, 1993; Abookire and Norcross, 1998; Gibson and Robb, 2000; Le Pape *et al.*, 2003). The juveniles of many flatfish appear to be concentrated in shallow and muddy habitats, especially in estuarine areas (Le Pape *et al.*, 2003). Juveniles of *S. solea* and *M. variegatus* were almost exclusively caught in large numbers in the northwestern Thermaikos Gulf in a shallow and muddy habitat close to the mouths of three rivers. The preference of juvenile flatfish for such areas can been

Table 4. Synoptic table of the habitat-related trends in relative abundance of the studied species.

Species	Family	Trend with		
		Depth	% Sand	% Carbonates
Group A				
C. lucernus	Triglidae	↘	↘↗*	↘
E. gurnardus	Triglidae	Peak at 100 m	↘↗*	↘
L. dieuzeidei	Triglidae	Peak at 270 m	Peak at 44%	ns
L. naevus	Rajidae	Peak at 180 m	↗	↗
L. budegassa	Lophiidae	Peak at 155 m	Peak at 32%	ns
M. variegatus	Soleidae	↘	↘↗	↘↗
M. barbatus	Mullidae	↘	↗	↘↘
M. surmuletus	Mullidae	↘	↗	ns
R. clavata	Rajidae	High densities between 75 and 350 m	↗	↗
R. miraletus	Rajidae	↘*	↗	↗
S. notata	Scorpaenidae	↘	↗	Peak at 50%
S. solea	Soleidae	↘	↘	Peak at 45%
S. ligulatus	Cynoglossidae	↘	↗	ns
S. nigrescens	Cynoglossidae	High densities between 100 and 300 m	↗	Peak at 47%
T. lastoviza	Triglidae	Peak at 75 m	↗	Complex pattern
Group B				
D. maroccanus	Sparidae	Peak at 95 m	Complex pattern	ns
D. annularis	Sparidae	↘	↘*	Complex pattern
M. scolopax	Centriscidae	Peak at 180 m	ns	ns
M. merlangus euxinus	Gadidae	↘	↘	Complex pattern
M. merluccius	Merlucciidae	Peak at 250 m	Peak at 20%	↘
M. poutassou†	Gadidae	↗	Peak at 9%	ns
P. acarne	Sparidae	↘	Complex pattern	Peak at 14%
P. bogaraveo	Sparidae	↘	ns	ns
P. erythrinus	Sparidae	↘	Complex pattern	↗
P. blennoides	Phycidae	↗	Peak at 20%	Peak at 33%
T. minutus capelanus	Gadidae	Peak at 97 m	Complex pattern	Peak at 18%
Z. faber	Zeidae	Peak at 70 m	↗*	↗

*Variable selected by AIC but not-significant based on an ANOVA test.

†Pelagic species that makes nycthemeral vertical migrations, moving at surface waters at night and near the bottom during the day.

attributed both to the abundance of prey in these highly productive grounds and to the enhanced capability of juveniles to bury themselves in finer sediments (Gibson and Robb, 2000; Le Pape *et al.*, 2003).

However, different results have been reported for flatfish in certain areas. Jager *et al.* (1993) reported that 0-group plaice and flounder in Dollard (Waden Sea) are abundant in sandy areas and absent from muddy sites, and this distribution pattern was attributed to the distribution of the main prey species (Jager *et al.*, 1993). In the present study, Cynoglossidae (*S. ligulatus* and *S. nigrescens*) were absent from the estuarine grounds of the northwestern Thermaikos Gulf, and their population density was higher in sands or muddy sands (Fig. 5). Thus, the patterns of sediment preference of flatfish in the study area were found to be species-specific and no obvious general pattern was found. Neuman and Able (1998) have demonstrated that the sediment selectivity of the flatfish *Scophthalmus aquosus* decreased in the absence of food. Therefore behavioral responses to prey distribution and abundance may be an important determinant of the observed patterns of relative abundance of flatfish. Distribution of prey probably indirectly affected sediment type preference.

All skates in this study (Rajidae; *L. naevus*, *R. clavata*, *R. miraletus*) exhibited a preference for sandy substrates and their population density increased with increasing sand content of the sediment (Table 4; Fig. 5). Rajidae are bottom-dwellers, feeding on benthic invertebrates and demersal fish. A preference of many Rajidae species for specific substrate types (either sandy or muddy sediments) has been reported (e.g., Jardas, 1973; Skjæraasen and Bergstad, 2000), partly attributed to the distribution of their preferred prey (e.g., Robichaud *et al.*, 1991; Catalano *et al.*, 2007).

The observed seasonal pattern in relative density of some species is partly related to recruitment. When the new recruits enter the fishing grounds, relative abundance and catches increase. For example, recruitment of *M. poutassou* occurs in late spring (May) and summer (Bas and Calderon-Aguilera, 1989), probably causing the marked high density observed during summer in this paper (Fig. 8). The seasonally variable fishing effort (e.g., in Greece there is a closure of trawlers from beginning of June till the end of September) may also affect relative density jointly with recruitment. If recruitment of some target species occurs during the closure season, the increase of population density will be more pronounced than if it occurred during a period of intense fishing. Migration between the study area and adjacent areas (such as deeper bottoms or non-sampled spawning grounds) is also a potential reason for the observed seasonal variation in population density in the study area. Additionally, the sea–land interaction in the Aegean Sea maximized during autumn and winter due to the increased river discharges (as a result of enhanced precipitation). Lloret *et al.* (2001) showed that enhanced hydroclimatic conditions in the NW Mediterranean were favorable for the productivity of the fish and invertebrate stocks, and suggested the presence of a linkage between recruitment of Mediterranean species and river discharges. For species inhabiting areas close to river mouths during a part of their ontogeny or occasionally, such as *S. solea*, the seasonal variation of river discharges may also induce seasonal variation of their abundance in the surveyed area.

Depth has been stated to be the main gradient along which faunal changes occur when analyzing shelf and upper slope assemblages (Bianchi, 1992; Fujita *et al.*, 1995; Moranta *et al.*, 1998; Demestre *et al.*, 2000; Kallianiotis *et al.*, 2000). However, the direct effect of depth on species abundance (through the increase of hydrostatic pressure) is expected to be relative small in relation to the indirect effects of depth because of the correlation with depth of many crucial environmental parameters such as light intensity, temperature, nutrient concentration, primary and secondary productivity. In the absence of such data in studies of fish spatial distribution, depth is concluded to be the main predictor variable of population density. On the other hand, a good knowledge of bathymetric distribution of commercial fish is essential for fisheries management even though depth is not always a causal predictor of fish abundance.

Environmental drivers impact marine ecosystems and the fish stocks. Fishing may in some cases exacerbate the negative impacts of such drivers. Total landings in Greece showed an increasing trend recently, indicating that this could be happening. Improved knowledge of species–environment relationships through such studies as the current one could form an integral aspect of a precautionary approach arguing that fisheries should be conducted in a way that is robust to environmental change and thus that fish stocks should never be exploited to a point where they are not resilient to environmental change. To this end, the European Commission has specifically requested the Scientific, Technical and Economic Committee for Fisheries (STECF) and ICES to incorporate any existing knowledge about environmental drivers in the assessments of the ecosystems and fisheries and in the advice (EC, 2008).

Understanding the patterns of spatial distribution of fish can assist fisheries managers by identifying areas of high abundance and diversity, areas with species of conservation interest, and sites where particular life-history stages occur (such as spawning and nursery areas). Implementing plans and control schemes that would target specific species assemblages, based on a good knowledge of the species spatio-temporal distribution in relation to environment, could serve as a sustainable approach to fisheries management. The establishment of Marine Protected Areas (MPAs) in line with the recent trends for a holistic ecosystem-based management would also benefit from an improved understanding of the spatial distribution of demersal species. Protected areas are an important tool for protecting sensitive habitats and species within an ecosystem approach.

Improved knowledge of the spatial and temporal distribution of commercially important fish species (and, to large extent, of the fisheries) and their relationships with the marine environment (in terms of both habitat and environmental preferences) is essential for the successful implementation of the

ecosystem approach to fisheries management. This is because the main task of fisheries management within an ecosystem approach in an EU context is to keep direct and indirect impacts of fisheries on marine ecosystems within bounds in relation to healthy marine ecosystems and ecologically viable fish populations, by including all the knowledge we have about the interactions between fisheries and marine ecosystems in decisions under the CFP.

Finally, it should be noted that GAMs are one class of statistical techniques that can be used to model non-linear relationships. Other methods also exist, such as multiple adaptive regression splines (MARS; Friedman, 1991), boosted regression trees (BRT; Friedman, 2002), and artificial neural networks (ANN; Rumelhart *et al.*, 1986), and could also be used to study non-linear relationships between species and environmental variables. However, GAM is the most common and well developed method for modeling fish abundance and spatial distribution, and is widely applied in fisheries science (Valavanis *et al.*, 2008). Several evaluations of alternative approaches to model fish abundance demonstrated the good performance and properties of GAMs as well as their advantages in ecological interpretability, although in some cases other methods may have some comparative advantages (Lehmann *et al.*, 2002; Leathwick *et al.*, 2006; Valavanis *et al.*, 2008).

ACKNOWLEDGEMENTS

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