Habitat preferences among three top predators inhabiting a degraded ecosystem, the Black Sea

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Summary: This study investigated whether there is evidence of widespread niche partitioning based on environmental factors in the Black Sea and tested the hypothesis that physiographic factors may be employed as predictors. It addresses poorly researched areas with good habitat potential for the only three cetacean subspecies living in this area: the Black Sea short-beaked common dolphin (*Delphinus delphis* spp. *ponticus*), the Black Sea bottlenose dolphin (*Tursiops truncatus* spp. *ponticus*) and the Black Sea harbour porpoise (*Phocoena phocoena* spp. *relicta*). Generalized additive models (GAMs) were used to analyse data collected from multiple sources. In total, 745 sightings of the three species between 1998 and 2010 throughout the Black Sea were included. The analysis found depth and sea surface temperature to be the most important variables for separating the occurrence of the three species. Common dolphins occurred mainly in deep waters and in areas where the sea surface temperature was low, bottlenose dolphins were distributed primarily in shallower and warmer waters than common dolphins, and harbour porpoises were distributed in shallower waters with lower sea surface temperature than bottlenose dolphins. This study suggests strong niche segregation among the three cetacean species. The study is also the first contribution to the basic information of cetacean species distribution and habitat preferences in the Black Sea as a whole. Knowledge of the distribution of the three dolphin species in the study area is essential to establish conservation measures for these populations.

Keywords: Black Sea; bottlenose dolphin; common dolphin; GAM; habitat preferences; harbour porpoise; niche segregation; spatial modelling.

Preferencias de hábitat de tres superpredadores en el mar Negro

Resumen: El presente trabajo analiza si existen evidencias de partición de nicho en base a factores ecológicos básicos en el mar Negro, así como si dichos factores pueden ser empleados como predictores de distribución en zonas pobremente muestreadas con respecto a las tres especies de cetáceos que habitan el área: el delfín común del mar Negro (*Delphinus delphis* spp. *ponticus),* el delfín mular del mar Negro (*Tursiops truncatus* spp. *ponticus*) y la marsopa del mar Negro (*Phocoena phocoena* spp. *relicta*). Se usaron Modelos Aditivos Generalizados (GAMs) para analizar grupos de datos provenientes de múltiples fuentes. En total fueron incluidos 745 avistamientos de las tres especies entre los años 1998 y 2000. El análisis indica que las variables profundidad y temperatura superficial del mar fueron las más influyentes a la hora de segregar las especies espacialmente. La distribución del delfín común indicó una relación positiva con aguas más profundas y frías, mientras el delfín mular y la marsopa con aguas más superficiales y cálidas, tendiendo esta última a localizarse en aguas más frías con respecto al delfín mular. Este trabajo sugiere, por lo tanto, que existe una importante segregación de nicho entre las tres especies de cetáceos. Este análisis es la primera contribución con respecto a las preferencias de hábitat de estas tres especies para toda el área del mar Negro, siendo el conocimiento de la distribución espacial esencial a la hora de establecer medidas de conservación para sus poblaciones.

Palabras clave: delfín común; delfín mular; GAM; mar Negro; marsopa; modelos espaciales de distribución; preferencias de hábitat; segregación de nicho.

INTRODUCTION

The Black Sea is a naturally isolated body of water in which three subspecies of cetacean can be found: the Black Sea short-beaked common dolphin (*Delphinus delphis ponticus*) (Barabash 1935), the Black Sea bottlenose dolphin (*Tursiops truncatus ponticus*) (Barabash-Nikiforov 1940) and the Black Sea harbour porpoise (*Phocoena phocoena relicta*) (Abel 1905). These three species are at the top of the trophic web in the basin, with no natural predators (Kleinenberg 1956, Jefferson et al. 2008).

The status of these populations has been of a great concern since the second half of the 20th century (Smith 1982, Mikhalev 2004, Mikhalev et al. 2004). The main threat came from mass legal takes of cetaceans in commercial fishery of several riparian countries, which caused a dramatic decline of cetacean populations that brought them close to extinction (Smith 1982, Zemsky 1994, BSC 2008, Tonay and Öztürk 2012), and had a deep impact on the structure and dynamics of the ecosystem as a whole (Fontaine et al. 2012). The exact number of Black Sea cetaceans killed in the 19th and 20th centuries is unknown, but it has been estimated at more than five million (BSC 2008) cumulatively for all bordering countries. The dolphin harvest mainly focused on common dolphins and harbour porpoises. These activities were banned in the USSR, Bulgaria and Romania in 1966 and in Turkey in 1983 (Smith 1982, Tonay and Öztürk 2012). Nonetheless, a level of illegal catches has continued to be documented in recent years (Buckland et al. 1992, Gol'din and Gol'din 2004). This massive fishery has likely led both Black Sea harbour porpoise and bottlenose dolphin to be listed as Endangered and the Black Sea common dolphin as Vulnerable in the IUCN Red List of Threatened Species (Birkun 2008, 2012, Birkun and Franzis 2008).

Despite the ban on the cetacean fishery, the reduced populations did not recover due to prey depletion in the 1980s and early 1990s (Eremeev and Zuyev 2004). Eutrophication, increased pollutants and organic materials, and climate warming episodes, all enhanced by overfishing and the invasion of alien species (a lobate ctenophore, *Mnemiopsis leidyi*) had ecosystem-wide consequences and led to a four-fold reduction of the Black Sea fish landings in 1991 (Eremeev and Zuyev 2004). Commercially important species such as anchovy (*Engraulis encrasicolus*) and sprat (*Sprattus sprattus*) that play a crucial role in the Black Sea pelagic food webs (Daskalov et al. 2007) and are also cetacean main prey were dramatically decimated (Daskalov et al. 2007). Overfishing using trawling techniques and eutrophication caused a decrease in bottom oxygen content, particularly on the Northwest Shelf. This resulted in hypoxic conditions, further degrading and changing the diversity of benthic communities and reducing the dolphins' sources of food (Eremeev and Zuyev 2004, Anton et al. 2010). A certain level of recovery of some fish stocks has been recorded in the recent years but, overall, the ecosystem is out of balance as a result of decades of exploitation with no coordinated regional management, and it is unlikely that it will revert to the original state (BSC 2008, Bologa and Sava 2012). Reduced prey availability has also compromised cetacean health, increasing their susceptibility to viral infection (Birkun et al. 1999). Today, by-catch is the biggest threat for cetaceans in the Black Sea, especially for those living in the coastal waters (Tonay and Öztürk 2003, Gol'din and Gol'din 2004, Anton et al. 2010). There are indications that the annual level of harbour porpoise incidental captures may be in the thousands over the entire Black Sea (Tonay and Öztürk 2003), including incidental catches during illegal fishing practices (Öztürk 2013). Illegal, unreported and unregulated exploitation of marine biological resources is one of the major environmental, economic and social problems concerning the entire Black Sea region (Birkun et al. 2006, Öztürk 2013).

Although the three cetacean species are still under a great amount of anthropogenic pressure, the available information about their abundance, population trends and spatial distribution is limited. After the Soviet moratorium of the fishery, aerial surveys were conducted by Soviet scientists from 1967 to 1973 in the Black Sea and a joint USA-USSR shipboard survey was conducted in 1981. The first surveys provided abundance estimates by species that varied considerably from year to year and no obvious trends were identifiable (Smith 1982). The joint USA-URSS sighting cruise covered only 900 km of track in a small portion of the eastern Black Sea, which was insufficient to allow estimation of total abundance (Buckland et al. 1992). No final conclusions were made and the results have been criticized for a number of methodological and analytical reasons. Therefore, their use as indicators of absolute abundance is not recommended (Smith 1982, Buckland et al. 1992). In the last decade, however, local surveys have been conducted in several areas of the Black Sea in order to assess dolphin abundance and distribution (Birkun et al. 2004, Raykov and Panayotova 2012, Radu et al. 2013). Unfortunately, many studies have been published in non-peer-reviewed journals, which are not widely available, and none of these studies aim to review all the existing knowledge. Consequently, population size, distribution, and ecological factors driving the distribution of cetacean species inhabiting the Black Sea remain unknown (Bologa and Sava 2012, BSC 2008).

This study aims to assess niche segregation among the three dolphin species that inhabit the Black Sea waters and concludes with some implications of our findings for management and research. Our results show that data from a wide variety of datasets can result in robust ecological models and provide useful information on identifying possible spatial patches of preferred habitat for the three dolphin species across the Black Sea. Modelling species distribution represents a potentially powerful tool for predicting animal distribution and understanding the ecological processes determining these distributions (Redfern et al. 2006, Embling et al. 2010). Management of whale and dolphin populations can benefit from accurate, model-derived predictions of their habitat to mitigate anthropogenic effects such

as fisheries by-catch (Kaschner et al. 2012), foresee impacts of habitat alterations on ecosystem function (D'Amico et al. 2003), protect critical habitats or select suitable areas for protection (Cañadas et al. 2005, de Stephanis et al. 2008), and aid our understanding of the ecology of these animals (Hamazaki 2002). Environmental factors can then be applied to predict marine predator distribution based on the relationships between predator, prey and environment, allowing more robust results than when one relies on prey distribution alone (Torres et al. 2008). Therefore, by assuming that the distribution of a species is non-random relative to environmental variability, predictive models of distribution typically identify the ecological relationships between the environment and species habitat selection. In this study, GAM-based spatial modelling was used in order to provide an overview of the distribution of the three cetacean species inhabiting the Black Sea in the whole basin.

MATERIALS AND METHODS

Study area

The Black Sea is one of the most isolated seas and the largest anoxic body of water in the world. The upper 100 m layer of water is well oxygenated, while the deep layer (100 m to 2250 m) is anoxic and contains high sulphide concentrations (BSC 2008), so deep pelagic and benthic organisms are largely absent. These anoxic conditions, limited water exchange with the Mediterranean Sea, and strong inter-basin temperature and salinity contrasts render the Black Sea ecology more vulnerable to anthropogenic effects than open seas (Kideys 2002). Important features of the Black Sea are low salinity, due to high outflow of fresh water from rivers, and low water temperature, especially during the winter when the water usually freezes in the northeast (e.g. in the Sea of Azov; see UNEP 1996). The stratification is affected by the fresh water input and the Mediterranean inflow of highly saline water. The temperature shows more variation than the salinity, seasonally as well as regionally. The mean annual surface temperature varies from 16°C in the south to 13°C in the northeast and 11°C in the northwest (Balkas et al. 1990). Limited species exchange and lack of adaptation capability of Mediterranean species to the Black Sea maintains relatively low biodiversity. This low species diversity and absence of many local competitors has provided unoccupied ecological niches for exotic invaders and therefore made biodiversity extremely sensitive to bio-invasions (Oğuz and Oztürz 2011).

Datasets

Sighting information from a wide variety of published and unpublished sources was analysed between 1998 and 2010. The initial unpublished data set was collected by dedicated observers in the Turkish marine area of the Black Sea during an environmental and geotechnical survey. These data were collected aboard the MV *L'Espoir* between March and May 2010 on a survey on behalf of ExxonMobil. The second data set comprised of published data on cetacean sightings, the majority of which was collected by dedicated observers during surveys conducted in Romanian (Dede and Tonay 2010, Radu et al. 2013) Bulgarian (Raykov and Panayotova 2012), southwest Turkish (Dede and Tonay 2010) and northern and northeastern waters of the Black Sea (Birkun 2002, Gol'din and Gol'din 2004). Surveys were made from vessels, airplanes or land-based platforms. As the survey effort could not be controlled, a model using data pooled from 12 survey years (1998-2000) was built. It has been reported that when one is trying to minimize bias from unsystematic sampling associated with opportunistic data, it is likely to be more important to pool data from multiple years rather than several different areas (Moura et al. 2012). Only multispecies surveys were used in this analysis. Sightings data were digitalized from the maps presented in the publications and included in a database with Arc Map 10.0.

Species distribution models

The habitat preferences of cetaceans within the study area were investigated. The relationships between the spatial occurrence of the cetaceans and environmental variables were assessed using generalized additive modelling (GAM) techniques (Hastie and Tibshirani 1990, Hammond et al. 2013, Notarbartolo di Sciara et al. 2015). Data exploration was applied following the protocol described in Zuur et al. (2010). The open-source statistical programming language R version 2.6.2 (http://cran.r-project.org) and the MGCV library within R were used (Wood 2001). Given that the majority of the data set came from different sources, effort information was not available for most of the surveys included in this study, so a model based on presence and "pseudo-absence" was used (Esteban et al. 2013). Only studies in which multispecies information was available were chosen for the analysis. A GAM with a Tweedie distribution and *logit link* function were used. The parameter p for the Tweedie distribution used was 1.1 and the γ (gamma) was 1.4, as recommended by Wood (2006) to prevent over-fitting.

All the cetacean sightings were treated as "sampling stations". As only multispecies datasets were used, this approach was chosen instead of a classical absence assigned randomly (Stockwell 1999) to reduce the bias. The models were fitted with the presence dataset, including sightings of the particular species obtained by different platforms, while all other sightings were treated as "pseudo-absences". At these locations, it was assumed that an observer was performing a dedicated watch, and when other species were sighted, that particular sighting was considered as pseudo-absence for the analysed species. The general structure of the model was

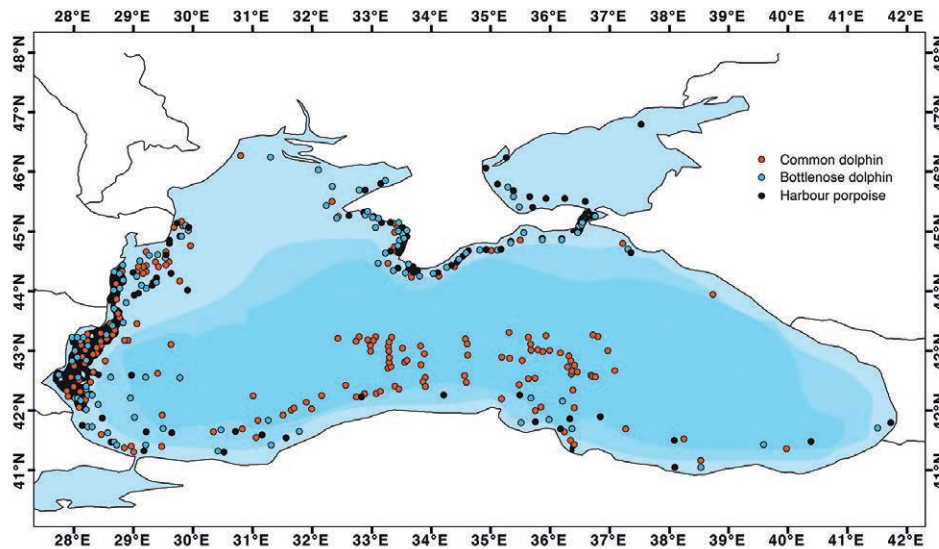$$E\left(p_i\right) = \exp\left[\theta_0 + \sum_k f_k\left(z_{ik}\right)\right] \qquad (1)$$

Fig. 1. – Visual sightings in the Black Sea between 1998 and 2010.

where p_i is the probability of finding the species ana-lysed at the ith sampling station, θ_0 is the intercept, f_k are smoothed functions of the explanatory covariates, and z_{ik} is the value of the kth explanatory covariate at the ith sampling station.

The environmental variables used in this study were sea bottom depth (its log was used, named as logbat) obtained from ETOPO2 (Amante and Eakins 2009), its derivate slope and aspect (obtained with the R li-brary SDMtools (Van der Wal et al. 2010)), distance to the coast, sea surface temperature (SST) and chlo-rophyll *a* concentration, obtained from satellite images of MODIS (Carder et al. 2003) when month and year information were available. In order to evaluate a pos-sible temporal variation, all models included year as covariate. Type of platform was also included in the models as a candidate covariate to minimize bias of the sampling method.

Model selection

A forward stepwise model selection was followed. All covariates were evaluated individually and chosen by a) the probability that each variable was included in the model by chance (less than 0.01), b) the generalized cross validation score (an approximation to the Aikake information criterion—the best model was the one with lowest value), and c) the percentage of deviance explained. The number of candidate environmental co-variates in a spatial modelling framework is potentially large, so variables of direct relevance to cetaceans were included. Based on these criteria, the best model was selected for the given species (see Table 2).

Environmental predictive models

The best GAM models were used to generate pre-dicted probability values of presence (0 to 1) on a grid of 2×2 km in the study area, which were plotted using ArcMap 10.0. In order to obtain the coefficient of vari-ation for the predictions and thus to optimize the pre-

dictive model accuracy, 200 bootstraps with replace-ment were run for each model, and a prediction grid was obtained for each bootstrap iteration. Coefficient of variations (CV) per-cell were estimated and plot-ted in Figure 3. Models were evaluated through CV. To make predictions over the entire Black Sea area, it was necessary to select values for the temporally vary-ing covariates. The predictive values from the GAM analysis were used to construct presence probability distribution maps for the three cetacean species. This model was then projected to the entire Black Sea. The summer season was selected (mean of July-August 2008-2009) because the majority of the observations were made during this time. This was presented as an example to avoid annual and month variability.

RESULTS

Survey observations

A total of 745 visual sightings of three species of cetaceans were obtained from surveys conducted be-tween 1998 and 2010. There were 242 observations of Black Sea common dolphin (*Delphinus delphis pon-ticus*), 302 of Black Sea bottlenose dolphin (*Tursiops truncatus ponticus*) and 201 of Black Sea harbour por-poise (*Phocoena phocoena relicta*) (Fig. 1).

Models

Log-transformed depth (logbat) and SST were the most significant environmental predictors for all three Black Sea species: common dolphin, bottlenose dol-phin and harbour porpoise. Statistical values for each species are shown in Table 1. Both were highly sig-nificant and explained 35.4%, 33.6% and 22.7%, of the deviance, respectively (Table 2). Presence probability of common dolphins was higher in water depths of more than 50 m (towards deepest waters), and towards cooler waters, between 5 and 18°C (Fig. 2A, B). Bot-tlenose dolphin presence was expected in waters below

Table 1. – Mean (with standard deviation) and ranges (min-max) for Black Sea common dolphin (*Delphinus delphis ponticus*), Black Sea bottlenose dolphin (*Tursiops truncatus ponticus*) and Black Sea harbour porpoise (*Phocoena phocoena relicta*) covariates shown to be significant.

Statistic		*Delphinus delphis ponticus*	*Tursiops truncatus ponticus*	*Phocoena phocoena relicta*
BAT (m)	Mean	918.72 (1000.22)	135.39 (345.45)	192.43 (407.18)
	Range	5-2437	1-2170	1-2272
SST (°C)	Mean	13.9±4.68	19.4±4.4	17.0±5.55
	Range	7.4-24.4	5.9-24.5	5.2-24.4
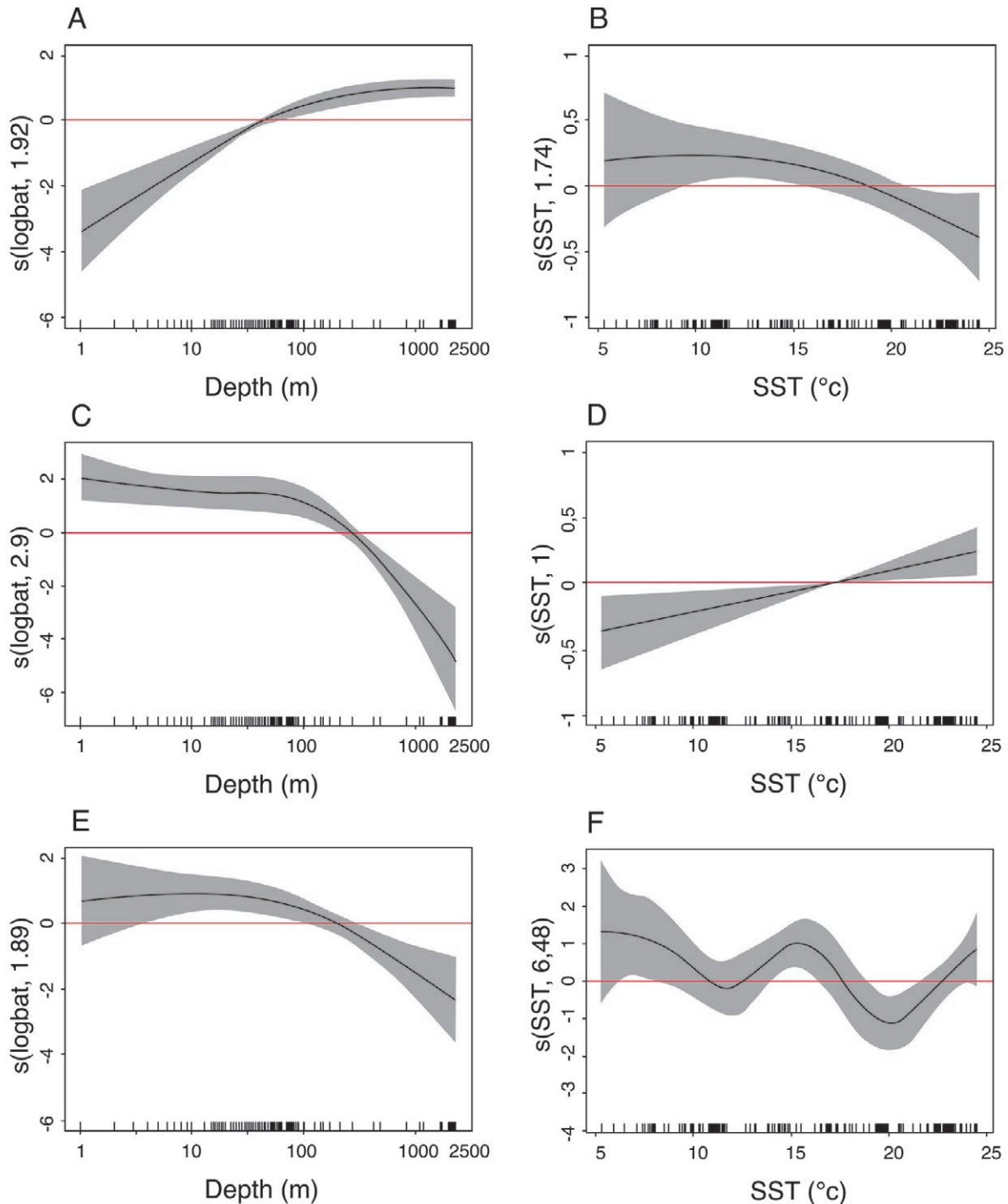
Fig. 2. – Relationships between observations of Black Sea common dolphin (*Delphinus delphis ponticus*) and (A) depth, (B) sea surface temperature (SST); between observations of Black Sea bottlenose dolphin (*Tursiops truncatus ponticus*) and (C) depth and (D) sea surface temperature (SST); and between observations of Black Sea harbour porpoise (*Phocoena phocoena relicta*) and (E) depth and (F) sea surface temperature (SST). Smooths are shown with the number of degrees of freedom in parentheses. Solid lines show the smooth estimate and grey areas the estimated 95% point-wise confidence intervals for the smoother. The zero line on the Y-axis is the mean of Y estimated by the model. The small vertical lines at the bottom of the graphs show the values at which there are observations.

Table 2. – Evaluation of different models for Black Sea common dolphin (*Delphinus delphis ponticus*), Black Sea bottlenose dolphin (*Tursiops truncatus ponticus*) and Black Sea harbour porpoise (*Phocoena phocoena relicta*). Sea surface temperature (SST), log-transformed depth (logbat), distance to coast (disthd), generalized cross validation score (GCV), difference between GCV score (ΔGCV), deviance explained by the model (%Dev) and degrees of freedom (df). Only covariates showing a significant relati onship are shown.

Covariates	GCV	ΔGCV	%Dev	df
Delphinus delphis ponticus				
SST+logbat	0.560	0	35.4%	4.67
disthd+SST	0.618	0.058	29.1%	5.77
disthd	0.675	0.115	21.6%	2.97
SST	0.694	0.134	19.5%	3.57
logbat	0.708	0.147	17.8%	2
Tursiops truncatus ponticus				
SST+logbat	0.583	0	33.6%	4.9
disthd+SST	0.633	0.049	29.2%	8.26
SST	0.752	0.169	12.9%	2
disthd	0.776	0.192	10.1%	3.19
logbat	0.790	0.206	8.7%	3.91
Phocoena phocoena relicta				
SST+logbat	0.531	0	22.7%	9.37
SST	0.583	0.052	14.7%	8.78
disthd+SST	0.612	0.081	9.8%	7.24
logbat	0.797	0.266	4.6%	2.01
disthd	0.797	0.263	5.2%	4.6

250 m depth (towards the mainland), with a higher preference for waters with SST between 18 and 24°C (Fig. 2C, D). Higher presence probability of harbour porpoises was predicted in water shallower than 200 m depth (towards the mainland) and SST below 18°C (Fig. 2E, F). No relationships were found between year or type of platform and any species of this study.

Model predictions of distribution

Prediction maps show a large area of presence probability of common dolphin in the centre of the basin, extending widely across the area (Fig. 3A). Bottlenose dolphin and harbour porpoise prediction maps show the highest presence probability in shallow waters, towards the mainland, the Northwest Shelf and the Sea of Azov (Fig. 3B, C).

DISCUSSION

This study provides a novel approach in studying the distribution of the top three predator species in the Black Sea. The kinds of datasets we used are statistically difficult to investigate due to the different surveying conditions and the lack of data related to observation effort. Therefore, no attempt is made to provide relative abundance estimations, as this study does not provide a framework for estimating detection functions. However, sightings of all the three species were enough to assess whether there is niche segregation, providing a measure of the species' distribution patches, as well as the habitat preferences relative to the other species recorded in the study area. Due to the high number of sightings of the three dolphin species in the study area, our "pseudo-absence" approach has been previously considered suitable for solving the heterogeneity of effort from different datasets by using other dolphins' presence as proxy for the given dolphin species' absence (Esteban et al. 2013).

Black Sea cetacean distribution and abundance has often been related to the patterns of fish migration and aggregations (Mikhalev et al. 2004, Dede and Tonay 2010, Raykov and Panayotova 2012), which depend on seasonal water temperatures along with other abiotic factors (BSC 2008). Distribution estimates can be highly uncertain for species that live in a dynamic environment and have complex behaviour and life histories (Isojunno et al. 2012). Although they can often be related to physical oceanographic features such as water depth, it is likely that prey abundance and movements are the most important factors in determining the occurrence and movements of cetaceans (Gaskin 1982, Evans 1987, Nøttestad et al. 2014). Oceanographic features have therefore been widely used as proxies of ecological variables such as prey distribution, which is difficult to obtain or cannot be measured (Torres et al. 2008). Different circulation features, bathymetric complexity, physico-chemical and strong weather patterns are known to exist within the study area and are well documented (Oğuz et al. 1995, BSC 2008). These com-
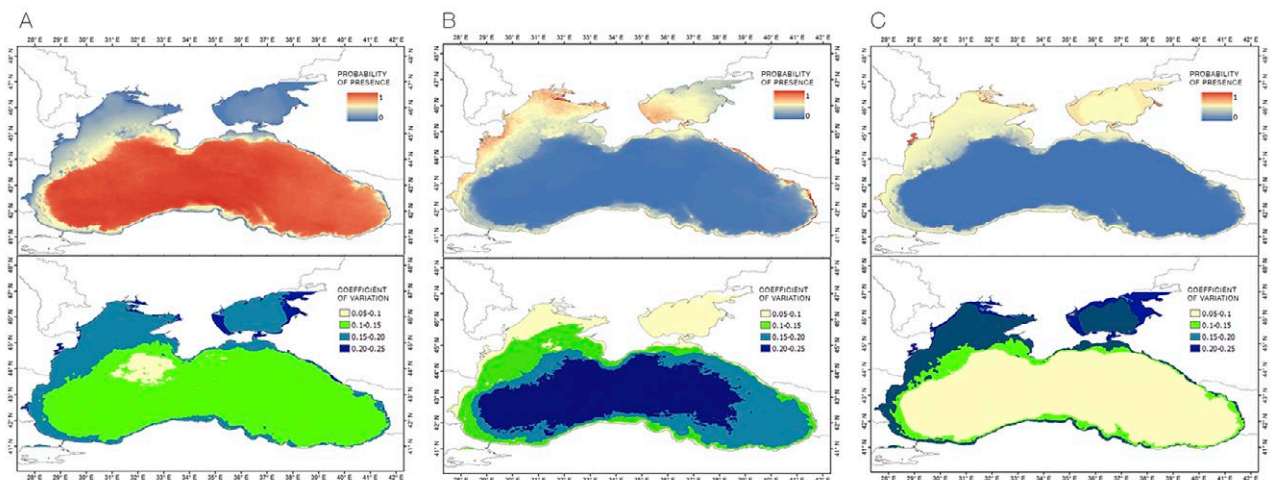

Fig. 3. – Spatial prediction pattern of coefficient of variation of the prediction models after 200 bootstrap resamples for (A) Black Sea common dolphin (*Delphinus delphis ponticus*), (B) Black Sea bottlenose dolphin (*Tursiops truncatus ponticus*) and (C) Black Sea harbour porpoise (*Phocoena phocoena relicta*) probabilities during the summer season of 2008-2009.

1970s have recorded bottlenose dolphins in the deep central part of the basin. Considering the changes to the marine ecosystem in the last few decades, it is suspected that the distribution, migrations, abundance and spawning areas of fish stock in the Black Sea will have been affected at a significant level (Bat et al. 2007, ahin and Hacimurtazaoğlu 2013). It is not unrealistic to suggest that the diet of bottlenose dolphins could have been more focused on pelagic fish prior to the fishery collapse in the 1980s and early 1990s than is currently the case. In support of this, bottlenose dolphins are considered to be opportunistic feeders that adapt their feeding habits to the availability of the most abundant prey species and thus respond to changes in their environment (Klinowska 1991, Jefferson et al. 2008). Changes in prey preferences of bottlenose dolphins in the Black Sea due to the decline among some demersal fish populations have also been suggested by Gladilina and Gol'din (2014). The authors also reported a more diverse diet in their sample. The diversity is comparable with the data from all the Mediterranean Sea (Miokovic et al. 1999, Blanco et al. 2001, Bearzi et al. 2005) or from the northeast Atlantic (Santos et al. 2007a). Such a wide diet range (a wide variety of schooling pelagic fish, benthic fish and cephalopods) is normal for the bottlenose dolphin (Santos et al. 2007b), but it has not been observed previously in the Black Sea. The central, deep waters need to be further surveyed to improve the model predictions and confirm whether the lack of bottlenose dolphins in deep waters in this study is due to the low effort of this study or to other ecological changes.

Harbour porpoise cover relatively continuously cold coastal waters of the North Pacific and the North Atlantic, around the UK and Ireland in their entirety, and south along the African coast to Senegal (Reid et al. 2003). The harbour porpoise has been found in the Aegean Sea (in the far eastern Mediterranean) and the western Mediterranean Sea (see Cañadas et al. 2005), but is absent in the rest of the Mediterranean basin (Frantzis et al. 2001). The predictive model for Black Sea harbour porpoises showed a higher preference for shallower waters than 200 m, similar to that of bottlenose dolphins. However, the results for the SST preference were different to those of bottlenose dolphin, indicating a preference for lower water temperatures (below 18°C). Depth also seems to be a significant predictor of harbour porpoise distribution (Watts and Gaskin 1985, Read and Westgate 1997, Raum-Suryan and Harvey 1998), pointing to a habitat preference for predominantly shelf waters between 50 to 150 m, with a lower preference for waters deeper than 100 m (Carretta et al. 2001, Embling et al. 2010). These results are consistent with the those of the literature, which have reported that harbour porpoises occur throughout the entire basin, including the Sea of Azov, Turkish Strait systems and across the shelf in shallow waters (Mikhalev 2004, Krivokhizhin and Birkun 2006, Tonay et al. 2007). This finding may be explained by the likely feeding habits of the harbour porpoise, which targets benthic fish such as whiting and gobies, which occur in shallow waters, and pelagic schooling fishes such as sprat and anchovy, which occur in both shallow and deep waters of the basin (Mikhalev 2004, Krivokhizhin and Birkun 2006, Tonay et al. 2007). In support of the results of this study in the Black Sea, Raykov and Panayotova (2012), who conducted a study in the Bulgarian coastal zone, noted that the bulk of observed cetaceans, including the harbour porpoise, which were observed between 50 and 100 m isobaths, are related to the highest catch of sprat per unit area.

The present study focuses on the influence of environmental factors in the whole basin over 12 years. The results of this study show robust evidence of niche partitioning among the three species. Depth and surface temperature appeared to have been good predictors for the distributions of the three species in the area, indicating a strong trend for bottlenose dolphins and harbour porpoises to be present in shallow waters across the shelf area, with the latter showing a higher preference for cooler waters than the former. Common dolphins appear to occur predominantly offshore throughout the Black Sea basin, in the colder water range. Further studies should focus on refining habitat predictions and examining relationships between the Black Sea cetacean distribution and environmental factors and niche segregation, especially in areas such as the central and southeast coast of the basin, where there is limited information available. The use of a long time-series of data would also minimize the likelihood of false correlations in the predictions, as there is a risk with short-time-interval window ('snapshot') studies for highly mobile species such as cetaceans (Cañadas et al. 2005). Studies comparing historic data sets (Smith 1982, Buckland et al. 1992) from decades ago with current data should also be conducted in order to provide a better knowledge of possible changes to cetacean population distributions due to the environmental changes that occurred in the Black Sea. In addition, potential competition between these species may be also be influencing their habitat preferences and the differentiation of their distributions could tend to reduce it. This study provides an important contribution to the basic knowledge on cetaceans in the Black Sea as a whole, assessing the presence of the three species in areas where data are not available or inexistent.

The Black Sea environment has improved slightly over the last decade (Kideys 2002), most probably associated with the deterioration of the economic situation in the countries along the Black Sea coast (Kuznetsov 2004). However, the whole ecosystem is different from that documented in the 1960s, and the composition and structure of the marine communities are constantly changing with the decline of certain species and the expansion of others (Zaitsev and Mamaev 1997). The quality of the Black Sea ecosystem is dependent, in particular, on the survival and welfare of these top predator populations, whether or not they are unique as subspecies, because they regulate the demography of species at lower trophic levels through a top-down regulation of the trophic food-web (Daskalov et al. 2007, Fontaine et al. 2012). The poor situation of these apex predators in the Black Sea ecosystem is still of major concern (Zaitsev and Mamaev 1997). Popula-

tions of small cetaceans are unlikely to have recovered significantly since the dolphin and porpoise fishery ban in 1983; in fact, the number of harbour porpoises is dropping (Fontaine et al. 2012, Radu et al. 2013). Despite the conservation effort in the last decade, including adoption of two essential instruments in 1996, the Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and Contiguous Atlantic Area (ACCOBAMS) and the Strategic Action Plan for the Rehabilitation and Protection of the Black Sea (BS SAP), there is still insufficient scientific information about cetacean ecology and it is widely acknowledged that this is the main obstacle in the way of their conservation (BSC 2008, Bologa and Sava 2012). A coordinated conservation effort between all the countries bordering the Black Sea is urgently required in to order to preserve this unique marine ecosystem and its unique vulnerable cetacean populations.

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