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RESEARCH ARTICLE

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Modelling dolphin distribution within an Important Marine Mammal Area in Greece to support spatial management planning

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Abstract

1. Understanding marine mammal distributions is essential for conservation, as it can help identify critical habitat where management action can be taken. The semi-enclosed Gulf of Corinth, Greece, has been identified as an Important Marine Mammal Area by the International Union for Conservation of Nature (IUCN) Marine Mammal Protected Areas Task Force, based on the regular occurrence of odontocete populations. A 7-year (2011–17) dataset of boat-based surveys was used to model and predict the distribution of striped dolphins, *Stenella coeruleoalba*, common dolphins, *Delphinus delphis*, and common bottlenose dolphins, *Tursiops truncatus*, in the entire Gulf (2400 km^2).
2. Multiple geographic, bathymetric, oceanographic, and anthropogenic variables were incorporated in a combined generalized additive model and generalized estimation equation (GAM-GEE) framework to describe dolphin occurrence and produce distribution maps.
3. Modelling indicated that striped and common dolphins prefer deep waters (>300 m) in the central and southern part of the Gulf, whereas bottlenose dolphins prefer shallow waters (<300 m) and areas close to fish farms along the northern–central shore.
4. Model-based maps of the predicted distribution identified a preferred habitat encompassing most of the Gulf, also revealing: (i) hot spots of dolphin distribution covering about 40% of the Gulf's surface; (ii) an almost complete overlap of striped and common dolphin distribution, consistent with the hypothesis that common dolphins modified their habitat preferences to live in mixed species groups with striped dolphins; (iii) a clear partitioning of striped/common and bottlenose dolphin habitat; and (iv) the important role played by fish farms for bottlenose dolphins, consistent with studies conducted elsewhere in Greece.
5. Evidence provided by this study calls for area-specific and species-specific management measures to mitigate anthropogenic impacts.

KEYWORDS

Delphinus delphis, distribution models, human impact, Important Marine Mammal Area, Mediterranean Sea, preferred habitat, *Stenella coeruleoalba*, *Tursiops truncatus*

1 | INTRODUCTION

Umbrella species such as marine mammals are ideal targets to inform marine spatial planning, because their protection can improve the conservation status of other key marine ecosystem components (Hooker & Gerber, 2004; Simberloff, 1998). Robust knowledge on cetacean distribution has supported the creation and management of a number of marine protected areas worldwide (Bailey & Thompson, 2009; Cañadas, Sagarminaga, De Stephanis, Urquiola, & Hammond, 2005; Hooker, Whitehead, & Gowans, 1999; Hoyt, 2005; Silva et al., 2012). Still, marine mammals have often been overlooked by national marine conservation efforts (Notarbartolo di Sciara et al., 2016). To improve this situation, the International Union for Conservation of Nature (IUCN) Marine Mammal Protected Areas Task Force recently formulated the concept of Important Marine Mammal Areas (IMMAs), intended to promote and prioritize the conservation of marine mammals within geographic areas of high ecological importance (IUCN, 2016; Notarbartolo di Sciara et al., 2016). IMMAs are defined as 'discrete portions of habitat, important to one or more marine mammal species, which have the potential to be delineated and managed for conservation' (Hoyt & Notarbartolo di Sciara, 2014). The semi-enclosed Gulf of Corinth in Greece is one of 26 areas characterized as IMMAs in the Mediterranean region (IUCN, 2017a). Its inclusion was based on the occurrence of isolated populations of the striped dolphin, *Stenella coeruleoalba*, and the common dolphin, *Delphinus delphis*. Common bottlenose dolphins, *Tursiops truncatus* (hereafter bottlenose dolphin), also occur regularly within this area (Bearzi et al., 2016; IUCN, 2017b).

Striped, common, and bottlenose dolphins in the Mediterranean are classified as Vulnerable, Endangered, and Vulnerable, respectively, in the IUCN Red List of Threatened Species (Aguilar & Gaspari, 2012; Bearzi, 2012; Bearzi, Fortuna, & Reeves, 2012). In the Gulf of Corinth, striped dolphins are relatively abundant (1324 individuals, 95% confidence interval (95% CI) 1158–1515), but geographic isolation exposes them to human impact and stochastic events (Bearzi et al., 2016). Common dolphins are few (22 individuals, 95% CI 16–31), and based on IUCN Red List criteria they would qualify as Critically Endangered within the Gulf (Santostasi, Bonizzoni, Gimenez, Eddy, & Bearzi, 2018). The Gulf of Corinth also hosts animals of intermediate striped × common dolphin pigmentation (55 individuals, 95% CI 36–83; Bearzi et al., 2016), recently confirmed to be individuals with mixed ancestry (hereafter 'admixed'; Antoniou, Frantzis, Alexiadou, Paschou, & Poulakakis, 2018). Whereas striped dolphins can be found in single-species groups, common and admixed dolphins occur only in mixed species groups with striped dolphins. Striped, common, and admixed dolphins are thought to be 'resident' within the Gulf (Bearzi et al., 2016). Bottlenose dolphins occur in low numbers (39 individuals, 95% CI 33–47; Bearzi et al., 2016), and at least some individuals are known to move in and out of the Gulf (Bearzi, Bonizzoni, & Gonzalvo, 2011b). In addition to cetaceans, the Gulf of Corinth hosts a variety of protected species listed in international conservation conventions such as the EU Habitats Directive (Bearzi et al., 2016; Issaris et al., 2012).

For several decades, the Gulf's remarkable odontocete fauna has been exposed to threats including prey depletion caused by overfishing, chemical contamination, habitat degradation (particularly because of the massive long-term dumping of industrial by-products), and acoustic disturbance from seismic surveys (Bearzi et al., 2016). Until recently, however, little was known about the abundance and distribution of cetaceans within the Gulf, and virtually no action was taken to protect them. The identification of preferred habitat can inform the management measures necessary to ensure the long-term protection of striped and bottlenose dolphins, and facilitate the recovery of a common dolphin population that is already on the brink of geographic eradication (Santostasi et al., 2018).

Previous research based on a smaller dataset has shown that striped dolphins favour deep oligotrophic waters, whereas bottlenose dolphins use continental shelf waters and areas near fish farms in the northern sector (Bearzi et al., 2016). No prediction was made on the actual spatial distribution of any cetacean species, however, and there was no information on the factors that influence the occurrence of common and admixed dolphins. This study aims to fill these gaps, based on 7 years of consistent survey effort. A combined generalized additive model and generalized estimation equation (GAM-GEE) framework was used to: (i) describe the habitat preferences of striped, common/admixed, and bottlenose dolphins; (ii) create maps of predicted distribution to identify critical dolphin habitat; and (iii) propose species-specific and area-specific management measures.

2 | METHODS

2.1 | Study area

The Gulf of Corinth is a deep semi-enclosed basin of approximately 2400 km^2, separating the Peloponnese from mainland Greece (Figure 1). The Gulf is roughly 128-km long and up to 35-km wide. It is separated to the west from the outer Gulf of Patras and the Ionian Sea by the 1.9-km-wide Rion-Antirion strait, and is bounded to the east by the narrow Corinth Canal (25-m wide). The western sector of the Gulf leading to open Ionian Sea waters is relatively shallow (Figure 1), with a maximum depth of 65 m under the Rion-Antirion bridge. The central sector of the Gulf includes a large basin with depths of 500–900 m. The waters are mostly oligotrophic and

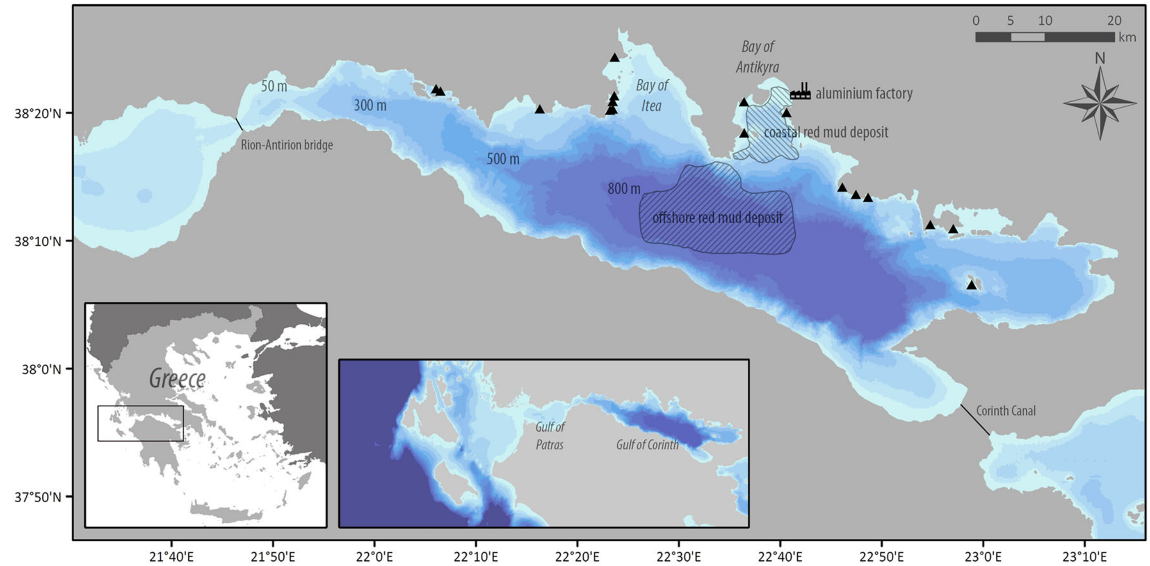

FIGURE 1 The study area, showing the position of the Gulf of Corinth in central Greece, some of the locations cited in the text, active fish farms (black triangles), the perimeter of coastal and offshore red mud deposits, and 50–800 m isobaths

transparent, with Secchi disk readings of 10–33 m (Bearzi, Bonizzoni, Agazzi, Gonzalvo, & Currey, 2011). On the northern coast, a large aluminium processing plant has been operating since 1966. Large volumes of tailings from the plant – also called 'red mud' – have been discarded into the Gulf between 1969 and 2011 (Iatrou, 2013; Issaris et al., 2012; www.alhellas.com), resulting in two main metalliferous deposits (Bearzi et al., 2016; Iatrou, 2013). The northern shore of the Gulf gives shelter to 17 fish farms (Figure 1) that produce mainly European sea bass, *Dicentrarchus labrax*, and gilthead seabream, *Sparus aurata*.

2.2 | Boat-based surveys

Boat-based visual surveys were conducted from a 5.8-m inflatable boat with rigid hull, powered by a 100-hp four-stroke outboard engine, between June and September 2011–17, totalling 283 days at sea and 27 079 km of navigation (Figure 2). Navigation was carried out under the following conditions: (i) daylight and no fog; (ii) sea state ≤2 Douglas; (iii) at least two experienced observers consistently scanning the sea surface by naked eye; and (iv) survey speeds of 26–31 km h^{-1}. A survey was interrupted if dolphins were sighted, when sea or weather conditions deteriorated, or when other factors (e.g. late hour) forced the crew to return to port. Binoculars were not used during navigation. Survey routes varied depending primarily on sea conditions, but attempts were made to obtain a homogeneous coverage of the study area. Because sea conditions can severely affect the probability of encountering dolphins (Buckland et al., 2001; Evans & Hammond, 2004), sea state was categorized using a fine-tuned scale (instead of a standard Beaufort or Douglas scale): S1 (flat), S2 (calm, but rippled), and S3 (non-breaking wavelets of less than 20-cm high). All data collected during unfavourable conditions (sea state above S3, observers not looking for dolphins, or navigation under non-standard conditions) were removed from the analysis to account for inaccuracy under those sampling conditions (Bonizzoni et al., 2014; Pirotta, Matthiopoulos, MacKenzie, Scott-Hayward, & Rendell, 2011). When dolphins were sighted, the research boat slowed down and stayed within 100 m of the animals. Boat disturbance was reduced by following the recommendations of Würsig and Jefferson (1990): e.g. operating the boat at the minimum speed and avoiding sudden

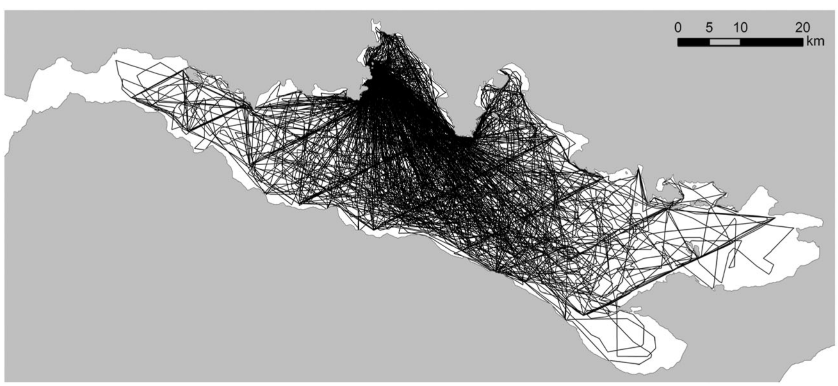

FIGURE 2 Survey effort in 2011–2017, totalling 27 079 km of navigation

changes of speed and direction, resulting in no apparent impact on dolphin movement patterns (Bearzi, Politi, & Notarbartolo di Sciara, 1999). The position of the boat was recorded via GPS at 1-min intervals throughout navigation and tracking, and was used as a proxy for dolphin position during dolphin group follows. Extensive photography was used to confirm the occurrence of common and admixed dolphins within striped dolphin groups (Bearzi et al., 2016). Admixed individuals (Antoniou et al., 2018) were combined with common dolphins for the purposes of this study. All navigation and group follow data were analysed with ARCMAP 10.4 (ESRI, Redlands, CA).

2.3 | Modelling framework

To account for a different probability of encountering dolphins depending on different effort conditions (Buckland et al., 2001; Evans & Hammond, 2004), the entire study area was divided into grid cells of 4 × 4 km (a resolution consistent with the remote-sensing data used), and a specific sampling 'effort index' (calculated as the number of 1-min GPS points within each grid cell, divided by the sea area in that cell) was assigned to each GPS point. All GPS points were linked with information obtained at sea (sea state, dolphin presence or

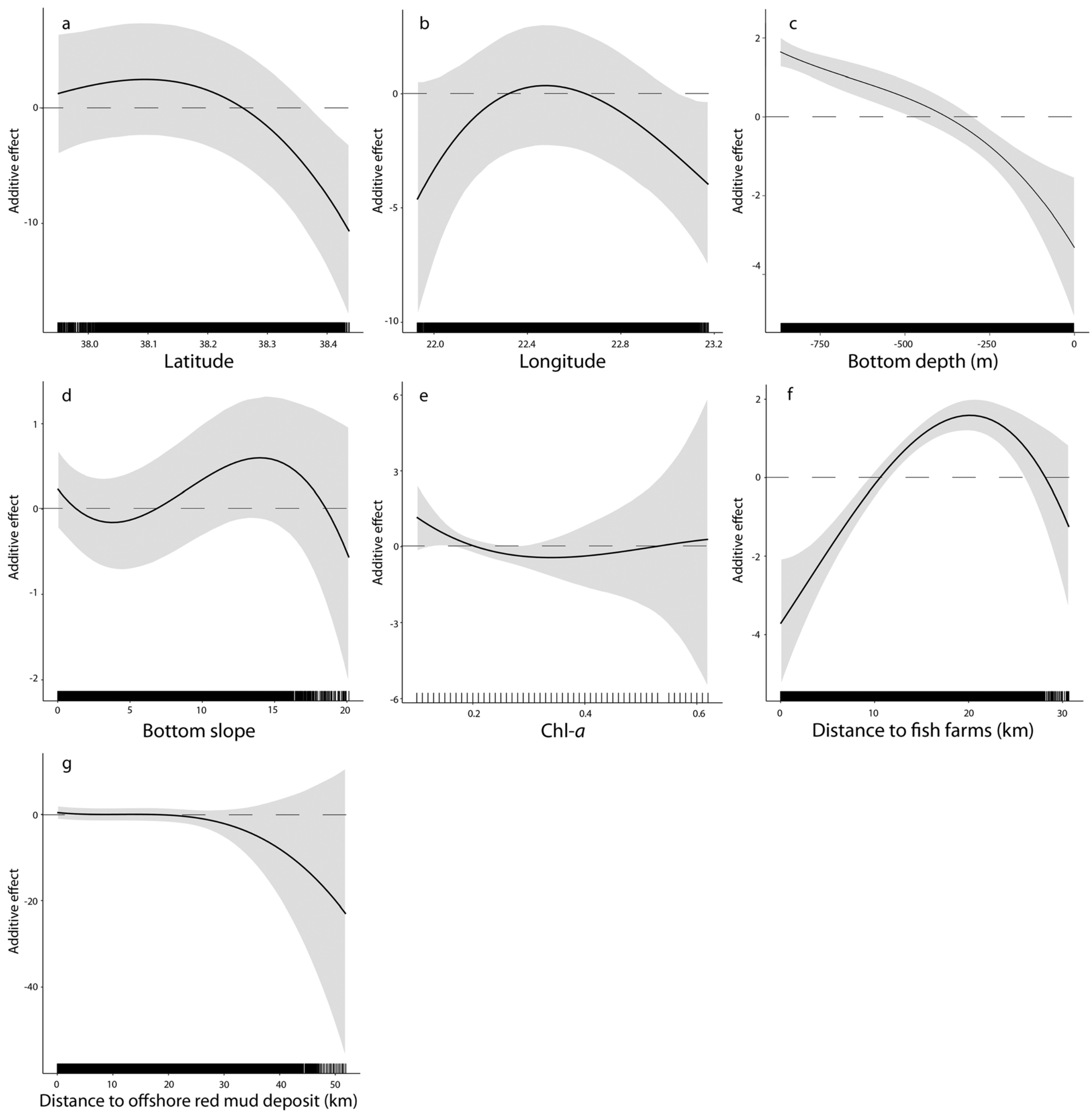

FIGURE 3 Response curves of the relationship between explanatory variables and striped dolphin occurrence: (a) latitude, (b) longitude, (c) bottom depth, (d) bottom slope, (e) chlorophyll *a* (Chl-*a*), (f) distance to fish farms, and (g) distance to the offshore red mud deposit. Shaded areas represent 95% confidence intervals, as calculated by the generalized estimation equation (GEE). Rug plots along the *x*-axis represent the sampling intensity across the variables range

absence), from online datasets (bottom depth, sea surface temperature (SST), chlorophyll *a* (Chl-*a*), and euphotic depth), from literature (location of red mud deposits), or calculated within ARCMAP (bottom slope, distances to features). Bottom depth was obtained from EMODnet (www.emodnet-bathymetry.eu) SST, Chl-a, and euphotic depth satellite data were obtained from NASA OceanColor (http://oceancolor.gsfc.nasa.gov) as monthly averaged MODIS-SMI products. The perimeter of red mud deposits was obtained by georeferencing a map in Iatrou (2013: Figure 4.40, p. 171). The bottom slope was calculated via the 'slope' spatial analysis tool in ARCMAP. All distances (m) were calculated as the minimum distance between the GPS points and the feature of interest, by using the 'cost distance' function within ARCMAP. The quantitative variables described above were linked to each GPS point, by using the 'extract multi values to points' tool in ARCMAP.

A generalized additive modelling (GAM) framework was used to identify which factors described above affected the distribution of dolphins in the Gulf of Corinth. GAMs are a non-parametric extension of generalized linear models (GLMs), and allow for flexible relationships between the response variable and explanatory variables (Hastie & Tibshirani, 1990; Wood, 2006). Here, binomial GAMs with a logit link were employed. To allow for the use of both navigation and dolphin group follow data, and consider the possibility of spatio-temporal

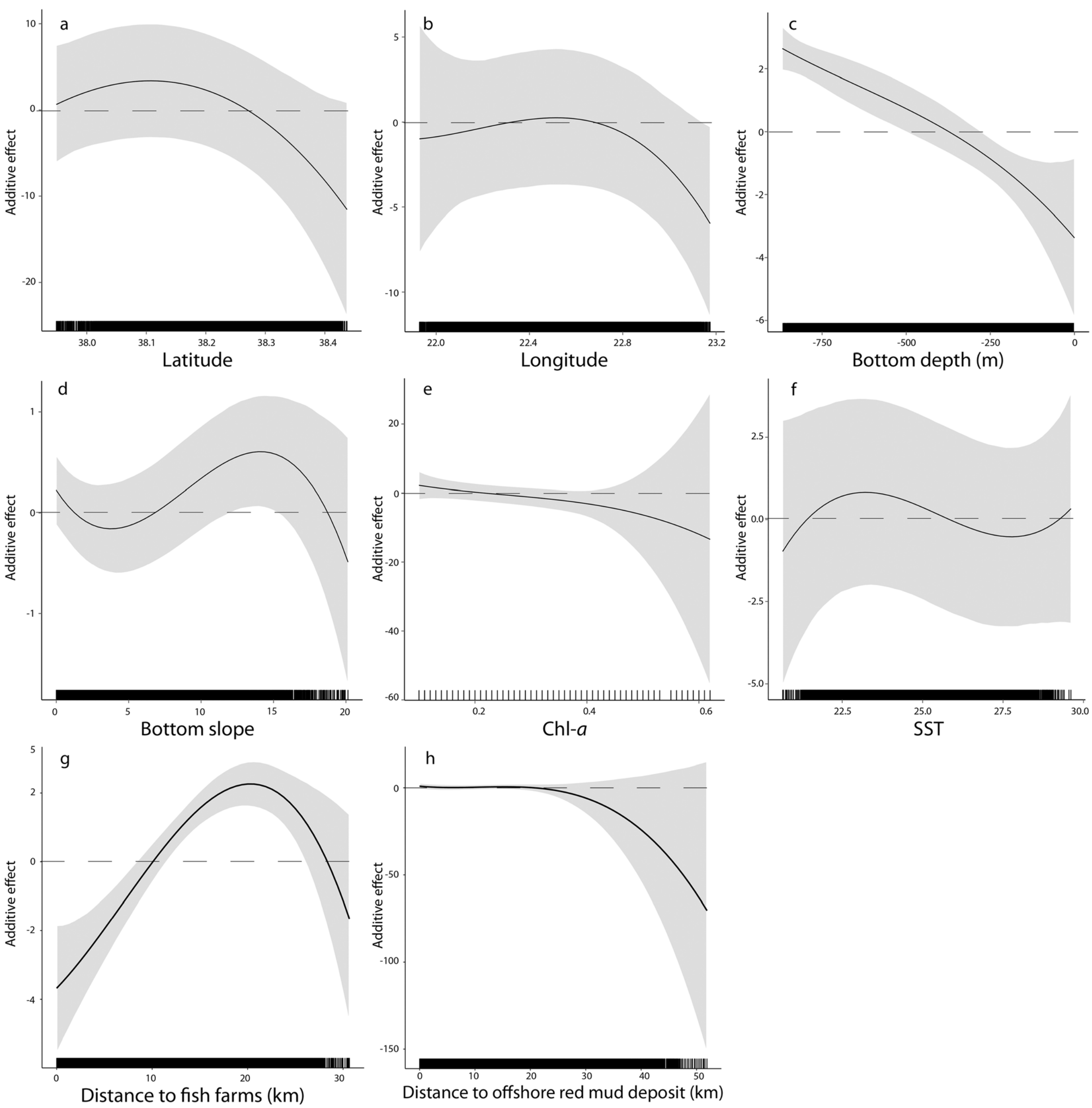

FIGURE 4 Response curves of the relationship between explanatory variables and common/admixed dolphin occurrence: (a) latitude, (b) longitude, (c) bottom depth, (d) bottom slope, (e) chlorophyll *a* (Chl-*a*), (f) sea surface temperature (SST), (g) distance to fish farms, and (h) distance to the offshore red mud deposit. Shaded areas represent 95% confidence intervals as calculated by the generalized estimation equation (GEE). Rug plots along the *x*-axis represent the sampling intensity across the variables range

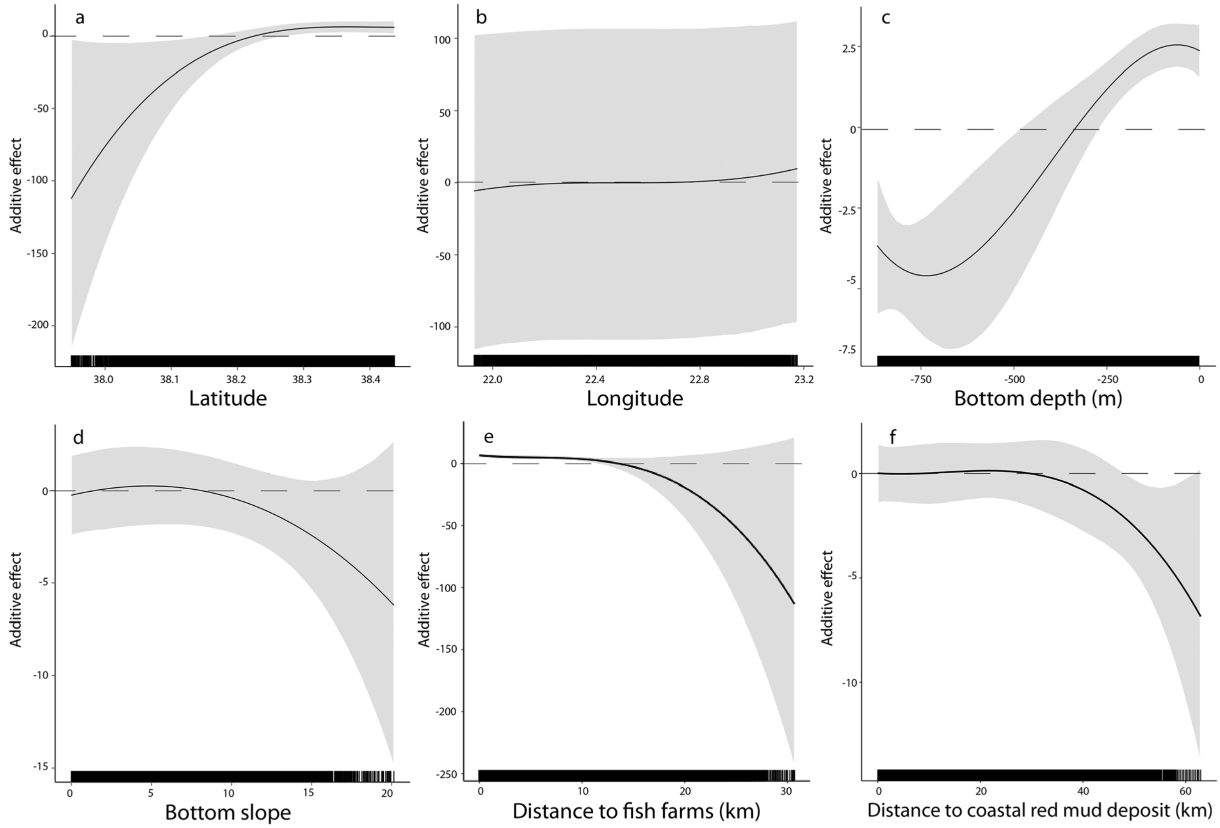

FIGURE 5 Response curves of the relationship between explanatory variables and bottlenose dolphin occurrence: (a) latitude, (b) longitude, (c) bottom depth, (d) bottom slope, (e) distance to fish farms, and (f) distance to the coastal red mud deposit. Shaded areas represent 95% confidence intervals, as calculated by the generalized estimation equation (GEE). Rug plots along the *x*-axis represent the sampling intensity across the variables range

autocorrelation caused by this continuous method of data collection, generalized estimation equations (GEEs) were used in combination with GAMs (Eguiguren, Pirotta, Cantor, Rendell, & Whitehead, 2019; Pirotta et al., 2011) within R 3.3.3 (R Core Team, 2017). All GPS points were grouped into individual blocks (Pirotta et al., 2011), defined as the set of continuous search points up to a dolphin sighting or the set of points associated with a dolphin group follow. Each day of sampling also designated a new block. These blocks were given a unique identifier to account for the autocorrelation between residuals within blocks. GEEs relax the assumption of independence between model residuals within blocks of data (Liang & Zeger, 1986), allowing for the use of all visual survey and group follow data while maintaining independence among blocks. Three model correlation structures (AR1, exchangeable, independence) were investigated based on different correlation structure estimators. When comparing quasi-likelihood under the independence model criterion (QIC) values, the working independence model performed better than the others and it was chosen for use in the modelling process (a choice consistent with the advice given by Pan, 2001).

Dolphin presence/absence data were modelled as a function of explanatory variables. We were interested in the impacts of several types of variables on dolphin distribution (geographic, bathymetric, environmental, and anthropogenic). Among these themes, there were too many variables to include all within an initial model to perform a selection process. There is also value in comparing submodels, each with distinct hypotheses (Planque, Loots, Petitgas, Lindstrøm, & Vaz, 2011). Consequently, four submodels were used (as described in Bonizzoni et al., 2014), each built with a specific set of explanatory variables: geographic (latitude and longitude), bathymetric (bottom depth and bottom slope), environmental (SST, Chl-*a*, and euphotic depth), and anthropogenic (distance to fish farms, distance to coastal red mud deposit, and distance to offshore red mud deposit). Each submodel included an effort index and sea state (to account for sampling bias), year (to account for any temporal variation among years), and block (to account for autocorrelation within blocks). Before model selection, multicollinearity was investigated in all four submodels using the variance inflation factor (VIF). Explanatory variables with the highest VIF value of ≥ 3 (Zuur, Ieno, Walker, Saveliev, & Smith, 2009) were individually removed from the submodel, and multicollinearity was re-checked to verify that the remaining variables were not correlated (Neter, Wasserman, & Kutner, 1990). Generalized linear models (GEE-GLMs) were constructed using the package GEEPACK within R (Højsgaard, Halekoh, & Yan, 2006). The package SPLINES was then used to build smoothing splines within the GEE-GLMs, generating GEE-GAMs. Models were fitted using the package MGCV. To prevent overfitting and to restrict flexibility, each continuous explanatory variable was given a maximum number of three degrees of freedom within each submodel (Ciannelli, Fauchald, Chan, Agostini, & Dingsor, 2008). The importance of variables was investigated by using a manual backward stepwise selection procedure to minimise the QIC.

Using submodels allows for comparison among different types of variables influencing animal distributions (Planque et al., 2011), but a primary objective of this project was to predict and map important habitats for each species, which required a single model. Variables retained in each of the four submodels were merged into final species-specific models, used to generate predictive maps of occurrence for striped, common/admixed, and bottlenose dolphins. Further multicollinearity investigations were performed, and explanatory variables with VIF ≥ 3 were removed. Using 4 × 4-km grid cells overlain across the entire Gulf, the values of the variables selected in the final species-specific models were extracted and linked to the centroid of each cell. For time-varying variables (i.e. remote sensing data) retained in the striped dolphin and common/admixed dolphin submodels, values related to the middle of the study period were used in the final predictive models, considering that the analyses did not show temporal variation of dolphin occurrence among years. The 'predict.gam' function in the MGCV library within R (Wood, 2006) was used to predict the probability of dolphin occurrence (a value of probability between 0 and 1), based on the final model for each species composed of the covariates retained by the submodels.

Two sets of predictive cell-based maps of dolphin distribution (Figure 6) were produced using: (i) a uniform scale of probability across species based on the species having the highest maximum probability value, i.e. the striped dolphin (Figure 6A1–A3); and (ii) species-specific scales of probability (Figure 6B1–B3). As the identification and protection of a species' habitat does not depend on the habitat preferences of a different species, the latter approach more appropriately identifies subareas where species-specific management action should be taken. The most frequently used portions of each species' preferred habitat (distribution hot spots) were identified visually in Figure 7 as grid cells with values of predicted species-specific occurrence greater than the mid value of the scale.

3 | RESULTS

3.1 | Dolphin occurrence and group follows

Dolphins (all species) were observed on 220 of the 283 days spent at sea, between 06:00 AM and 10:00 PM, for a total of 3171 km and 552 h of group follows (Figure 6A1–A3). Striped dolphins were observed on 176 days, for a total of 638 sightings. Their movements

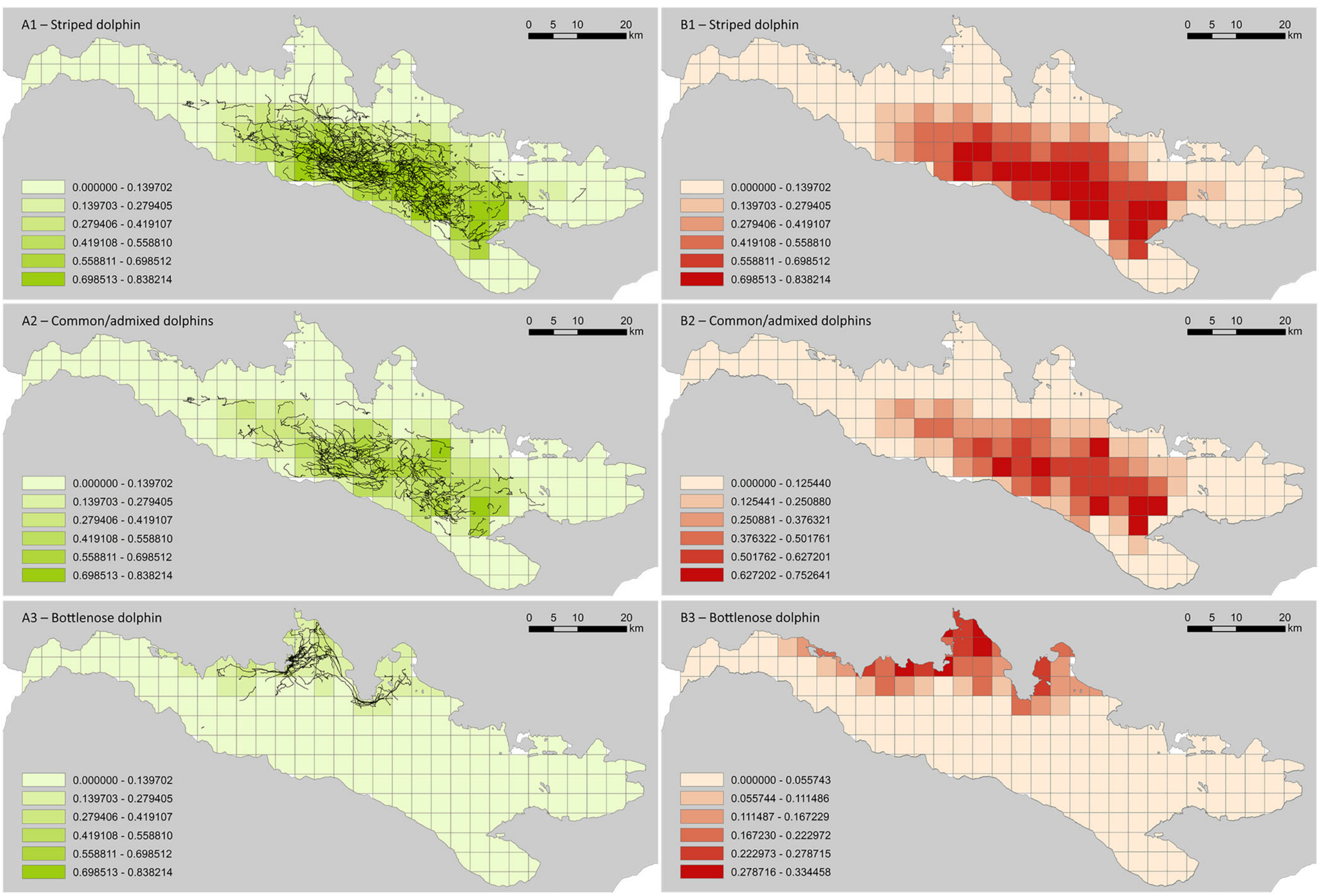

FIGURE 6 Cell-based maps of predicted dolphin occurrence in the Gulf of Corinth: 1, striped dolphin; 2, common/admixed dolphins; 3, bottlenose dolphin. Scale values in the A maps are uniform across species, whereas those in the B maps are species specific. Darker colours indicate preferred habitat. Black lines in A maps show dolphin movements tracked during group follows

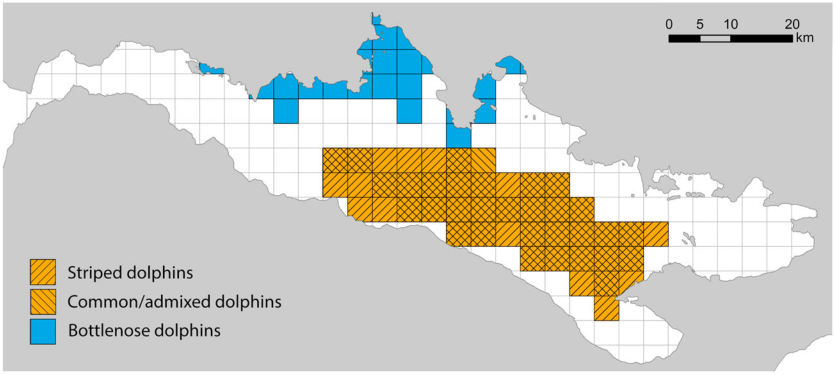

FIGURE 7 Predicted hot spots of dolphin distribution in the Gulf of Corinth. Orange cells: striped and common/admixed dolphins (cross-hatched cells indicate distribution hot spots for both striped and common/admixed dolphins). Blue cells: bottlenose dolphins

were tracked for a total of 414 h 27 min (mean = 39 min, SD = 43.1 min), encompassing 2492 km. Common and admixed dolphins were always found within striped dolphin groups, observed on 103 days (162 sightings) and tracked for 190 h 26 min (mean = 71 min, SD = 51.0 min), encompassing 1092 km. Bottlenose dolphins were observed on 72 days (98 sightings, never in mixed species groups) and tracked for 137 h 34 min (mean = 84 min, SD = 71.2 min), encompassing 679 km.

3.2 | Striped dolphins

The variable year was never retained in the four submodels, suggesting no significant interannual differences in striped dolphin occurrence. Latitude and longitude were retained in the geographic submodel, bottom depth and slope were retained in the bathymetric submodel, Chl-*a* was retained in the environmental submodel, and distance to fish farms and distance to the offshore red mud deposit were retained in the anthropogenic submodel. Although latitude and longitude have wide confidence intervals, they drop under the zero line towards high values, indicating a higher occurrence in the central and southern sectors of the Gulf (Figure 3a, b). Occurrence was higher in waters deeper than 300 m (with an almost linear increase of occurrence as depth increases; Figure 3c) and away from fish farms (Figure 3f). Occurrence was lower away from the offshore red mud deposit (Figure 3g), but the confidence intervals are wide for this factor. Confidence intervals in the response curves for bottom slope and Chl-*a* are also wide (Figures 3d, 3e), preventing interpretation.

3.3 | Common and admixed dolphins

Common and admixed dolphins responded similarly to striped dolphins. The variable year was never retained in the four submodels. Latitude and longitude were retained in the geographic submodel, bottom depth and slope were retained in the bathymetric submodel, Chl-*a* and SST were retained in the environmental submodel, and distance to fish farms and to the offshore red mud deposit were retained in the anthropogenic submodel. Latitude and longitude plots are suggestive of a higher occurrence in the central and southern sectors of the Gulf (Figures 4a, 4b), but the confidence intervals are wide. Occurrence was higher in waters deeper than 300 m (with an almost linear increase of occurrence as depth increases; Figure 4c) and away from fish farms (Figure 4g). Occurrence was lower in waters with high Chl-*a* values (Figure 4e) and away from the offshore red mud deposit (Figure 4h), but the confidence intervals are wide. The response curves for bottom slope and SST are unclear (Figures 4d, 4f).

3.4 | Bottlenose dolphins

Three of the four submodels retained the variable year, suggesting that bottlenose dolphin occurrence in the Gulf varied among years. Latitude and longitude were retained in the geographic submodel, bottom depth and slope were retained in the bathymetric submodel, and distance to fish farms and to the coastal red mud deposit were retained in the anthropogenic submodel. Occurrence was higher at latitudes above approximately 38.2°N (Figure 5a), in waters shallower than 300 m (Figure 5c), and in areas within approximately 10 km of fish farms (Figure 5e). The response curve for longitude (Figure 5b) has extremely wide confidence intervals. Plots of bottom slope (Figure 5d) and distance to the coastal red mud deposit (Figure 5f) suggest a drop in occurrence at high values, but the confidence intervals are wide.

3.5 | Preferred habitat

The final model for striped dolphins included longitude, bottom depth, bottom slope, Chl-*a*, distance to fish farms, and distance to the offshore red mud deposit. Predictive values of striped dolphin occurrence varied between 0 and 0.84 (Figure 6B1). The model predicted the preferred habitat to be situated in the central/southern sector of the Gulf, with a dolphin distribution hot spot encompassing 696 km^2 (Figure 7). The final model for common/admixed dolphins included latitude, longitude, bottom depth, bottom slope, Chl-*a*, SST, and distance to the offshore red mud deposit. Predictive values of common/admixed dolphin occurrence varied between 0 and 0.75 (Figure 6B2). The model predicted a preferred habitat situated in the central/southern sector of the Gulf, largely overlapping that of striped dolphins, with a distribution hot spot encompassing 512 km^2 (Figure 7). The final model for bottlenose dolphins included longitude, bottom depth, bottom slope, and distance to fish farms. Predictive values of bottlenose dolphin occurrence varied between 0 and 0.33 (Figure 6B3). The model predicted a preferred habitat situated in the northern/central coastal sector of the Gulf, with distribution hot spots encompassing 231 km^2 (Figure 7).

Overall, the models fit the data fairly well (Figure 6 shows the dolphin movements tracked during group follows), consistent with an extensive observation effort across the 7 years of study. Of 201 grid cells of the sea surface considered in the predictive analyses (total water surface 2381 km^2), 69 (total water surface 943 km^2; 39.6%) were identified as distribution hot spots for one or more species (Figure 7). None of the cells representing distribution hot spots for bottlenose dolphins were hot spots for striped or common/admixed dolphins. Conversely, 31 cells (496 km^2) were identified as distribution hot spots for both striped and common/admixed dolphins, indicating a broad overlap in the distribution of the two species (cross-hatched cells in Figure 7).

4 | DISCUSSION

Odontocete species living in coastal and inland areas impacted by overexploitation, extraction, and development face considerable risks. Whereas some of the most resilient species may adapt to some extent, and even coexist with humans (Bearzi, Piwetz, & Reeves, 2019), other species will decline if effective management and conservation action is not taken. In the waters of Greece, a variety of binding national, regional, and international legislative instruments require the protection of all cetacean species (for a review of the international legal framework for marine mammal conservation in the Mediterranean, see Scovazzi, 2016). Management action is therefore mandatory to protect marine biodiversity and to maintain (or restore) cetacean species and habitats to a favourable conservation status. The Gulf of Corinth hosts populations of three protected odontocete species exposed to significant anthropogenic threats. The population of common dolphin is classified as Endangered in the Mediterranean (Bearzi, 2012), and would qualify as Critically Endangered within the Gulf (Santostasi et al., 2018), whereas those of striped and bottlenose dolphins are classified as Vulnerable in the Mediterranean (Aguilar & Gaspari, 2012; Bearzi et al., 2012). This study shows that the Gulf of Corinth contains important habitat for these species, and identifies areas within the Gulf where management action must be taken to ensure effective protection.

4.1 | Striped and common/admixed dolphins

Striped and common/admixed dolphins were found to have largely similar habitat preferences. The striped dolphin preference for waters deeper than 300 m is consistent with the findings from other Mediterranean areas (e.g. Cañadas, Sagarminaga, & Garcia-Tíscar, 2002; Carlucci, Fanizza, Cipriano, Paoli, & Russo, 2016; Panigada et al., 2008), and with a diet based on pelagic and bathypelagic prey species living in the water column (including bony fishes of the families Gadidae, Sparidae, and Gonostomiatidae, and perhaps more importantly cephalopods of the families Histiotheuthidae, Ommastrephidae, Enoploteuthidaea, and Onychoteuthidaea; Aguilar, 2000). For instance, the stomach contents of striped dolphins bycaught in fishing gear off Turkey suggest that oceanic and bioluminiscent cephalopods with wide vertical distribution and diurnal movements are important prey (Dede, Salman, & Tonay, 2016; Öztürk, Salman, Öztürk, & Tonay, 2007). Although studies of striped dolphin diet were not conducted in the Gulf of Corinth, repeated findings of fresh and wounded dead specimens of the long-armed squid *Chiroteuthys veranyi* occurred while tracking striped dolphins, suggesting that these squids could have been killed by them (Bearzi et al., 2016).

Common dolphins in Greece (and elsewhere in the Mediterranean) normally prefer continental shelf waters (Bearzi et al., 2003; 2005; Frantzis et al., 2003; Giannoulaki et al., 2017), where they target epipelagic schooling fish such as European anchovy, *Engraulis encrasicholus*, and the European pilchard, *Sardina pilchardus* (Bearzi et al., 2005; 2010; Bearzi, Politi, Agazzi, & Azzellino, 2006). In the Gulf of Corinth, the unusual preference for deep waters documented in this study is consistent with the hypothesis of common dolphins having modified their behaviour to associate with larger striped dolphin groups. Across the 7 years of this study, common and admixed dolphins were observed exclusively within mixed species groups with striped dolphins. During 190 h of observation, the few common dolphins scattered within large striped dolphin groups (Bearzi et al., 2016) were never observed schooling and chasing epipelagic fish at the surface (a typical behaviour of common dolphins in other Mediterranean areas; Bearzi et al., 2003, 2006), suggesting behavioural and diet modifications. Sharing deep-water habitat with striped dolphins and perhaps adapting to their foraging behaviour may come at a cost for common dolphins, considering that the two species have different diets (Aguilar, 2000; Bearzi et al., 2003) and that common dolphins have higher metabolic costs (Spitz et al., 2012). In other Mediterranean areas where large numbers of common and striped dolphins coexist and share the same habitat (occasionally also forming mixed species groups), common dolphins tend to stay closer to the coast, and admixed individuals were not reported (Giménez et al., 2017).

Sharing habitat and living within mixed species groups with the more abundant striped dolphins probably developed as an adaptation to low common dolphin numbers (Frantzis & Herzing, 2002). Mixed species groups may provide social and foraging advantages as well as improved avoidance of predators (Stensland, Angerbjörn, & Berggren, 2003); however, striped and common dolphins are closely related and intermating is known to occur in the Gulf of Corinth (Antoniou et al., 2018). The resulting hybridization and introgression are significant threats for rare species coexisting with more abundant species (Allendorf, Leary, Spruell, & Wenburg, 2001; Levin, 2002). Hybridization may lead to the local eradication of a population through genetic swamping (where 'pure' species are progressively replaced by hybrids) or demographic swamping (where population growth rates are reduced by the expression of deleterious alleles and the production of maladaptive hybrids; Todesco et al., 2016). In the Gulf of Corinth, the documented production of viable and fertile hybrid offspring (Antoniou et al., 2018) may ultimately be the swansong of the small and isolated population of common dolphins (Antoniou et al., 2018; Bearzi et al., 2016 ; Santostasi et al., 2018).

The preferred habitat of striped and common/admixed dolphins, shown in Figure 6, probably includes most of the geographical range of these isolated populations (Bearzi et al., 2016; Santostasi et al., 2018). Distribution hot spots encompassed 696 km^2 for striped dolphins and 512 km^2 for common/admixed dolphins (Figure 7). Such a restricted geographical distribution, combined with genetic isolation (Bearzi et al., 2016; Gkafas et al., 2007; Moura, Natoli, Rogan, & Hoelzel, 2013), makes these populations especially vulnerable to human impacts and extreme mortality events (Davidson, Hamilton, Boyer, Brown, & Ceballos, 2009; Santostasi et al., 2018).

4.2 | Bottlenose dolphins

Neither striped nor common/admixed dolphins were ever observed associated with, or in the proximity of, bottlenose dolphins across the 7 years of this study. Habitat partitioning, consistent with the differences in diet and foraging strategies among these differently sized species, was confirmed by the maps of predicted dolphin occurrence (Figure 6). Bottlenose dolphins preferred continental shelf waters close to fish farms, with a higher predicted occurrence in the shallower northern part of the Gulf where the fish farms are concentrated (Figure 1). Particularly large and active fish farms located on the western shores of the bays of Itea and Antikyra (Galaxidi Marine Farm S.A., www.gmf-sa.gr) possibly contribute to making this part of the Gulf of Corinth more appealing to bottlenose dolphins (Figure 6). The preference for waters within 10 km of fish farms, with a high occurrence in their immediate vicinity (Figure 5e), is consistent with findings in other semi-enclosed areas of Greece, where bottlenose dolphins have adapted to opportunistic foraging near fish farm cages (Bonizzoni et al., 2014; Bonizzoni, Eddy, Würsig, & Bearzi, 2015; Piroddi, Bearzi, & Christensen, 2011). Fish farms are known to attract a great variety of organisms, probably because of artificial substrate and infrastructure, combined with the input of nutrients or manufactured fish feed (Bacher, Gordoa, & Sagué, 2012; Callier et al., 2018; Dempster, Sanchez-Jerez, Bayle-Sempere, Gimenez-Casalduero, & Valle, 2002). The concentration of wild prey, including key bottlenose dolphin prey (Bearzi, Fortuna, & Reeves, 2008; Machias et al., 2006), is thought to attract the dolphins, whereas the infrastructure itself may facilitate prey capture (Díaz López, 2006).

Preferred bottlenose dolphin habitat also included areas away from fish farms (Figure 6), and at least some of the individuals photo-identified during this study are known to travel extensively and to exit the Gulf (Bearzi, Bonizzoni, & Gonzalvo, 2011). East–west movements (possibly from one fish farm area to the next) may explain other responses by the models, such as the weak effect of longitude, whereas movements in and out of the Gulf may contribute to the observed interannual variability in bottlenose dolphin occurrence (Bearzi et al., 2016). Interannual variability within the Gulf and long-distance movements may be a response to the low density and patchy distribution of prey, while also allowing access to potential reproductive partners that would be necessary to maintain a sufficient gene flow (Bearzi et al., 2016; Bearzi, Fortuna, & Reeves, 2008; Silva et al., 2008).

4.3 | Management scenario and important threats

The management actions necessary to protect cetaceans in Greece were outlined in the National Strategy and Action Plan for the conservation of cetaceans in Greece, 2010–2015 (Notarbartolo di Sciara & Bearzi, 2010), which identified the Gulf of Corinth as an area of special conservation importance. Earlier, in 2007, the Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea, and Contiguous Atlantic Area (ACCOBAMS), ratified by Greece, had already listed the Gulf of Corinth as an area of special importance for common dolphins and other cetaceans, calling for the creation of a marine protected area (resolution 3.22; ACCOBAMS, 2007). In the same year, Greenpeace proposed the creation of a marine reserve (Greenpeace, 2007). Parts of the Gulf of Corinth were included in a proposed network of marine protected areas (Giakoumi et al., 2012; Issaris et al., 2012; Stelzenmüller et al., 2013; Vassilopoulou et al., 2012). In recent years, much more detailed information has become available on the abundance, distribution, movements, and genetics of dolphin populations within the Gulf (Antoniou et al., 2018; Bearzi et al., 2016; Bearzi, Bonizzoni, Agazzi, et al., 2011; Bearzi, Bonizzoni, & Gonzalvo, 2011; Santostasi, Bonizzoni, Bearzi, Eddy, & Gimenez, 2016), on the critical conservation status of common dolphins (Santostasi et al., 2018), and on the specific anthropogenic impacts threatening marine mammals in this area (Bearzi et al., 2016). So far, however, all this information has not produced management action that can ensure a favourable conservation status for dolphin populations in the Gulf, let alone prevent the eradication of common dolphins (Santostasi et al., 2018).

The reduced availability of important prey caused by overfishing has long been identified as one of the primary reasons behind the dramatic decline of common dolphins in the Mediterranean (Bearzi et al., 2003; Bearzi, Notarbartolo di Sciara, Reeves, Cañadas, & Frantzis, 2004), and in western Greece in particular (Bearzi et al., 2006; Bearzi et al., 2008; Piroddi, Bearzi, & Christensen, 2010; Piroddi, Bearzi, Gonzalvo Villegas, & Christensen, 2011). The effects of prey depletion and food web competition also threaten Mediterranean striped and bottlenose dolphins (Aguilar & Gaspari, 2012; Bearzi, Fortuna, & Reeves, 2008; Gómez-Campos, Borrell, Cardona, Forcada, & Aguilar, 2011). The impact of fishing in the Gulf of Corinth may be underestimated, considering that illegal fishing (including unreported, misreported, or undersize landings) is common throughout Greece (Moutopoulos, Prodromitis, Mantzouni, & Koutsikopoulos, 2016; Stergiou, Moutopoulos, & Armenis, 2009). For instance, illegal purse seining and beach seining within coastal areas where this fishing gear is banned was observed repeatedly during the 7 years of this study. The cumulative damage caused by legal and illegal fishing is exacerbated by the mechanical and biological damage caused to the sea bed by destructive fishing methods such as trawling and seining, known to cause dramatic alterations of the substrate and to reduce the biomass and biodiversity of benthic ecosystems, compromising their functionality, productivity, and complexity (Cabral, Duque, & Costa, 2003; Dayton, Thrush, Agardy, & Hofman, 1995; Eigaard et al., 2017; Hiddink et al., 2017; Jones, 1992; Katsanevakis, Maravelias, Vassilopoulou, & Haralabous, 2010; Løkkeborg, 2005; Stergiou, Economou, Papaconstantinou, Tsimenides, & Kavadas, 1998). Beyond the fishing pressures within the Gulf (Issaris et al., 2012; Vassilopoulou et al., 2012), high fishing pressure in the adjacent waters of the Gulf of Patras and Inner Ionian Sea Archipelago is likely to affect and limit movements of marine organisms into the Gulf of Corinth, including those of fish species that represent important dolphin prey (Giannoulaki et al., 2008; Tsagarakis et al., 2008; Tserpes, Politou, Peristeraki, Kallianiotis, & Papaconstantinou, 2008).

Other extant threats to dolphins in the Gulf include fishing-related mortality, anthropogenic noise, and pollution. Though incidental mortality in fishing gear is a major threat to many odontocete populations worldwide (Read, Drinker, & Northridge, 2006; Reeves, McClellan, & Werner, 2013; Taylor et al., 2017), and its occurrence and impact should be assessed rigorously, at present there is little evidence that bycatch represents a primary threat to dolphin populations in the Gulf of Corinth. Geophysical research and seismic surveys are not infrequent (Beckers et al., 2015; Taylor et al., 2011), and the intensive noise produced during these surveys can displace, harm, and kill cetaceans (Nowacek, Thorne, Johnston, & Tyack, 2007; Würsig & Richardson, 2009). Cargo ships and motor yachts of all sizes cross important dolphin habitat (Bearzi et al., 2016). Colossal volumes of hazardous industrial waste have been disposed off into the Gulf for over half a century (Bearzi et al., 2016; Issaris et al., 2012). Although the disposal of red mud at sea stopped in 2011 (Issaris et al., 2012; www.alhellas.com), contamination through the food web may expose dolphins to the immunotoxic and other detrimental effects of persistent environmental pollutants (Botsou & Hatzianestis, 2012; Desforges et al., 2016; Jepson et al., 2016; Malea, Haritonidis, & Kevrekidis, 1994; Tsangaris et al., 2011). Preferred dolphin habitat overlaps with areas of red mud disposal and dolphins show no avoidance of red mud areas (Bearzi et al., 2016), as further documented in this study.

4.4 | Urgent management action

Based on the available information on the impact of trawling and seining, and taking into account the binding national and international commitments to protect cetaceans and marine biodiversity, an immediate and total ban of bottom trawling, purse seining, and beach seining within the Gulf of Corinth would be the most important single management measure to protect dolphins and marine biodiversity. Such a measure would help maintain a favourable conservation status of striped and bottlenose dolphins and would contribute to the recovery of common dolphins. The ban would protect marine biodiversity at large, facilitating the recovery of depleted fish stocks and benefiting the local community of small-scale artisanal fishers operating trammel nets, gillnets, and longlines (Bearzi et al., 2016). Such management action would support the local and traditional fishing economy of the Gulf of Corinth, and would also promote nature tourism, leading to a sustainable use of marine resources consistent with Greece's natural and cultural heritage.

A ban of trawling and seining would not be new to Greece, as similar regulations have been adopted to protect other semi-enclosed areas (such as the Amvrakikos Gulf, where trawlers and seiners have been banned for more than 50 years; Gonzalvo, Giovos, and Moutopoulos, 2015). Although temporal and spatial fishing bans already exist in the Gulf of Corinth (Kapantagakis, 2007; Vassilopoulou et al., 2012), current regulations clearly cannot prevent the geographic eradication of common dolphins (Santostasi et al., 2018). The ecosystem and marine biodiversity of the Gulf needs to recover from decades of resource mismanagement, dumping of industrial waste, overexploitation, and illegal fishing practices. Research in a nearby area in the eastern Ionian Sea showed that high fishing pressure was the main reason behind the precipitous decline of common dolphins (Bearzi et al., 2006, 2010; Bearzi, Agazzi, et al., 2008), and ecosystem modelling predicted that a ban of trawling and seining would allow common dolphins to recover (Piroddi, Bearzi, Gonzalvo Villegas, & Christensen, 2011). The creation of a no-take area where only small-scale fishing is allowed (based on strict criteria for the issuing of new artisanal fishing licences) would not only be the most meaningful remedial action: it would also be welcomed by the great majority of fishers operating in the Gulf of Corinth, who perceive trawlers and seiners as the main threat to fish stock viability (Bearzi et al., 2016).

4.5 | Area-specific and species-specific management action

Strict partitioning of dolphin habitat provides a rationale for separate area-specific and species-specific management measures. Whereas a ban of trawling and seining in the entire Gulf would benefit all dolphin species, other management measures can be effective within smaller subareas. In striped and common/admixed dolphin distribution hot spots, anthropogenic noise must be kept to low and biologically acceptable levels, primarily through strict regulations for seismic surveys and hydrocarbon exploration and exploitation. Shipping and leisure boat traffic and speed should be regulated through appropriate codes of conduct to prevent harassment, displacement, and physical harm to dolphins. In bottlenose dolphin distribution hot spots, no measures that may result in harm or habitat loss (e.g. by means of acoustic devices) should be taken to deter the animals from approaching fish farm cages and from foraging in their vicinity. To such extent, education and awareness campaigns should be designed to encourage coexistence with bottlenose dolphins and to promote tolerance by fish farmers and fishers (Bearzi et al., 2019; Notarbartolo di Sciara & Bearzi, 2010). Although the flexible diet and opportunistic behaviour of bottlenose dolphins (including depredation on fishing gear, scavenging, and other kinds of opportunistic foraging) may allow the species to persist in areas that are far from pristine (Bearzi et al., 2019), management action in dolphin distribution hot spots should be taken to reduce noise, direct disturbance, and habitat degradation. Food-web contamination resulting from the past disposal of red mud into the Gulf should be monitored to better assess any impacts on dolphins and other marine species.]

5 | CONCLUSIONS

Indifference to science-based management recommendations and formal commitments to protect marine biodiversity (often in the name of short-term gain for fisheries and industrial lobbies) is eroding the valuable biodiversity and natural heritage of the Gulf, and may soon result in the loss of common dolphins from yet another Mediterranean area (Santostasi et al., 2018). The fate of dolphins inhabiting the Gulf of Corinth depends on strict conservation measures to mitigate the known human impacts, as well as on precautionary action to prevent harm from threats that are less understood. An immediate and fully enforced total ban of trawling and seining would be the single most effective management measure to protect marine mammals and marine biodiversity in this vulnerable inland sea. The recent formal inclusion of the Gulf of Corinth in the EU Natura 2000 network (Area code GR2520007, Law 4519/2018, February 2018) may set the stage for such a ban, provided that commitments and designations 'on paper' are soon followed by concrete and properly enforced conservation action.

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