



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Original article

Common dolphin (*Delphinus delphis*) habitat preferences using data from two platforms of opportunityAndré E. Moura^{a,*}, Neftalí Sillero^b, Ana Rodrigues^c^a School of Biological and Biomedical Sciences, Durham University, South Road, Durham, DH1 3LE, UK^b Centro de Investigação em Ciências Geo-Espaciais (CICGE), Universidade do Porto, Faculdade de Ciências, 4169-007 Porto, Portugal^c Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO), Campus Agrário de Vairão, 4485-661, Portugal

ARTICLE INFO

Article history:

Received 31 March 2011

Accepted 25 August 2011

Available online 13 September 2011

Keywords:

Ecological niche modelling

Cetacea

Common dolphin

Maxent

Portugal

ABSTRACT

Cetaceans are difficult to observe in the wild, and demand complex logistics for dedicated collection of biological data. As such, the distribution of most cetacean species is still poorly understood. Ecological niche models are useful in studying species distributions and their ecological determinants, and platforms of opportunity (e.g. commercial nautical operators) can provide an alternative source for that data in cetaceans. In this study, we modelled common dolphin (*Delphinus delphis*) habitat preferences using ecological niche modelling and presence data obtained from distinct platforms of opportunity in two different areas in the Portuguese coast (west and south mainland Portugal) for the period 2005–2007. Models from southern Portugal were projected to western Portugal and vice-versa, to check for robustness in predicting the species ecological niche. Our results show that data from platforms of opportunity can result in robust ecological models and provide extremely useful information on cetacean ecology. We found that common dolphins exhibit a patchy distribution pattern over the Portuguese coastline, and identified key habitats for their occurrence. The most important variable associated with this species' distribution was chlorophyll concentration which, given the results from previous research, we hypothesise reflects an ecological specialisation on pelagic schooling fish. Given that the most abundant schooling fish species in Portugal is increasingly overexploited and in constant decline, more attention should be given to the conservation of common dolphin in Portuguese waters.

© 2011 Elsevier Masson SAS. All rights reserved.

1. Introduction¹

The study of species' distributions can provide important information regarding their ecology (Guisan and Zimmermann, 2000). Ecological niche models (ENM) can be useful in predicting species movement ranges, identifying habitat preferences and potential population breaks, as well as ecological barriers to species dispersal (Austin et al., 1996; Gottfried et al., 1999; Osborne et al., 2001; Bentivegna et al., 2007; Isari et al., 2007; Ravago-Gotanco et al., 2007; Skov et al., 2008; for a review see Sillero et al., 2010). ENM can be particularly helpful in studying species with large distribution ranges and low sighting rates, where detailed distribution information can be very difficult to obtain (Guisan et al.,

2006). In the case of highly mobile oceanic species, geographical barriers are extremely uncommon, leading to what has been called the marine-speciation paradox (Bierne et al., 2003). One hypothesis states that adaptation to different environments (and not physical barriers) would effectively stop gene flow between groups (Palumbi, 1994; Jackson and Cheetham, 1999; Schluter, 2001; Via, 2001), thus ecological niche modelling studies might also be an important tool in identifying ecological barriers in mobile marine organisms.

Despite its name, the common dolphin (*Delphinusspp.*) has been surprisingly ill studied, especially when compared to its closely related species, the bottlenose dolphin (*Tursiops spp.*). Common dolphins are considered opportunistic feeders, targeting pelagic schooling fish, usually the most abundant local species (e.g.: Silva, 1999; de Pierrepoint et al., 2005; Meynier et al., 2008). Although ocean wide genetic differentiation tends to be low (Natoli et al., 2006; Mirimin et al., 2009), controversy over its alpha taxonomy is ongoing (Rosel et al., 1994; Kingston and Rosel, 2004; Natoli et al., 2006). Natoli et al. (2006) suggested that the described differences in common dolphin morphology (Heyning and Perrin, 1994) might

* Corresponding author. Tel.: +44 07521042848.

E-mail address: a.e.v.moura@durham.ac.uk (A. E. Moura).

¹ AUC – Area Under the Curve; EGV – Ecogeographical Variables; ENM – Ecological Niche Models; WWC – Whale Watching Companies; ROC – Receiver Operated Characteristics; SD – Standard Deviation; SPEA – Society for the Study of Birds; SST – Sea Surface Temperature.

be the result of local adaptation rather than incipient speciation (Kingston and Rosel, 2004). The study of its distribution however, has been faced with a large degree of uncertainty and dramatic changes in the established knowledge. With a large dispersal potential and spending most of their time underwater, observations in the wild can be notoriously difficult. It was once widely accepted that common dolphins had an ubiquitous worldwide pantropical distribution (e.g.: Carwardine, 1995). However, more recently the common dolphin has been represented as having an essentially coastal distribution and being effectively absent from many of the pantropical coastlines of the world (Folkens et al., 2002). Further to this, a recent analysis of common dolphin records in the eastern coasts of the North and South American continents concluded that confirmed sightings of the species were only restricted to three discrete areas within that coastline (Jefferson et al., 2009). Although these studies tend to be conservative, they show that this species might actually occupy only certain “restricted” habitats. These habitats appear to overlap with regions having oceanographic characteristics usually related to high productivity (Reilly, 1990; Reilly and Fiedler, 1994; Fiedler and Reilly, 1994; Cañadas et al., 2005; Jefferson et al., 2009). However, very few studies have tested which environmental variables best correlate with common dolphin distribution. Previous studies have found that it tends to occupy areas with good upwelling conditions (Reilly, 1990; Reilly and Fiedler, 1994; Fiedler and Reilly, 1994; Jefferson et al., 2009). Cañadas and Hammond (2008) showed chlorophyll concentration to be correlated with common dolphin abundance but did not determine the species spatial ecological niche (Sillero, 2011).

Dedicated cetacean surveys are rare owing to their complex and expensive logistics, and few institutions are capable of promoting them. Researchers have alternatively relied on two types of platforms of opportunity to collect such data: (1) surveys with constant linear route efforts, such as commercial transportation services (e.g.: Wall et al., 2006; Williams et al., 2006); and (2) targeted observational efforts, such as whale-watching companies (Hauser et al., 2006) or nature watching enthusiasts (Evans and Hammond, 2004). Both types are suboptimal and have inherent procedural limitations, but can provide information that would otherwise be unavailable. Although both opportunistic data sources have been used in previous studies, no study to date compared the relative performance of each type in analysing dolphin distribution.

The Iberian Peninsula stands as a very interesting region to carry out ecological niche studies. Standing in the transition between two very different environments (the Mediterranean Sea and the North Atlantic), it exhibits a high level of habitat complexity (Alcaraz et al., 2006). The common dolphin is the most commonly stranded cetacean species on this coast (Sequeira et al., 1996), and it exhibits a considerable level of morphological variation (Murphy et al., 2006). However, high occurrence of strandings may not reflect a homogeneous distribution along the coast; moreover, patterns of distribution of common dolphins in Portugal remain unknown. In fact, after performing three years of fieldwork on this species for another study (A. Moura, unpublished data), we hypothesised that the species is not distributed uniformly along the coast, but it exhibits patches of higher probability of occurrence.

In our study, we first aimed at modelling common dolphin habitat preferences using ecological niche modelling and distribution data obtained from two platforms of opportunity (constant linear route and targeted observational data sources), over a period of several years and for two geographical areas. Second, we test whether or not there might be spatial patches of preferred habitat for common dolphins along the Portuguese coast, and whether these are constant through time. Finally, we compare the models obtained by the two opportunity data sources and discuss their

inherent strengths and limitations. With this study, we hope to highlight the potential for both data sources to be used in modelling cetacean distribution, and thus encourage the use of such data, in many regions the only available from these animals.

2. Materials and methods

2.1. Species datasets and study areas

We used data from two different platforms of opportunity over a period of three years (2005–2007): (1) records from constant linear routes performed by the Society for the Study of Birds (hereafter, SPEA dataset) along the western coast of Portugal to a maximum distance of 38 nautical miles from the coastline (Fig. 1A); and (2) records from targeted observational efforts collected by the whale-watching company “Dolphin Seafaris” (hereafter, WWC dataset) along part of the south coast of Portugal, or Algarve region, to a maximum distance of 27 nautical miles from the coastline (Fig. 1B). Sighting data of WWC dataset was recorded almost daily from May to September over the three years, while there was no seasonality in the SPEA sighting effort.

2.2. Environmental data

We collected monthly data of three environmental variables (surface sea temperature, SST; chlorophyll concentration; and

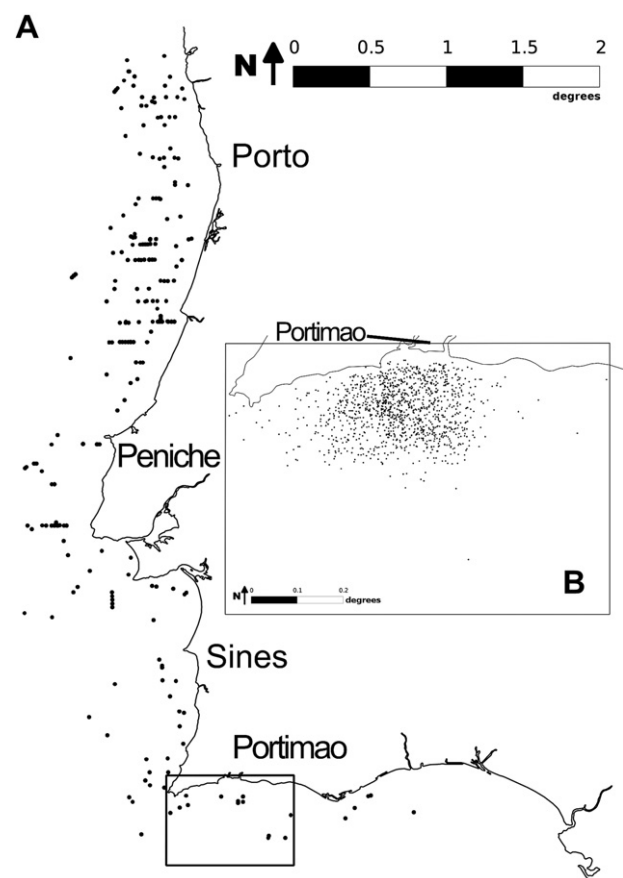


Fig. 1. Distribution of *Delphinus delphis* records collected by two different platforms of opportunity during 2005–2007: (A) constant linear routes performed by the Society for the Study of Birds (SPEA) dataset along the western coast of Portugal; and (B) targeted observational points collected by whale watching company (WWC) dataset along the south coast of Portugal (Algarve region). Sighting data of WWC dataset was recorded from May to September over the three years.

depth) from May to September during 2005–2007. Environmental variables were retrieved from the NASA's online PO.DAAC Ocean ESIP Tool (POET) (<http://podaac.jpl.nasa.gov/poet>), the OceanColor website (<http://oceancolor.gsfc.nasa.gov/>) and the GEBCO website (<http://www.gebco.net/>), respectively. We further derived the standard deviation (SD) of the monthly data series SST across all years to examine average intra-annual (seasonal) variability. We derived the SD of depth using a filter where the SD of one pixel is computed using the nine surrounding pixels. Therefore, the models were calculated including five variables in total. The original spatial resolution was 0.042° (4.7 km approximately). This spatial resolution was kept during the calculation of the ENMs.

2.3. Ecological niche models

We modelled the realized niche (*sensu* Hutchinson, 1957; see Sillero, 2011) of *Delphinus delphis* in the two study areas (western coast of Portugal with the Society for the Study of Birds – SPEA – dataset, and south coast of Portugal or Algarve region with the whale watching companies – WWC – dataset; Fig. 1).

In the Algarve coastal area, we built a model using each of the following: mean values of variables for all the three years sampled (2005–2007); mean values for each year individually; and mean values for each month from May to September (by averaging individual months across years). The model including data from all three years was projected to the Portuguese western coast (SPEA study area). Models were calculated for each year and month in order to evaluate temporal patterns in the spatial distribution of common dolphins.

In the Portuguese western coast, we built a model using data pooled from the three survey years (2005, 2006 and 2007), as each annual SPEA survey covered different regions within the Portuguese coastline. This model was then projected to the Algarve coastal area (WWC study area). The WWC projected model was

compared with the SPEA model and vice-versa, using a spatial correlation analysis, to evaluate the predictive capabilities of each model. In both cases, the study areas did not go beyond the areas covered by the surveys.

2.4. Maximum entropy models

We built Maximum Entropy models, as implemented in Maxent 3.3.1 software (www.cs.princeton.edu/~schapire/maxent), to identify which environmental variables correlated better with the species distribution, as well as areas of potential occurrence. This is a general-purpose machine learning method that uses presence-only occurrence data (Phillips et al., 2004, 2006; Phillips and Dudik, 2008), and thus calculates the realized ecological niche (*sensu* Hutchinson, 1957; see Sillero, 2011). The Maxent output for the realized niche model is a map representing the suitability of habitats through an index (Sillero, 2011). This index is continuous from very suitable habitats (value 1) to very unsuitable habitats (value 0) for the species. Maxent is particularly well suited to noisy or sparse information and it is capable of dealing with continuous and categorical ecogeographical variables (EGV) at the same time (Phillips et al., 2006). Maxent models consistently outperform more established methods, either presence-only methods (Bioclim, Domain) or presence-absence methods (GAM, GLM), especially when samples sizes are low (Elith et al., 2006; Hernandez et al., 2006).

Maximum Entropy looks for the statistical model that produces the most uniform distribution but still infers as accurately as possible the observed data. It compares the presence-only records with data extracted randomly from all the background (including the species records; see Phillips et al., 2009). These background data were extracted by Maxent automatically. Hence, Maxent calculated a set of ten models for each datasets through an iterative process and performed an average ensemble model (Araújo and

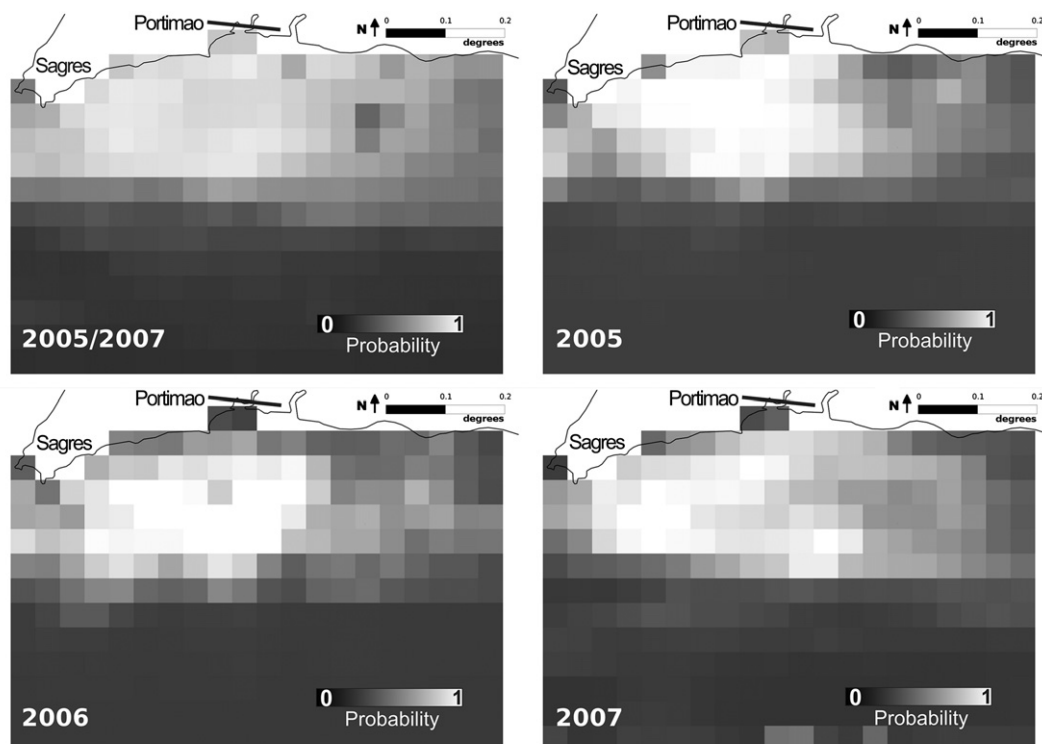


Fig. 2. Ensemble Maxent models for whale watching company (WWC) dataset for years 2005–2007 together, and separately for years 2005, 2006 and 2007.

New, 2007; Sillero, 2009, 2010). Maxent estimates the range of a species with the constraint that the expected value of each environmental variable (or its transform and/or interactions) should match its empirical average, i.e. the average value for a set of sample points taken from the species distribution (Phillips et al., 2004, 2006). Maxent weights each EGV by a constant and the estimated probability distribution is exponential in the sum of the weighed features, divided by a scaling constant to ensure that the probability values range from 0.0 to 1.0 and sum to 1.0. The program starts with an uniform probability distribution (gain = 0) and iteratively alters one weight at a time to maximize the likelihood of the occurrence dataset. The algorithm converges to the optimum probable distribution, and thus, the gain can be interpreted as representing how much better the distribution fits the sample points than the uniform distribution (Phillips et al., 2004, 2006; Phillips and Dudik, 2008).

Maxent was run with autoselecting randomly selecting 70% of the presence records as training data and 30% as test data. Default parameters were used in order to allow different models to be comparable. Models were evaluated with receiver operated

characteristics (ROC) plots. The area under the curve (AUC) of the ROC plot was taken as a measure of the overall fit of the Maxent model (Liu et al., 2005). AUC was selected because it is independent of prevalence (the proportion of presence in relation to the total dataset size; see Van der Wal et al., 2009). The importance of each EGV for explaining the species distribution was determined by: (1) jackknife analysis of the average AUC with training and test data; and (2) average percentage contribution of each environmental factor to the models. This was done by creating a model excluding one environmental variable, followed by the creation of a model using only the excluded individual variable. This procedure was repeated for each individual variable.

3. Results

All Maxent ensemble models using the whale watching company (WWC) dataset predicted similar suitable areas for the models including data from: all years pooled (2005–2007; Fig. 2); for each year separately (2005, 2006 and 2007; Fig. 2); and for each month (from May to September; Fig. 3). The most suitable habitats

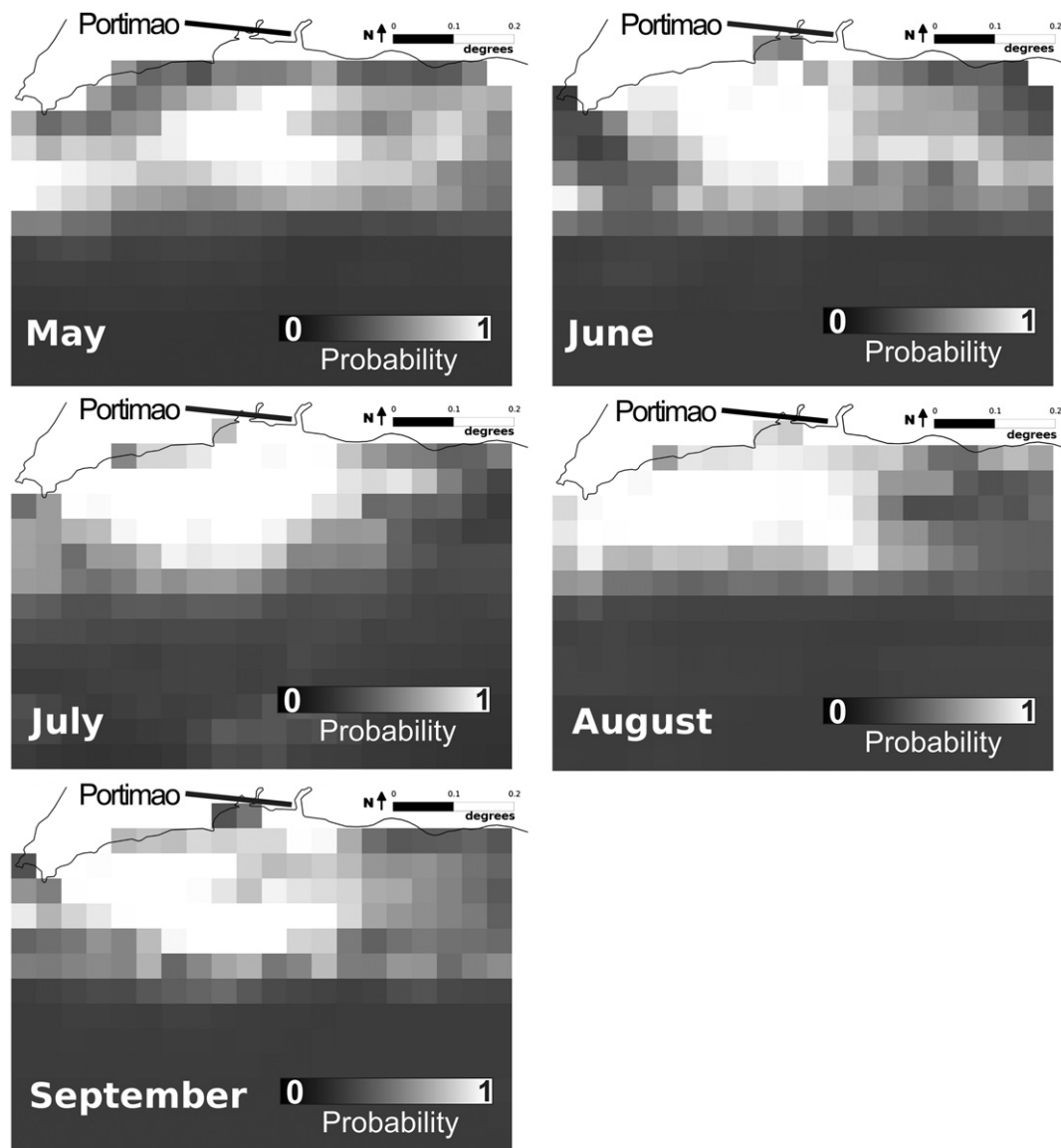


Fig. 3. Ensemble Maxent models for whale watching company (WWC) dataset for months May to September separately.

were located close to the coast, around the main group of common dolphin records (Figs. 2 and 3). This pattern was similar in the Maxent ensemble model using the Society for the Study of Birds (SPEA) dataset (Fig. 4) as in the most suitable habitats were located close to the coast.

The projected models of the WWC dataset to the Portuguese western coast (Fig. 5), and of the SPEA dataset to the Algarve coast (Fig. 4) were similar to the respective ensemble models of SPEA (Fig. 4; spatial correlation: $R = 0.877$) and WWC dataset (Fig. 2; spatial correlation $R = 0.769$). In the projected models of the WWC dataset to the Portuguese western coast, suitable habitats had, in general, a lower suitability index (WWC projection: range = 0.02–0.65, mean = 0.31 ± 0.14 ; SPEA model: range = 0.01–0.72, mean = 0.19 ± 0.21 ; Fig. 5). In the projected model of the SPEA dataset to the Algarve coast, the most suitable habitats were displaced to the west (Fig. 4).

All Maxent ensemble models of WWC dataset obtained mean AUC values higher than 0.8 when using the training data; in some cases, AUC was higher than 0.9 (Table 1). The respective AUC values for the test data were always higher than 0.75 (Table 1). The ensemble models of SPEA dataset obtained an AUC = 0.9 with the training data, and an AUC = 0.83 with test data.

In the WWC ensemble models, the variables chlorophyll concentration and sea surface temperature (SST) contributed more to the explained variation in the model, in almost all group models (all sampling years; years 2005, 2006, 2007; and months July and August; Table 2). There were three exceptions: in May, the variable SD of SST substituted SST; in June and September, the depth substituted SST. Therefore, chlorophyll concentration was the most important variable in all groups (Table 2). These patterns can be observed in the jackknife analysis of AUC and gain values of training and test data, for models calculated with only one variable and

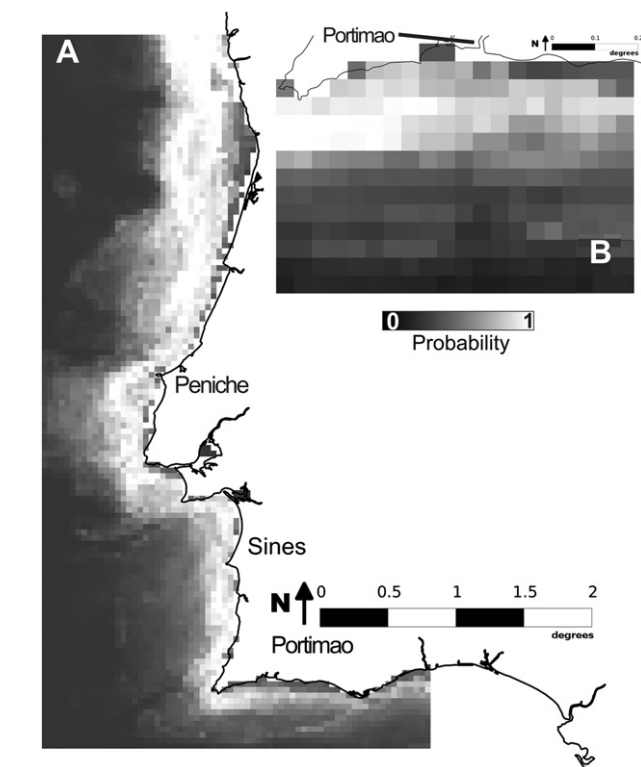


Fig. 4. Ensemble (western Portuguese coast) and projected (Algarve coast) Maxent models for Society for the Study of Birds (SPEA) dataset.

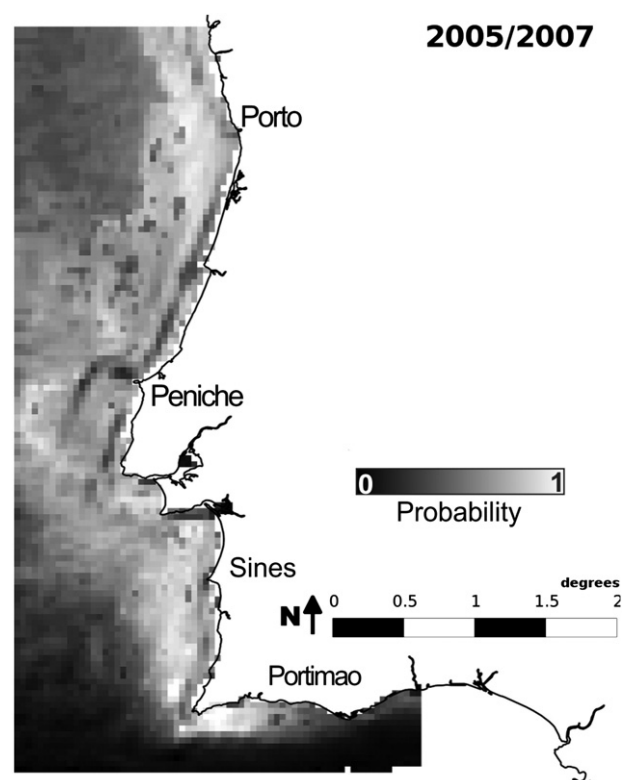


Fig. 5. Projected Maxent models for whale watching company (WWC) dataset for years 2005–2007 together.

models calculated without that variable (Table 3). Although the pattern is not always observed, in most cases, chlorophyll concentration and SST were the most important variables (Table 3).

In the SPEA ensemble model, the variables chlorophyll concentration and depth contributed more to the explained variation in the model: 49.54% and 35.67%, respectively. The other variables had very low contribution values: SST = 7.43%; SD of depth = 3.75%; and SD of SST = 3.61%. Like in the WWC ensemble models, these two variables were the most important in the jackknife analysis of AUC and gain values of training and test data, for models calculated with only one variable and models calculated without that variable (Table 4).

4. Discussion

Our results showed that common dolphins exhibit a patchy distribution over the Portuguese coastline. However, the exact

Table 1

Mean results of the area under the curve (AUC) of the receiver operated characteristics (ROC) plots for *Delphinus delphis* Maxent ensemble models of the whale watching company (WWC) dataset (all years: 2005–2007; years 2005, 2006 and 2007; and months May, June, July, August and September).

Year	Training	Testing
All years	0.83	0.77
2005	0.91	0.88
2006	0.91	0.86
2007	0.88	0.84
May	0.92	0.89
June	0.91	0.86
July	0.88	0.8
August	0.9	0.83
September	0.92	0.85

Table 2

Mean percentage contribution of each variable to the whale watching company (WWC) ensemble Maxent models (all years: 2005 to 2007; years 2005, 2006 and 2007; and months May, June, July, August and September). The two most important variables are presented in bold.

Variables	All years	2005	2006	2007	May	June	July	August	September
Depth	3.19	4.06	9.15	8.21	5.67	21.34	6.81	2.79	22.31
Chlorophyll	73.5	62.26	55.17	58.08	79.26	51.05	77.32	84.76	61.19
Depth SD	1.67	1.66	4.6	4.99	4.34	4.99	3.55	1.8	6.85
SST SD	6.68	8.97	7.65	14.69	8.09	6.12	3.67	2.15	7.82
SST	14.96	23.04	23.43	14.02	2.64	16.5	8.65	8.49	1.83

spatial patterns changed in different years, thus suggesting a more continuous distribution when observations are analysed over a longer time frame. Nevertheless, some areas consistently result as preferential habitats, supporting the hypothesis that there are patches of higher probability of occurrence for common dolphins in the study area. Some of these areas are consistent with observations made during field expeditions (A. Moura, unpublished data). As an example, the coastal region around Porto (northern Portugal) has the lowest recorded encounter rate during field efforts and consistently results as a low probability area in the models. Contrastingly, Peniche (central Portugal) consistently results as a high probability area in the models, and was in fact one of the areas with the highest encounter rate in the field.

Common dolphin distribution in the area analysed in this study was best predicted by chlorophyll concentration. In this context, chlorophyll concentration does not itself determine the distribution of common dolphin, but acts as a proxy for other biological factors. Chlorophyll concentration is known to reflect a higher incidence of pelagic schooling fish (Solanki et al., 2005; Ware and Thomson, 2005; Zainuddin et al., 2006), and previous studies describe the common dolphin as feeding on such prey (Silva, 1999; de Pierrepont et al., 2005; Pusineri et al., 2007; Meynier et al., 2008). In our study area, the most common prey item found in stomach contents was the sardine (*Sardina pilchardus*) (Silva, 1999), which is the most abundant pelagic schooling fish in the Portuguese coast (Marques et al., 2003). On the western coast of Portugal, sardine is known to feed mainly on available species of plankton (Garrido et al., 2008), reflecting a filter feeding strategy of this species (Garrido et al., 2007). Furthermore, a correlation was found between chlorophyll concentration and both stomach phytoplankton content and feeding intensity of sardine (Garrido et al., 2008), suggesting that distribution of this fish species is also correlated with chlorophyll concentration in our study area. As such, we believe the high predictive values of chlorophyll concentration obtained in this study reflect a strong local dependency on sardine as a prey item. Previous studies on common dolphin distribution elsewhere, also found an association with regions of high chlorophyll concentration (Cañadas and Hammond, 2008) or upwelling (Reilly, 1990; Reilly and Fiedler, 1994; Fiedler and Reilly, 1994; Jefferson et al., 2009). No data on local common dolphin prey choice was available in these previous studies, but studies on the species feeding ecology around Europe describe it as an opportunist feeder on locally abundant pelagic fish, with sardine being replaced by other such species outside the Portuguese coast (de Pierrepont et al., 2005; Pusineri et al., 2007; Meynier et al., 2008). The strong association with regions of high chlorophyll concentration found in this and previous studies (Reilly, 1990; Reilly and Fiedler, 1994; Fiedler and Reilly, 1994; Cañadas and Hammond, 2008; Jefferson et al., 2009), further supports the idea that although the common dolphin might be a generalist in terms of species consumed, it is possibly an ecological specialist restricted to small pelagic schooling fish. This pattern appears to be a characteristic of common dolphin, as other dolphin species do not show such patterns. In the bottlenose dolphin, for example, depth and relief

are consistently the most important variables predicting its distribution (Azzellino et al., 2008; Cañadas et al., 2005; Cubero-Pardo, 2007; Davis et al., 2002; Hastie et al., 2003; Lusseau and Wing, 2006), which coupled with the wide diversity of feeding strategies observed in this species (e.g.: Silber and Fertl, 1995; Smolker et al., 1997; Bearzi et al., 1999), suggests a more plastic ecology.

4.1. Platforms of opportunity data limitations

Our results showed that data obtained through platforms of opportunity can be extremely useful in studying cetacean ecology. Several limitations have been pointed out in such data as compared to data obtained from dedicated surveys, the most important being: (1) unsystematic sampling effort leading to biased results (e.g. Wall et al., 2006); and (2) unreliability of species identification due to inexperienced observers collecting data (e.g. Hauser et al., 2006). As for unsystematic sampling, our results show that only the direct observational effort data (i.e. whale watching company – WWC – dataset) show such a problem, with results overlapping strongly with the cloud of data points. However, when the models were projected for the rest of the coast, the results were very consistent with the Society for the Study of Birds (SPEA) dataset models, particularly the model where data from all years was pooled. Although there are differences, the most important environmental variables were consistent and the suitable areas overlapped largely, showing that the WWC dataset model was relatively transferable. Therefore, when trying to minimize bias from unsystematic sampling associated with opportunistic data, it appears to be more important to pool data from multiple years rather than several different areas.

Inexperienced observers can mistake striped dolphins (*Stenella coeruleoalba*) for common dolphins in Portuguese waters (pers. obs.). Although it is definitely a possibility as no records were validated, records from the SPEA dataset together with our own field experience in the area indicate that the striped dolphin is observed much less frequently than the common dolphin; as such we do not believe it significantly affected our results. Additionally, both independent datasets gave similar results, which are consistent with previous studies showing that common dolphins tend to occur in highly productive areas (Reilly, 1990; Reilly and Fiedler, 1994; Fiedler and Reilly, 1994; Cañadas and Hammond, 2008; Jefferson et al., 2009) and feed almost exclusively on pelagic schooling fish (Silva, 1999; de Pierrepont et al., 2005; Pusineri et al., 2007; Meynier et al., 2008).

4.2. Conservation implications

Given our data, we suggest that a decline in sardine populations could result in a reduction of local common dolphin populations. While sardine abundance estimate and port landings experience strong cycles (Santos et al., 2001; Borges et al., 2003; Marques et al., 2003), both have shown a decreasing trend in the last 20 years (Borges et al., 2003; Marques et al., 2003), and signs of sardine overfishing in the Portuguese mainland coast are documented (Baeta et al., 2009).

Table 3

Jackknife analysis of area under the curve (AUC) of receiver operated characteristics (ROC) plots, and gain percentile values for each environmental variable when used in isolation and when omitted in Maxent models of whale watching company (WWC) dataset (all years: 2005–2007; years 2005, 2006 and 2007; and months May, June, July, August and September). Gain values corresponded to the average values over Maxent iterative runs. For models calculated with only one variable, the variable or variables with the highest value are in bold; for models calculated without that variable, the variable or variables with the lowest value are in bold. Tr G: Training gain; Te G: Test gain; AUC: area under the curve of ROC plots; W–: without that variable; W+: only with that variable.

2005–2007	Tr G W–	Tr G W+	Te G W–	Te G W+	AUC W–	AUC W+
Depth	0.64	0.49	0.49	0.4	0.77	0.71
Chlorophyll	0.65	0.52	0.51	0.41	0.77	0.73
Depth SD	0.65	0.25	0.51	0.13	0.77	0.63
SST SD	0.61	0.17	0.47	0.06	0.76	0.62
SST	0.61	0.53	0.45	0.52	0.76	0.77
2005	Tr G W–	Tr G W+	Te G W–	Te G W+	AUC W–	AUC W+
Depth	1.09	0.76	1.07	0.76	0.88	0.82
Chlorophyll	1.09	0.79	1.09	0.81	0.88	0.82
Depth SD	1.09	0.44	1.11	0.43	0.88	0.72
SST SD	1.06	0.18	1.09	0.2	0.88	0.68
SST	1.01	0.81	1.03	0.93	0.87	0.85
2006	Tr G W–	Tr G W+	Te G W–	Te G W+	AUC W–	AUC W+
Depth	1.03	0.73	0.89	0.72	0.85	0.8
Chlorophyll	1.06	0.72	0.95	0.75	0.86	0.81
Depth SD	1.05	0.31	0.98	0.28	0.86	0.7
SST SD	1.01	0.09	0.94	0.08	0.86	0.61
SST	0.89	0.71	0.76	0.79	0.82	0.82
2007	Tr G W–	Tr G W+	Te G W–	Te G W+	AUC W–	AUC W+
Depth	0.77	0.52	0.84	0.54	0.84	0.76
Chlorophyll	0.8	0.52	0.86	0.58	0.85	0.76
Depth SD	0.77	0.29	0.83	0.29	0.84	0.67
SST SD	0.72	0.34	0.78	0.37	0.83	0.72
SST	0.72	0.61	0.79	0.67	0.83	0.81
May	Tr G W–	Tr G W+	Te G W–	Te G W+	AUC W–	AUC W+
Depth	0.93	0.7	1.12	0.77	0.87	0.78
Chlorophyll	0.92	0.74	1.07	0.94	0.87	0.85
Depth SD	0.93	0.37	1.12	0.39	0.87	0.69
SST SD	0.9	0.23	1.11	0.18	0.88	0.68
SST	0.96	0.67	1.13	0.76	0.88	0.81
June	Tr G W–	Tr G W+	Te G W–	Te G W+	AUC W–	AUC W+
Depth	0.95	0.73	0.89	0.71	0.85	0.79
Chlorophyll	1.05	0.65	0.98	0.59	0.86	0.77
Depth SD	1.04	0.38	0.95	0.3	0.86	0.67
SST SD	0.98	0.24	0.88	0.24	0.85	0.7
SST	0.93	0.38	0.82	0.43	0.83	0.76
July	Tr G W–	Tr G W+	Te G W–	Te G W+	AUC W–	AUC W+
Depth	0.81	0.53	0.47	0.47	0.8	0.77
Chlorophyll	0.75	0.65	0.42	0.57	0.79	0.79
Depth SD	0.83	0.33	0.62	–0.07	0.81	0.67
SST SD	0.83	0.04	0.53	0.04	0.8	0.56
SST	0.81	0.14	0.49	0.13	0.8	0.62
August	Tr G W–	Tr G W+	Te G W–	Te G W+	AUC W–	AUC W+
Depth	1.06	0.73	0.8	0.47	0.83	0.77
Chlorophyll	0.95	0.92	0.63	0.8	0.81	0.84
Depth SD	1.06	0.5	0.76	0.45	0.83	0.74
SST SD	1.05	0.07	0.8	–0.01	0.84	0.52
SST	1.03	0.16	0.75	0.08	0.83	0.61
September	Tr G W–	Tr G W+	Te G W–	Te G W+	AUC W–	AUC W+
Depth	1	0.78	0.79	0.7	0.84	0.79
Chlorophyll	1.01	0.72	0.85	0.59	0.84	0.79
Depth SD	1.05	0.44	0.8	0.33	0.83	0.67
SST SD	1.06	0.1	0.85	0.03	0.84	0.59
SST	1.1	0.49	0.91	0.44	0.85	0.75

Table 4

Jackknife analysis of area under the curve (AUC) of receiver operated characteristics (ROC) plots, and gain percentile values for each environmental variable when used in isolation and when omitted in Maxent models of Society for the Study of Birds (SPEA) dataset (years 2005, 2006 and 2007). Gain values corresponded to the average values over Maxent iterative runs. For models calculated with only one variable, the variable or variables with the highest value are in bold; for models calculated without that variable, the variable or variables with the lowest value are in bold. Tr G: Training gain; Te G: Test gain; AUC: area under the curve of ROC plots; W–: without that variable; W+: only with that variable.

2005–2007	Tr G W–	Tr G W+	Te G W–	Te G W+	AUC W–	AUC W+
Depth	0.82	0.66	0.7	0.64	0.82	0.8
Chlorophyll	0.85	0.69	0.72	0.63	0.82	0.8
Depth SD	0.89	0.29	0.78	0.27	0.83	0.7
SST SD	0.91	0.2	0.8	0.19	0.83	0.68
SST	0.9	0.36	0.79	0.29	0.83	0.71

been described where once abundant species declined drastically and became endangered in a surprisingly short time frame, mainly due to overexploitation or habitat interference (Gaston and Fuller, 2008). In fact, a drastic decline in the occurrence of common dolphin in the Mediterranean coincided with the peak in total fisheries landings in the area (Bearzi et al., 2006), a scenario that, in light of the present results, should not be ruled out in the Portuguese coast or other locations throughout the species distribution when considering conservation efforts. The occurrence of abundant species is, paradoxically, quite rare, and when they do occur, they tend to have disproportionate effects on their ecosystems (Gaston and Fuller, 2008), and should thus be the focus of conservation attention.

5. Concluding remarks

Our results show a high dependency of the common dolphin on a well-defined habitat that is increasingly overexploited and in constant decline. Therefore, we propose that more attention should be given to the conservation of common dolphin in Portuguese waters. A locally abundant species relying on an overexploited habitat is one of the cases identified as requiring more urgent conservation measures (Gaston and Fuller, 2008). In fact, being a specialized animal with long generation times, the common dolphin is in the group of organisms more likely to suffer from extinction debt, which is characterized by an apparent resistance to habitat perturbation followed by a population crash once the habitat is stabilized in a new state (Kuussaari et al., 2009). As such, although it might seem counter-intuitive, the moment to apply conservation measures might be now that the potential for perturbation is being identified rather than later when a decrease in the population becomes apparent.

Declaration of interests

Funding bodies had no role in neither the study design; in the collection, analysis and interpretation of the data; nor in the decision to write and submit the manuscript.

Acknowledgements

We are deeply grateful to the whale-watching company Dolphin Seafaris for providing data for common dolphin sightings. We are also indebted to Iván Ramírez and Ana Meirinho from Sociedade Portuguesa de Estudo das Aves (SPEA) for granting us access to their common dolphin sightings data, which were collected during Marine IBAs LIFE Project (LIFE04 NAT/PT/000213). Pedro Tarroso helped with obtaining and preparing environmental data.

Based on both WWC and SPEA records, it becomes clear that the common dolphin is disproportionately more abundant than any other cetacean species in the Portuguese coast (data not shown). However, that is not the case in other European locations such as the North Sea (Hammond et al., 2002) or the Mediterranean Sea (Bearzi et al., 2006; Segura et al., 2006). Several examples have

Malgorzata Pilot provided useful comments to the manuscript. AM and NS are supported respectively by a doctoral grant (SFRH/BD/28012/2006) and a post-doctoral position (SFRH/BPD/26666/2006) from FCT (Portugal). We also acknowledge the comments from two anonymous reviewers that greatly improved initial versions of the manuscript.

References

- Alcaraz, D., Paruelo, J., Cabello, J., 2006. Identification of current ecosystem functional types in the Iberian Peninsula. *Global Ecol. Biogeogr.* 15, 200–212.
- Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. *Trends Ecol. Evol.* 22, 42–47.
- Austin, G.E., Thomas, C.J., Houston, D.C., Thompson, D.B., 1996. Predicting the spatial distribution of buzzard *Buteo buteo* nesting areas using a geographical information system and remote sensing. *J. Appl. Ecol.* 33, 1541–1550.
- Azzellino, A., Gaspari, S., Airolidi, S., Nani, B., 2008. Habitat use and preferences of cetaceans along the continental slope and the adjacent pelagic waters in the western Ligurian Sea. *Deep-Sea Res. Part I* 55, 296–323.
- Baeta, F., Costa, M.J., Cabral, H., 2009. Changes in the trophic level of Portuguese landings and fish market price variation in the last decades. *Fish. Res.* 97, 216–222.
- Bearzi, G., Politi, E., Agazzi, S., Azzellino, A., 2006. Prey depletion caused by overfishing and the decline of marine megafauna in eastern Ionian Sea coastal waters (central Mediterranean). *Biol. Conserv.* 127, 373–382.
- Bearzi, G., Politi, E., Notarbartolo-di-Sciara, G., 1999. Diurnal behavior of free-ranging bottlenose dolphins in the Kvarneric (northern Adriatic Sea). *Mar. Mamm. Sci.* 15, 1065–1097.
- Bentivegna, F., Valentino, F., Falco, P., Zambianchi, E., Hochscheid, S., 2007. The relationship between loggerhead turtle (*Caretta caretta*) movement patterns and Mediterranean currents. *Mar. Biol.* 151, 1605–1614.
- Bierne, N., Bonhomme, F., David, P., 2003. Habitat preference and the marine-speciation paradox. *Proc. R. Soc. Lond. B* 270, 1399–1406.
- Borges, M.F., Santos, A.M.P., Crato, N., Mendes, H., Mota, B., 2003. Sardine regime shifts off Portugal: a time series analysis of catches and wind conditions. *Sci. Mar.* 67, 235–244.
- Cañadas, A., Hammond, P.S., 2008. Abundance and habitat preferences of the short-beaked common dolphin *Delphinus delphis* in the southwestern Mediterranean: implications for conservation. *Endang. Species Res.* 4, 309–331.
- Cañadas, A., Sagarmínaga, R., de Stephanis, R., Urquiola, E., Hammond, P.S., 2005. Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. *Aquat. Conserv.* 15, 495–521.
- Carwardine, M., 1995. Whales, Dolphins, and Porpoises. Dorling Kindersley, London.
- Cubero-Pardo, P., 2007. Environmental factors governing the distribution of the bottlenose (*Tursiops truncatus*) and the spotted dolphin (*Stenella attenuata*) in golfo dulce, South Pacific, off Costa Rica. *Investigaciones Marinas* 35, 15–23.
- Davis, R.W., Ortega-Ortiz, J.G., Ribic, K.A., Evans, W.E., Biggs, D.C., Ressler, P.H., Cady, R.B., Leben, R.R., Mullin, C.D., Würsig, B., 2002. Cetacean habitat in the northern oceanic Gulf of Mexico. *Deep-Sea Res. Part I* 49, 121–142.
- de Pierrepont, J.F., Dubois, B., Desormonts, S., Santos, M.B., Robin, J.P., 2005. Stomach contents of english channel cetaceans stranded on the coast of Normandy. *J. Mar. Biol. Ass. UK* 85, 1539–1546.
- Elith, J., Graham, C., Anderson, R., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R., Huettmann, F., Leathwick, J., Lehmann, A., Li, J., Lohmann, L., Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R., Soberón, J., Williams, S., Wisz, M., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Evans, P.G.H., Hammond, P.S., 2004. Monitoring cetaceans in European waters. *Mamm. Rev.* 34, 131–156.
- Fiedler, P.C., Reilly, S.B., 1994. Interannual variability of dolphin habitats in the eastern tropical Pacific. II: effects on abundances estimated from tuna vessel sightings, 1975–1990. *Fish. Bull.* 92, 451–463.
- Folkens, P.A., Reeves, R.R., Stewart, B.S., Clapham, P.J., Powell, J.A., 2002. Guide to Marine Mammals of the World. Alfred A. Knopf.
- Garrido, S., Ben-Hamadou, R., Oliveira, P.B., Cunha, M.E., Chicharo, M.A., van der Lingen, C.D., 2008. Diet and feeding intensity of sardine *Sardina pilchardus*: correlation with satellite-derived chlorophyll data. *Mar. Ecol. Prog. Ser.* 354, 245–256.
- Garrido, S., Marçalo, A., Zwolinski, J., van der Lingen, C.D., 2007. Laboratory investigations on the effect of prey size and concentration on the feeding behaviour of *Sardina pilchardus*. *Mar. Ecol. Prog. Ser.* 330, 189–199.
- Gaston, K.J., Fuller, R.A., 2008. Commonness, population depletion and conservation biology. *Trends Ecol. Evol.* 23, 14–19.
- Gottfried, M., Pauli, H., Reiter, K., Grabherr, G., 1999. A fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by climate warming. *Divers. Distrib.* 5, 241–251.
- Guisan, A., Broennimann, O., Engler, R., Vust, M., Yoccoz, N.G., Lehmann, A., Zimmermann, N.E., 2006. Using niche-based models to improve the sampling of rare species. *Conserv. Biol.* 20, 501–511.
- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecol. Model.* 135, 147–186.
- Hammond, P.S., Berggren, P., Benke, H., Borchers, D.L., Collet, A., Heide-Jørgensen, M.P., Heimlich, S., Hiby, A.R., Leopold, M.F., Øien, N., 2002. Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. *J. App. Ecol.* 39, 361–376.
- Hastie, G.D., Wilson, B., Thompson, P.M., 2003. Fine-scale habitat selection by coastal bottlenose dolphins: application of a new land-based video-montage technique. *Can. J. Zool.* 81, 469–478.
- Hauser, D.D.W., Vanblaricom, G.R., Holmes, E.E., Osborne, R.W., 2006. Evaluating the use of whalewatch data in determining killer whale (*Orcinus orca*) distribution patterns. *J. Cetacean Res. Manage.* 8, 273–281.
- Hernandez, P.A., Graham, C.H., Master, L.L., Albert, D.L., 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29, 773–785.
- Heyning, J.E., Perrin, W.F., 1994. Evidence for two species of common dolphin (genus *Delphinus*) from the eastern north pacific. *Nat. Hist. Mus. Los Ang. County Contrib. Sci.* 442, 1–35.
- Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Harb. Symp. Quant Biol.* 22, 415–427.
- Isari, S., Psarra, S., Pitta, P., Mara, P., Tomprou, M., Ramfos, A., Somarakis, S., Tselepidis, A., Koutsikopoulos, C., Fragopoulou, N., 2007. Differential patterns of mesozooplankters distribution in relation to physical and biological variables of the northeastern Aegean Sea (eastern Mediterranean). *Mar. Biol.* 151, 1035–1050.
- Jackson, J.B.C., Cheetham, A.H., 1999. Tempo and mode of speciation in the sea. *Trends Ecol. Evol.* 14, 72–77.
- Jefferson, T.A., Fertl, D., Bolaños-Jiménez, J., Zerbini, A.N., 2009. Distribution of common dolphins (*Delphinus* spp.) in the western Atlantic ocean: a critical re-examination. *Mar. Biol.* 156, 1109–1124.
- Kingston, S.E., Rosel, P.E., 2004. Genetic differentiation among recently diverged delphinid taxa determined using AFLP markers. *J. Hered.* 95, 1–10.
- Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M., Steffan-Dewenter, I., 2009. Extinction debt: a challenge for biodiversity conservation. *Trends Ecol. Evol.* 24, 564–571.
- Liu, C., Berry, P.M., Dawson, T.P., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28, 385–393.
- Lusseau, S.M., Wing, S.R., 2006. Importance of local production versus pelagic subsidies in the diet of an isolated population of bottlenose dolphins *Tursiops* sp. *Mar. Ecol. Prog. Ser.* 321, 283–293.
- Marques, V., Morais, A., Pestana, G., 2003. Distribuição, Abundância e Evolução do Manancial de Sardinha Presente na Plataforma Continental Portuguesa Entre 1995 e 2002. *Relat. Cient. Téc. IPIMAR, Série digital*. <http://ipimar-iniap.ipimar.pt> 10, 29.
- Meynier, L., Pusineri, C., Spitz, J., Santos, M.B., Pierce, G.J., Ridoux, V., 2008. Intra-specific dietary variation in the short-beaked common dolphin *Delphinus delphis* in the Bay of Biscay: importance of fat fish. *Mar. Ecol. Prog. Ser.* 354, 277–287.
- Mirimin, L., Westgate, A., Rogan, E., Rosel, P., Read, A., Coughlan, J., Cross, T., 2009. Population structure of short-beaked common dolphins (*Delphinus delphis*) in the North Atlantic Ocean as revealed by mitochondrial and nuclear genetic markers. *Mar. Biol.* 156, 821–834.
- Murphy, S., Herman, J.S., Pierce, G.J., Rogan, E., Kitchener, A.C., 2006. Taxonomic status and geographic cranial variation of common dolphins (*Delphinus*) in the Eastern North Atlantic. *Mar. Mamm. Sci.* 22, 573–599.
- Natoli, A., Cañadas, A., Peddemors, V.M., Aguilar, A., Vaquero, C., Fernández-Piqueras, P., Hoelzel, A.R., 2006. Phylogeography and alpha taxonomy of the common dolphin (*Delphinus* sp.). *J. Evol. Biol.* 19, 943–954.
- Osborne, P.E., Alonso, J.C., Bryant, R.G., 2001. Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. *J. App. Ecol.* 38, 458–471.
- Palumbi, S.R., 1994. Genetic divergence, reproductive isolation, and marine speciation. *Annu. Rev. Ecol. Syst.* 25, 547–572.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190, 231–259.
- Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31, 161–175.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* 19, 181–197.
- Phillips, S.J., Dudík, M., Schapire, R.E., 2004. A maximum entropy approach to species distribution modeling. In: *Proceedings of the Twenty-First International Conference on Machine Learning*, pp. 655–662.
- Pusineri, C., Magnin, V., Meynier, L., Spitz, J., Hassani, S., Ridoux, V., 2007. Food and feeding ecology of the common dolphin (*Delphinus delphis*) in the oceanic northeast Atlantic and comparison with its diet in neritic areas. *Mar. Mamm. Sci.* 23, 30–47.
- Ravago-Gotanco, R.G., Magsino, R.M., Juinio-Meñez, M.A., 2007. Influence of the north equatorial current on the population genetic structure of *Tridacna crocea* (mollusca: tridacnidae) along the eastern Philippine seaboard. *Mar. Ecol. Prog. Ser.* 336, 161–168.
- Reilly, S.B., 1990. Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. *Mar. Ecol. Prog. Ser.* 66, 1–11.
- Reilly, S.B., Fiedler, P.C., 1994. Interannual variability of dolphin habitats in the eastern tropical Pacific. I: research vessel surveys, 1986–1990. *Fish. Bull.* 92, 434–450.

- Rosel, P.E., Dizon, A.E., Heyning, J.E., 1994. Genetic analysis of sympatric morphotypes of common dolphins (genus *Delphinus*). Mar. Biol. 119, 159–167.
- Santos, A.M.P., Borges, M.F., Groom, S., 2001. Sardine and horse mackerel recruitment and upwelling off Portugal. ICES. J. Mar. Sci. 58, 589–596.
- Schluter, D., 2001. Ecology and the origin of species. Trends Ecol. Evol. 16, 372–380.
- Segura, A.G., Crespo, E.A., Pedraza, S.N., Hammond, P.S., Raga, J.A., 2006. Abundance of small cetaceans in waters of the central Spanish Mediterranean. Mar. Biol. 150, 149–160.
- Sequeira, M., Inácio, A., Silva, M.A., Reiner, F., 1996. Arrojamentos de mamíferos marinhos na costa continental Portuguesa entre 1989 e 1994. ICN, Lisboa.
- Silber, G.K., Fertl, D., 1995. Intentional beaching by bottlenose dolphins (*Tursiops truncatus*) in the Colorado River delta, Mexico. Aquatic Mammals 21, 183–186.
- Sillero, N., 2009. Potential distribution of the new populations of *Hyla meridionalis* in Salamanca (Spain). Acta Herpetologica 4, 83–98.
- Sillero, N., 2010. Modelling new suitable areas for *Hyla meridionalis* in a current and future expansion scenario. Amphibia-Reptilia 31, 37–50.
- Sillero, N., 2011. What does ecological modelling model? A proposed classification of ecological niche models based on their underlying methods. Ecol. Model. 222, 1343–1346.
- Sillero, N., Barbosa, M., Martínez-Freiría, F., Raimundo, R., 2010. Los modelos de nicho ecológico en la herpetología ibérica: pasado, presente y futuro. Boletín de la Asociación Herpetológica Española 21, 2–24.
- Silva, M.A., 1999. Diet of common dolphins, *Delphinus delphis*, off the Portuguese continental coast. J. Mar. Biol. Ass. UK 79, 531–540.
- Skov, H., Gunnlaugsson, T., Budgell, W.P., Horne, J., Nottestad, L., Olsen, E., Soiland, H., Vikingsson, G., Waring, G., 2008. Small-scale spatial variability of sperm and sei whales in relation to oceanographic and topographic features along the mid-Atlantic ridge. Deep-Sea Res. Part II 55, 254–268.
- Smolker, R., Richards, A., Connor, R., Mann, J., Berggren, P., 1997. Sponge carrying by dolphins (delphinidae, *Tursiops* sp.): a foraging specialization involving tool use? Ethol. 103, 454–465.
- Solanki, H.U., Mankodi, P.C., Nayak, S.R., Somvanshi, V.S., 2005. Evaluation of remote-sensing-based potential fishing zones (PFZs) forecast methodology. Cont. Shelf Res. 25, 2163–2173.
- Van der Wal, J., Shoo, L.P., Graham, C., Williams, S.E., 2009. Selecting pseudo-absence data for presence-only distribution modelling: how far should you stray from what you know? Ecol. Model. 220, 589–594.
- Via, S., 2001. Sympatric speciation in animals: the ugly duckling grows up. Trends Ecol. Evol. 16, 381–390.
- Wall, D., O'Brien, J., Meade, J., Allen, B.M., 2006. Summer distribution and relative abundance of cetaceans off the west coast of Ireland. Biol. Environ. Proc. R. Ir. Acad. B. 106, 135–142.
- Ware, D.M., Thomson, R.E., 2005. Bottom-up ecosystem trophic dynamics determine fish production in the northeast pacific. Science 308, 1280–1284.
- Williams, R., Hedley, S.L., Hammond, P.S., 2006. Modelling distribution and abundance of Antarctic baleen whales using ships of opportunity. Ecol. Soc. 11, 1.
- Zainuddin, M., Kiyofuji, H., Saitoh, K., Saitoh, S.I., 2006. Using multi-sensor satellite remote sensing and catch data to detect ocean hot spots for albacore (*Thunnus alalunga*) in the northwestern north pacific. Deep-Sea Res. Part II 53, 419–431.