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## TITLE

*Habitat preferences of baleen whales in a mid-latitude habitat*

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## ABSTRACT

Understanding the dynamics of baleen whale distribution is essential to predict how environmental changes can affect their ecology and, in turn, ecosystem functioning. Recent work showed that mid-latitude habitats along migratory routes may play an important role on the feeding ecology of baleen whales. This study aimed to investigate the function of a mid-latitude habitat for blue (*Balaenoptera musculus*), fin (*B. physalus*) and sei (*B. borealis*) whales occurring in sympatry during spring and summer months and to what extent their environmental niches overlap. We addressed those questions by developing environmental niche models (ENM) for each species and then making pairwise comparisons of niche overlap and relative habitat patch importance among the three species. ENMs were created using sightings from the Azorean Fisheries Observer Program from May to November, between 2004 and 2009, and a set of 18 predictor environmental variables. We then assessed monthly (April-July) overlap

among ENMs using a modified Hellinger's distance metric ( $I$ ). Results show that the habitat niches of blue and fin whales are strongly influenced by primary productivity and sea surface temperature and are highly dynamic both spatially and temporally due to the oceanography of the region. Niche overlap analyses show that blue and fin whale environmental niches are similar and that the suitable habitats for the two species have high degree of spatial coincidence. These results in combination suggest that this habitat may function as a mid-latitude feeding ground to both species while conditions are adequate. The sei whale model, on the other hand, did not include variables considered to be proxies for prey distribution and little environmental niche overlap was found between this species and the other two. We argue that these results suggest that the region holds little importance as a foraging habitat for the sei whale.

## **1. Introduction**

Marine ecosystems are facing increasing changes and deteriorating rapidly, due to the combined effect of global climate change and of a significant increase in the human utilization of marine space and resources (McCauley et al., 2015; Worm et al., 2006; Worm et al., 2003). These changes may unbalance marine ecosystems, to the point of causing regime shifts, with detrimental effects not only on the natural communities but also to the ecosystem services they provide to human societies (Möllmann et al., 2015; Worm et al., 2006). To counteract the deterioration of marine ecosystems we need effective management and conservation policies that incorporate the most recent advances in population biology and community ecology (Soulé et al., 2005). In that respect, understanding the processes, functioning and interrelationships among ecosystem components is essential for proper ecosystem-based management (Borja, 2014).

Pelagic marine ecosystems are highly dynamic and vast, and many pelagic predators regularly move thousands of kilometers among different regions of the ocean (Block et al., 2011). Obtaining information to understand the ecology of pelagic species and ecosystems in order to be able to predict how changes may affect pelagic communities is a complex task that is further hampered by logistical and financial constraints (Borja, 2014; Game et al., 2009; McClellan et al., 2014). One of the great challenges for accurately predicting patterns and features of pelagic communities is to identify the

mechanisms leading to the presence of a given species in a specific geographical area at a specific moment in time (Verity et al., 2002).

In face of the data scarcity for pelagic ecosystems, one of the approaches commonly used is to describe the habitat requirements of a species by fitting niche models and then use those models to identify its potential distribution by projecting the models on environmental space (Robinson et al., 2011; Tyberghein et al., 2012). Niche models can be 1) mechanistic, informed by species' physiological tolerances and behavior; 2) correlative, which try to identify statistical relationships between species occurrences and environmental conditions; 3) a combination of the above (Anderson, 2012, 2013). Mechanistic methods depend on a profound knowledge of the organism's physiology and behavior that is not available for the vast majority of species, especially in the case of pelagic taxa (Anderson, 2013; Robinson et al., 2011). By far, most niche models utilize a correlative approach, taking advantage of the availability of a wealth of digital data sources on species occurrences and environmental conditions (Franklin, 2010; Guisan and Thuiller, 2005; Peterson et al., 2011; Tyberghein et al., 2012). The correlative approach is rooted in the Grinnellian notion of environmental niche, assuming that the natural distribution of a species is chiefly controlled by abiotic preferences, food requirements and microhabitat characteristics (Grinnell, 1904; Hutchinson, 1991).

In the present work we explore the potential of using environmental niche models to investigate the processes involved in the utilization of a mid-latitude pelagic habitat by different species of baleen whales.

It is a well-known fact that most baleen whales undertake large annual migrations to highly productive areas during the summer, where they store large amounts of energy in the form of fat deposits that are believed to finance most of the activities over the next season (Stern, 2009). Their breeding and calving success during the following season, and even their survival, is probably dependent on the outcome of this feeding period (Webster et al., 2002). Based on stomach contents obtained from whaling catches, it was long believed that baleen whales feed only opportunistically when on breeding grounds and during migration, although some energetic models suggest that they may actually need to consume some food between feeding seasons (Lockyer, 1981).

However recent work has shown that habitats along migratory routes may play an important role on the feeding ecology of baleen whales. There is mounting evidence that at least some individuals interrupt their migration to high-latitude feeding grounds to forage in mid-latitude waters. Feeding behavior in mid-latitude sites during spring and summer was reported for southbound humpback whales off Australia and New Caledonia, as well as in the South Atlantic (Barendse et al., 2010; Garrigue et al., 2010; Stockin and Burgess, 2005); similarly, in the Northeast Pacific, sighting data and satellite telemetry suggest that blue whales forage at different latitudes in discrete sites during their entire migratory cycle (Bailey et al., 2009; Mate et al., 1999; Reilly and Thayer, 1990).

In the central North Atlantic, recent studies investigating the movements and behavior of blue, fin (*B. physalus*) and sei whales (*B. borealis*), occurring in sympatry in the Azores region (37-40°N) during their northbound migration to summering grounds, yielded distinct results.

Blue and fin whales instrumented with satellite transmitters in the Azores remained foraging at middle latitudes for periods varying from a few days to months (Silva et al., 2013). Foraging behavior in fin whales was only detected in the vicinity of the Azores islands and north of 56°N, suggesting the species alternate periods of active migration with periods of extended use of specific habitats along the migratory route (Silva et al., 2013). In contrast, sei whales tagged in the Azores did not interrupt their migratory journey and their movement patterns gave no indication of foraging activity until whales reached the Labrador Sea, a known feeding ground for this species (Prieto et al., 2014).

Visser et al. (2011) investigated the association between baleen whale relative abundance in the Azores with the timing of three stages of phytoplankton bloom development (the onset, maximum, and end of bloom). Peak relative abundance of baleen whales was better explained by the onset of the spring bloom and occurred with a lag of 11 to 14 weeks and standard deviation (SD) of 1.5 weeks, 14 to 16 weeks (SD = 1.2 weeks), and 14 to 17 weeks (SD = 2.1 weeks) respectively for the blue, fin and sei whales. Although the results by Visser et al. (2011) show some inter-annual variation, which is more pronounced in the case of the sei whale, they suggest that whales may synchronize their migration to the North Atlantic phytoplankton spring bloom.

Clearly, more investigation is necessary to understand the processes leading to the choice and utilization of mid-latitude pelagic habitats by migrating baleen whales, and to understand if these habitats have distinct ecological roles for these animals.

Our study focused on three baleen whale species (blue, fin and sei whales) occurring in sympatry in a mid-latitude habitat (the Azores islands) during their migratory season towards high-latitude feeding grounds. We developed dynamic monthly environmental niche models using a presence only modelling approach based on the maximum entropy principle (Phillips et al., 2006), in order to characterize the environmental niche of each of the three species in the study area, and to understand how the habitat conditions change over time. We then quantified the environmental niche overlap among the three species (Warren et al., 2008) to assess to which degree their environmental niches are similar while they are in the region.

## **2. Methods**

### *2.1. Study region*

Data were collected in waters off the Azores islands, between 36°30'N 24°30'W and 40°00'N 31°45'W (Figure 1). The Azores are an isolated archipelago of nine volcanic islands disposed in three groups (Eastern, Central and Western) aligned along a NW-SE orientation, extending over 600 km. The archipelago is crossed by the Mid-Atlantic Ridge (MAR) between the Central and Western groups. The islands are positioned over the Azores plateau rising from the abyssal plain (~4,000 m), and defined roughly by the 2,000 m depth isobath. As other volcanic oceanic islands, the Azores are characterized by steep slopes and narrow or absent island-shelves (Tempera et al., 2012). Additionally to the islands, more than 460 seamounts are found within the archipelago EEZ (Morato et al., 2008). These characteristics combine to create a wide range of habitat types and are responsible for complex circulation patterns that increase the ability of the archipelago to capture and retain particles and small organisms (Sala et al., 2015). The region is largely dominated by two eastward flows generating from the Gulf Stream: the cold southern branch of the North Atlantic Current that crosses the MAR to the north of the Azores (45-48°N), and the warm Azores Front/Current system, a quasi-permanent feature located south of the islands (34-36°N). Average sea surface temperature varies from 15 to 20°C in winter and 20-25°C in summer.

## 2.2. *Whale occurrence data*

Occurrences of blue, fin and sei whales were obtained from the Azorean Fisheries Observer Program (POPA), from May to November, between 2004 and 2009 (Figure 1). POPA places trained observers aboard tuna-fishing vessels to monitor and collect information on the fishery and on the presence and behavior of cetaceans, seabirds and turtles. Cetacean surveying effort is conducted when the vessel is cruising or searching for fish schools. During on-effort periods, vessel position and environmental conditions are recorded every 30 minutes or whenever vessel course changes  $>20^\circ$ . All sightings and vessel positions are georeferenced using global positioning system with datum WGS84. Sightings are coded according to reliability of species identification, from 0 (low confidence) to 3 (definitive). In this study we analyzed only sightings recorded during on-effort survey periods conducted in sea states on the Beaufort scale  $\leq 3$  and with an identification score of 3.

## 2.3. *Environmental data*

A set of 18 candidate environmental variables (Table 1) were selected based on perceived potential ecological relevance for cetaceans (Baines and Reichelt, 2014; Baumgartner et al., 2001; Cañadas et al., 2002; Davis et al., 2002; Mannocci et al., 2014; Mannocci et al., 2015; Yen et al., 2004). **Depth** was obtained from the grid-centered bedrock version of the ETOPO-1 digital elevation model (Amante and Eakins, 2008). Remotely sensed **night-time sea surface temperature** (NSST) was derived from standard mapped images (level 3, monthly average composite) collected by the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument aboard NASA's Aqua satellite and obtained from the Ocean Color Discipline Processing System (Campbell et al., 1995). Remotely sensed near-surface primary productivity indicated by **Chlorophyll-a concentration** (Chl-a) data was used as a proxy for secondary production and was also derived from data collected by Aqua MODIS, with the same spatial and temporal resolutions as NSST. We tried to use finer temporal resolutions (weekly, daily) for NSST and Ch-a as this is believed to improve model performance (Becker et al., 2012; Forney et al., 2015; Forney et al., 2012). However, due to the study region being frequently overcast, using these finer scale data would have meant discarding great part of the whale occurrences for not having complete sets of environmental variables. To maintain a reasonable sample size for all species, we opted

to use monthly composites for dynamic variables. Additionally, a recent investigation has shown that model accuracy can decrease substantially due to data loss from cloudy conditions, and that in those cases the use of environmental data fields at coarser temporal resolutions may be preferable (Scales et al., 2016). **Seamount** location and physiography were obtained from Morato et al. (2008) and digitized as a georeferenced database.

The remaining variables were derived from those four using a Geographic Information System (ArcGIS 10.1; ESRI, Inc.; hereby referred as ArcGIS). Variables based on distance/area calculation were first processed in UTM zone 26N with horizontal datum WGS84, and then all variables were projected to an Equidistant Cylindrical projection with horizontal datum WGS84 and resampled to the same extent, with 2.5 arc-minute resolution. Derived variables were: terrain **slope**; **distance to shore**, **distance to bathymetric isoline** ( $\text{Dist}_{(n)}$ , with 'n' representing isoline); **seamount density** (d-Seamounts); **minimum depth of seamount** (Seamount\_dpt); **time-lagged Chlorophyll-a concentration** for one ( $\text{Chl-a}_{(-1m)}$ ) and two ( $\text{Chl-a}_{(-2m)}$ ) months prior to the sighting date; **local variation of Chlorophyll-a concentration** (V-Chl-a; calculated as standard deviation within a 8x8 pixel kernel); **time-lagged local variation of Chlorophyll-a concentration** for one ( $\text{V-Chl-a}_{(-1m)}$ ) and two ( $\text{V-Chl-a}_{(-2m)}$ ) months prior to the sighting date; and **local variation of night-time sea surface temperature** (V-NSST; calculated as standard deviation within a 3x3 pixel kernel).

Collinearity between environmental variables was investigated by calculating the Kendall's correlation coefficient ( $\tau$ ) in R (R Development Core Team 2012). Kendall's correlation coefficient  $|\tau| > 0.7$  was interpreted as indicating high collinearity between pairs of environmental variables (Dormann et al., 2013; Warren et al., 2013).

## 2.4. Environmental niche models

### 2.4.1. Modelling procedure

All models were fitted using the software MaxEnt 3.3.3k (Dudík et al., 2007; Phillips et al., 2006), available at <http://www.cs.princeton.edu/~schapire/maxent>. MaxEnt is a machine learning method for modelling species distributions from presence-only data as a function of a set of environmental covariates (background). MaxEnt predictive performance has been shown to be consistently competitive with other well-established

methods, including those using presence-absence data (Aguirre-Gutiérrez et al., 2013; Duan et al., 2014; Elith and Graham, 2009; Elith et al., 2006). Studies evaluating the effect of sample size on the performance of several niche modelling algorithms have demonstrated that MaxEnt is one of the most consistent across sample sizes, even when using less than 10 occurrences (Aguirre-Gutiérrez et al., 2013; Hernandez et al., 2006; Pearson et al., 2007; Wisz et al., 2008). However, best performance is achieved when models are based on 20 or more occurrences (Pearson et al., 2007; Shcheglovitova and Anderson, 2013). In MaxEnt presences are assumed to be drawn from a probability distribution  $\pi$  over the study region, constrained by environmental variables that are ecologically relevant to the species of interest and represent the available (although possibly incomplete) information about the species distribution (Phillips et al., 2006). The method uses the maximum entropy principle to estimate the set of constraints that are likely to be satisfied by  $\pi$  and to single-out the distribution of maximum entropy among all distributions satisfying those constraints. Simple functions (features in machine learning terminology) are used to express the distribution of environmental variable values over the presence sites in order to set those constraints (Dudík et al., 2004; Phillips et al., 2006). The maximum entropy distribution will be the most unconstrained or, in other words, that which will produce the least under-specified model across the entire study region (Dudík et al., 2004).

Sample selection bias strongly affects model performance in presence-only methods (Phillips et al., 2009). In MaxEnt, predictions can be considerably improved by drawing the background data from a distribution of locations with the same sample selection bias as the occurrence data (Kramer-Schadt et al., 2013; Phillips et al., 2009). POPA survey effort is neither randomly nor uniformly distributed across the study region (Silva et al., 2002; Silva et al., 2011), as it is dependent on fish distribution and fishing strategies of the boat captains. To improve model performance, background environmental data were obtained using a set of 10,000 randomly chosen vessel data points, ensuring that presence and background data had the same spatial and temporal bias (Figure 1).

Cetacean occurrences and background data points were merged with candidate environmental variables in ArcGIS, producing 'sample with data' (SWD) datasets. Occurrences with missing corresponding environmental variables were discarded. If environmental values were missing for a background data point, that data point was



discarded and another was randomly chosen until all background data points had a complete set of corresponding environmental variable values.

During test trials we verified that the default 500 iterations were not sufficient to guarantee model convergence. Thus the number of maximum iterations was set to 5,000 for all models. During the same trials we ran models with MaxEnt default settings and obtained biologically unreasonable variable response curves (ie, highly jagged or multimodal) for more complex functions (product, threshold, and hinge). Although complex, multimodal response curves can have ecological justification in some cases, they may also be caused by excessive complexity of the models and lead to overfitting (Merow et al., 2013; Peterson et al., 2011; Phillips and Dudík, 2008). Merow et al. (2014) advocate that model complexity should be constrained based on the attributes of the data and study objectives, favoring simpler models when in the presence of small sample sizes and strong sampling bias, and when the aim is to infer environmental niches. In view of that, we changed MaxEnt settings to use only the simpler linear and quadratic functions (Merow et al., 2013; Phillips and Dudík, 2008).

We used the multivariate similarity surface (MESS) function in MaxEnt (Elith et al., 2010) to test the similarity among environmental conditions found during model fitting and the prediction area. Predictions were restricted to an area chosen according to results of the MESS analysis. The 'fade by clamping' option in MaxEnt was enabled to prevent extrapolations outside the environmental range of the training data (Owens et al., 2013). Due to the large number of models, MaxEnt was run in command line mode using scripts.

Individual species models were fitted using all available occurrences for that species, after variable pruning (see Section 2.4.2 below). After individual species model fitting, monthly (April-July) habitat suitability maps were produced for the three whale species, by projecting the models to the specific environmental conditions of each month considered (Elith et al., 2011). Dynamic environmental variables used to create those suitability maps (sea surface temperature, chlorophyll-a, and derived variables) were based on monthly climatologies covering the study period (2004-2009). Maps were produced by MaxEnt using logistic habitat suitability scores varying from 0 (unsuitable habitat) to 1 (highly suitable habitat), and exported in rasterized format. Based on the analysis of maps produced by MaxEnt with the results of the MESS analysis (not

shown) the extent of the habitat suitability maps was restricted to 150 nautical miles around the islands to avoid extrapolating to environmental conditions outside the range of the training data.

To quantify the temporal change in habitat suitability, the suitable habitat for each species was calculated for individual months using ArcGIS. We assumed better than average habitat suitability when suitability scores were  $\geq 0.5$  (Elith et al., 2011; Phillips and Dudík, 2008).

#### *2.4.2. Selection of environmental variables*

Pilot models using all 18 candidate variables were built for each species and relative variable importance was evaluated using the 'permutation importance' (PI) scores reported by MaxEnt. By randomly permuting the values among data-points for a given variable (presence and background) and measuring the resulting decrease in the training area under the receiver operating characteristic curve metric values (AUC), the PI measures the contribution of each variable to the final model. Searcy and Schaffer (2016) have shown that the PI score is biologically realistic, reflecting actual aspects of a species' ecology. Variables with a high PI score likely play an important role in defining the environmental niche of the species and driving its distribution; conversely, variables with low PI scores have little explanatory power regarding the species distribution, making this metric useful in sorting relevant variables from variables of marginal importance (C. Searcy, Personal communication).

Variables with a PI score  $< 5$  were considered to have little predictive power and were excluded for improved parsimoniously (Hastie et al., 2009; Merow et al., 2013), creating a new, pruned set of variables. Since unknown interactions among variables may be at play, eliminating variables may result in a change regarding the nature of those interactions and require re-estimation of the functions for the other variables. Thus this pruning process was repeated iteratively until no more variables with a PI score  $< 5$  were detected.

After pruning, individual models were built with only the retained variables for each species. The marginal response curves that show how individual variables affect the predictions when utilized alone to create a model, were used to investigate the possible ecological influence of the variables on the species predicted habitat.

### 2.4.3. Model evaluation

Ideally, evaluation of model performance should be carried out utilizing spatially independent data. Even for data collected independently in the same region, model performance measures are inflated by the effect of dependence between training and test data, which is created by spatial autocorrelation (Bahn and McGill, 2013). Unfortunately, we had no independent data for model evaluation and thus had to resort to resampling, utilizing K-fold cross-validation instead. K-fold cross-validation is a well-established resampling method that works by splitting data in mutually exclusive subsets, or folds (Hastie et al., 2009). In K-fold cross-validation model performance is assessed by successively removing each subset for evaluation, while the remaining K-1 subsets are used to fit (train) the model. The process is repeated iteratively to produce K models and obtain the evaluation metrics for each of these models. In this way, occurrences are not used simultaneously to fit and test model performance and no single occurrence will be used more than once to test the models; however the predictive performance calculated using K-fold cross validation may still be inflated (Peterson et al., 2011).

In this study we used the cross-validation tool in MaxEnt to split occurrences in training (90% of occurrences) and test (10% of occurrences) subsets using 10-fold cross-validation (Elith et al., 2011). To evaluate the predictive performance of the models, we used the resulting mean test AUC, which measures the model ability to discriminate between randomly chosen presence and absence sites (or background sites in the case of MaxEnt) (Fielding and Bell, 1997; Phillips et al., 2006). With presence-absence data, AUC values range from 0 to 1, with a value of 0.5 indicating model accuracy not better than random and a value of 1 indicating perfect model fit (Fielding and Bell, 1997). When using presence-only data, the maximum achievable AUC is a quantity  $1-a/2$  (where “a” is the fraction of the geographical area covered by the species’ unknown true distribution); consequently, in that case, AUC always assumes a value  $<1$  (Phillips et al., 2006; Wiley et al., 2003). However, given reasonable sampling of the background, the AUC score is still useful for predicting non-random patterns even when using presence-only data (Phillips et al., 2006). It is generally assumed that AUC values between 0.7 and 0.9 indicate reasonable model performance and above 0.9 high performance (Peterson et al., 2011).

## 2.5. Environmental niche overlap analyses

We assessed monthly (April-July) overlap among environmental niche models (ENMs) for the three whale species using the *I* statistic (Warren et al., 2008), and the relative rank metric (RR) (Warren and Seifert, 2011).

The *I* statistic is obtained by comparing the habitat suitability scores in each cell of suitability maps produced by MaxEnt models for two species, after normalizing each map so that all suitability scores sum to 1. The statistic is computed as  $1 - \text{“Hellinger’s distance”}$  from probability theory, ranging between 0 (ENMs for pairs of species are completely distinct) to 1 (ENMs are identical). The statistic is especially suited for comparing suitability maps produced by MaxEnt since it treats the suitability maps as probability distributions and does not assume that the suitability scores are proportional to species abundance (Warren et al., 2008). The resulting score of the *I* statistic for a given pair of species quantifies the environmental niche shared by two pairs of species.

The RR metric, on the other hand, estimates the probability that a given grid cell has equivalent habitat suitability ranking in two models, regardless of the absolute difference of habitat suitability scores among the two models (Warren and Seifert, 2011). It is estimated by iteratively and randomly sampling without replacement two points in geographic space (A and B), and asking whether the inferred relationship between them (i.e.,  $A > B$  or  $A < B$ ) is the same for the two models and dividing the number of matches by number of comparisons (Warren and Seifert, 2011). The RR metric also takes values between 0 and 1, and is useful to investigate if discrete areas have the same relative importance for two species sharing the same geographical space.

To calculate these metrics we first created new MaxEnt ‘combined’ models for the three whale species, combining the variables retained in each individual model. This procedure was necessary because quantitative comparison of environmental niche models requires that models are fitted to the same variables. We then produced monthly habitat suitability maps from April to July for the three whale species using ‘raw’, instead of logistic, suitability scores.

We used the software ENMTools (Warren et al., 2010) to calculate the *I* statistic and the RR metric among pairs of species within each month. We applied the ‘niche equivalency test’ (Warren et al., 2008), to assess whether the environmental niche

models for each species were significantly different from each other. We performed the niche equivalence test by comparing the niche overlap values ( $I$ ) of pairs of whale species to null distributions of 100 overlap values. Niches in pairwise comparisons were considered non-equivalent if the overlap value of the species being compared was significantly ( $P \leq 0.05$ ) lower than the overlap values from the null distribution. See Warren et al. (2008) for a detailed explanation of the process. All calculations were carried out in ENMTools (Warren et al., 2010).

### **3. Results**

#### *3.1 Individual environmental niche models*

After excluding sightings without corresponding environmental variables, a total of 17 blue whale, 31 fin whale, and 33 sei whale sightings were used to fit the models. These sample sizes are modest for this type of studies, especially in the case of the blue whale with less than 20 occurrences (Shcheglovitova and Anderson, 2013). This was in part the reason for choosing MaxEnt as the modelling technique, as it is one of the more robust methods for small sample sizes (Pearson et al., 2007; Wisz et al., 2008).

Strong collinearity between pairs of predictor variables was not detected based on the Kendall's correlation coefficient ( $|\tau| < 0.7$  for all pairs). Pilot models were thus run with all 18 variables and the number of variables was reduced for each model using the pruning process explained above in Section 2.4.2. Variables retained for each species model varied, according to their relative contribution to the models given by the PI scores (Table 2).

The models for blue and fin whales had mean AUC values well above the 0.7 threshold, indicating a reasonable predictive performance (Table 2). In contrast, the model for the sei whale had a more modest performance, with an AUC marginally below 0.7 (Table 2).

##### *3.1.1 Blue whale*

The mean AUC reported for the blue whale model was high (0.82) indicating that the model has a very good performance in discriminating presence and background sites (Table 2).

For blue whales, most of the contribution to the model came from the Chlorophyll-a concentration of the previous month to the sighting date (Chl-a<sub>(-1m)</sub>; Table 2). Other variables that were also retained included the variation of Chl-a concentration recorded two months before the sighting date (V-Chl-a<sub>(-2m)</sub>), local variation of night-time sea surface temperature (V-NSST), and distance to shore. The marginal response curves showed increasing habitat suitability with higher values for all the variables used to fit the model (Figure S1).

The predictions show a degradation of the habitat suitability for blue whales as the seasons progress (from April to July), with a strong latitudinal component, with conditions degrading progressively from south to north (

Figure 2). The degradation of the habitat quality is also reflected in a decrease of the predicted area with suitability greater than average (suitability score  $\geq 0.5$ ) from April to July (Table 3).

### *3.1.2 Fin whale*

Although slightly worse than the blue whale model, the fin whale model also performed relatively well with an AUC = 0.79 (Table 2).

Night-time sea surface temperature (NSST) contributed most to the fin whale model, followed by Chl-a<sub>(-1m)</sub>, with V-Chl-a<sub>(-2m)</sub> having a modest contribution (Table 2). No other variable was retained in this model. The marginal response curves showed that habitat suitability decreased with increasing NSST and enhanced habitat suitability at intermediate values of both Chl-a<sub>(-1m)</sub>, and V-Chl-a<sub>(-2m)</sub> (Figure S2).

As with the blue whale, there was a progressive degradation of the habitat suitability over consecutive months with a strong latitudinal component (Table 3;

Figure 3).

### *3.1.3 Sei whale*

The sei whale model had a poor performance based on the mean AUC score attained (0.69).

None of the primary productivity variables, considered here as proxies for secondary production, were retained in the model (Table 2). The variable with the largest contribution to the model was NSST, followed by distance to shore and by V-NSST. The other 15 variables evaluated were rejected during the pruning phase. The shapes of the marginal response curves indicate a degradation of the habitat conditions with an increase of both NSST and V-NSST (Figure S3). Habitat suitability initially improves with increasing distance to shore but then decreases with higher values of that variable (Figure S3).

The monthly predictions, as well as the computation of the monthly area with above than average habitat suitability (Table 3;

Figure 4) show a progressive degradation of the habitat conditions. However, unlike the results for blue and fin whales, no latitudinal component is apparent. Instead, the highest values of habitat suitability are found around the islands and deteriorate progressively towards more coastal waters (

Figure 4).

### *3.2 Environmental niche overlap*

The combined models used for the niche overlap analyses performed similarly to the individual models (Table S1) and yielded analogous predictions of habitat suitability both spatially and temporally (not shown).

Both the niche similarity *I* statistic and the relative ranking (RR) of habitat patches show a greater similarity of the monthly environmental niches between blue and fin whales than between any of those species and the sei whale (Table 4). For all the pairwise comparisons that included the sei whale, the niche equivalency hypothesis was rejected, showing that the predicted environmental niches being compared differed significantly ( $P \leq 0.05$ ); in contrast, for comparisons between blue and fin whales the hypothesis was rejected only regarding predictions for July (Table 4), indicating that these species are utilizing the same environmental niche for most of the time while in the study region. Furthermore, the high RR values obtained for the pairwise

comparisons among blue and fin whales, indicate that those species are utilizing similar habitats in the Azores region.

## **4. Discussion**

### *4.1. Habitat function*

We characterized the environmental niche of blue, fin and sei whales in an open-ocean mid-latitude migratory habitat in the North Atlantic. To the best of our knowledge this is the first time that this was attempted.

Silva et al. (2013) proposed that migrating blue and fin whales may extensively use stop-over sites along their migratory routes to renew energy reserves prior to arriving at high productive foraging grounds at northern latitudes. Notwithstanding, contrasting results for the sei whale (Prieto et al., 2014) raised the possibility that the same habitat could hold diverse functions to different species.

Our models do not explicitly account for behavior and as a result cannot adequately distinguish foraging habitats from those used for migrating or resting. However we argue that although our methodology does not permit to directly test the role of the region as a feeding ground, we can still draw some conclusions about the habitat use by considering model results and the set of environmental variables that were most influential in each model.

The models for blue and fin whales show high suitability scores for most of the study area during April and May. Conditions deteriorate rapidly in the following months, with a consequent decrease of the area with higher than average suitability in June and July (Table 3;

Figure 2 and 3). For both species models show a progressive deterioration of the favorable habitat conditions from lower to higher latitudes. The Azores region shows strong seasonal warming of the waters, with a sharp increase in sea surface temperature (SST) from April onwards, along a south-north latitudinal gradient (Bashmachnikov et al., 2004; Martins et al., 2007). The temperature gradient is inversely related to the primary production in the region, which shows zonal bands of increasing Chlorophyll-a concentration (Chl-a) from south to north and a progressive reduction of the Chl-a



values with increasing temperature from spring to summer months (Martins et al., 2007). The progressive degradation of favorable habitat conditions captured by the blue and fin whale models is clearly influenced by these trends in SST and Chl-a.

Results by Visser et al. (2011) suggest that the timing of baleen whale presence in the Azores follow the onset of spring bloom by several weeks. By fitting a behavior discriminant model to satellite telemetry data, Silva et al. (2013) were able to show that blue and fin whales instrumented with satellite transmitters interrupted their migration for weeks to months to feed in the vicinity of the Azores. Silva et al. (2013) suggested that the whales were taking advantage of enhanced productivity created by local oceanographic processes and topographic features, in order to gain energy prior to their arrival to high-latitude foraging grounds.

Our results support those hypotheses for blue and fin whales. Chlorophyll-a from the month preceding the sighting date was the most and second most influential variable, respectively to the blue and fin whale models. Zooplankton have generation and maturation times in excess of one month, resulting in delayed response to changes in primary productivity (Clark et al., 2001; Croll et al., 2005; Santora et al., 2010). The variable response curves shown in Figure S1 were created by producing a model fit only to the corresponding variable and must be interpreted with caution. Having that in mind, results for the blue whale show increasing habitat suitability for higher values of Chl-a, indicating a preference for areas that harbored a phytoplankton bloom the month preceding the sighting. For the fin whale the results are not as clear, since there seems to be a preference for intermediate Chl-a values (Figure S2). However that may be due to the fact that the variable was not the most influential in the model, creating a sub-optimal model.

It is noteworthy that other variables retained in the blue and fin whale models included standard deviation of Chl-a (two months earlier) and of NSST (only blue whale). Both variables indicate the presence of localized variation or gradients in primary productivity or surface temperature that can be caused by oceanographic processes and topographic features (Nieto et al., 2012). These can be permanent or transient in nature but may create conditions for increased prey densities that may in turn be exploited by the whales (Bost et al., 2009).

These results in combination suggest that, in addition to using the Azores as a migratory habitat, blue and fin whales may utilize the region as a mid-latitude feeding ground while conditions are optimal, possibly taking advantage of productivity enhancing and concentration phenomena as proposed by Silva et al. (2013).

In contrast to the blue and fin whale models, the sei whale model did not retain variables related to primary production (Table 2). Prey preferences of sei whales partially overlap with those of blue and fin whales. Sei whales in the North Atlantic rely heavily on calanoid copepods as prey, which are seldom taken by blue and fin whales (Gavrilchuk et al., 2014; Prieto et al., 2012). Notwithstanding, similarly to blue and fin whales, euphausiid zooplankton may comprise the bulk of sei whale prey in some parts of the North Atlantic (Prieto et al., 2012). If the Azores region held a marked role as a foraging ground for the sei whale, analogously to the other two species, we would expect a greater influence from variables known to affect availability of potential prey than those retained in the sei whale model (Baines and Reichelt, 2014; Letessier et al., 2009; Murase et al., 2014).

The fact that the sei whale model performed more poorly than the blue and fin whale models suggests that the variables considered in that model have reduced influence in driving the presence of the species within the study area. Prieto et al. (2014) report that sei whales instrumented with satellite tags in the Azores only engaged in foraging behavior when approaching the Labrador Sea. Before that, whales showed a near constant speed and orientation indicative of migratory behavior (Prieto et al., 2014). If sei whales are only travelling through the region while migrating, it is not expectable that their distribution is strongly related with any specific environmental variable, unless some variables represent features used as navigational cues. The variable with most contribution to the sei whale model was NSST, but in light of the low model performance it is possible that the importance of the variable is just a reflection of the seasonality of the species, and is devoid of other ecological significance. The habitat suitability maps also show a relevant influence of distance to shore in the predictions (

Figure 4). Navigational landmarks are widely utilized by migratory species (Åkesson and Hedenström, 2007; Bauer et al., 2013; Garrigue et al., 2015; Wiener et al., 2011). It is plausible that sei whales utilize the islands as topographic aids in navigation, although

that is impossible to determine from our data. Finally, the standard deviation of NSST (V-NSST) was also retained in the model (Table 2), but the response curve for that variable shows a preference for low values, indicating a lack of affinity for localized variation or gradients in surface temperature (Figure S3).

#### *4.2. Environmental niche overlap*

As noted above, results from the sei whale models suggest that the variables considered here have limited ability in predicting the presence of the species in the region, which has impacted model performance. In light of that, it can be argued that performing a niche overlap analysis comparing the sei whale to the other two species becomes unwarranted. However, we believe that including the sei whale in the niche overlap analyses is still valuable. From the strikingly different results shown by the sei whale model, we can hypothesize that in the study area the sei whale does not share the same environmental niche with either of the two other species. The results from the niche equivalency test show that the environmental niche utilized by the sei whale is significantly distinct from those of the blue and fin whales for all months evaluated (Table 4), confirming that hypothesis. Notwithstanding, it is important to stress that those results hold only for the specific environmental niche defined by the variables considered in the combined models.

The scores of pairwise comparison of habitat suitability relative ranking (RR) comparing the sei whale with the two other species were also consistently low for all months, suggesting little spatial overlap of areas with similar relative importance for the sei whale and either the blue whale or the fin whale (Table 4).

In contrast, the predicted blue and fin whale environmental niches are essentially identical from April to June, and there is a high concordance on the relative importance of the same geographic areas among the two species (Table 4).

These results reinforce the notion that the Azores may hold different ecological roles depending on the species considered. The niche equivalency test failed to detect statistically significant differences between the environmental niches of blue and fin whales for most of the months evaluated, which suggests that these two species are influenced by a similar set of environmental conditions when they are in the region. Additionally, results from the relative ranking of habitat suitability between these two

species suggest that the habitat quality varies spatially in a similar way for both species. Thus it seems reasonable to assume that the Azores hold a similar ecological role for the blue and the fin whales.

In contrast, based on the environmental niche similarity analyses, the quality of the sei whale habitat in the Azores does not seem to be influenced by the same set of environmental conditions, or even have a similar spatial distribution. It is thus plausible to assume that the ecological role that the Azores plays to the sei whale is, at least partially, different than that it plays for the blue and fin whales.

Identifying and describing the ecological interactions and mechanisms of coexistence among species are essential steps to understand the functioning of any ecosystem (Chase and Leibold, 2003). Our methodology does not allow investigating ecological interactions among species. Notwithstanding, the niche overlap results suggest that blue and fin whales may be targeting the same type of resources in the Azores. Both species are known to prey upon northern krill (*Meganyctiphanes norvegica*) in the region (Silva et al., 2013; Visser et al., 2011). Behavioral observation and analysis of fecal samples indicate that sympatric blue and fin whales in the Azores often feed on krill within hundreds of meters from each other and possibly over the same prey patches (Silva and Prieto, unpublished data). If indeed, as our results suggest, blue and fin whales are targeting the same resources in the Azores, then it would be important to conduct further investigation to understand if these species present any type of biotic interactions between, either positive (mutualism, facilitation) or negative (competition).

## **5. Concluding remarks**

Environmental disturbances, such as climate change, fisheries, deep-sea mineral exploration or increasing noise pollution, are likely to cause perturbations in ocean circulation, timing of biological events such as productivity blooms, changes in ecological community assemblages, among other. It is expected that these changes will alter the spatial and temporal distribution of food resources for many predators as well as their ability to find and capture those prey (Hazen et al., 2013; MacLeod, 2009; McGregor et al., 2013).

Having a good understanding of the drivers and dynamics of marine predators' distributions is essential not only to enable monitoring animal populations but also to

forecast effects of future change. Our results clearly illustrate the continuous change that pelagic ecosystems undergo and how that may affect marine predators. These results support the notion that ocean management must be dynamic and take into account both the spatial and the temporal scales (Game et al., 2009; Maxwell et al., 2015). The present work demonstrates the potential of environmental niche modelling in informing and supporting efforts towards dynamic ocean management.

The reason the Azores becomes a temporary stopover for blue and fin whales seems to be related to a combination of environmental conditions that create suitable habitat for these species for a brief period. As those specific conditions change, the habitat ceases to be of value. As consequence of climate change, heat content of the oceans is increasing at a fast rate, leading to changes in water temperature, circulation and sea level (Roemmich et al., 2015). Although the North Atlantic is undoubtedly responding to climate change, predicting how these changes will affect the North Atlantic oceanography has shown to be extremely difficult (Msadek et al., 2014). However, it is expectable that the environmental conditions that create a stopover habitat for blue and fin whales in the region will change. Recently it has been shown that baleen whales present remarkable plasticity in their migratory phenology. Humpback whale (*Megaptera novaeangliae*) and fin whale date of arrival at a feeding ground in the Gulf of St Lawrence (Canada) has retroceded at a rate of one day per year over a period of nearly three decades, in response to ocean warming leading to earlier ice break-up (Ramp et al., 2015). However, the effect that this rate of change has on the resilience of the populations is still unclear. Different phases of the annual cycle of migratory animals are inextricably linked. The events of one phase will influence the next phase to an extent that can be relevant not only at the individual level but also to the population (Webster et al., 2002). Further investigation is necessary to understand the importance of the mid-latitude pelagic habitat around the Azores to these whales and how changes to the oceanography in the region can affect their phenology and, ultimately, their populations.

Although the present work has advanced our understanding on the mechanisms involved in the creation of suitable habitat for the blue and fin whales, several challenges still lay ahead. Our methodology did not allow uncovering which, if any, environmental conditions drive the presence of the sei whale in the region, and why conditions that are apparently favorable for the other two species do not seem to be

important for that species. Our results also raise questions about biotic interactions and resource partitioning between blue and fin whales, enabling their coexistence in the region. To advance our understanding about the functioning of this mid-latitude pelagic ecosystem, it would be valuable to characterize the biotic interactions about these and other species occurring in the region.

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Table 1: Candidate environmental variables used in pilot MaxEnt models.

Table 2: Retained environmental variables and predictive performance of MaxEnt models for blue (*Balaenoptera musculus*), fin (*B. physalus*), and sei (*B. borealis*) whales. Standard deviations (SD) around the mean area under the receiver operating characteristic curve (AUC) calculated over ten cross-validation folds. The permutation importance score returned by MaxEnt for each variable is given, with the variables contributing most to each model highlighted in bold.

Table 3: Monthly (April-July) area with above than average habitat suitability scores ( $\geq 0.5$ ) from predictions based on the environmental niche models developed in MaxEnt for blue (*Balaenoptera musculus*), fin (*B. physalus*), and sei (*B. borealis*) whales.

Table 4: Pairwise environmental niche comparisons among blue (*Balaenoptera musculus*), fin (*B. physalus*), and sei (*B. borealis*) whales. Results of habitat patch relative ranking (RR) and niche similarity (I) are given for pairs of species for monthly (April-July) predictions of the combined MaxEnt models. The results and interpretation of the niche equivalency test is shown. \*denotes significantly distinct ( $P \leq 0.05$ ) environmental niches among pairs of species.

Table S1: Retained environmental variables and predictive performance of combined MaxEnt models for blue (*Balaenoptera musculus*), fin (*B. physalus*) and sei (*B. borealis*) whales, used in niche comparison analyses. Standard deviations (SD) around the mean area under the receiver operating characteristic curve (AUC) calculated over ten cross-validation folds. The permutation importance score returned by MaxEnt for each variable is given, with the variables contributing most to each model highlighted in bold.

Table 1

Table 1: Candidate environmental variables used in pilot MaxEnt models.

Environmental variable	Acronym	Transformation	Resolution Spatial/temporal	Units	Source
Depth	Depth	none	1 arc-minute/static	m	NationalGeophysicalDataCenter(NGDC), National OceanicandAtmospheric Administration(NOAA) <a href="http://www.ngdc.noaa.gov/mgg/global/global.html">http://www.ngdc.noaa.gov/mgg/global/global.html</a> . (Amante & Eakins 2008)
Night-time sea surface temperature	NSST	none	2.5 arc-minute/month	°C	National Aeronautics and Space Administration (NASA) Goddard Space Flight Center's Ocean Data Processing System (ODPS) <a href="http://oceancolor.gsfc.nasa.gov">http://oceancolor.gsfc.nasa.gov</a> . (Campbell et al. 1995).
Chlorophyll-a concentration	Chl-a	log10	2.5 arc-minute/month	mg/m <sup>3</sup>	National Aeronautics and Space Administration (NASA) Goddard Space Flight Center's Ocean Data Processing System (ODPS) <a href="http://oceancolor.gsfc.nasa.gov">http://oceancolor.gsfc.nasa.gov</a> . (Campbell et al. 1995).
Seamounts	<i>None</i>	none	10 meters	unitless	<a href="http://www.int-res.com/articles/suppl/m357p017_app.pdf">www.int-res.com/articles/suppl/m357p017_app.pdf</a> . (Morato et al. 2008).
<i>Derived environmental variables</i>					<i>Original variable</i>
Slope within a 3x3 pixel kernel	Slope	log10	1 arc-minute/static	degrees from the horizontal	Depth
Euclidean distance to shoreline	Distance to shore	square root	1 arc-minute/static	m	Depth
Euclidean distance to 200 meters isobath	Dist(200)	square root	1 arc-minute/static	m	Depth
Euclidean distance to 500 meters isobath	Dist(500)	square root	1 arc-minute/static	m	Depth
Euclidean distance to 1000 meters isobath	Dist(1000)	square root	1 arc-minute/static	m	Depth
Euclidean distance to 2000 meters isobath	Dist(2000)	square root	1 arc-minute/static	m	Depth
Seamount density within 8x8 pixel kernel	d-Seamounts	none	1 arc-minute/static	seamounts/km <sup>2</sup>	Seamounts



Minimum depth seamounts	Seamount_dpt	none	1 arc-minute/static	m	Seamounts
Time-lagged Chlorophyll-a concentration (-1 month)	Chl-a (-1m)	log10	2.5 arc-minute/month	mg/m <sup>3</sup>	Chl-a
Time-lagged Chlorophyll-a concentration (-2 months)	Chl-a (-2m)	log10	2.5 arc-minute/month	mg/m <sup>3</sup>	Chl-a
Chlorophyll-a local variation (calculated as standard deviation within a 8x8 pixel kernel of log-transformed Chlorophyll-a)	V-Chl-a	none	2.5 arc-minute/month	SD log10(mg/m <sup>3</sup> )	Chl-a
Time-lagged Chlorophyll-a local variation (-1 month)	V-Chl-a (-1m)	none	2.5 arc-minute/month	SD log10(mg/m <sup>3</sup> )	Chl-a
Time-lagged Chlorophyll-a local variation (-2 months)	V-Chl-a (-2m)	none	2.5 arc-minute/month	SD log10(mg/m <sup>3</sup> )	Chl-a
Nigh-time sea surface temperature local variation (calculated as standard deviation within a 3x3 pixel kernel of NSST)	V-NSST	none	2.5 arc-minute/month	SD °C	NSST

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**Table 2**

Table 2: Retained environmental variables and predictive performance of MaxEnt models for blue (*Balaenoptera musculus*), fin (*B. physalus*), and sei (*B. borealis*) whales. Standard deviations (SD) around the mean area under the receiver operating characteristic curve (AUC) calculated over ten cross-validation folds. The permutation importance score returned by MaxEnt for each variable is given, with the variables contributing most to each model highlighted in bold.

	<i>Blue whale</i>	<i>Fin whale</i>	<i>Sei whale</i>
Number of sightings used in model	17	31	33
Mean AUC $\pm$ SD	0.821 $\pm$ 0.135	0.794 $\pm$ 0.111	0.691 $\pm$ 0.128
<i>Retained environmental variables</i>	<i>Permutation importance</i>		
Time-lagged log <sub>10</sub> Chlorophyll-a concentration (-1 month)	<b>47.2</b>	28.6	-
Time-lagged Chlorophyll-a local variation (-2 months)	24.4	8.8	-
Night-time sea surface temperature	-	<b>62.6</b>	<b>49.8</b>
Night-time sea surface temperature local variation	14.5	-	22.6
Square root of Euclidean distance to shoreline	13.9	-	27.6

Table 3: Monthly (April-July) area with above than average habitat suitability scores ( $\geq 0.5$ ) from predictions based on the environmental niche models developed in MaxEnt for blue (*Balaenoptera musculus*), fin (*B. physalus*), and sei (*B. borealis*) whales.

	<i>Area in km<sup>2</sup> / % of total area (563,176 km<sup>2</sup>)</i>			
	<i>April</i>	<i>May</i>	<i>June</i>	<i>July</i>
Blue whale	421,462 / 74.8%	363,979 / 64.6%	151,004 / 26.8%	44,981 / 8%
Fin whale	562,597 / 100%	487,694 / 86.6%	192,264 / 34.1%	0 / 0%
Sei whale	192,763 / 34.2%	142,473 / 25.3%	63,919 / 11.3%	91 / 0%

**Table 4**

Table 4: Pairwise environmental niche comparisons among blue (*Balaenoptera musculus*), fin (*B. physalus*), and sei (*B. borealis*) whales. Results of habitat patch relative ranking (RR) and niche similarity (I) are given for pairs of species for monthly (April-July) predictions of the combined MaxEnt models. The results and interpretation of the niche equivalency test is shown. \*denotes significantly distinct ( $P \leq 0.05$ ) environmental niches among pairs of species.

Species pairs	Month	RR	I	<i>Interpretation of niche equivalency test</i>
Sei whale-Blue whale	April	0,257	0,852*	Different
Sei whale-Fin whale	April	0,379	0,887*	Different
Fin whale-Blue whale	April	0,777	0,993	Equivalent
Sei whale-Blue whale	May	0,426	0,862*	Different
Sei whale-Fin whale	May	0,456	0,882*	Different
Fin whale-Blue whale	May	0,859	0,993	Equivalent
Sei whale-Blue whale	June	0,473	0,781*	Different
Sei whale-Fin whale	June	0,504	0,854*	Different
Fin whale-Blue whale	June	0,923	0,984	Equivalent
Sei whale-Blue whale	July	0,468	0,717*	Different
Sei whale-Fin whale	July	0,523	0,808*	Different
Fin whale-Blue whale	July	0,928	0,983*	Different

Table S1: Retained environmental variables and predictive performance of combined MaxEnt models for blue (*Balaenoptera musculus*), fin (*B. physalus*) and sei (*B. borealis*) whales, used in niche comparison analyses. Standard deviations (SD) around the mean area under the receiver operating characteristic curve (AUC) calculated over ten cross-validation folds. The permutation importance score returned by MaxEnt for each variable is given, with the variables contributing most to each model highlighted in bold.

Combined Niche Models	<i>Blue whale</i>	<i>Fin whale</i>	<i>Sei whale</i>
Number of sightings used in model	17	31	33
Mean AUC $\pm$ SD	0.829 $\pm$ 0.097	0.786 $\pm$ 0.083	0.681 $\pm$ 0.132
<i>Retained environmental variables</i>	<i>Permutation importance</i>		
Time-lagged log <sub>10</sub> Chlorophyll-a concentration (-1 month)	<b>56.5</b>	32.9	0.3
Time-lagged Chlorophyll-a local variation (-2 months)	18.5	7.9	0.1
Night-time sea surface temperature	1.4	<b>54.9</b>	<b>44.5</b>
Night-time sea surface temperature local variation	11.5	0	37.6
Square root of Euclidean distance to shoreline	12	4.3	17.5

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### Habitat preferences of baleen whales in a mid-latitude habitat

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<http://dx.doi.org/10.1016/j.dsr2.2016.07.015>

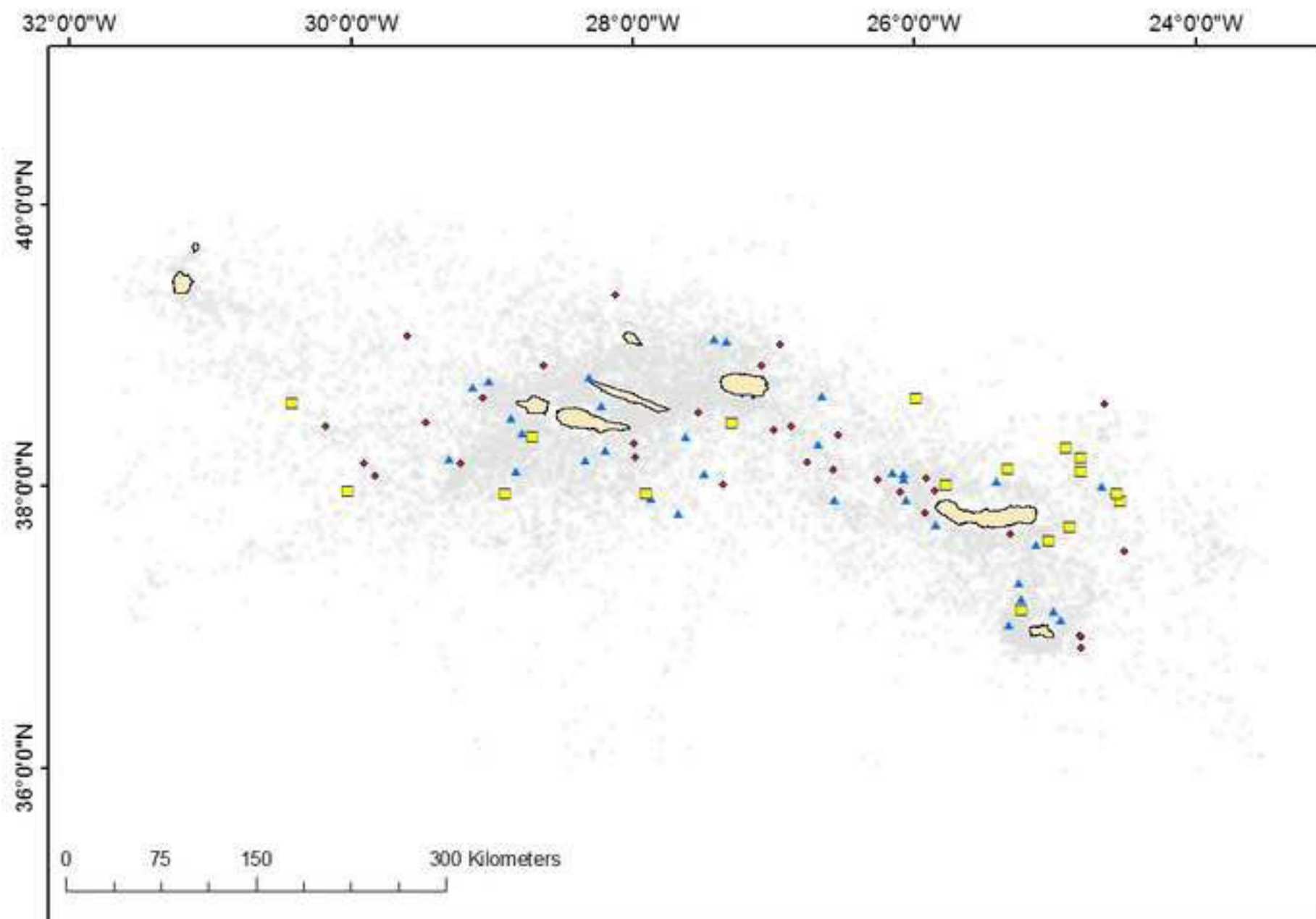
Figure 1: Distribution of occurrences (2004-2009) of blue (*Balaenoptera musculus*) (squares), fin (*B. physalus*) (circles) and sei (*B. borealis*) (triangles) whales, and background points (crosses), used to fit the MaxEnt models.

Figure 2: Blue whale (*Balaenoptera musculus*) predicted habitat suitability maps off the Azores islands. Habitat suitability represented by color shade, with warmer (darker) colors corresponding to higher suitability.

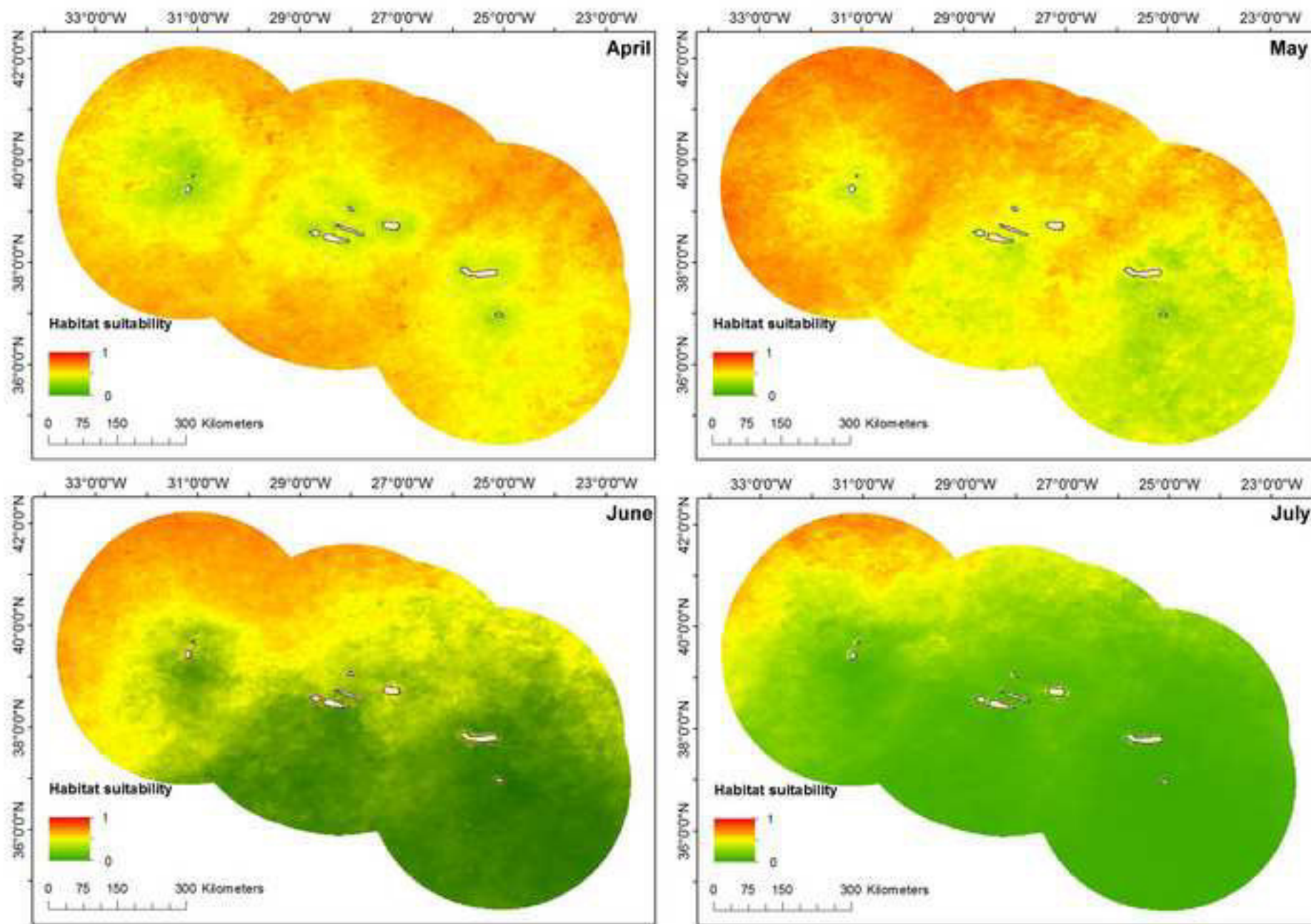
Figure 3: Fin whale (*Balaenoptera physalus*) predicted habitat suitability maps off the Azores islands. Habitat suitability represented by color shade, with warmer (darker) colors corresponding to higher suitability.

Figure 4: Sei whale (*Balaenoptera borealis*) predicted habitat suitability maps off the Azores islands. Habitat suitability represented by color shade, with warmer (darker) colors corresponding to higher suitability.

Figure 1  
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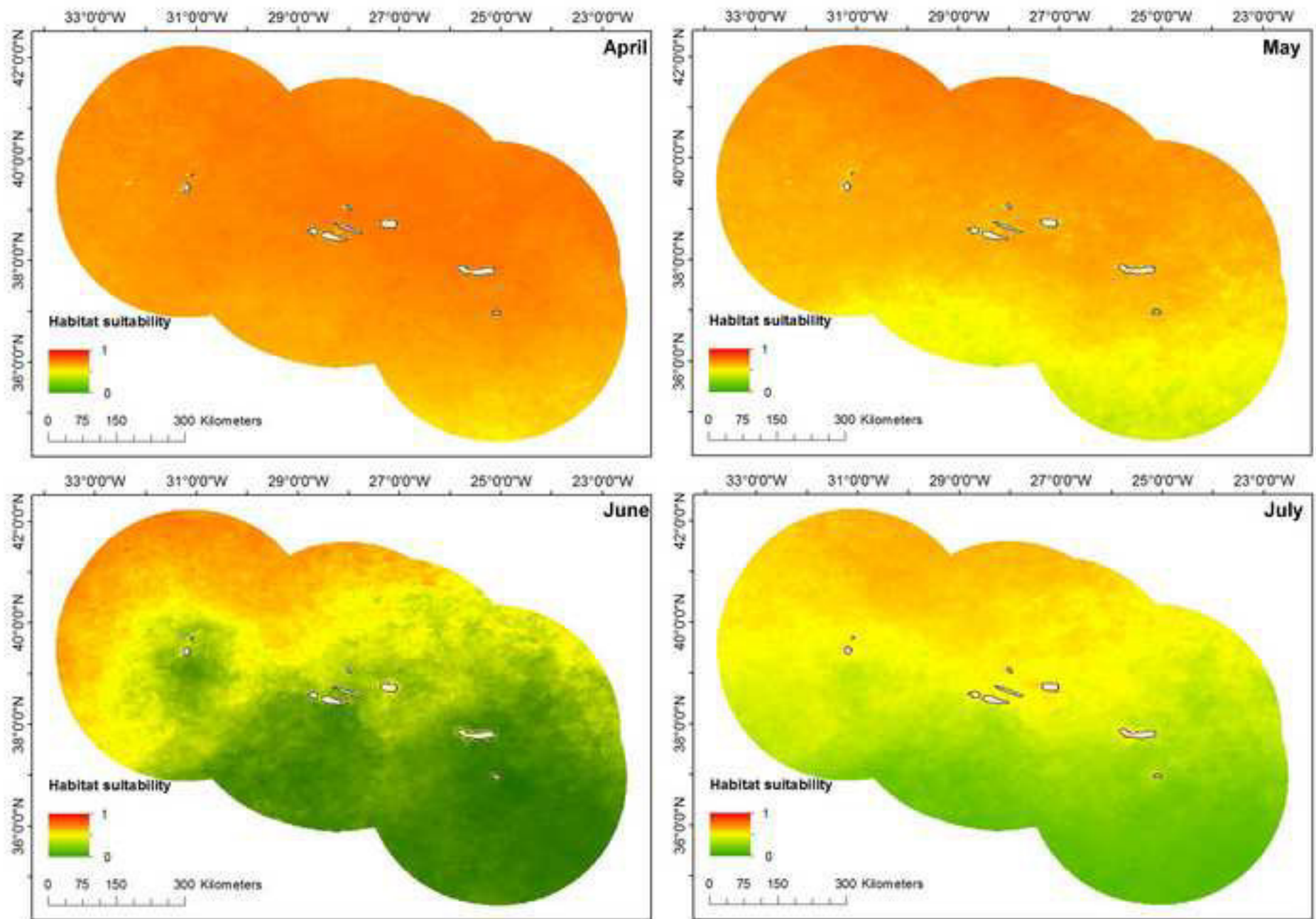


**Figure 2**  
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**Figure 3**  
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**Figure 4**  
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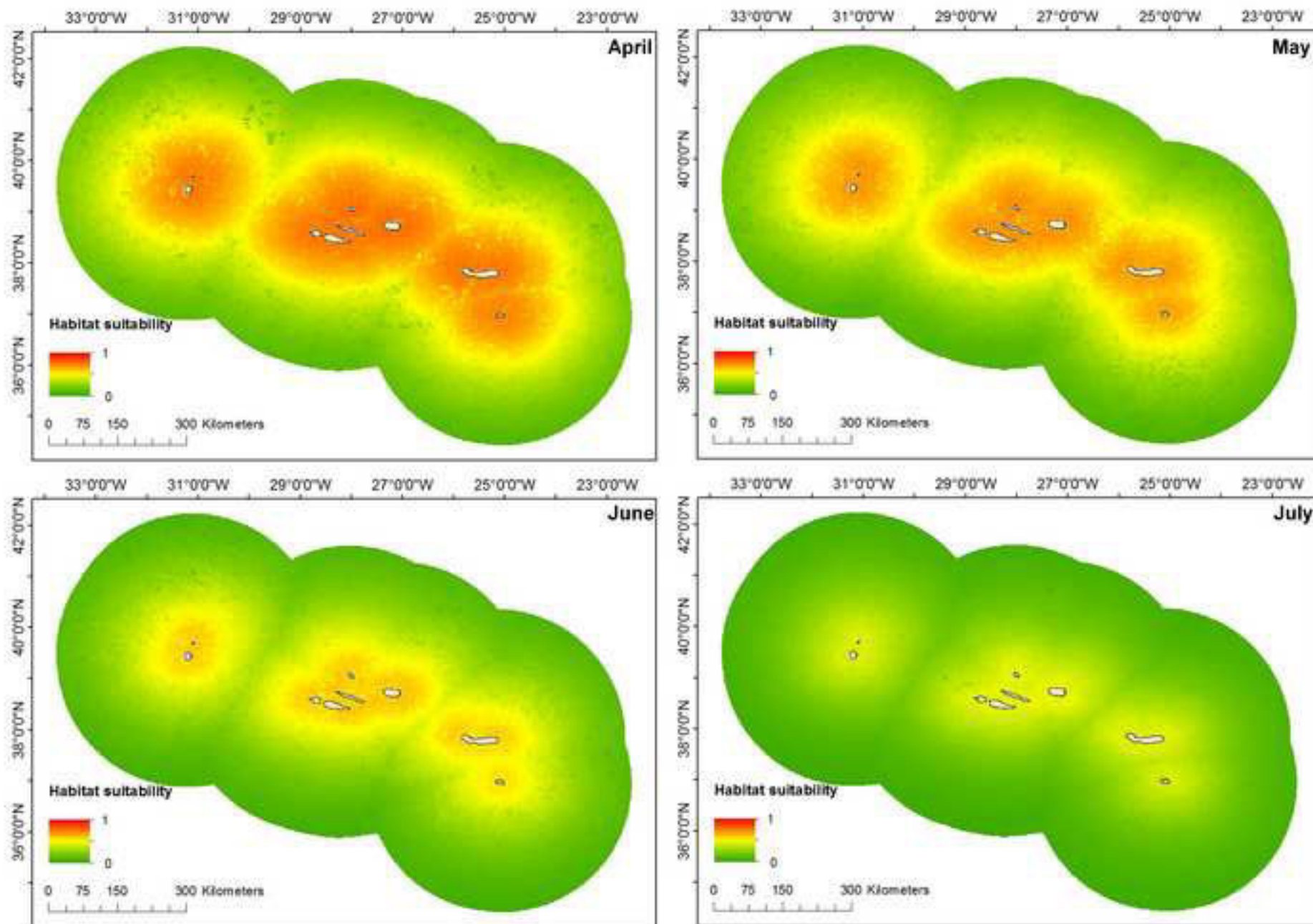


Figure S1: Marginal response curves of models built for the blue whale (*Balaenoptera musculus*) using only the respective variable. Chl\_a(-1m): Time lagged Chlorophyll-a concentration, prior month to the sighting date; V-Chl\_a( - 2m): Time-lagged Chlorophyll-a local variation (-2 months); V-NSST: Night-time sea surface temperature local variation.

Figure S2: Marginal response curves of models built for the fin whale (*B. physalus*) using only the respective variable. NSST: Night-time sea surface temperature; . Chl\_a(-1m): Time lagged Chlorophyll-a concentration, prior month to the sighting date; V-Chl\_a( - 2m): Time-lagged Chlorophyll-a local variation (-2 months).

Figure S3: Marginal response curves of models built for the sei whale (*B. borealis*) using only the respective variable. NSST: Night-time sea surface temperature; V-NSST: Night-time sea surface temperature local variation.

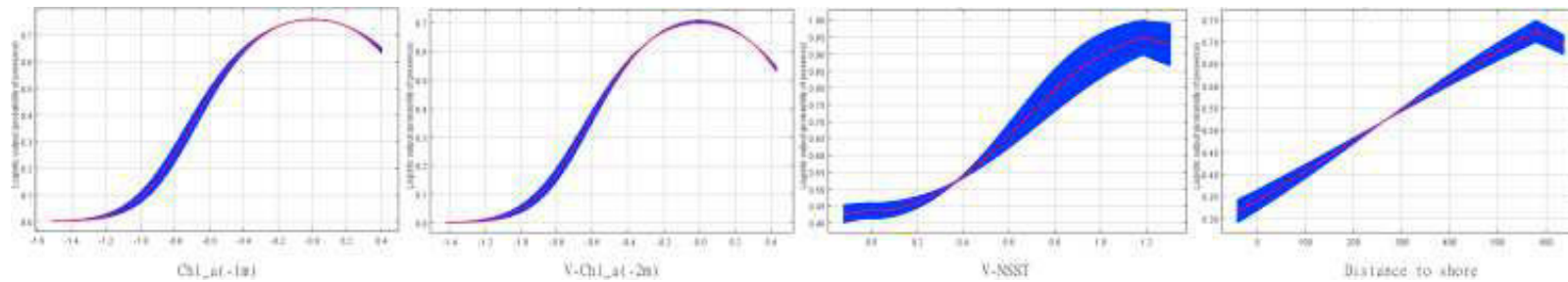


Fig. S1. Marginal response curves of models built for the blue whale (*Balaenoptera musculus*) using only the respective variable. Chl\_a(-1 m): Time lagged Chlorophyll-a concentration, prior month to the sighting date; V-Chl\_a(-2 m): Time-lagged Chlorophyll-a lo...

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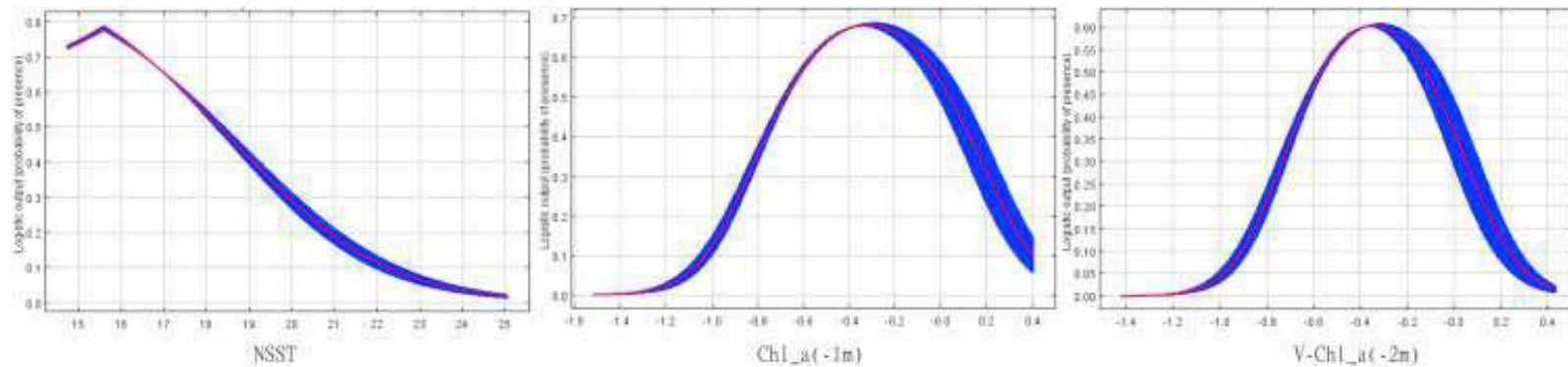


Fig. S2. Marginal response curves of models built for the fin whale (*Balaenoptera physalus*) using only the respective variable. NSST: Night-time sea surface temperature; . Chl\_a(-1 m): Time lagged Chlorophyll-a concentration, prior month to the sighting date; ...

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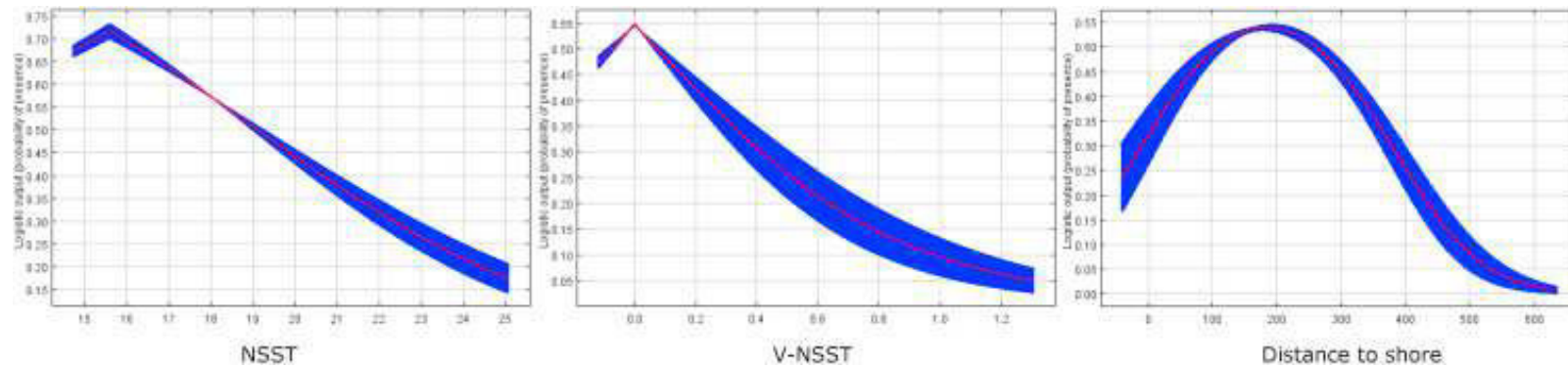


Fig. S3. Marginal response curves of models built for the sei whale (*Balaenoptera borealis*) using only the respective variable. NSST: Night-time sea surface temperature; V-NSST: Night-time sea surface temperature local variation.

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