A matter of timing: how temporal scale selection influences cetacean ecological niche modelling

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ABSTRACT: Modelling in the marine environment faces unique challenges that place greater emphasis on model accuracy. The spatio-temporal variability of this environment presents challenges when trying to develop useful habitat models. We tested how different temporal scales influence model predictions for cetaceans with different ecological requirements. We used 7 years of (opportunistic) whale watching data (>16000 cetacean sightings) collected in the Azores archipelago under the MONICET platform. We modelled the distribution of 10 cetacean species with a sampling bias correction. Distribution modelling was performed at 2 spatial scales (2 and 4 km) and 2 temporal resolutions (8 d vs. monthly averages). We used a MAXENT analysis with 3 different validation procedures. Generally, the 8 d means produced better results. In some cases (e.g. baleen whales), predictions using monthly means were no better than null models. Finer temporal grains provided essential insights, especially for species influenced by dynamic variables (e.g. sea surface temperature). For species more influenced by static variables (e.g. bathymetry), differences between temporal scales were smaller. The selection of the right temporal scale can be essential when modelling the niches of cetaceans. Datasets with high temporal resolution (e.g. whale watching data) can provide an excellent basis for these analyses, allowing use of finer temporal grains. Our models showed good predictive performance; however, limitations related to the spatial coverage were found. Merging datasets with different temporal and spatial resolutions could help to improve niche estimates. Models with better predictive capacity and transferability are needed to implement more efficient protection and conservation measures.

KEY WORDS: Ecological niche models • Temporal scales • Marine environments • Whale watching • Cetaceans • Azores

INTRODUCTION

Knowledge of species' geographic distributions is important for conservation efforts. In the absence of comprehensive distribution data, habitat models can be useful alternatives, e.g. to identify key habitats and areas of concern for vulnerable populations (Guisan et al. 1999), manage anthropogenic threats (Redfern et al. 2013) and evaluate climate change effects (Keith et al. 2014). In recent times, the ecological niche modelling field has experienced enormous growth (Peterson et al. 2011), in part driven by easy access to biodiversity records through opportunistic datasets and citizen science programmes. In general, data obtained through platforms of opportunity can be considered as a low-cost option, but they provide only limited information for an understanding of factors affecting distribution and abundance (Evans & Hammond 2004). However, Redfern et al. (2006) claimed that cetacean habitat modelling data collected opportunistically can be considered to be almost equivalent to data collected using designed surveys if all potential sources of bias are taken into consideration. Several studies have demonstrated the utility of opportunistic data in a variety of applications, such as distribution studies (van Strien et al. 2013), Red List assessments (Maes et al. 2015) and population trends (McPherson & Myers 2009). Modelling in the marine environment faces unique challenges that place greater emphasis on model accuracy. Difficulties arise from the characteristics of some marine species, such as their large ranges, low detectability or large-scale migrations. Furthermore, taking into consideration the spatio-temporal variability of the marine environment is crucial when trying to develop useful habitat models (Redfern et al. 2006).

Despite their widespread use, there are still some concerns regarding the accuracy of species distribution models (Peterson et al. 2011). Typically, the temporal and spatial resolutions of analyses are determined by the availability of environmental data rather than by an assessment of species' characteristics (Barry & Elith 2006, Jetz et al. 2012). Different species might have different relationships with their environments; while some might prefer more stable conditions, others could be more dependent on dynamic habitat features (Roberts et al. 2016, Fernandez et al. 2017, Scales et al. 2017). Moreover, different variables used for modelling procedures can show significant variation over a range of timescales. Recent studies tested the effects of different temporal grain selection of environmental variables when modelling cetacean distributions (e.g. Mannocci et al. 2014, Fernandez et al. 2017, Scales et al. 2017). While Mannocci et al. (2014) found that climatological time scales (e.g. seasonal or annual) might produce better distribution estimates for cetaceans, others found that finer temporal grain (e.g. weekly data) produce better results (Fernandez et al. 2017, Scales et al. 2017). Therefore, the selection of an adequate temporal grain for niche modelling can be a complex issue. Both Mannocci et al. (2017) and Fernandez et al. (2017) suggested that the selection of the temporal scale to be used is dependent on many factors, such as the study goal or the nature of the data collected. Other potential problems might be related to the logistic difficulties associated with sampling the marine environment. Therefore, niche models for mobile marine species need to have enough flexibility to accommodate all of the factors described.

Cetaceans are top predators and therefore represent a key element of the oceanic ecosystem. However, it can be difficult to obtain accurate data for good abundance or distribution estimates, due to certain cetacean characteristics, such as their entirely pelagic ecology. To manage the potential hazards to these highly mobile populations increasingly requires a detailed understanding of their seasonal distributions and habitat (Roberts et al. 2016).

The Azores harbour a high diversity of cetaceans, with 28 species registered to date (Silva et al. 2014). Silva et al. (2014) found that some species are highly migratory and only occur during specific time periods (e.g. Atlantic spotted dolphins during summer–early autumn or blue whales during spring–early summer) while others are observed in the area year round (e.g. sperm whales). Silva et al. (2014) also found important variations in the encounter rates for some species (e.g. bottlenose dolphins and Risso’s dolphins). Silva et al. (2013) found evidence of the importance of the Azores for feeding purposes for some baleen whales (blue and fin whales). Two main studies focussed on cetacean distribution patterns in the area. Silva et al. (2014) used a long-term dataset (1999–2009) obtained from opportunistic (Azores Fisheries Observer Programme, POPA) and dedicated boat surveys, together with land-based observations, to analyse the spatial and temporal distributions of 24 cetacean species. Recently, Tobeña et al. (2016) produced distributional models for 15 cetacean species using data obtained from POPA, from May to November, between 2004 and 2009.

Here, we investigated the role of using different temporal scales when modelling the niches of cetaceans, focussing on dynamic marine environments and using a set of 10 cetacean species with different ecological characteristics. Four different modelling scenarios were tested: (1) spatial coverage of environmental predictors; (2) temporal coverage of environmental predictors; (3) spatio-temporal generation of background points; and (4) total number of background points generated. Dynamic distributional maps for those species in the Azores were created, using the ‘best’ scenarios.

METHODS

Study area

The study area is located in the Azores archipelago, a group of North Atlantic oceanic islands located approximately 1800 km west of Lisbon, Portugal. The region is strongly influenced by the Gulf Stream and all branches of this current. Its large-scale oceanic circulation is dominated by the Azores Current, which generates considerable mesoscale variability (Santos et al. 1995). Data were restricted to 4 of the 9 islands of the archipelago where whale watching activities are concentrated: São Miguel, Terceira, Pico and Faial (Fig. 1).

Occurrence data

Cetacean occurrence data were obtained from the MONICET platform for the period from January 2009 to December 2015. MONICET (www.monicet.net) is an online platform created in 2008 which collects standardized data of commercial whale watching companies and stores the data in a flexible and stable online database. Presently 7 Azorean whale watching companies contribute with 2 kinds of data: sightings locations and photographs for photo-identification purposes. On each whale watching trip, companies collect a minimum set of basic data (including geographical coordinates, species identification, sea state, number of individuals and activity state), which is checked and validated by qualified personnel for quality control.

We selected 10 cetacean species (short-beaked common dolphin, sperm whale, bottlenose dolphin, Atlantic spotted dolphin, fin whale, Risso’s dolphin, short-finned pilot whale, sei whale, striped dolphin and blue whale) based on data availability and ecological significance (Table 1). The chosen species cover a wide range of ecological characteristics, from baleen whales, which feed mainly on small crustaceans, to deep divers such as sperm whales that feed on deep-water squid.

Environmental variables

Five terrain variables (depth, slope, distance to the 200 m and 1000 m bathymetric lines and distance to canyon-like features) were derived from a digital elevation model (DEM) of the EMODnet Bathymetry portal (www.emodnet-bathymetry.eu/): depth was directly read from the DEM; slope and distances to the 200 m and 1000 m bathymetric lines were calculated using QGIS 2.14.3. The topographic position index (TPI) measures where a point is in the overall landscape/seascape in order to identify features such as ridges, canyons, or midslopes (Wright & Heyman 2008). We calculated the TPI with the SAGA GIS (www.saga-gis.org/) implementation (based on Guisan et al. 1999, Weiss 2001), using a small radius of 2000 m and a bigger radius of 6000 m. We selected features corresponding to V-shape river valleys and deep narrow canyons (Weiss 2001). We applied a filter (<3 km) to eliminate artefacts and small features. Distance to the edge of these canyon-like features was calculated (Fig. 2).

Three oceanographical variables (sea surface temperature, distance to thermal fronts and chlorophyll *a* [chl *a*]) were used for this study. Two of these were calculated using NASA’s multi-scale ultra-high resolution (MUR) sea surface temperature (SST), which merges many satellite infrared and passive microwave datasets into global daily maps at 1 km resolution. Thermal ocean fronts were detected from each MUR SST daily map (Miller 2009). We then generated 8 d and monthly ocean front metrics from the composite front maps (Miller et al. 2015). The variable Fdist (front distance) quantifies the distance to the closest major front.

Biological productivity was indicated using satellite ocean colour estimates of chl *a*, from the ESA Ocean Colour Climate Change Initiative based on monthly and 8 d composites (Version 2.0 dataset, OC4v6 algorithm, 4 km resolution, www.esa-oceancolour-cci.org). Lagged chl *a* products for 2 and 4 wk before each study period were calculated. All variables were tested for correlation using the variance inflation factors (VIF) implemented on the usdm R package, setting a VIF threshold of 10 (Naimi et al. 2014). No correlation was found between the environmental variables.

Temporal and spatial resolutions

Two spatial (2 and 4 km) and 2 temporal (8 d and 1 mo) resolutions for the eco-geographical variables were used. Two grids of 2 and 4 km were created using QGIS; environmental variables were resampled using a cubic interpolation. Data were divided in 8 d and monthly periods (averaged when necessary) and projected on the respective spatial grids (Table 1). A complete set of environmental layers was constructed for each spatial grid and temporal resolution.

Modelling techniques and evaluation procedures

MAXENT modelling (Phillips et al. 2006) was used to test the effects of different grouping and data filter scenarios. For each species and modelling scenario, 10 runs were performed using the default MAXENT settings. The variables to be used for each species modelling were selected using an iterative process. The percentage contribution, permutation importance and the jackknife test given by MAXENT were used to select the variables used in the final models (Kalle et al. 2013).

Data bias corrections

Bias correction can have an important influence on model performance (Phillips et al. 2009, Varela et al. 2014). We used a spatial filtering of the presences together with a target background approach to correct for sampling bias.

Whale watching activities in the Azores are characterized by the use of land-based lookouts (Magalhães et al. 2002) which guide the boats to the animals. Once the boats arrive at the animals, the sighting event and recording begins. It is common for multiple whale watching companies to record the same sighting event as several boats cluster around easily accessible animals. Therefore, a spatial data filtering (or data thinning) procedure was applied (Peterson et al. 2011). Sightings were filtered based on temporal and spatial proximity. Occurrence registers of the same species completed by any whale watching company within 1 h of the first sighting within a 2 and 4 km radius were considered duplicate and filtered out.

For each model run, a total of 10000 and 50000 background points were selected (Phillips & Dudík 2008) using 2 different techniques: (1) a non-targeted and (2) a targeted background approach. Points were always selected from the area contained in the minimum sampled area (MSA) obtained by drawing a minimum convex polygon (MCP) around the sightings of each trip (see Fig. S1.1 in Supplement 1 at www.XXXXXXXX). A trip is defined as the time between the boat leaving the main harbour and its return. The area inside the polygon was defined as the area sampled on the trip. For each day with at least 1 whale watching trip, an MSA was established. If several trips were made on a day, then the total sampled area was calculated by merging all of the MSAs.

For non-targeted background, points were randomly selected from all daily MSAs. For the targeted background, points were selected using detectability as a vector of probability weights. For both approaches, no specific temporal or spatial structure was used for the background points selection. Ten iterations were performed to minimize potential biases derived from randomization. Detectability functions were constructed using a modified distance sampling approach. These methods are based on line or point transect sampling. The main assumption is one of imperfect detection: objects located on the lines or points are always seen, but become harder to detect with increasing distance to the line or point (Thomas et al. 2002). This study uses the 'detectability index' of Thompson & George (1994). Lookout stations are 'sampling points', and detectability decreases with distance from these points. We applied a multiple-covariate model, where method detection functions are modelled based on distance and additional covariates (Marques et al. 2007). Species were placed into 4 main groups: small dolphins, large dolphins, sperm whales and baleen whales. Two covariables were used: the mean sea state (a proxy for visibility) and the company that collected the data (assuming observer skills vary between companies). The mean sea state was calculated using all of the registers collected by the companies for each trip and categorized in 2 groups (Beaufort ≤3 and >3). Important differences were found for distance of sightings to the main lookout points between the companies collecting the data (see Supplement 1). Species detectability was calculated for each grid of the MSA. Grids with presences of other species were assumed to be visited by boats, and therefore set to maximum detectability. On grids sampled more than once per day, only the highest detectability value was kept.

Model performance evaluation

Models were evaluated using 3 methodologies: (1) a cross-validation based on a space/time evaluation structure, (2) a restricted independent dataset and (3) a null model.

(1) A cross-validation based on a geographically structured approach (Araújo & Rahbek 2006, Jiménez-Valverde et al. 2011, Peterson et al. 2011) was applied by segregating our data into different spatio-temporal bins (Radosavljevic & Anderson 2014). Although any environmental biases present in the overall dataset still exist, this approach segregates such biases temporally or geographically, allowing for evaluations capable of detecting overfitting to any corresponding environmental biases. We applied a masked spatio-temporal structured approach, by screening out the environmental data for background sampling from the time period (and area in some cases) corresponding to the localities used for model evaluation. Each bin corresponds to a temporally independent evaluation dataset, including, in some cases, unsampled areas. Five folds of equal size were created for each species, determined by the extension of the sampling periods.

(2) An independent dataset was used, collected with the 11.9 m sailing boat 'Anacaona', from the Groupe de Recherche sur les Cétacés (GREC). The survey took place around São Miguel Island, divided into 22 d of effort in 2013 and 18 d of effort in 2014, for a total of 280.1 h of effort. Due to data limitations, this test was only performed with a reduced set of 6 species. See Supplement 2 for more information.

(3) Null models using only the geographic coordinates of sighting locations as explanatory variables were constructed for evaluation using a MAXENT algorithm. Null model predictions were tested with both of the previously described validation datasets (temporal cross-validation and independent dataset).

For all of the evaluation procedures, the area under the curve (AUC) for the receiver operator curve (ROC) of each fold was used to quantify model performance. A total of 50 AUC values were obtained for the cross-validation scenario (10 runs × 5 folds) and 10 AUC values for the independent dataset (10 runs). A Kruskal-Wallis test with a Nemenyi post hoc test was used to look for significant differences between the different scenarios tested. All modelling and data filtering analysis was produced using R 3.2.2 (R Core Team 2015) with the Distance2 (Miller 2015), raster (Hijmans 2016), qdap (Rinker 2013), MASS (Venables & Ripley 2002), dismo (Hijmans et al. 2017), SDMTools (VanDerWal et al. 2014), pROC (Robin et al. 2011) and PMCMR (Pohlert 2014) packages.

RESULTS

Model performance

In general, niche models for all species produced high AUC values for the spatio-temporal masked cross-validation approach, with consistent differences in performance depending on the temporal resolution used (Fig. 3). The number of background points selected or the spatial resolution of the environmental data did not influence the models. Overall the choice of both finer temporal scale and target background selection produced significantly different AUC values: models based on 8 d environmental means typically outperformed those based on monthly data, whereas models using a targeted background approach performed significantly better than those using a non-targeted background selection in nearly all cases. Both methods outperformed the null models in the case of the 8 d temporal scale. However, for the monthly scale, null models outperformed the non-targeted approach, and no significant differences were found with the targeted selection.

When looking into a more detailed analysis, the niche of each species was influenced by a different set of environmental variables (Tables S3.1, S3.2 & S3.3 in Supplement 3), and model performance varied by species and method (Tables 2 & 3). Looking at the best results for each species, almost all AUC values for the masked cross-validation test varied between 0.75 and 0.94, i.e. in the fair to excellent range (Araújo et al. 2005 based on Swets 1998). However, the values obtained for bottlenose dolphins and common dolphins were consistently poor ($0.53 < AUC < 0.59$). For the independent dataset, the best results for the AUC values ranged between 0.67 and 0.82. Nearly all models using environmental variables as explanatory factors produced better results than null models (except for Risso’s dolphin and bottlenose dolphin models in the cross-validation tests).

The use of a targeted background approach improved model performance for all species (except common dolphin) on the cross-validation test, but results were variable in the independent validation. An overlapping of the standard deviations was found for some species (e.g. sperm whale).

Model performance differed according to the temporal resolution of environmental data and species. The 3 deep-diving species (sperm whale, Risso’s dolphin and short-finned pilot whale) showed no difference between 8 d or monthly means. Furthermore, for the first 2 species, no differences were found between null models and 'regular' models in any temporal scenario. In the case of the sperm whale, differences were present for the independent dataset (null models performed poorly). However, significant differences were found between the 2 temporal grain sizes for baleen whales and small delphinid species. For 5 species highly influenced by dynamic variables (striped dolphin, Atlantic spotted dolphin, sei whale, fin whale and blue whale) the 8 d scale produced better results. In the case of the striped dolphin, differences in AUC were smaller (ΔAUC = 0.02); however, for the other species differences on AUC values were important (ΔAUC between 0.1 and 0.15). Likewise for those species, significant differences were found between null models and 'regular' models in the 8 d scenarios (ΔAUC between 0.05 and 0.12), yet these differences were not present for the monthly scenario. For some species (such as baleen whales), the null model, when using monthly resolution, had better predictive capabilities.

To summarize, no (or relatively small) differences were found for all species when modelling their niches using different spatial resolution for the environmental variables or number of background points. On the other hand, the temporal grain of the environmental variables and the method of selection of the background points had different effects depending on the species modelled (Table 4).

Species patterns

Depth was selected as an important variable for almost all species studied (see Supplement 3 for tables and figures), but especially for 2 deep-diving species (sperm and pilot whales) and a small delphinid (striped dolphin). Together with Risso's dolphins, they showed a preference toward areas closer to canyon-like features (Fig. S3.1–4 in Supplement 3). Moreover, they were strongly influenced by the 1000 m depth contour. Striped dolphins also preferred deep-water environments and moderate SST values (16–26°C, peaking at 21°C; Fig. S3.4). Atlantic spotted dolphins showed a preference for warm (18–26°C, peaking at 24°C) and relatively deep waters around the 1000 m bathymetric line (Table S3.2 & Fig. S3.5). Common dolphins showed a preference for relatively shallow waters closer to the 200 m bathymetric lines (Fig. S3.6). Bottlenose dolphins had similar results, although this species seems to be less restricted to those areas (Fig. S3.7).

Chlorophyll was only relevant as an explanatory variable for baleen whales. The models for blue whales showed better performances when including chl *a* measured 2 wk before the sightings; for sei whales, the best results were obtained when using chl *a* at the time of sighting. No model showed improved performance using chl *a* measured 4 wk prior to sighting. Response curves for blue whales (Fig. S3.8) showed a very restricted niche strongly influenced by SST (14–20°C, peaking at 17°C), with a preference for deeper and off-shore waters. Sei whale response curves indicated a wide range of SST values (14–24°C, peaking at 16°C), but with a strong preference for colder waters (Fig. S3.10). Both species preferred moderate to high chlorophyll values (blue whales from 1 to 4 mg m^{-3} and sei whales from 2 to 6 mg m^{-3}). Chlorophyll did not influence models for fin whales, which showed a wider range of suitable SST values (14–25°C, peaking at 18–19°C) relative to other Balaenopteridae (Fig. S3.9).

Seasonal variability in suitable habitat depended on the species (Supplement 4). While some deep-diving species showed fewer differences through time (sperm whales and Risso's dolphins), some small odontocetes seem to be more influenced by environmental changes (Atlantic spotted dolphins and striped dolphins). For all baleen whales, differences in habitat suitability were found between seasons. In general, species highly influenced by dynamic variables followed this pattern, with high variability of suitability values in some months (Fig. 4 and suitability maps in Supplement 4).

DISCUSSION

This study elucidates the effects of using different temporal scales for the environmental variables when modelling mobile species with different ecological characteristics. From the 4 scenarios tested, the use of different spatial scales and the number of background points had little or no influence on the results. Similar results of the spatial grain effects were found by other studies focussing on cetaceans (Redfern et al. 2008, Becker et al. 2010, Scales et al. 2017). Opinions are divided on the number of background points to be used in a presence/background model. Phillips & Dudík (2008) found that 10000 background points is optimal for Maxent, whereas Renner et al. (2015) suggested that a greater number of background points is preferred. Therefore in the present study we used 2 approaches: 10000 and 50000 background points. No differences were found between the 2 methods, in agreement with the findings of Phillips & Dudík (2008). Differences in model performance were found for the 2 other scenarios tested: targeted sampling of background points and temporal resolution of environmental variables. The targeted sampling approach to select the background points proved to be effective, as better results were obtained when applying a targeted background approach. In general, the use of a finer temporal grain provided better results, particularly for species highly influenced by dynamic variables.

Our results also demonstrate the significant value of an opportunistic dataset for niche modelling procedures. The availability of observations with a high sampling rate allowed the use of a finer grain for environmental variables (8 d), which is relevant particularly for species with a distribution that is highly influenced by dynamic variables. Occurrence datasets with high temporal resolution are therefore important to provide accurate estimates of the temporal dimension of the niche.

Sampling background corrections

The use of a sampling background approach based on a minimum sampled area and a detectability index proved to be useful. Sample bias corrections can lead to a strong improvement in model performance (Phillips et al. 2009). However, for some species, especially when using an independent dataset for evaluation, better results were obtained with a non-targeted background approach (such as bottlenose dolphins). The target background (or background selection) method used in this study has the potential to impact model prediction and performance (VanDerWal et al. 2009). Previous studies generally preferred a random selection of background points (e.g. Warton & Shepherd 2010, Barbet-Massin et al. 2012), yet recent studies suggested that targeted background points can improve the results in some cases (Stolar & Nielsen 2015, Ranc et al. 2017). An excessive reduction or increase of the spatial (or temporal) range of the background data can lead to inaccurate results (Thuiller et al. 2004, VanDerWal et al. 2009). Ranc et al. (2017) suggested that the usefulness of target-group bias correction is highly dependent on the system investigated. The selection of background data can be extremely useful, yet it should be undertaken with a good knowledge of the dataset, associated biases and species ecology (Fourcade et al. 2014).

Spatial and temporal scale

Significant differences were found between temporal scales, but not spatial scales. Temporal scales have been suggested to be a key element to test when building niche models in the marine environment (Scales et al. 2016, Fernandez et al. 2017, Mannocci et al. 2017). As expected, the use of different temporal scales of the environmental variables strongly affected the results of the models built. Differences between monthly means and 8 d means were not important for species mostly influenced by topographic variables (sperm whale, pilot whale, Risso's dolphin and striped dolphin). No differences between null models and models using environmental variables were found for 2 of these species (Risso's dolphins and sperm whales) in the cross-validation tests. Those species are extremely dependent on bathymetric features (e.g. canyon-like features, high-slope areas), and therefore will prefer some specific geographic areas where those features are present. Due to the small study area used in this study, when species use the same regions regularly, models based solely on spatial coordinates might be able to predict those areas (as they remain constant through time). Nevertheless, for sperm whales, when validating the models with the independent dataset (which includes geographic areas not used for the training), null models performed poorly compared to the other approaches. For species specifically influenced by variables with higher dynamism (blue whale, fin whale, sei whale and Atlantic spotted dolphin), temporal scale differences were important. Incorporating 8 d environmental data can produce better models for some species. In general, models for migratory, or seasonal species, may benefit from fine-scale temporal resolutions, while for resident species, the use of broader temporal grain might be appropriate. Nevertheless, we recommend treating each species individually when investigating the appropriate scale to obtain accurate distributional estimates.

Caveats and bias

Data collected by highly opportunistic sources have some obvious limitations. Our data, for instance, were confined to coastal areas around the islands where whale watching operations are performed. Using data from a fisheries observer programme, Silva et al. (2014) found many offshore sightings around the Azores, which might represent a different set of environmental relationships. The inshore bias of our data leads to an environmental and spatial truncation which affects the predictive capabilities of our models outside the study area (Peterson et al. 2007, 2011, Owens et al. 2013). Nevertheless, for some species (such as the sperm whale), our models proved to have a good predictive capability in coastal areas, even for unsampled locations such as the north coast of São Miguel Island.

Despite this spatial bias, the models produced accurate estimates able to characterize the temporal dimension of the niche. Although touristic operations peak during the summer months, there are trips all year around, which allow detection of interesting temporal patterns and the use of a finer temporal grain. In this case, the use of a high-resolution temporal occurrence dataset allowed us to obtain a clear picture of the effects of dynamic oceanographic variables (such as SST, chlorophyll or frontal areas).

Of the 10 species evaluated in this study, 2 were consistently difficult to model: common and bottlenose dolphins. This could be due to a number of factors. Firstly, both species are widely distributed and present throughout the year in high numbers (Silva et al. 2014). Obtaining accurate models for generalist/common species can be challenging (McPherson & Jetz 2007), and the models can be particularly sensitive to the data used (Jiménez-Valverde et al. 2008). Silva et al. (2008) hypothesized that bottlenose dolphins living in the Azores carry out extensive movements and have large home ranges. These characteristics can also be challenging for modelling procedures (Peterson et al. 2011). However, even if our models failed to predict the temporal niche of bottlenose dolphins (AUC < 0.55), results for the independent dataset were fairly good (AUC = 0.68). Furthermore, it is possible that there are other environmental drivers for these species, occurring at a finer temporal and/or spatial scale, which we were not able to include in the modelling process. Influential variables that might improve the models are those related to behavioural events (e.g. foraging, migration, reproduction; Bailey et al. 2009, Roever et al. 2014), interspecific relationships (Ehrlén & Morris 2015) or even anthropogenic factors (e.g fisheries interactions, whale watching disturbance; Stone et al. 1997, Lusseau 2005).

Implications for cetacean species ecology

Sperm whales showed an important relationship with depth, associated with canyon-like features and with higher suitability values in summer (warmer SST). Skov et al. (2008) found an influence of bottom complexity on the presence of sperm whales, which may be similar to the influence we found with canyons. Recent studies have shown how sperm whales use submarine canyons in different ways for feeding purposes (Fais et al. 2015, Guerra et al. 2017). For the Azores area, Tobeña et al. (2016) found an influence of chlorophyll for this species, which was not detected in our study. Whitehead et al. (2010) also noted that the addition of satellite-derived measures of productivity did not improve predictive capacity of explanatory models for deep-water cetacean diversity.

The other 2 deep-diving species (short-finned pilot whale and Risso’s dolphin) showed a strong relationship with depth, although this factor was more important for the short-finned pilot whale. This species seems to be restricted to deeper waters, as described in previous studies for *Globicephala* spp. in the Azores (Silva et al. 2014, Tobeña et al. 2016). Additionally, we found a strong influence of temperature, such as Fullard et al. (2000) found for some populations of long-finned pilot whale. For Risso’s dolphins, we found an influence of distance to the 1000 m contour line, which agrees with the findings of Baumgartner (1997) and Olavarría et al. (2001) for different areas (Gulf of Mexico and Chile). Another important factor for Risso’s dolphins is the distance to canyons. Hartman et al. (2014) hypothesized that squid distribution might be a key element for their social structure and distribution in the Azores, thus the relationship with canyon-like features could be related to the presence of squid.

Striped dolphins presented a well-marked seasonal distribution, with suitability maps reflecting strong variation between summer and spring, which agrees with Tobeña et al. (2016). However, we also found depth and distance to canyon-like features to be relatively important predictors, similar to the preference for deeper and warmer waters reported for the species in the Mediterranean (Panigada et al. 2008). SST was important for Atlantic spotted dolphins, with a preference for warmer and deep waters, in line with the findings of Hamazaki (2002) for the mid-west North Atlantic and Tobeña et al. (2016) for the Azores. While results of common dolphins in the present study should be interpreted with caution (especially on the temporal dimension), we found a preference for shallower waters, close to the 200 m bathymetric lines. In a deep-water environment such as the Azores, these findings might indicate a preference for island-like features or seamounts, as noted by Tobeña et al. (2016) and Morato et al. (2008). The slight preference for shallow coastal areas of bottlenose dolphins agrees with Tobeña et al. (2016).

All baleen whales were strongly influenced by dynamic variables, with significantly better results when using 8 d means. This reinforces the importance of high-resolution temporal datasets, which are able to provide enough data to run models with finer temporal grain. The most restricted niche found corresponds to the blue whale with a relatively short window of occurrence strongly dependent on SST, which leads to a highly seasonal occurrence for this species. In contrast, fin whales were the most flexible of the 3 species modelled, with a wider range of temperature and no dependence on productivity. Our models predict a higher percentage of suitable habitat for fin whales during spring and autumn; however, even if more restricted, there is still a portion of suitable area during summer months, agreeing with previous observations of Silva et al. (2014). Sei whales showed a more restricted habitat than fin whales, but were more flexible than blue whales. In contrast, Prieto et al. (2017) found a relatively similar niche for blue and fin whales (both influenced by chl *a*) and a different niche for sei whales (with no influence of chl *a*). These differences might be related to the temporal grain of the environmental variables. The low number of presences available to those authors (a maximum of 35 presences in an area of 278 km around the entire archipelago, compared to a minimum of 100 presences in an area of about 37 km around 4 islands used in the present study), limited the use of the temporal scale to monthly means. In our study, the results obtained with the 8 d grouping clearly outperformed the monthly ones, with differences in AUC values higher than 0.15.

Final remarks

This study demonstrates how the use of finer temporal scales provides essential insights, especially for cetacean species highly dependent on dynamic environmental conditions. Opportunistic, high temporal resolution occurrence data (such as the ones collected by whale watching operations) can be a useful source for modelling mobile species distributions in dynamic environments, provided the effects of the associated biases are corrected. Dynamic distributional models, such as the ones presented here, can be extremely valuable for dynamic ocean management (DOM) applications. DOM approaches are emerging in several places globally, replacing static management, and are proving to be an effective tool to respond to potential conflicts around ocean resources (Lewison et al. 2015). Tools such as WhaleWatch (Hazen et al. 2017) use these products to provide near real-time probability of occurrence, including temporal variability, to reduce human impacts (e.g. ship strikes or loud underwater sounds).

However, we do acknowledge the limitations of the data used in this study due to its low spatial coverage. Generally, there is a trade-off between high temporal resolution and good spatial coverage. Therefore, we want to highlight the advantages of data complementarity between different sampling methodologies to produce better distribution estimates. Redfern et al. (2006) suggested that accurate and flexible cetacean distribution estimates should be based on different spatial and temporal resolutions. While sampling programmes covering an extended area can provide a clear image of the spatial patterns, other sampling methods with high periodicity in relatively small areas can help to clarify temporal patterns (as supported in this study). Models with better predictive capacity and transferability are needed to implement more efficient protection and conservation measures.

Acknowledgements. The data used in this paper were obtained through the MONICET platform from the following Azorean whale watching companies: Terra Azul – Azores Islands Whales and Dolphins, Picos de Aventura – Animação e Lazer Lda., Horta

Cetáceos Whale and Dolphin Watching – Azores Experiences, Ocean Emotion Azores Whale Watching, SeaColors Expeditions and Futurismo – Azores Whale Watching. We are very thankful to all of these companies and the guides, skippers and lookouts who joined and helped us during this process. The sampling data collection for this study was only possible through the collaboration of the Groupe de Recherché sur les Cétacés (GREC). All sampling campaigns were done under permission from the local authorities: licenses 30/2013/DRA and SAI/DRA/2014/1260. M.F. is supported by grant M3.1.2/F/028/2011 from the Fundo Regional para a Ciência e Tecnologia (Azores Government). This research was partially supported by the European Regional Development Fund (ERDF) through the COMPETE - Operational Competitiveness Programme and national funds through FCT - Foundation for Science and Technology, under the project 'PEst-C/MAR/LA0015/2013', by the Strategic Funding UID/Multi/04423/2013 through national funds provided by FCT - Foundation for Science and Technology and European Regional Development Fund (ERDF), in the framework of the program PT2020 and by cE3c funding (Ref: UID/BIA/00329/2013). It was also partly supported by the Centro de Investigação de Recursos Naturais, University of the Azores (CIRN) and the Interdisciplinary Centre of Marine and Environmental Research, Porto, Portugal (CIIMAR).

LITERATURE CITED

Araújo MB, Rahbek C (2006) How does climate change affect biodiversity? Science 313:1396–1397 PubMed doi:10.1126/science.1131758

Araújo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species–climate impact models under climate change. Glob Change Biol 11:1504–1513 doi:10.1111/j.1365-2486.2005.01000.x

Bailey H, Mate BR, Palacios DM, Irvine L, Bograd SJ, Costa DP (2009) Behavioural estimation of blue whale movements in the Northeast Pacific from state-space model analysis of satellite tracks. Endang Species Res 10:93–106 https://doi.org/10.3354/esr00239

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol Evol 3:327–338 doi:10.1111/j.2041-210X.2011.00172.x

Barry S, Elith J (2006) Error and uncertainty in habitat models. J Appl Ecol 43:413–423 doi:10.1111/j.1365-2664.2006.01136.x

Baumgartner MF (1997) The distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiography of the northern Gulf of Mexico. Mar Mamm Sci 13:614–638 doi:10.1111/j.1748-7692.1997.tb00087.x

Becker EA, Forney KA, Ferguson MC, Foley DG, Smith RC, Barlow J, Redfern JV (2010) Comparing California Current cetacean–habitat models developed using *in situ* and remotely sensed sea surface temperature data. Mar Ecol Prog Ser 413:163–183 doi:10.3354/meps08696

De Reu J, Bourgeois J, Bats M, Zwertvaegher A and others (2013) Application of the topographic position index to heterogeneous landscapes. Geomorphology 186:39–49 doi:10.1016/j.geomorph.2012.12.015

Ehrlén J, Morris WF (2015) Predicting changes in the distribution and abundance of species under environmental change. Ecol Lett 18:303–314 PubMed doi:10.1111/ele.12410

Evans PGH, Hammond PS (2004) Monitoring cetaceans in European waters. Mammal Rev 34:131–156 doi:10.1046/j.0305-1838.2003.00027.x

Fais A, Aguilar Soto N, Johnson M, Pérez-González C, Miller PJO, Madsen PT (2015) Sperm whale echolocation behaviour reveals a directed, prior-based search strategy informed by prey distribution. Behav Ecol Sociobiol 69:663–674 doi:10.1007/s00265-015-1877-1

Fernandez M, Yesson C, Gannier A, Miller P, Azevedo JMN (2017) The importance of temporal resolution for niche modelling in dynamic marine environments. J Biogeogr 44:2816–2827

Fourcade Y, Engler JO, Rödder D, Secondi J (2014) Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PLOS ONE 9:e97122 PubMed doi:10.1371/journal.pone.0097122

Fullard KJ, Early G, Heide-Jørgensen MP, Bloch D, Rosing-Asvid A, Amos W (2000) Population structure of long-finned pilot whales in the North Atlantic: a correlation with sea surface temperature? Mol Ecol 9:949–958 PubMed doi:10.1046/j.1365-294x.2000.00957.x

Guerra M, Hickmott L, van der Hoop J, Rayment W, Leunissen E, Slooten E, Moore M (2017) Diverse foraging strategies by a marine top predator: Sperm whales exploit pelagic and demersal habitats in the Kaikōura submarine canyon. Deep-Sea Res I 128:98–108 doi:10.1016/j.dsr.2017.08.012

Guisan A, Weiss SB, Weiss AD (1999) GLM versus CCA spatial modeling of plant species distribution. Plant Ecol 143:107–122 doi:10.1023/A:1009841519580

Hamazaki T (2002) Spatiotemporal prediction models of cetacean habitats in the mid-western North Atlantic Ocean (from Cape Hatteras, North Carolina, U.S.A. to Nova Scotia, Canada). Mar Mamm Sci 18:920–939 doi:10.1111/j.1748-7692.2002.tb01082.x

Hartman KL, Fernandez M, Azevedo JMN (2014) Spatial segregation of calving and nursing Risso's dolphins (*Grampus griseus*) in the Azores, and its conservation implications. Mar Biol 161:1419–1428 doi:10.1007/s00227-014-2430-x

Hazen EL, Palacios DM, Forney KA, Howell EA and others (2017) WhaleWatch: a dynamic management tool for predicting blue whale density in the California Current. J Appl Ecol 54:1415–1428

Hijmans RJ (2016) raster: geographic data analysis and modeling. R package version 2.5-8

Hijmans RJ, Phillips S, Leathwick J, Elith J (2017) dismo: species distribution modeling. R package version 1.1-4

Jetz W, McPherson JM, Guralnick RP (2012) Integrating biodiversity distribution knowledge: toward a global map of life. Trends Ecol Evol 27:151–159

Jiménez-Valverde A, Lobo JM, Hortal J (2008) Not as good as they seem: the importance of concepts in species distribution modelling. Divers Distrib 14:885–890 doi:10.1111/j.1472-4642.2008.00496.x

Jiménez-Valverde A, Peterson AT, Soberón J, Overton J, Aragón P, Lobo JM (2011) Use of niche models in invasive species risk assessments. Biol Invas 13:2785–2797 doi:10.1007/s10530-011-9963-4

Kalle R, Ramesh T, Qureshi Q, Sankar K (2013) Predicting the distribution pattern of small carnivores in response to environmental factors in the Western Ghats. PLOS ONE 8:e79295 PubMed doi:10.1371/journal.pone.0079295

Keith DA, Elith J, Simpson CC (2014) Predicting distribution changes of a mire ecosystem under future climates. Divers Distrib 20:440–454 doi:10.1111/ddi.12173

Lewison R, Hobday A, Maxwell S, Hazen E and others (2015) Dynamic ocean management: identifying the critical ingredients of dynamic approaches to ocean resource management. BioScience 65:486–498 doi:10.1093/biosci/biv018

Lusseau D (2005) Residency pattern of bottlenose dolphins *Tursiops* spp. in Milford Sound, New Zealand, is related to boat traffic. Mar Ecol Prog Ser 295:265–272 doi:10.3354/meps295265

Maes D, Isaac NJB, Harrower CA, Collen B, van Strien AJ, Roy DB (2015) The use of opportunistic data for IUCN Red List assessments. Biol J Linn Soc 115:690–706 doi:10.1111/bij.12530

Magalhães S, Prieto R, Silva M, Gonçalves J, Afonso-Dias M, Santos RS (2002) Short-term reactions of sperm whales (*Physeter macrocephalus*) to whale-watching vessels in the Azores. Aquat Mamm 28:267–274

Mannocci L, Laran S, Monestiez P, Dorémus G, Van Canneyt O, Watremez P, Ridoux V (2014) Predicting top predator habitats in the Southwest Indian Ocean. Ecography 37:261–278 doi:10.1111/j.1600-0587.2013.00317.x

Mannocci L, Boustany AM, Roberts JJ, Palacios DM and others (2017) Temporal resolutions in species distribution models of highly mobile marine animals: recommendations for ecologists and managers. Divers Distrib 23:1098–1109 doi:10.1111/ddi.12609

Marques TA, Thomas L, Fancy SG, Buckland ST, Handel CM (2007) Improving estimates of bird density using multiple-covariate distance sampling. Auk 124:1229–1243 doi:10.1642/0004-8038(2007)124[1229:IEOBDU]2.0.CO;2

McPherson J, Jetz W (2007) Effects of species' ecology on the accuracy of distribution models. Ecography 30:135–151

McPherson JM, Myers RA (2009) How to infer population trends in sparse data: examples with opportunistic sighting records for great white sharks. Divers Distrib 15:880–890 doi:10.1111/j.1472-4642.2009.00596.x

Miller P (2009) Composite front maps for improved visibility of dynamic sea-surface features on cloudy SeaWiFS and AVHRR data. J Mar Syst 78:327–336 doi:10.1016/j.jmarsys.2008.11.019

Miller DL (2015) Distance2: simple distance sampling models. R package version 0.1. https://github.com/DistanceDevelopment/Distance2

Miller PI, Scales KL, Ingram SN, Southall EJ, Sims DW (2015) Basking sharks and oceanographic fronts: quantifying associations in the north-east Atlantic. Funct Ecol 29:1099–1109 doi:10.1111/1365-2435.12423

Morato T, Varkey DA, Damaso C, Machete M and others (2008) Evidence of a seamount effect on aggregating visitors. Mar Ecol Prog Ser 357:23–32 doi:10.3354/meps07269

Naimi B, Hamm NAS, Groen TA, Skidmore AK, Toxopeus AG (2014) Where is positional uncertainty a problem for species distribution modelling? Ecography 37:191–203 doi:10.1111/j.1600-0587.2013.00205.x

Olavarría C, Aguayo-Lobo A, Bernal R (2001) Distribution of Risso's dolphin (*Grampus griseus*, Cuvier 1812) in Chilean waters. Rev Biol Mar Oceanogr 36:111–116 doi:10.4067/S0718-19572001000100011

Owens HL, Campbell LP, Dornak LL, Saupe EE and others (2013) Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. Ecol Model 263:10–18 doi:10.1016/j.ecolmodel.2013.04.011

Panigada S, Zanardelli M, MacKenzie M, Donovan C, Mélin F, Hammond PS (2008) Modelling habitat preferences for fin whales and striped dolphins in the Pelagos Sanctuary (Western Mediterranean Sea) with physiographic and remote sensing variables. Remote Sens Environ 112:3400–3412 doi:10.1016/j.rse.2007.11.017

Peterson AT, Papeş M, Eaton M (2007) Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. Ecography 30:550–560 doi:10.1111/j.0906-7590.2007.05102.x

Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB (2011) Ecological niches and geographic distributions. Monographs in Population Biology 49. Princeton University Press, Princeton, NJ

Phillips SJ, Dudík M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31:161–175 doi:10.1111/j.0906-7590.2008.5203.x

Phillips S, Anderson R, Schapire R (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259 doi:10.1016/j.ecolmodel.2005.03.026

Phillips SJ, Dudík M, Elith J, Graham CH, 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 PubMed doi:10.1890/07-2153.1

Pohlert T (2014) The pairwise multiple comparison of means ranks package (PMCMR)

Prieto R, Tobeña M, Silva MA (2017) Habitat preferences of baleen whales in a mid-latitude habitat. Deep-Sea Res II 141:155–167 doi:10.1016/j.dsr2.2016.07.015

R Core Team (2015) R: a language and environment for statistical computing. Version 3.2.2. R Foundation for Statistical Computing, Vienna

Radosavljevic A, Anderson RP (2014) Making better Maxent models of species distributions: complexity, overfitting and evaluation. J Biogeogr 41:629–643 doi:10.1111/jbi.12227

Ranc N, Santini L, Rondinini C, Boitani L, Poitevin F, Angerbjörn A, Maiorano L

(2017) Performance tradeoffs in target-group bias correction for species distribution models. Ecography 40:1076–1087 doi:10.1111/ecog.02414

Redfern JV, Ferguson MC, Becker EA, Hyrenbach KD and others (2006) Techniques for cetacean–habitat modeling. Mar Ecol Prog Ser 310:271–295 doi:10.3354/meps310271

Redfern JV, Barlow J, Ballance LT, Gerrodette T, Becker EA (2008) Absence of scale dependence in dolphin–habitat models for the eastern tropical Pacific Ocean. Mar Ecol Prog Ser 363:1–14 doi:10.3354/meps07495

Redfern JV, McKenna MF, Moore TJ, Calambokidis J and others (2013) Assessing the risk of ships striking large whales in marine spatial planning. Conserv Biol 27:292–302 PubMed doi:10.1111/cobi.12029

Renner IW, Elith J, Baddeley A, Fithian W and others (2015) Point process models for presence-only analysis. Methods Ecol Evol 6:366–379 doi:10.1111/2041-210X.12352

Rinker TW (2013) qdap: quantitative discourse analysis, R Package. 2.2.5. University at Buffalo, Buffalo, NY

Roberts JJ, Best BD, Mannocci L, Fujioka E and others (2016) Habitat-based cetacean density models for the U.S. Atlantic and Gulf of Mexico. Sci Rep 6:22615 PubMed doi:10.1038/srep22615

Robin X, Turck N, Hainard A, Tiberti N, Lisacek F, Sanchez JC, Müller M (2011) pROC: an open-source package for R and S+ to analyze and compare ROC curves. BMC Bioinformatics 12:77 PubMed

Roever CL, Beyer HL, Chase MJ, van Aarde RJ (2014) The pitfalls of ignoring behaviour when quantifying habitat selection. Divers Distrib 20:322–333 doi:10.1111/ddi.12164

Santos RS, Hawkins S, Monteiro LR, Alves M, Isidro EJ (1995) Marine research, resources and conservation in the Azores. Aquat Conserv 5:311–354 doi:10.1002/aqc.3270050406

Scales KL, Hazen EL, Jacox MG, Edwards CA, Boustany AM, Oliver MJ, Bograd SJ (2017) Scale of inference: on the sensitivity of habitat models for wide-ranging marine predators to the resolution of environmental data. Ecography 40:210–220 doi:10.1111/ecog.02272

Silva MA, Prieto R, Magalhães S, Seabra MI, Santos RS, Hammond PS (2008) Ranging patterns of bottlenose dolphins living in oceanic waters: implications for population structure. Mar Biol 156:179–192 doi:10.1007/s00227-008-1075-z

Silva MA, Prieto R, Jonsen I, Baumgartner MF, Santos RS (2013) North Atlantic blue and fin whales suspend their spring migration to forage in middle latitudes: building up energy reserves for the journey? PLOS ONE 8:e76507 PubMed doi:10.1371/journal.pone.0076507

Silva MA, Prieto R, Cascão I, Seabra MI, Machete M, Baumgartner MF, Santos RS (2014) Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. Mar Biol Res 10:123–137 doi:10.1080/17451000.2013.793814

Skov H, Gunnlaugsson T, Budgell WP, Horne J and others (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 II 55:254–268 doi:10.1016/j.dsr2.2007.09.020

Stolar J, Nielsen SE (2015) Accounting for spatially biased sampling effort in presence-only species distribution modelling. Divers Distrib 21:595–608 doi:10.1111/ddi.12279

Stone G, Kraus S, Hutt A, Martin S (1997) Reducing by-catch: Can acoustic pingers keep Hector's dolphins out of fishing nets? Mar Technol Soc J 31:3–7

Swets JA (1988) Measuring the accuracy of diagnostic systems. Science 240:1285–1293 PubMed doi:10.1126/science.3287615

Thomas L, Buckland ST, Burnham KP, Anderson DR, Laake JL, Borchers DL, Strindberg S (2006) Distance sampling. In: Encyclopedia of environmetrics. John Wiley & Sons, Ltd

Thompson SK, George AFS (1994) Detectability in conventional and adaptive sampling. Biometrics 50:712–724 PubMed doi:10.2307/2532785

Thuiller W, Brotons L, Araújo MB, Lavorel S (2004) Effects of restricting environmental range of data to project current and future species distributions. Ecography 27:165–172 doi:10.1111/j.0906-7590.2004.03673.x

Tobeña M, Prieto R, Machete M, Silva MA (2016) Modeling the potential distribution and richness of cetaceans in the Azores from fisheries observer program data. Front Mar Sci 3:202

VanDerWal J, Shoo LP, Graham C, Williams SE (2009) Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? Ecol Model 220:589–594 doi:10.1016/j.ecolmodel.2008.11.010

VanDerWal J, Falconi L, Januchowski S, Shoo L, Storlie C (2014) SDMTools: species distribution modelling tools: tools for processing data associated with species distribution modelling exercises. R package version 1.1-221

Varela S, Anderson RP, Garcia-Valdes R, Fernandez-Gonzalez F (2014) Environmental filters reduce the effects of sampling bias and improve predictions of ecological niche models. Ecography 37:1084–1091

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York, NY

Warton DI, Shepherd LC (2010) Poisson point process models solve the 'pseudo-absence problem' for presence-only data in ecology. Ann Appl Stat 4:1383–1402 doi:10.1214/10-AOAS331

Weiss AD (2004) Topographic position index and landform classification. Working draft Indus Corp EPA Region 10

Whitehead H, O'Brien K, Worm B (2010) Diversity of deep-water cetaceans and primary productivity. Mar Ecol Prog Ser 408:1–5 doi:10.3354/meps08619

Wright DJ, Heyman WH (2008) Introduction to the special issue: marine and coastal GIS for geomorphology, habitat mapping, and marine reserves. Mar Geod 31:223–230 doi:10.1080/01490410802466306

Table 1. Number of total cetacean sightings for the different combinations of spatial resolutions (2 and 4 km). The last column represents the number of presence grids available after filtering for no-data pixels when using chlorophyll as the covariate. NA:

Common name	Scientific name	Total	2 km	4 km	4 km/chl
Short-beaked common dolphin	*Delphinus delphis*	5648	2909	2824	NA
Sperm whale	*Physeter macrocephalus*	5278	2085	1944	NA
Bottlenose dolphin	*Tursiops truncatus*	1843	1467	1422	NA
Atlantic spotted dolphin	*Stenella frontalis*	1777	1322	1281	NA
Fin whale	*Balaenoptera physalus*	801	575	549	234
Risso’s dolphin	*Grampus griseus*	731	576	552	NA
Short-finned pilot whale	*Globicephala macrorynchus*	559	260	193	NA
Sei whale	*Balaenoptera borealis*	381	237	231	159
Striped dolphin	*Stenella coeruleoalba*	341	287	286	NA
Blue whale	*Balaenoptera musculus*	281	194	189	104

Table 2. Test values for the area under the curve (AUC) obtained when testing predictive capacity of models (targeted background, non-targeted background and null) at 2 km spatial resolution with no chlorophyll variables. AUC was obtained using a spatio-temporal masked cross-validation approach and an independent dataset. Results show the means (±SD) of all AUC runs. For the cross-validation scenario, SD was calculated from 10 runs and 5 folds (50 AUC values). For the independent dataset, it was calculated from the AUC values obtained from 10 runs of the model (10 AUC values). Values in **bold**

	8 d			Month		
	Target	Non-target	Null	Target	Non-target	Null
Cross-validation						
Sperm whale	**0.84** **(±0.01)**	0.81 (±0.02)	0.83 (±0.02)	**0.84** **(±0.01)**	0.81 (±0.02)	0.83 (±0.02)
Pilot whale	**0.91** **(±0.02)**	0.86 (±0.02)	0.87 (±0.06)	0.9 (±0.02)	0.85 (±0.02)	0.86 (±0.06)
Risso’s dolphin	0.73 (±0.04)	0.69 (±0.04)	**0.75** **(±0.02)**	0.73 (±0.04)	0.69 (±0.03)	**0.76** **(±0.03)**
Striped dolphin	**0.86** **(±0.01)**	0.79 (±0.01)	0.81 (±0.02)	0.84 (±0.01)	0.76 (±0.01)	0.81 (±0.02)
Atlantic spotted dolphin	**0.85** **(±0.04)**	0.81 (±0.01)	0.75 (±0.07)	0.72 (±0.08)	0.64 (±0.07)	0.75 (±0.07)
Sei whale	**0.81** **(±0.04)**	0.80 (±0.04)	0.73 (±0.08)	0.72 (±0.04)	0.69 (±0.04)	0.73 (±0.08)
Fin whale	**0.89** **(±0.02)**	0.87 (±0.02)	0.75 (±0.07)	0.73 (±0.08)	0.67 (±0.09)	0.75 (±0.07)
Blue whale	0.92 (±0.08)	**0.93** **(±0.03)**	0.81 (±0.07)	0.8 (±0.05)	0.75 (±0.05)	0.81 (±0.07)
Short-beaked common dolphin	0.58 (±0.04)	**0.59** **(±0.02)**	0.57 (±0.02)	**0.59** **(±0.04)**	**0.59** **(±0.02)**	0.57 (±0.02)
Bottlenose dolphin	0.55 (±0.04)	0.53 (±0.03)	**0.58** **(±0.04)**	0.55 (±0.03)	0.52 (±0.03)	**0.58** **(±0.04)**
Independent dataset						
Sperm whale	0.81 (±0.01)	**0.82** **(±0.01)**	0.66 (±0.01)	0.79 (±0.01)	**0.82** **(±0.02)**	0.61 (±0.02)
Risso’s dolphin	**0.71** **(±0.01)**	0.63 (±0.01)	0.7 (±0.01)	0.65 (±0.02)	0.63 (±0.01)	0.67 (±0.02)
Striped dolphin	0.56 (±0.01)	0.63 (±0.01)	0.58 (±0.08)	0.59 (±0.01)	**0.67** **(±0.01)**	0.6 (±0.10)
Atlantic spotted dolphin	0.64 (±0.01)	**0.66** **(±0.01)**	0.51 (±0.01)	0.58 (±0.01)	0.6 (±0.01)	0.54 (±0.01)
Short-beaked common dolphin	0.51 (±0.01)	**0.64** **(±0.01)**	0.52 (±0.02)	0.45 (±0.01)	0.63 (±0.01)	0.52 (±0.02)
Bottlenose dolphin	0.37 (±0.01)	**0.68** **(±0.01)**	0.29 (±0.01)	0.39 (±0.01)	0.66 (±0.02)	0.31 (±0.01)

Table 3. Test values for the area under the curve (AUC) obtained when testing predictive capacity of models (targeted background, non-targeted background and null) at 4 km spatial resolution with chlorophyll variables included. AUC was obtained using a spatio-temporal masked cross-validation approach. Results show mean (±SD) AUC. Values in **bold**

	8 d			Month		
	Target	Non-target	Null	Target	Non-target	Null
Sei whale	**0.82 (±0.05)**	0.81 (±0.05)	0.72 (±0.05)	0.67 (±0.09)	0.64 (±0.09)	0.70 (±0.08)
Fin whale	**0.88 (±0.05)**	0.87 (±0.06)	0.77 (±0.06)	0.7 (±0.06)	0.64 (±0.07)	0.75 (±0.08)
Blue whale	**0.94 (±0.02)**	0.93 (±0.06)	0.82 (±0.05)	0.77 (±0.08)	0.72 (±0.09)	0.81 (±0.07)

Table 4. Effects of the 4 scenarios tested on the modelling processes using all results: (1) spatial coverage of environmental predictors (2 vs. 4 km); (2) temporal coverage of environmental predictors (8 d vs. monthly); (3) spatio-temporal generation of background points (targeted vs. random selection) and (4) total number of background points generated (10000 vs. 50000). Results are presented for each species and as a general overview. Arrows and mathematical symbols indicate the performance of each method when compared to the alternative (: equal, ≅: almost equal, ↑: better, ↓: worse).

	Spatial scale		Temporal scale		Selection background points		No. background points	
	2 km	4 km	8 d	Month	Targeted	Random	10000	50000
Sperm whale	≅		≅		↑≅	↓≅	=	
Pilot whale	≅		↑	↓	↑	↓	=	
Risso’s dolphin	≅		≅		↑	↓	=	
Striped dolphin	≅		↑	↓	↑	↓	=	
Atlantic spotted dolphin	≅		↑	↓	↑	↓	=	
Sei whale	≅		↑	↓	↑≅	↓≅	=	
Fin whale	≅		↑	↓	↑≅	↓≅	=	
Blue whale	≅		↑	↓	↑≅	↓≅	=	
Short-beaked common dolphin	≅		≅		↓≅	↑≅	=	
Bottlenose dolphin	≅		≅		↓≅	↑≅	=	
General	≅		↑≅	↓≅	↑≅	↓≅	=	

Fig. 1. Study area, showing 2 km grids sampled from 2009 to 2015 by the whale watching companies in the eastern and central groups of the Azores Islands. Lines represent the 1000 m bathymetric lines

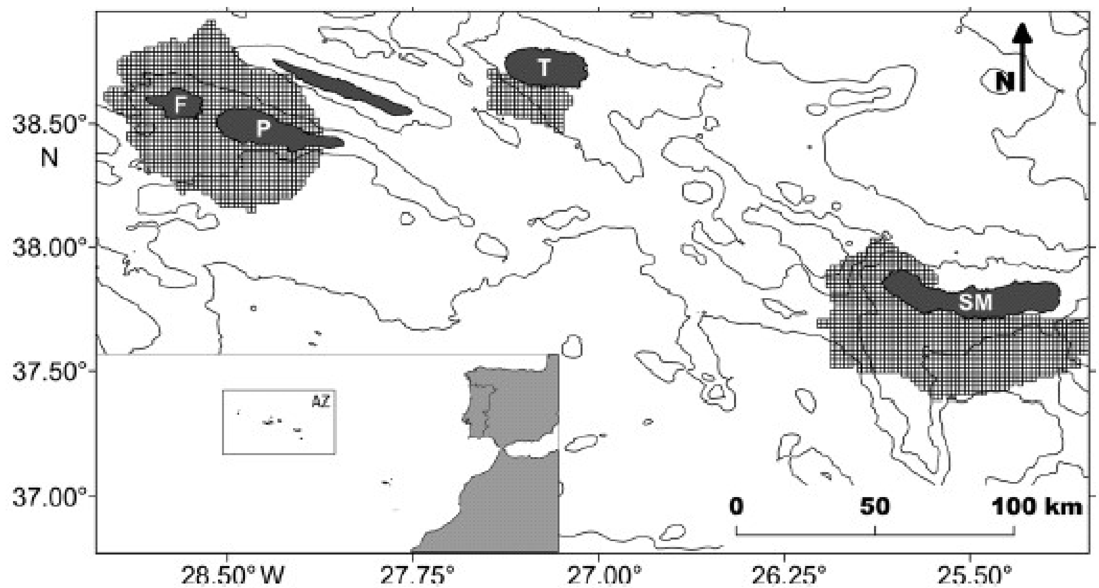

Fig. 2. Canyon-like features (represented in black) from the central and eastern groups of the Azores area derived from the EMODnet Bathymetry using the topographic position index

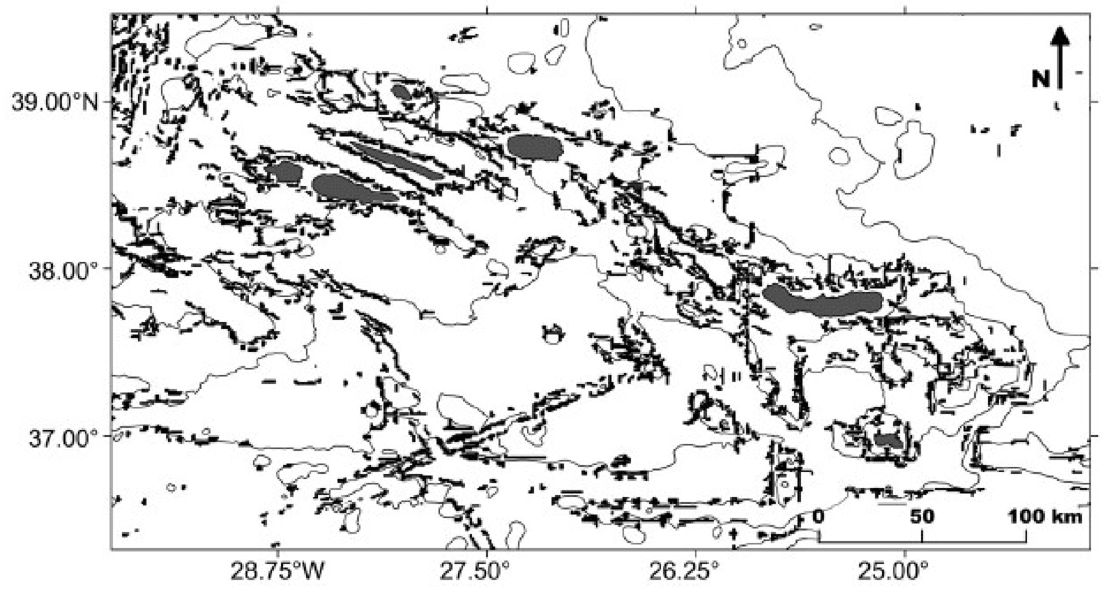

Fig. 3. Comparison of the general area under the curve (AUC) test when using the spatio-temporal cross-validation approach and pooling together results for all species, folds and iterations for: (1) targeted background (target, T), non-targeted background (non-target, NT) and null models; (2) environmental variables at temporal scales (8 d versus 1 mo) and environmental variables at spatial scales (2 versus 4 km). Significant differences calculated using a Kruskal-Wallis with a Nemenyi post hoc test are noted with letters

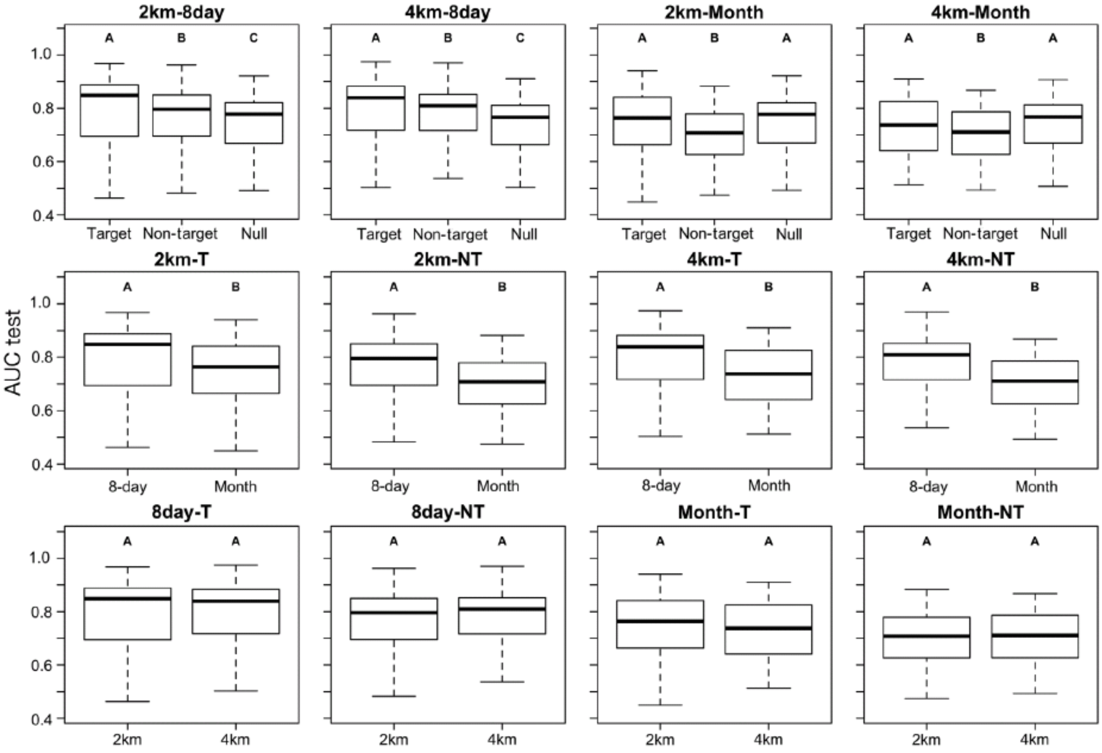

Fig. 4. Example of suitability maps (together with SD) for Atlantic spotted dolphins on a 20 km radius around São Miguel island (Azores) for 4 months (February, May, July, November), representing 4 seasons (winter, spring, summer, autumn). Left column refers to the monthly averaged suitability; right column refers to suitability SD for all weeks corresponding to that month. Maps are presented in 2 × 2 km grid. Maps for all species and months are presented in Supplement 4