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# Alongside but separate: Sympatric baleen whales choose different habitat conditions in São Miguel, Azores

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## ABSTRACT

Fin whales and sei whales are two migratory baleen whale species sighted every year across the waters of the Azores. Improved understanding of the ecological niche and habitat requirements of these baleen whales is needed to identify persistent or predictable oceanographic events that may set the time of their migration, as well as local or ephemeral oceanographic features that may aggregate their prey in a particular area. In dynamic environments such as the open ocean, mesoscale and submesoscale features can become decisive to determine the distributions of highly mobile species such as baleen whales. In this study, we analyse the habitat preferences of fin whales and sei whales around São Miguel Island (Azores) using environmental variables at different temporal and spatial scales. For both species, model results showed a clear influence of variables linked with primary production and therefore, prey availability; as well as a noticeable preference for oceanographically dynamic areas which directly affect distribution and aggregation of prey. Those environmental choices may indicate different levels of foraging habitat use for both species. Differences were found between the species, highlighting preferences for colder waters in fin whales and areas with stronger sea surface temperature gradients in sei whales. Model results obtained for fin whales were similar with those previously published for blue whales, suggesting that both species make similar use of the waters around São Miguel, often foraging during the migration across these waters. Results for sei whale, however, emphasize dynamic variables, indicating that travelling may prevail over feeding behaviour during their migration by the Azores.

## 1. Introduction

Interference between coexisting species is generally considered to be minimal when food is not limited (Crombie, 1945; Connell, 1983; Schoener, 1983). However, similar ecological niches or limited resources may cause interspecific interactions such as: (1) competition, as suggested by Kasamatsu et al. (2000) in Antarctica for minke and blue whales, and by Whitehead and Carlson (1988) in Newfoundland for fin and humpback whales; (2) or habitat or niche partitioning (in response to competition), for example to maximize resource exploitation, as suggested by Friedlaender et al. (2009) in Antarctica for minke and humpback whales, or through different feeding strategies as observed by Friedlaender et al. (2015) in California for fin and blue whales. Sympatric species may therefore react differently to changes in the environment, shifting their distribution and/or adapting their behaviour. For instance, in the Western North Atlantic, sympatric baleen whales (fin, blue, sei and humpback whales) have shifted their distributions differently in the last decade, following shifts in the distributions of their

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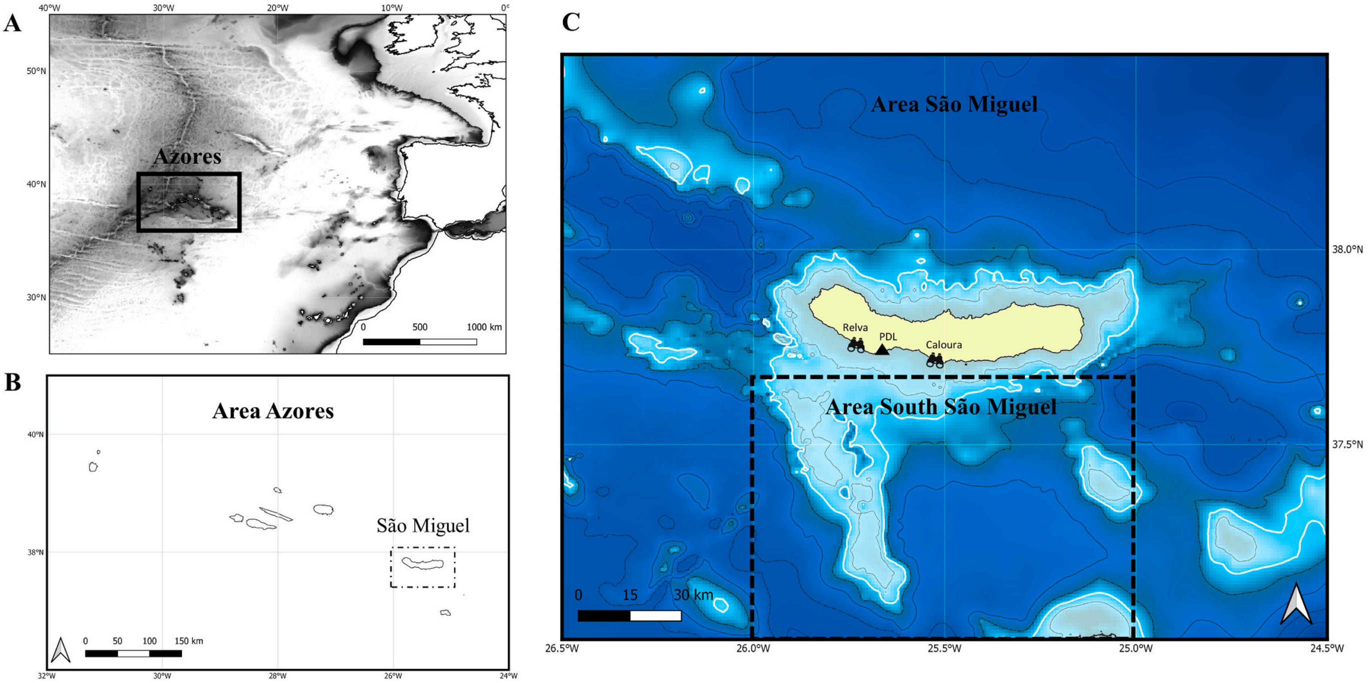

**Fig. 1.** Study area. **A)** Location of the Azores archipelago (black square) in the Atlantic. **B)** Enlarged view of the Azores archipelago in which our study area São Miguel Island is marked with a dotted black square (enlarged in C). **C)** São Miguel bathymetric map with depth contour lines every 500 m; in white bold colour is highlighted the 1000 m bathymetric line. The main two lookout points (Relva and Caloura) and the main base harbour (Ponta Delgada -PDL-) are indicated. The three indicated areas, Azores – in panel B -, and São Miguel and Area south São Miguel – in panel C - are the ones considered to calculate the environmental variables.

prey, which at the same time are likely to have been related to changes in their environment (Davis et al., 2020).

In the Azores, fin whale *(Balaenoptera physalus)* and sei whale *(Balaenoptera borealis)* are sighted every year in spring and summer (Visser et al., 2011; Silva et al., 2003, 2013, 2014; González García, 2019). Until February 2018, both species were listed by the IUCN as endangered due to the decline of their populations by at least 70% over the last three generations (i.e., over periods of approximately 78 and 93 years respectively) (Reilly et al., 2008, 2013; Cooke, 2018a). Since 2018, fin whales have been categorised as vulnerable (Cooke, 2018b) because the estimated rates of decline over the last three generations exceed the threshold of 50%.

At least some of the individuals of both species sighted in the archipelago are known to perform a long migration between North Atlantic feeding grounds used in summer and wintering lower latitude breeding areas (Olsen et al., 2009; Silva et al., 2013; Prieto et al., 2014; Pérez-Jorge et al., 2020). Some fin whales sighted in the Macaronesia region are thought to migrate along shorter routes (Aguilar, 2009; Edwards et al., 2015; Valente et al., 2019), or even to undertake alternative migration routes. For instance, individuals sighted in autumn in the mainland coast of NW Iberia were recorded in Azorean waters during summer (Díaz López and Méthion, 2019; Silva et al., 2019). Findings using acoustic detection suggest that the Azores is a wintering area for fin whales, which have been acoustically detected from autumn to spring; but mainly a transit route for sei whales, which have been acoustically detected in spring and autumn, according to the timing of the expected migration (Nieukirk et al., 2004; 2012; Romagosa et al., 2020).

Nevertheless, there are several possible reasons for these baleen whales to occur in the Azores: it may be the location of the archipelago in mid-Atlantic waters that makes it an excellent topographic cue along whales' migration route (e.g., Bauer et al., 2011; Luschi, 2013; Garrigue et al., 2015), or it could be due to the excellent foraging opportunities arising around the islands and/or related to the complex oceanographic regime of the region (Sala et al., 2015; Caldeira and Reis, 2017; González García et al., 2018). Silva et al. (2013) showed that fin whales perform "Area Restricted Search" (indicative of foraging behaviour (MacArthur and Pianka, 1966; Emlen, 1968) during most of their time around the Azores. They apparently forage for a few days in the Azores before continuing their migration further north. Visser et al. (2011) suggested that feeding behaviour of baleen whales around the islands was synchronized with the spring bloom. However, Prieto et al. (2014) reported no indications of foraging in sei whales around the Azores. Those findings were also supported by analyses of whale occurrence data from the Azorean Fisheries Observer Program (POPA) with environmental niche models in which primary production related variables were retained for fin and blue whales, but not for sei whales (Prieto et al., 2016; Tobeña et al., 2016).

Species distributions are usually driven by the distribution of their food. Fin whales feed mainly on euphausiids, but they also eat small schooling fish such as capelin, herring, and blue whiting and even zooplankton such as copepods (Christensen et al., 1992). Sei whales have a more varied diet, including copepods, euphausiids, amphipods, decapods, cephalopods and fish. In the North Atlantic, they feed primarily on calanoid copepods such as *Calanus fimmarchicus,* switching in some Atlantic areas to euphausiids (Prieto et al., 2012). Both fin and sei whales can vary their diet according to local and seasonal prey availability (Christensen et al., 1992; Sigurjonsson and Vikingsson, 1997; Prieto et al., 2012).

Our understanding of the interactions between the marine environment and its inhabitants, at different scales, also allows us to perceive how the same ecological niche for large mobile marine species might change geographically over time. These insights should enable us to devise appropriate management and conservation plans for threatened migratory species, such as the baleen whales considered here.

In this paper we use Generalized Additive Models (GAMs) to explore the habitat preferences at multiple environmental scales, of the two most frequently sighted baleen whale species (fin whale and sei whale) in São Miguel (Azores) between 2008 and 2014. We use cetacean sightings collected by a whale watching company, and environmental

**Table 1**
Main environmental variables used in this study.

| VARIABLES (source, units) | SPATIAL RESOLUTION | TEMPORAL RESOLUTION |
|---|---|---|
| **Depth** (GEBCO-08, m) | 30”arc (∼1 km) | static |
| **Distance to the coastline** (IH, m) | High resolution | – |
| **CHL** (GlobColour, mg/m$^3$) | 1 km | Daily, 8-days, monthly |
| **MSLA-UV** (AVISO, m/s) | ¼° | Daily |
| **SST** (OSTIA, K) | 0.05° grid (∼6 km) [*10*–100 km *effective*] | Daily |
| **SST** (MetOp, K) | 1 km | 3-5 images/day |
| **WIND** (ECMWF, m/s) | 0.5° grid (∼54 km) [79 km *effective*] | 6 h |

Abbreviations used are: **GEBCO-08**: General Bathymetric Chart of the Oceans. **IH:** Instituto Hidrográfico de Portugal. **CHL**: chlorophyll concentration. **GlobColour**: European Node for Global Ocean Colour. **MSLA-UV**: Mean Sea Level Geostrophic Velocity Anomalies. **AVISO**: satellite altimetry data. **SST**: Sea Surface Temperature. **OSTIA**: Operational SST and Sea Ice Analysis. **MetOp**: Advanced Very High Resolution Radiometer (AVHRR) on board the Meteorological Operational satellite. **ECMWF**: European Centre for Medium-Range Weather Forecasts.

data at three temporal resolutions (daily, weekly and monthly) and two spatial resolutions (low −0.5°- and high −0.05°-) in order to encompass the scales at which relevant oceanographic processes occur in the region. Consideration of larger scales/coarser resolutions allows us to account for well-established or persistent events such as the spring bloom, which can be a major reason for whales to be attracted to the region every year. Working at smaller scales/finer resolutions allow us to capture more ephemeral or local processes, such as local upwelling or smaller fronts, filaments, or eddies, which can affect the short-term local distribution of the whales once they have arrived in the region. We analyse the temporal distribution of the two species over the seven years of study and address their habitat preference around São Miguel, investigating the role that the Azores may play in their migration journeys.

## 2. Methods

### 2.1. Study area

The Azores archipelago is located in mid-Atlantic waters (36-41°N, 24-32°W) and comprises nine volcanic islands surrounded by deep waters. Our study area is in the Oriental group, off the south coast of São Miguel Island (37-38.5°N, 26.5–24.5°W) (Fig. 1). The archipelago has a very dynamic oceanographic regime which also shows a well-defined seasonality. Eddies and filaments arise mainly from the North Atlantic Current (NAC) (at the north of the archipelago) and the Azores Front/Current System (AF/AC) (at the south), which limits the North Atlantic Subtropical Gyre (Pérez et al., 2003; Dave et al., 2015; Amorim et al., 2017; Caldeira and Reis, 2017). These features are known to enhance and retain primary production, thus enhancing secondary production throughout the trophic chain and favouring the aggregation of marine life. Minimum temperatures (around 15 °C) are usually reached in March, while the warmest period is usually in late summer-early autumn, when temperature rises to around 25 °C. Chlorophyll concentration usually peaks in spring, when the spring bloom takes place, and decreases to its minimum in summer months.

Our study area, around São Miguel Island, is characterized by deep waters very close to the shore. It includes two oceanic trenches with more than 3600 m deep (Fossa do Hirondelle and Bacia de São Miguel, NW and SE of the island respectively) and a shallower platform (500–1000 m) that extends 50 km south on the SW of the island (Fig. 1C). This area is also frequently affected by the presence of mesoscale and submesoscale oceanographic features derived from the AF/AC, and its interaction with the surrounding bathymetry (González García et al., 2018).

### 2.2. Cetacean data

Cetacean occurrence data were collected between May 2008 and December 2014 along the south coast of São Miguel (Azores) during whale watching tours run from Ponta Delgada. Cetaceans were located from strategic observation points on land by experienced observers. These lookouts started searching for animals every day before boats go out at sea, scanning the area with powerful binoculars (Steiner 20 × 80 mm). The two more frequently used lookout locations were Caloura and Relva (Fig. 1C). Boats then travelled towards the cetaceans following the indications given from land and complying with the requirements of the regional legislation (DLR nº 10/2003/A and DLR nº13/2004/A) mainly regarding the direction and speed of approach, distances to be maintained, number of boats in the area and duration of the observations. Once the boat was close to the animals, species, GPS location, behaviour, number of individuals, group composition, association with other cetacean species and other relevant information were noted by on-board observers. Only sightings with a reliable location and a confirmed species identification (except for beaked whales, for which identification to genus was accepted) were considered for analyses, approximately, 93% of the records.

Whale watching tours were conducted year-round but were more frequent in summertime, when the sea conditions and numbers of tourists were more favourable for the activity. Since sightings were recorded mostly following land observations, it is not possible to derive a meaningful measure of search effort. Although number of trips per year varied considerably (minimum of 227 in the six months surveyed in 2008, maximum of 422 in the entire year 2014), overall, this variation was reasonably consistent throughout the study period, with no significant difference in number of trips across the seven years (Kruskal-Wallis Chi-squared = 4.6437, df = 6, p = 0.5903). Further information about the study area and observation protocols can be found in González García et al. (2018).

### 2.3. Environmental data

We used the static variables depth (from GEBCO) and slope (derived from depth) with a resolution of 30 arc-seconds (∼1 km) (Table 1). Distance to the coast was calculated with reference to a high-resolution vector of coastline data provided by the *Instituto Hidrográfico de Portugal*. We calculated the available depth in the study area considering the sampled area the Minimum Convex Polygon containing 100% of the sightings recorded.

The dynamic variables were all downloaded for the study years (2008–2014) and prepared at three different temporal scales (daily, weekly and monthly) (Table 1). For Sea Surface Temperature (SST) we also used two different spatial resolutions. The high spatial resolution SST product was obtained from the Advanced Very High-Resolution Radiometer (AVHRR) on board the Meteorological Operational satellite (MetOp). It provides data with a spatial resolution of around 1 km (EUMETSAT/OSI-SAF, 2008), which allow us to account for local and short-term oceanographic events, providing a more detailed view of the study area. For the subsequent analyses, we discarded values with a poor quality index (“bad”, “not usable” and “unprocessed”). The low spatial resolution SST product, the Operational SST and Sea Ice Analysis (OSTIA), reduces data loss and simplifies data processing, accounting at the same time for well-established or more persistent features. It has a gridded resolution of 0.05°, although the effective spatial resolution is around 50 km (Reynolds et al., 2013). From this latter dataset, thermal fronts were derived using a Canny edge function (Canny, 1987) with an upper threshold of 1 °C/100 km and a lower threshold of 0.4 °C/100 km. Note that thermal fronts have been established within a threshold of gradients to select only representative fronts. For MetOp and OSTIA

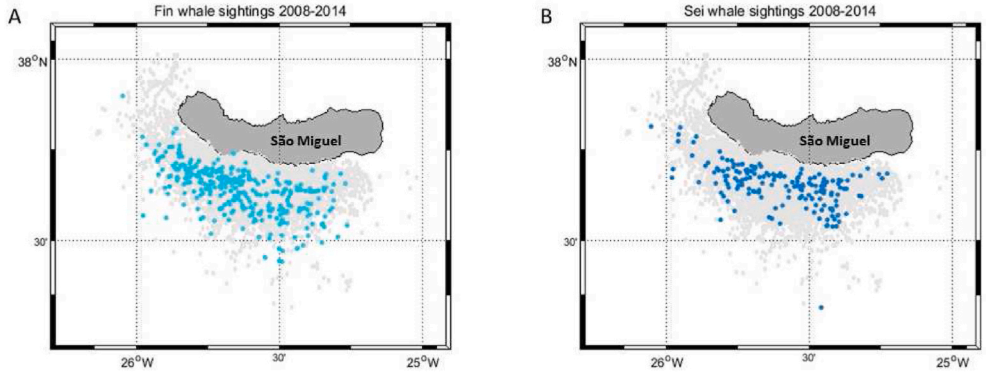

**Fig. 2.** Fin whale (A) and sei whale (B) sightings registered between 2008 and 2014 in blue, with sightings of all the non-targeted species during the same period (used as pseudo-absences for modelling) in grey as background.

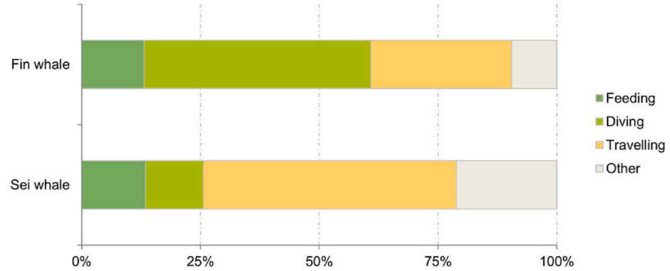

**Fig. 3.** Fin whale and sei whale behaviour registered during the study period. Percentages of feeding, diving (likely including foraging dives), travelling, and other behaviours (such as socialising, resting or not identified ones).

data, daily, weekly and monthly gradients, averages and standard deviations were calculated for each sighting and for São Miguel (37-38.5°N, 26.5–24.5°W) and the entire archipelago (35-42°N, 33-23°W). Climatological means were calculated for each day of the year, each week and each month over the entire study period. An SST anomaly for each sighting was calculated, expressing the SST at the sighting location in relation to the climatological mean value.

Chlorophyll concentration is usually used as a proxy for primary production. It was retrieved from GlobColour (http://globcolour.info), with a spatial resolution of 1 km on daily and 8-day composites. Monthly composites were calculated from the 8-day files. Mean and standard deviation (daily, weekly and monthly) were calculated for each sighting and for the three areas considered: the Azores archipelago (35-42°N, 33-23°W), São Miguel (37-38.5°N, 26.5–24.5°W) and south of São Miguel (37-37.7°N, 26-25°W). Mean chlorophyll concentrations, at a given location, from 1 to 17 weeks prior to a sighting were also calculated. Three chlorophyll Indices were created to place the concentration of chlorophyll in the study area in the context of average concentration in

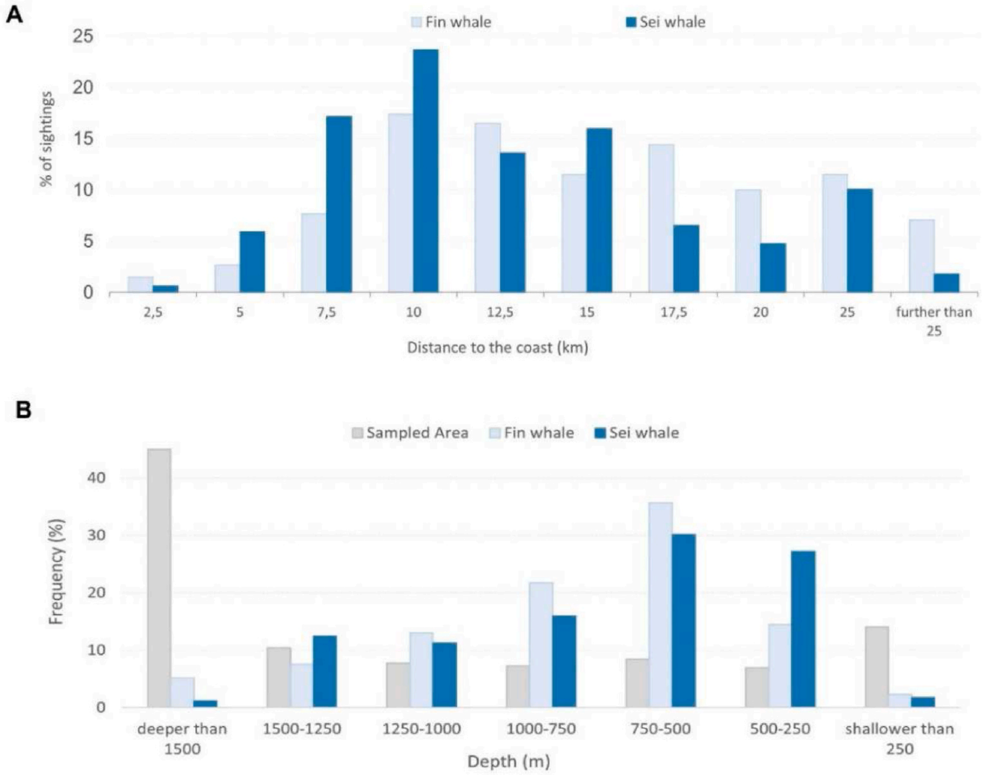

**Fig. 4.** A) *Distance to the coast* of fin and sei whale sightings. On the x-axis, distance to the coast with intervals of 2.5 km; on the y-axis, percentage of sightings of fin whales (light blue) and sei whales (dark blue). Notice sei whale sightings are usually closer to the shore. **B) *Depth* values of the sampled area, fin and sei whale sightings.** On the x-axis, depth intervals of 250 m; on the y-axis, percentage of sightings of fin whales (light blue), sei whales (dark blue) and percentage of grid cells of the sampled area (grey), which corresponds to the area of the Minimum Convex Polygon containing 100% of the sightings.

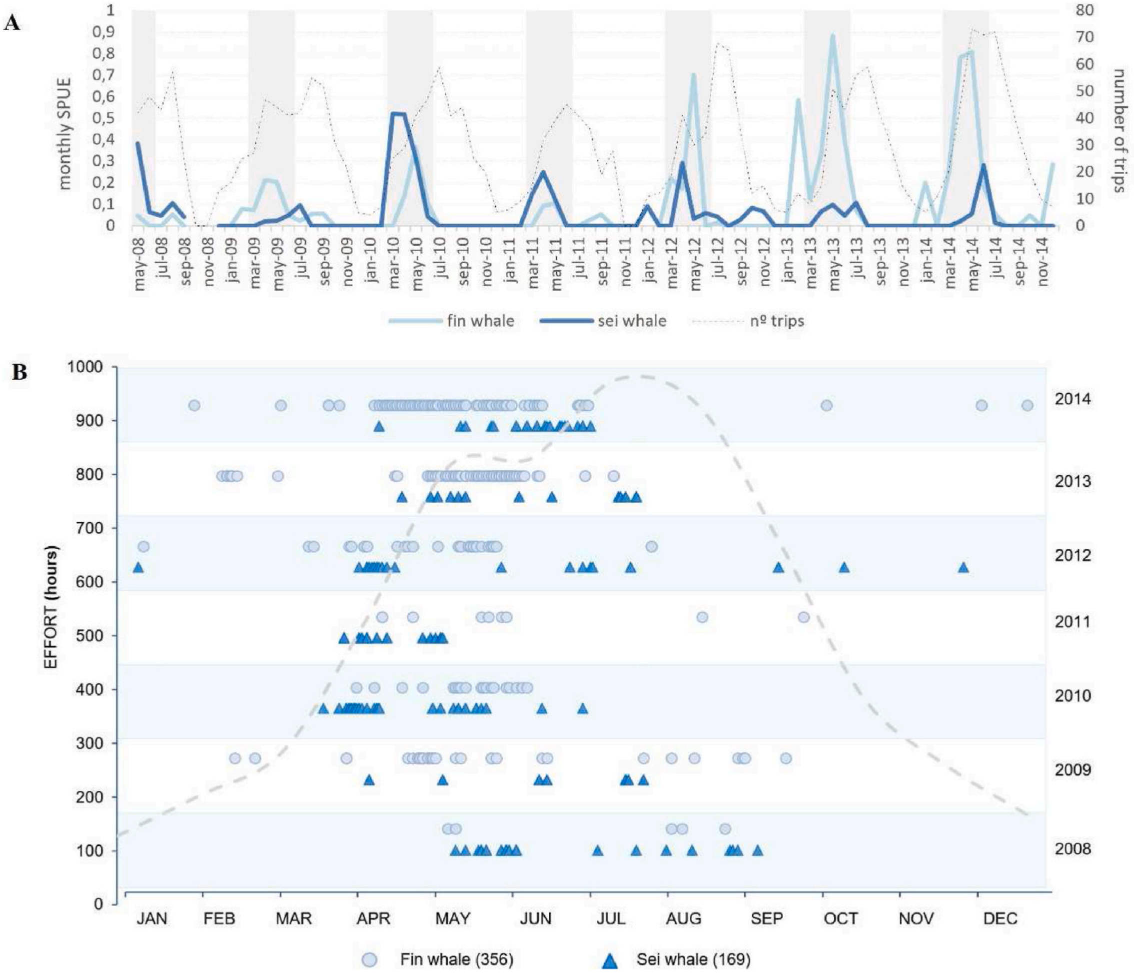

**Fig. 5.** Temporal distribution of fin and sei whales between May 2008 and December 2014. A) Monthly SPUE for fin and sei whales (number of sightings/number of trips) (light and dark blue lines, read on the left y-axis) and number of trips per month (black dotted line, read on the right y-axis). **B)** Daily sightings and hours of effort recorded. Left y-axis corresponds to the monthly number of hours spent at sea (effort) during the study period, represented with a dashed line in the graph. Right y-axis shows the years, and x-axis, the months.

the surrounding area. They were calculated as ratios between the highest values of chlorophyll in a small area and the average concentration over a bigger area (Supp. Fig. 1). Index 1 was a ratio between the highest value in coastal São Miguel (37.65–37.75°N, 25.8–25.3°W) and the average for São Miguel (37-38.5°N, 26.5–24.5°W); Index 2 compared south São Miguel (37-38°N, 26-25°W) with a bigger area south of the Azores (30-38°N, 32-22°W); and Index 3 compared the Azores (35-42°N, 33-25°W) and a bigger Atlantic area (30-48°N, 38-15°W).

To account for the oceanographic mesoscale dynamism, we calculated the Eddy Kinetic Energy (EKE) from the gridded geostrophic velocity anomalies (Mean Sea Level Anomalies: MSLA-UV) distributed by AVISO (now accessible at http://marine.copernicus.eu/). We calculated seasonal EKE, considering as winter December-January-February; spring March-April-May; summer June-July-August; and autumn September-October-November.

Wind data were obtained, only for the daily datasets, from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA-Interim 0’5 6-hourly surface analysis. This provides a gridded resolution of 0.5° (~54 km), but an effective spatial resolution of around 79 km (Dee et al., 2011).

After processing the data retrieved, we created six extensive sets of environmental variables: low spatial resolution daily (39 variables), weekly (37) and monthly (27); and high spatial resolution daily (40 variables), weekly (40) and monthly (21) (Supp. Tables 1-7). In order to reduce the number of variables contained in each dataset, we followed a selection process. Firstly, we analysed collinearity using Pearson correlation matrices, which were visualized as dendrograms. We retained all the variables with a distance of at least 0.8 from each other (Marubini et al., 2009; MacLeod et al., 2008) and for lower distance values, at least one variable per dendrogram branch, prioritizing those with fewer missing values. We also calculated the Variance Inflation Factors (VIF) for each set of variables, removing (one by one) the variables with the highest VIF. Only the variables with VIF lower than 5 were retained (Rogerson, 2001). We thus ended up with six reduced datasets (Supp. Tables 1-7): low spatial resolution daily (19 variables), weekly (17) and monthly (17), and high spatial resolution daily (22 variables), weekly (20) and monthly (15).

### *2.4. Spatio-temporal analyses*

Total number of sightings, and number of sightings of fin whales and sei whales were mapped in a grid of 5 × 5 $\text{km}^2$ using QGIS (version 3.10.10 - A Coruña) to look for potential differences in their spatial distribution. Histograms were used to visualize distance to the coast for both species, also depth values for the surveyed area, considered as the Minimum Convex Polygon containing 100% of the sightings.

Temporal distribution was analysed for each species considering Sightings Per Unit of Effort (SPUE) to account for the search effort. We considered as unit of effort a whale watching trip, which is commercially

**Table 2**

Summary of the GAM results for the six obtained models for fin whale distribution.

| FIN WHALE | | LOW SPATIAL RESOLUTION | HIGH SPATIAL RESOLUTION |
|---|---|---|---|
| **DAILY** | **AUC** | 0.805 | 0.725* |
| | **AUC SD** | 0.138 | 0.132* |
| | **TSS** | 0.572 | 0.326* |
| | **DEV (%)** | 29 | 22.9 |
| | **n** | 6962 | 3354 |
| | **Explanatory Variables** | Depth, dist. coast, SST gradient São Miguel, SST climatological daily mean, chlorophyll week 8, chlorophyll week 12, EKE seasonal São Miguel | Dist. coast, SST mean São Miguel, EKE seasonal São Miguel |
| **WEEKLY** | **AUC** | 0.812 | 0.785 |
| | **AUC SD** | 0.146 | 0.147 |
| | **TSS** | 0.600 | 0.550 |
| | **DEV (%)** | 34.1 | 31.5 |
| | **n** | 6905 | 7246 |
| | **Explanatory Variables** | Depth, slope, dist. coast, SST gradient São Miguel, SST gradient Azores, SST climatological weekly mean, SST anomaly São Miguel, chlorophyll south São Miguel, chlorophyll Azores, chlorophyll week 12, EKE seasonal São Miguel | Depth, slope, dist. coast, SST climatological weekly mean, chlorophyll SD south São Miguel, chlorophyll Azores, chlorophyll week 8, EKE seasonal São Miguel, EKE seasonal Azores |
| **MONTHLY** | **AUC** | 0.756 | 0.795 |
| | **AUC SD** | 0.104 | 0.117 |
| | **TSS** | 0.534 | 0.539 |
| | **DEV (%)** | 32.2 | 29.3 |
| | **n** | 7509 | 7361 |
| | **Explanatory Variables** | Depth, dist. coast, SST gradient São Miguel, SST gradient Azores, SST SD gradient Azores, SST anomaly São Miguel, SST anomaly Azores, chlorophyll south São Miguel, chlorophyll SD Azores, chlorophyll month 3 | Dist. coast, SST of the nearest front, chlorophyll SD São Miguel, chlorophyll index 4, chlorophyll month 4, EKE seasonal São Miguel, EKE seasonal Azores |

Abbreviations used are: **AUC**: Area Under the Curve of the Receiving Operating Characteristic plot. **AUC SD**: Standard Deviation of the AUC. **TSS:** True Statistic Skill. **DEV (%)**: Percentage of deviance explained in the model. **n**: total number of cetacean records (including presence and pseudo-absence) used in the model. **SST**: Sea Surface Temperature. **EKE**: Eddy Kinetic Energy.

* For this model, k-fold cross-validation could not be done for all subsets due to missing values.

defined by the company in duration and time schedule and has been maintained under the same standards throughout the study period. Each trip usually starts with an initial route informed by the on-land observers followed by a period of 2.5–3 h at sea (2.8 ± 0.17 h for our study period). Land observers start searching for animals around 1–1.5 h earlier than the departure time and remain on their position looking for animals until the boat finalizes the observations for the trip. Trips are carried out in the morning and/or afternoon. It should be noted that cetaceans might not be seen on every trip (absent in $<1\%$) and that the boat could encounter further whales or dolphins not originally spotted from land. The SPUE was defined as the number of sightings of each whale species divided by the total number of trips over each month or whale season. The whale season was considered as extending from March to June every year, a period that includes 89.4% of the recorded sightings of fin whales and 83.4% of sei whales over the study period.

## *2.5. Habitat preference*

Habitat preferences for fin and sei whales were analysed following the modelling approach used by González García et al. (2018) for blue whales. Six different explanatory models were obtained for each species, one for each environmental dataset: low resolution daily, weekly, and monthly, and high resolution daily, weekly, and monthly. To avoid pseudo-replication, a data-thinning process was applied, excluding from modelling sightings of the same species recorded in the same area less than 1 h after the previous sighting, unless photo-identification confirmed that different individuals were involved. We applied Generalized Additive Models with a *logit* link function (which is appropriate for the probability associated with an observation that has only two possible outcomes -presence or absence-) and a binomial distribution. The presence/pseudo-absence approach applied, considers the sightings of the target species as presences, and the sightings of the non-target species as pseudo-absences (Esteban et al., 2013). Note that, when multispecies sightings occur, and therefore, different species are recorded in the same location and time, only one record is kept as a pseudo-absence. This way, we ensure that the location was surveyed at a defined date and time. The selection of uniformly or randomly distributed pseudo-absence points from the study region may fail to account for sample selection bias, as some areas (and times) are more likely to be surveyed than others. As the number of pseudo-absences used here is high (compared to the number of presences), they could be considered as targeted background, as they are representative of the overall conditions in which survey was carried out, and both presence and pseudo-absence (or background points) share the same potential biases (Phillips et al., 2009). In the modelling process, a backwards stepwise selection was applied. The first model for each dataset included all the variables, with the number of splines *(k)* set to 4. Low *k* prevents overfitting as it limits the complexity of the fitted curve. Variables were removed sequentially based on its significance in the model. The overall goodness of fit was compared within nesting models mainly following the Akaike Information Criteria (AIC). Higher number of observations used in the models often increased the AIC, specially on high resolutions, but a compromise was done between sample size and not considerably higher AIC. The best possible final model was chosen selecting the lowest AIC. In some cases, when the p-values and confidence bands of the predictors were rather large, we added some extra model selection steps to discard any variable that did not significantly improve the AIC or the deviance explained of the model (Zuur et al., 2007). Models were evaluated with a k-fold cross-validation, in which we used data from six of the seven years to train the model, and data from the remaining year to test it. To compare models, we calculated the mean Area Under the Curve (AUC) and its standard deviation, across all test years, and the mean True Statistic Skill (TSS) across all test years for each model. An AUC of 0.5 indicate no discrimination better than random, while an AUC of 1 corresponds to a test with perfect discrimination. TSS ranges between $-1$ and $+1$, where $+1$ indicates perfect agreement and values of zero or less indicate a performance no better than random (Allouche et al., 2006). Modelling and validation were analysed in the open-source software R 4.0.3 (R Core Team, 2020). GAM's were conducted using the '*mcgv*' library (Wood, 2011), AUC was obtained with the '*pROC*' package (Robin et al., 2011), and TSS was calculated using '*dismo*' (Hijmans et al., 2011) and '*caret*' (Kuhn, 2008) packages, using as a threshold the value at which sensitivity and specificity were maximized.

In order to test for potential spatial autocorrelation, the residuals from all final models were analysed. Firstly, covariograms were plotted using the R package '*gstat*' (Pebesma, 2004; Gräler et al., 2016), to indicate how covariance changes as a function of the geographical distance between points. Secondly, Moran's I test was applied using the '*DHARMa*' package for R (Hartig, 2022). This test quantifies spatial correlation in two dimensions (i.e., geographically). In order to run the test, jittering was applied to location data to avoid repeated coordinates.

To account for any potential spatial bias effect resulting from data

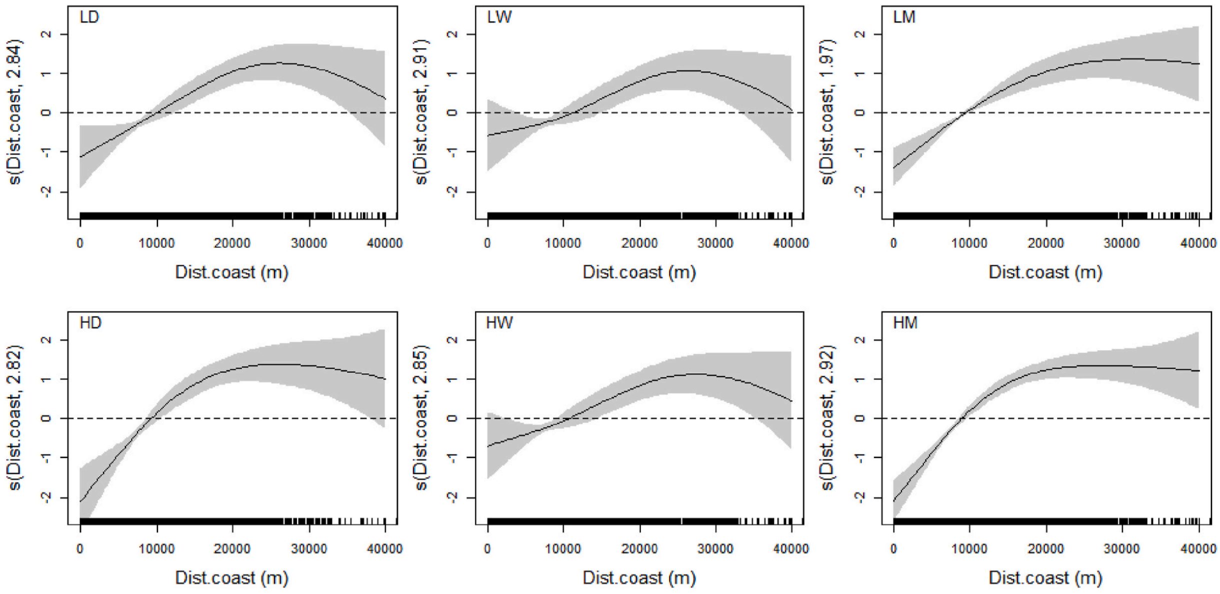

**Fig. 6.** Smoothers for *distance to the coast*, variable selected in all the final GAMs for fin whales. LD = Low resolution daily model. LW = Low resolution weekly model. LM = Low resolution monthly model. HD = High resolution daily model. HW = High resolution weekly model. HM = High resolution monthly model. Black marks on the x-axis indicate the distribution of the observations.

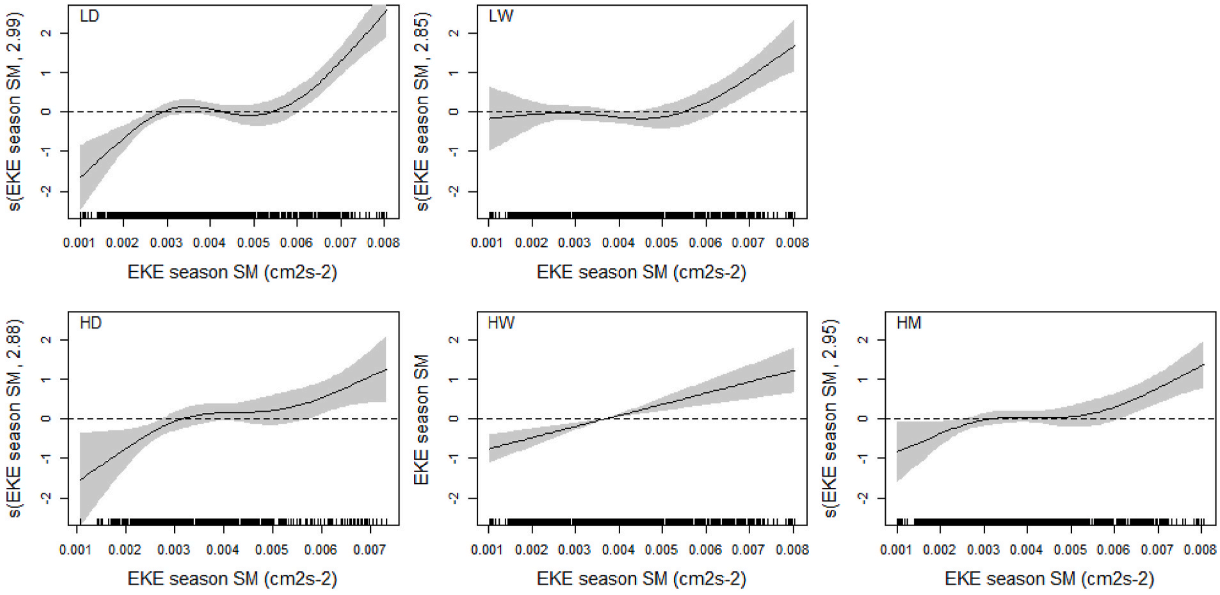

**Fig. 7.** Smoothers for *seasonal Eddy Kinetic Energy (EKE) in São Miguel*, variable selected in all the final GAMs for fin whales, except in the low resolution monthly model. LD = Low resolution daily model. LW = Low resolution weekly model. HD = High resolution daily model. HW = High resolution weekly model. HM = High resolution monthly model. EKE season SM = seasonal Eddy Kinetic Energy in São Miguel. Black marks on the x-axis indicate the distribution of the observations.

collection during the commercial whale watching trips, which departed from Ponta Delgada, the models were fitted again, but using the logarithm of distance to Ponta Delgada as an offset. Distance to Ponta Delgada was not significantly correlated with any predictor. The offset weights sightings according to their distance from the base port, assuming that further locations have less chance of being surveyed. The modelling process otherwise followed the approach already described.

In order to obtain a direct comparison of habitat preferences between the two species studied, GAMs were also applied using only sightings of fin and sei whales as a binary variable (using records of fin whales as presences, and records of sei whales as pseudo-absences), i.e., not considering sightings of any other species as pseudo-absence records. A model was fitted for each dataset. Due to the much smaller sample size, variables with large number of missing values were removed to allow the models to run. AUC and TSS were calculated for the final model without cross-validation.

Behaviour and other field notes were checked to provide more evidence of the possible habitat use of the two baleen whale species considered. However, these data were not recorded in a standardized way over the study period, so they were not used in statistical analyses and are presented only as additional information.

## 3. Results

A total number of 7721 sightings of twenty different species of cetaceans was recorded during the 2364 trips over 1386 non-consecutive

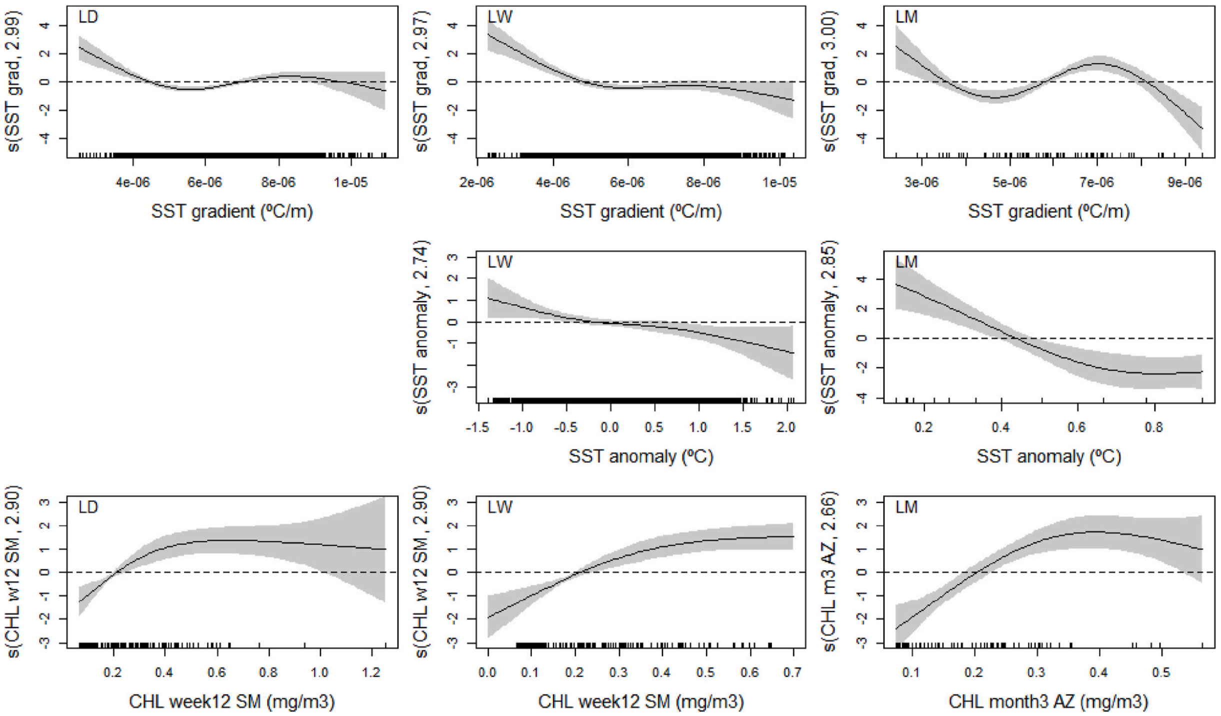

**Fig. 8.** Smoothers of three of the selected variables in the low spatial resolution final GAMs for fin whales. Sea Surface Temperature (SST) gradient in São Miguel, SST anomaly in São Miguel, and chlorophyll concentration around São Miguel 12 weeks (or 3 months) before the sighting. LD = Low resolution daily model. LW = Low resolution weekly model. LM = Low resolution monthly model. SM = São Miguel. AZ = Azores. Black marks on the x-axis indicate the distribution of the observations.

days between May 2008 and December 2014.

Fin whales were recorded on 340 occasions over 193 different days (Fig. 2A). In most of the sightings (73.5%) they were alone or in pairs, although a maximum of 15 individuals were recorded during the same observation. Sei whales were sighted 169 times over 108 days (Fig. 2B): 38% of sightings were of single individuals, and almost 50% were of two or three animals together. The maximum sei whale group size recorded was seven individuals. We should note that the group sizes registered referred to the animals sighted from the boat, and not to the animals present in the area, which could be spread in a larger zone belonging nonetheless to the same group.

After the data thinning process, we retained 304 sightings of fin whales and 156 of sei whales. On six occasions fin whales were observed together with blue whales, and only once together with sei whales.

According to the field notes, fin whales were feeding in 13.2% of the sightings and sei whales in 13.5% (Fig. 3). Diving continuously, especially without following a specific direction moving around over the same area, often is linked with foraging behaviour in baleen whales. This kind of behaviour was noted for fin whales in 47.7% of the records and in 12.2% for sei whales. A high percentage of sei whale sightings were recorded travelling (53.2%), compared to 29.6% for fin whales. Krill patches and whale faeces (mostly from fin whales) were observed on several occasions in the vicinity of the sighting (Supp. Fig. 2). Fin whale faeces were reddish-brownish in colour, while sei whale faeces (described only once in our dataset, in June 2012), were bright yellow.

### 3.1. Spatial distribution

Fin whales and sei whales seem to occupy approximately the same area during the study period (Fig. 2). However, number of sightings for both species was unevenly distributed within the surveyed area (Supp. Fig. 3), with fin whales being sighted more frequently in waters south and south-west of Ponta Delgada. The available depths in the sampled area range from 0 to 3237 m. Around 45% of the sampled area corresponds to waters deeper than 1500 m. Fin whales were found between 0.5 and 37.2 km from the shore (median: 14.4 km) (Fig. 4A). The maximum depth assigned to a fin whale sighting was 3095 m (range: 23–3095 m, median 722 m) (Fig. 4B). Sightings of fin whales were associated with wide range of temperatures (SST): from 15.1 to 24.6 °C (median: 16.8 °C). Sei whales were usually recorded closer to the shore (min. 2.0 km; median 10.3 km) (Fig. 4A). However, the maximum distance at which a whale was recorded during our study period (53.9 km) was also associated with a sei whale. Sei whales were observed within a range of depths between 90 and 2203 m (30.2% of the sightings were recorded between 500 and 750 m; median 660 m) (Fig. 4B). They were sighted in waters with SST between 18.1 and 24.9 °C (median: 20.2 °C).

### 3.2. Temporal distribution

Fin whales and sei whales were sighted every year and their occurrences quite often overlapped in time (Fig. 5). Most of the sightings of both species were recorded between March and June: 89.4% of fin whale sightings and 83.4% of sei whale sightings. To note that survey effort was higher from June to August every year, when 45.5% of the whale watching trips registered were carried out (Fig. 5B). Fin whales were sighted earlier than sei whales in several years. However, sei whales usually extended their occurrence through the summer (and even into the autumn), particularly in 2008 (when they were sighted regularly until September) and 2012 (when there were occasional sightings in September, October and November). The overall SPUE for the whale season (March–June) was 0.291 sightings/trip for fin whales, while for sei whales it was much lower (0.125 sightings/trip).

Over the seven years of the study, fin whales were seen at least once in every calendar month except in November. The SPUE for the whale season varied among years: it was particularly low in 2008 (although in 2008 records started only in May) and 2011 (0.022 and 0.05 sightings/trip respectively), especially if compared with the highest seasonal SPUE, which was 0.581 in 2013. In 2014 was recorded the maximum

**Table 3**
Summary of the GAM results for the six obtained models for sei whale distribution.

| SEI WHALE | | LOW SPATIAL RESOLUTION | HIGH SPATIAL RESOLUTION |
|---|---|---|---|
| **DAILY** | **AUC** | 0.764 | 0.682 |
| | **AUC SD** | 0.105 | 0.106 |
| | **TSS** | 0.447 | 0.458 |
| | **DEV (%)** | 12.9 | 12.8 |
| | **n** | 6943 | 5092 |
| | **Explanatory Variables** | SST gradient São Miguel, SST SD gradient São Miguel, chlorophyll week 12 | Dist. coast, chlorophyll SD south São Miguel, chlorophyll week 12, EKE seasonal Azores |
| **WEEKLY** | **AUC** | 0.686 | 0.700 |
| | **AUC SD** | 0.137 | 0.143 |
| | **TSS** | 0.432 | 0.387 |
| | **DEV (%)** | 18.2 | 16.6 |
| | **n** | 6943 | 6943 |
| | **Explanatory Variables** | Depth, SST climatological weekly mean, chlorophyll south São Miguel, chlorophyll SD south São Miguel, chlorophyll week 12, EKE seasonal Azores | SST gradient São Miguel, SST SD gradient São Miguel, chlorophyll SD south São Miguel, chlorophyll week 12, EKE seasonal Azores |
| **MONTHLY** | **AUC** | 0.618 | 0.722 |
| | **AUC SD** | 0.141 | 0.109 |
| | **TSS** | 0.483 | 0.470 |
| | **DEV (%)** | 21.1 | 15.8 |
| | **n** | 7489 | 7341 |
| | **Explanatory Variables** | Depth, SST gradient São Miguel, SST SD gradient São Miguel, SST gradient Azores, SST SD gradient Azores, SST anomaly SM, distance to the nearest SST front, chlorophyll south São Miguel, chlorophyll Index 3, chlorophyll month 3, EKE seasonal Azores | Dist. coast, SST SD gradient São Miguel, SST of the nearest front, chlorophyll SD São Miguel, chlorophyll month 4, EKE seasonal Azores |

Abbreviations used are: **AUC**: Area Under the Curve of the Receiving Operating Characteristic plot. **AUC SD**: Standard Deviation of the AUC. **TSS:** True Statistic Skill. **DEV (%)**: Percentage of deviance explained in the model. **n**: total number of cetacean records (including presence and pseudo-absence) used in the model. **SST**: Sea Surface Temperature. **EKE**: Eddy Kinetic Energy.

number of fin whale sightings (120), with May as the month with more (19.4% of the overall). In general, the highest monthly SPUE for fin whales was in May (0.484 sightings/trip) (Fig. 5B).

Sei whales were sighted every year, at least once in every calendar month except in February and December (Fig. 5A). The highest monthly SPUE was seen in April (0.181 sightings/trip). Interannual differences were also found, with 2010 by far the year with the highest seasonal SPUE (0.303 sightings/trip), followed by 2008 with 0.21. The lowest seasonal SPUE was in 2009 (0.025 sightings/trip), when only eight sightings were recorded in the entire year (Fig. 5B).

### 3.3. Habitat preference

Fin whale models performed reasonably well in terms of AUC (0.72–0.80), TSS (0.33–0.60) and deviance explained (22.9–34.3%) (Table 2). AUC standard deviation ranged between 0.10 and 0.15 for all models, pointing to no big between-year differences in model performances. It should be noted that the daily high spatial resolution model had the smallest sample size (44% of the total number of sightings) due to many missing values for the high-resolution environmental variables, which did not allow a complete cross-validation. Waters further than 10 km from the coast were preferred in all the final models (Fig. 6). Seasonal EKE for São Miguel was selected in all but one model, the exception being the low resolution monthly model (Fig. 7). The most favourable conditions were those with the highest EKE values available around São Miguel, i.e., EKE stronger than 0.006 $cm^2s^{-2}$.

Three variables were also common for the low spatial resolution models: depth, with slightly preferred waters around 800 m depth; SST gradient around São Miguel, for which low values increase habitat suitability; and chlorophyll concentration 12 weeks (or three months) before the sighting, with a positive influence of values $> 0.2$ mg/m$^3$ (Fig. 8). SST anomaly was selected in weekly and monthly low spatial resolution models, showing a clear preference for colder waters (Fig. 8). In both weekly models, high concentrations of chlorophyll in the archipelago ($>$1.5 mg/m$^3$) increased habitat suitability.

Sei whale models were weaker in terms of both AUC (0.62–0.76), TSS (0.387–0.483) and deviance explained (12.8–21.1%) (Table 3). Performance of all models did not vary notably among years as supported by the slight variations of the AUC standard deviations (0.11–0.14). As for fin whales, the high spatial resolution daily model had a smaller sample size due to missing values in the environmental data products. Nevertheless, 67% of the sightings were used for the model. High values of SST gradient around São Miguel ($>6 \times 10^{-6}$ °C/m) seem to be more suitable in three of the models (low spatial daily and monthly and high spatial weekly) (Fig. 9). The chlorophyll concentration 12 weeks (or three months) before the sighting was retained in all final models except in the high spatial resolution monthly model, in which the concentration four months (instead of three) before the sighting was selected (Fig. 10). Habitat suitability increased generally when the lagged chlorophyll concentrations were higher than 0.2 mg/m$^3$. In both weekly models, habitat suitability increased with high SD values for chlorophyll concentration in the south of São Miguel.

Covariograms of residuals from all final models indicated values of covariance close to zero at all distances. Moran's I tests indicated significant spatial autocorrelation for the high spatial resolution weekly model for fin whale ($p < 0.01$) and weakly significant spatial autocorrelation ($p < 0.05$) for two other models, the low spatial resolution monthly model for fin whale, and the low spatial resolution daily model for sei whale. To account for spatial autocorrelation, Generalized Additive Mixed Models were applied using the *'mgcv'* package for R (Wood,

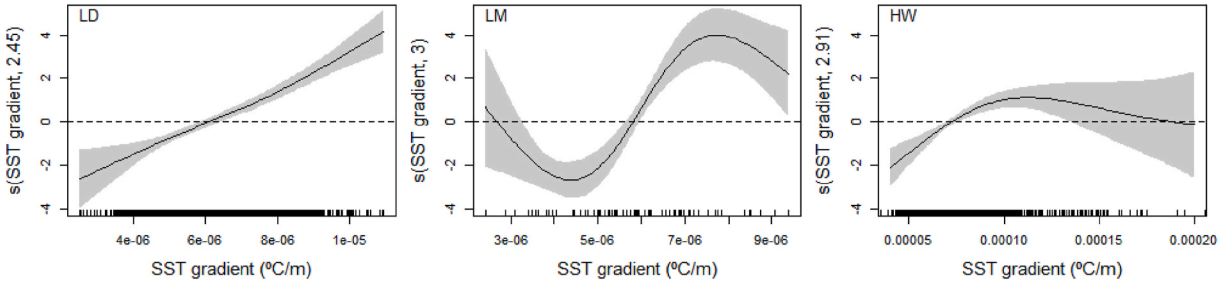

**Fig. 9.** Smoothers of the *Sea Surface Temperature gradient in São Miguel* selected in three of the final GAMs for sei whales. LD = Low resolution daily model. LM = Low resolution monthly model. HW = High resolution weekly model. Black marks on the x-axis indicate the distribution of the observations.

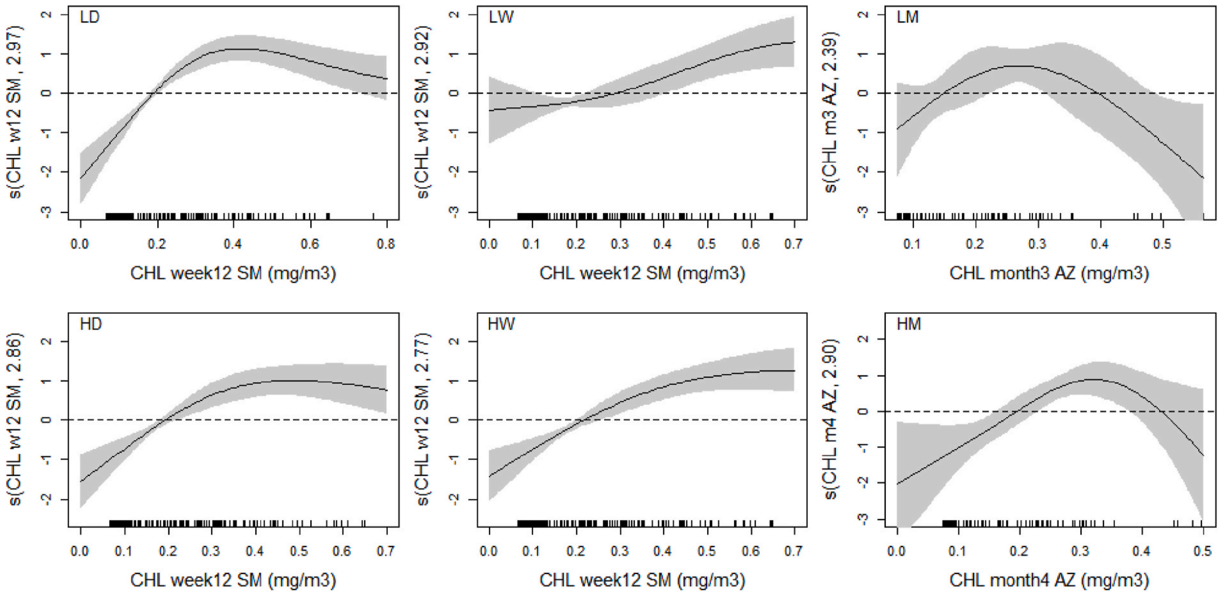

**Fig. 10.** Smoothers for *chlorophyll concentration around São Miguel 12 weeks* (or three-four months) before the sighting, variable selected in all the final GAMs for sei whales. LD = Low resolution daily model. LW = Low resolution weekly model. LM = Low resolution monthly model. HD = High resolution daily model. HW = High resolution weekly model. HM = High resolution monthly model. SM = São Miguel. AZ = Azores. Black marks on the x-axis indicate the distribution of the observations.

2011). In this case, we added an exponential spatial correlation structure based on the variogram shape of the residuals, and null random effects. The GAMM was implemented for the high spatial resolution weekly model for fin whale. While it could be run for small subsets of the dataset, it did not converge for the whole dataset. Therefore, particular caution is needed in the interpretation of the results of the original GAM in this case.

Models including distance to Ponta Delgada as an offset yielded rather similar results to those from the models without an offset variable. Performance was generally lower in terms of deviance explained (maximum difference of 5.2%) and AUC and TSS (differences <0.15). The main variables selected in the final models were common for the original and the offset models for every scale analysed, and exactly the same variables were selected in four of the models executed (see Supp. Table 8 for details).

Models using only fin whale and sei whale sightings as the binary response (n = 304 and 156 respectively) had quite high deviance explained values (ranging from 26.8 to 39.1%), as might be expected from the smaller datasets, with good AUC (from 0.83 to 0.9) and TSS (from 0.53 to 0.67) values (Table 4). A high spatial resolution daily model could not be run due to the small sample size available. Habitat suitability for fin whale, relative to that of sei whale, progressively increased until approximately 20 km from the coast. At greater distances, there are wide confidence intervals, and it is not possible to distinguish the two species. Regarding SST gradient around São Miguel, sei whales generally present a preference for stronger gradients than do fin whales. In the low spatial resolution weekly models (Fig. 11), fin whale habitat shows lower weekly SST means and higher chlorophyll concentrations, compared to that of sei whale, both to the south of São Miguel and in the entire archipelago.

## 4. Discussion

### 4.1. Dealing with opportunistic data

Opportunistic data are usually collected under a parent project or activity, which covers most of the costs of the data collection. In the Azores, whale watching companies provide a useful and highly valuable source of long-term data and, particularly in São Miguel, these data are collected year-round and with a good spatial coverage. However, such whale watching data have some disadvantages, such as lack of well-quantified effort due to the initial land search for the animals and possible spatial or temporal bias due to commercial interests such as shorter distances to the coast or more sheltered areas. These limitations can nevertheless be largely overcome with an appropriate methodology and a good knowledge of the dataset, avoiding incorrect conclusions. In this case, for instance, abundance estimates were not possible, but we can be more confident about the habitat preference analysis, using exploratory models rather than predictive, aided by a data-thinning process to avoid pseudo-replication and using a presence/pseudo-absence approach that minimises biases due to effort variation in space and time (as this bias affect equally both categories).

To control for spatial bias due to the commercial schedule of the trips, we also fitted models using distance to the main harbour (Ponta Delgada) as an offset. Models with the offset yielded very similar results to the original ones, selecting the same main environmental variables. Additionally, it should be noted that, spatial bias in the presence records would likely be mirrored in the absences, due to our use of sightings of other species as pseudo-absences, effectively controlling for bias. Therefore, the influence of the distance to the main harbour was not considered to be important in these analyses. Smoothers of the predictors show the same effects on the response variable in both types of models, thus supporting the main results of the original models.

We also tested residuals from all the original models for spatial autocorrelation. Covariograms did not show strong indications of spatial autocorrelation in the models. When applying Moran's I test, nine of the twelve models presented, showed no significant spatial autocorrelation, and two showed weak spatial autocorrelation ($0.01 < p < 0.05$). We attempted to apply GAMM, which are generally indicated to work with autocorrelated data, especially with small datasets (Zuur et al., 2009). In this case we applied an exponential spatial correlation structure but, when using the full dataset, the model failed to converge. Therefore, although autocorrelation was not an issue for the majority of the final models, in the cases where it was present and we were not able to control for it, results of the original GAM (particularly in relation to the statistical significance of the partial effects detected) should be interpreted cautiously.

Models using only fin and sei whale sightings highlighted some of the

**Table 4**
Summary of the GAM results for the five obtained models for direct comparison of habitat selection of fin and sei whales.

| FIN-SEI | | LOW SPATIAL RESOLUTION | HIGH SPATIAL RESOLUTION |
|---|---|---|---|
| **DAILY** | **AUC** | 0.83 | |
| | **TSS** | 0.53 | |
| | **DEV (%)** | 26.8 | |
| | **n** | 460 | |
| | **Explanatory Variables** | Dist. coast, SST gradient São Miguel, SST climatological daily mean, EKE seasonal São Miguel, EKE seasonal Azores | |
| **WEEKLY** | **AUC** | 0.88 | 0.89 |
| | **TSS** | 0.64 | 0.63 |
| | **DEV (%)** | 37.9 | 38.8 |
| | **n** | 460 | 457 |
| | **Explanatory Variables** | Dist. coast, SST gradient São Miguel, SST gradient Azores, SST climatological weekly mean, chlorophyll south São Miguel, chlorophyll SD south São Miguel, chlorophyll Azores | Dist. coast, SST gradient São Miguel, SST SD gradient São Miguel, SST climatological weekly mean, chl. south São Miguel, chl. SD south São Miguel, chl. Azores, chl. index 3, chl. week 4 and week 12, EKE seasonal São Miguel |
| **MONTHLY** | **AUC** | 0.89 | 0.9 |
| | **TSS** | 0.67 | 0.6 |
| | **DEV (%)** | 39.1 | 30% |
| | **n** | 460 | 460 |
| | **Explanatory Variables** | Dist. coast, SST gradient São Miguel, SST SD gradient São Miguel, SST anomaly São Miguel, distance to the nearest front, chlorophyll south São Miguel, chlorophyll index 2 | Dist. coast, SST SD gradient São Miguel, SST SD gradient São Miguel, SST of the nearest front, chlorophyll SD São Miguel |

Abbreviations used are: **AUC**: Area Under the Curve of the Receiving Operating Characteristic plot. **TSS:** True Statistic Skill. **DEV (%)**: Percentage of deviance explained in the model. **n**: total number of cetacean records (including presence and pseudo-absence) used in the model. **SST**: Sea Surface Temperature. **EKE**: Eddy Kinetic Energy.

main differences in habitat selection between the two species. These models expressed the preferences of one species in relation to those of the other and do not necessarily provide an adequate picture of absolute habitat preferences for each species.

Despite of the limitations, opportunistic data have important advantages. Namely, long term regular cover and considerably high number of sightings, allow analyses of long-term variation on distribution and occurrence of species, which are not possible with traditional dedicated surveys usually limited in space and time. Furthermore, objectives should be defined according to the nature of the dataset and conclusions must be done under a sound comprehension of the field methodology and resulting dataset. Further discussion about the limitations of these data and how to overcome them can be found in González García et al. (2018).

### 4.2. *Living in sympatry*

Fin whales and sei whales were sighted every year in the Azores mostly in spring months, even though observer effort at sea reaches a maximum in summertime. These two species occur in the same geographic area, sometimes even within a few hundred metres one of another, suggesting at least a partial overlap of their ecological niches. However, their sightings seem to be concentrated in different zones. They clearly change their distribution over time, probably dependent on the environmental conditions and without relying on a specific favourite location around the island, i.e., adapting to the dynamic location of their ecological niche. The use of fine-scale environmental variables, and not only coarse resolutions, in the analysis of their habitat requirements helped us to identify different preferences among the two species. Fin whales were the first species to be sighted every year, but usually the first sightings were of single individuals, and the majority of the animals arrived later in spring, generally after the arrival of blue whales (see González García et al., 2018). The arrival date of sei whales varied, although again, during the study period, most arrived during spring, remaining usually until later in the season than fin whales. In other areas, such as Antarctica, a similar timing has been found with blue whales arriving first, followed by fin and then sei whales (Mizroch et al., 1984). Sympatric fin and blue whales have been reported in several areas, such as Ireland, California, St. Lawrence or Antarctica (Baines et al., 2017; Friedlaender et al., 2015; Gavrilchuk et al., 2014; Širović et al., 2004 respectively). Sightings of other whales at the same time and in the same location as sei whales are less common, but fin and sei whales have been recorded together in Greenland (Laidre et al., 2010), also sei whales and sperm whales in the Azores (González García, Pers. Obs.) and sei, fin and blue whales together in NW Spain (Diaz Lopez and Méthion, 2019).

Baleen whale feeding habits, or more precisely, the feeding habits of their prey, can partially explain the preference for different chlorophyll concentrations in the models obtained for each species. In general, weekly models provided a more detailed ecological view, especially regarding chlorophyll influence. Daily chlorophyll values change rapidly and provide only a snapshot of the area when the satellite passes (and there are no clouds), which may not reliably represent the prevailing conditions. Monthly averages, on the other hand, may overlook short-term features, and thus fail to detect their effect on the whales. Notwithstanding, statistical model performance was fairly good for all the temporal resolutions (all AUC and TSS showed that the models were better than random), and when variables were selected in all models for the species, trends were rather similar in all of them, providing some confidence that they were biologically meaningful.

### 4.3. *Fin whales: high chlorophyll concentrations and dynamic areas*

Fin whales preferred intermediate to high chlorophyll concentrations in the archipelago, even when chlorophyll values were very low in the south of São Miguel. There is an implicit biological delay between phytoplankton blooms and fin whale presence. Fin whales' main prey, euphausiids, can feed both on phytoplankton and other zooplankton, including copepods of the genus *Oithona* and *Calanus* (Schmidt, 2010). Recent findings have shown that fin whales sighted in the Azores feed at higher trophic levels than blue or sei whales in the same area (Silva et al., 2019); therefore, the relationship between chlorophyll concentration and fin whale occurrence could be weaker in fin whales than for blue or sei whales. On another hand, there is also a possible spatial displacement of the phytoplankton and the subsequent trophic levels of the food chain. In other words, prey for whales will not necessarily occur where high chlorophyll concentrations are/were found. Furthermore, the chlorophyll concentration varies with depth, and surface values (as used in this study) may not be representative of the real conditions in the water column.

Fin whales, as was the case for blue whales studied in the same area and period (González García et al., 2018), showed a preference for dynamic areas (e.g., high EKE, high SST gradients), in agreement with Pérez-Jorge et al. (2020), supporting the hypothesis of oceanographic features acting as prey retention or aggregation mechanisms, probably favouring the availability of food and increasing their foraging efficiency. Both species, fin and blue whales, have been recorded feeding during our study period, consistent with previous research results for the

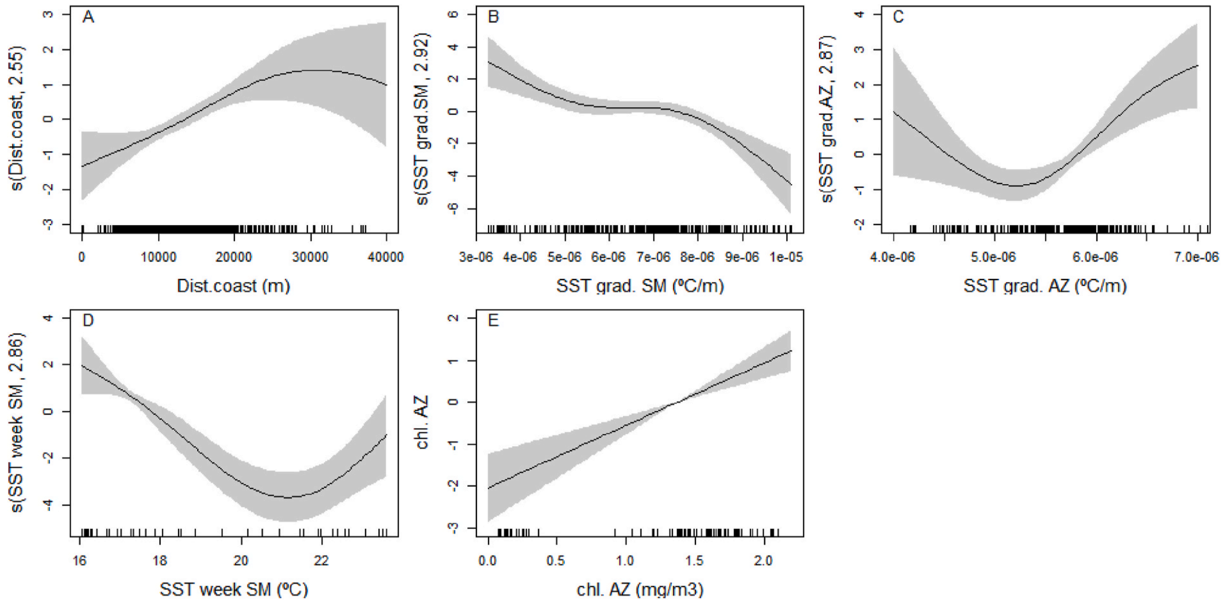

**Fig. 11.** Smoothers for five of the seven variables selected in the best fitting GAM with presences of fin whales and absence of sei whales for low spatial weekly resolution. A. Distance to the coast. **B.** SST gradient in São Miguel. **C.** SST gradient in Azores. **D.** Weekly climatological SST mean in São Miguel. **E.** Weekly chlorophyl concentration in the Azores. Black marks on the x-axis indicate the distribution of the observations.

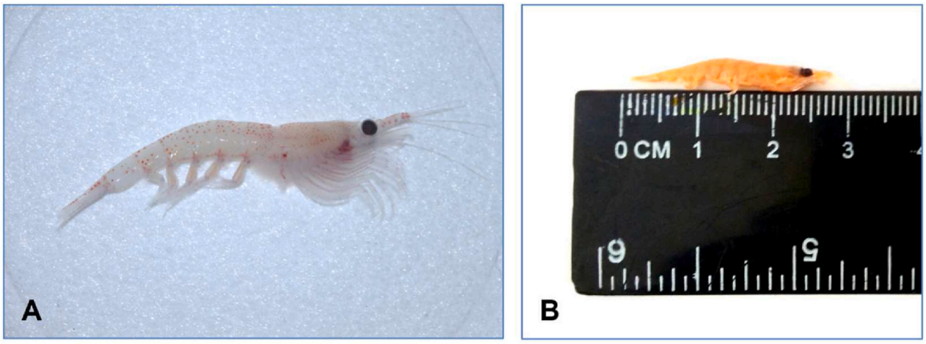

**Fig. 12.** A) Sample of krill collected in May 2014. **B)** Measurement of krill collected south of São Miguel: approx. 25 mm. Photos taken with Futurismo Azores Adventures by (A) Wesley Zadelhoff and (B) Victor Ojeda.

Azores (Silva et al., 2013; Prieto et al., 2016; Tobeña et al., 2016). Furthermore, inter and intra-annual variation in location within the study area, support the hypothesis of fin whales selecting temporary suitable habitat conditions in different areas over time, i.e., taking advantage of the dynamic environment.

Although fin whales were seen in waters with the widest temperature range, their habitat suitability increased (in the low-resolution models) in colder waters, usually 1.5 to 2 °C colder than the climatological mean. The temperature of the nearest front was significant only for this species, and only in the high spatial resolution monthly model, reinforcing the preference for colder waters. The selection of lower temperatures may be related with oceanographic features such as local upwelling or eddies, which at the same time, may be related with higher chlorophyll concentrations. Anticyclonic eddies have warm core and cold surroundings, while cyclonic eddies have cold core and warm surroundings. In both cases the maximum productivity is found within their cold part, which at the same time may host more available prey for the whales.

Final models performed well for all resolutions considered, except for the high spatial resolution daily model, which has a very low sample size due to data gaps in environmental variables. However, the use of different spatial scales did yield interesting results. For instance, SST anomaly, which had a significant effect in all low spatial resolution models for fin whales, suggesting a preference for colder anomalies across all temporal resolutions, was not selected in any of the high spatial resolution models. This highlights the possibility that different environmental features may be relevant at different scales.

### 4.4. *Sei whale: less feeding, more travelling*

Statistical performance of sei whale models was lower than for fin whale models. Nevertheless, AUC and TSS showed better goodness of fit than random, indicating that the selected environmental explanatory variables did have an effect on the response variable. The apparent weak relationship existing between the explanatory variables considered and the occurrence of sei whales limits the utility of the models, highlighting the need of further exploration with other variables. Environmental factors related with migration, such as travelling efficiency or current direction, might shed some light in future models.

Four of the six sei whale models (low spatial resolution daily and monthly and high spatial resolution weekly and monthly) showed increased habitat suitability in areas of high SST gradients with low standard deviations in São Miguel. This indicates a preference for well-defined oceanographic features, like eddies or fronts, whose presence has previously been found to favour sei whale occurrence (Kawamura, 1974; Horwood, 1987). However, high SST gradients can also indicate the presence of stronger currents, in this case, in the upper water column where the temperature gradients were observed. This latter argument agrees with the results of Skov et al. (2008), who shows a strong sei whale response to flow gradients, especially in waters shallower than 100 m.

The models obtained showed how habitat suitability for sei whales increased, even with low chlorophyll concentrations, when the SD of chlorophyll was higher around São Miguel and in its south coast, thus, showing a more uneven distribution. However, regarding chlorophyll concentration, models were not as consistent as those for blue or fin whales, despite the likely existence of a more direct relationship between phytoplankton and copepods, which were described as the most common prey of sei whales (Prieto et al., 2012); than between phytoplankton and euphausiids, the main described prey for fin or blue whales, which belong to a higher trophic level than copepods. The final models, in contrast with the models obtained by Prieto et al. (2016), retained variables related to primary production (chlorophyll concentration and its variation). It is worth pointing out that, although Prieto et al. (2014) did not observe any foraging behaviour south of 48°N in his work, 13.5% of the sei whale sightings considered in our study were registered as feeding. Evidence was observed such as lunging behaviour or swimming on the side taking huge mouthfuls of water and krill clearly visible on the surface (Supp. Fig. 4). In addition, on several occasions during our research, whale faeces were noted in the area of the sighting. Thus, we can assert that at least some of the individuals sighted were feeding around the islands, although probably in a lesser extent than blue or fin whales.

The greater variety of sei whales' possible prey (although feeding on visible krill has been clearly confirmed for fin, sei and blue whales in the Azores), may result in reduced success in defining their preferences in the model, as not all their prey items will be equally linked to primary production and, therefore, the niche occupied by the whales may be broad. Additionally, 53.2% of the sei whale sightings recorded were noted as travelling, a much higher percentage than for blue or fin whales (29.2 and 29.6% respectively). Therefore, variables related with feeding ecology or prey distribution may not largely cover the niche requirements for sei whales in the Azores, as feeding is not the only – and apparently seldom the main - purpose of their stay around the islands.

### 4.5. *Some common choices*

Notwithstanding the different preferences noted for fin and sei whales (and for blue whales, see González García et al., 2018), some choices were common for them. All the low spatial resolution and the high spatial daily models for fin whales, and all the models for sei whales except the high spatial resolution monthly, retained chlorophyll concentration 12 weeks (or three months) before the sighting. Successful krill spawning is known to occur just after phytoplankton blooms, since krill females need to build up enough resources for the reproductive season and critical larval stages require appropriate feeding conditions. A time of less than three months after spawning has been enough for *Meganychtiphanes norvegica* to achieve juvenile stages in the Clyde Sea (Scotland) (Tarling and Cuzin-Roudy, 2003) and for several krill species in Monterey Bay to achieve their peak after the phytoplankton bloom (Croll et al., 2005). The growth rate of the krill varies with prevailing environmental conditions and, in particular, it increases with warmer temperatures (Cuzin-Roudy et al., 2004), so a period of three months in the Azores probably is enough for krill to reach a suitable size to be eaten by baleen whales. Krill samples in the Azores, although very scarce, reached sizes between 16 and 27 mm (Villa et al., 2011; González García, Pers. Obs. – Fig. 12), which can correspond to juvenile-adult stages (Labat and Cuzin-Roudy, 1996; Silva et al., 2017).

As seen before, fin whales, sei whales and blue whales can feed on zooplankton, namely krill, but even if they may take similar prey, different habitat preferences for each species are suggested by the models. Although not representing an unquestionable proof, the different colours of whale faeces recorded (more reddish-brownish for fin whale, yellow for sei whale and reddish for blue whale) are consistent with different diets in the Azores for the three species. Although with certain preference for copepods and euphausiids, sei whales are the species with the most diverse diet, fin whales generally feed mostly on euphausiids (although in the Azores seem to feed in higher trophic levels), and blue whales are stenophagous, feeding almost exclusively on euphausiids (Horwood, 1987; Christensen et al., 1992; Sigurjonsson and Víkkingsson, 1997; Schmidt, 2010; Prieto et al., 2012; Silva et al., 2019). Our results suggest the possibility of resource partitioning that may reduce interspecific competition. To assess this hypothesis, further research is needed on whale foraging behaviour, such as diving profiles, dive duration, faecal sample analysis, etc. Furthermore, to the best of our knowledge, there is no reliable information published about the occurrence or life cycle of krill in the Azores, neither with surface nor water column sampling; this is also a gap that needs to be filled.

### 4.6. *Future expectations in a warming context*

According to the latest IPCC report, in the 21st century ocean temperature is expected to increase by a factor of 2–8 (depending on the different scenarios of future emissions) with respect to the last 30 years (IPCC, 2021). In the Atlantic, changes related with climate change have already affected ocean circulation, weakening the Gulf Stream as a result of a salinity decline in high latitudes (Yang et al., 2016; Chen et al., 2019; Caesar et al., 2021). Recent data show an increase of 2.7 °C of SST in the Azores per century (Siemer et al., 2021). This points to an obvious and inevitable change in the ocean environment, that will affect the distribution of marine life in the entire Atlantic basin. In the Azores, the interaction of oceanographic features (such as eddies, fronts and filaments derived from the main streams – AF/AC, NAC, main branches of the Gulf Stream-) with the diverse topography of the archipelago plays an essential role enhancing temporary localized resources that provide better conditions for marine life than surrounding oceanic waters (Caldeira and Reis, 2017; Sala et al., 2015; Amorim et al., 2017). However, within a warming context, a northward expansion or shift of the oligotrophic subtropical gyre is expected. Therefore, also a northward shift in the location of the phytoplankton bloom and/or its decrease in productivity might induce more oligotrophic conditions around the islands (Yang et al., 2020; Siemer et al., 2021).

Species undertaking long-migrations, such as the baleen whales sighted in Macaronesia, are likely to act as sentinels of changes in the ocean environment. They rapidly can change the timing of their migrations, or even shift their range to adapt to the new conditions. In fact, Sousa et al. (2021) have already suggested that such changes are occurring in fin whales in Macaronesia. In the Azores, as our final models suggest, fin whales might track high productivity conditions closer to the islands (with conditions similar to the ones analysed) or further north (i.e., not in reach of coastal or whale watching observers) if warming conditions induce the phytoplankton bloom to shift northward. Diet adaptability would also be a key factor, as lower levels of the trophic chain might be located closer to the phytoplankton concentrations, and therefore likely to be further from the islands in an ocean warming context. According to our results, sei whales would rather be less influenced by food availability (and could nevertheless benefit from occasional and advantageous foraging opportunities), and perhaps rely on the islands more as a topographic cue for migration instead of a stop for supply.

## 5. Conclusions

Models for fin whales show better performance than those for sei whales. Environmental variables linked with primary production and prey distribution explained reasonably well the habitat preferences for fin whales, which appear to spend a substantial part of their time around the Azores engaged in foraging. These results are similar to those for blue whales in the same area (González García et al., 2018), highlighting similarities in the habitat preferences of both species. However, sei whale models showed a much lower performance, probably due to more limited foraging activity in the area, where they spend more time travelling than feeding.

Fin whales, sei whales and blue whales were present in sympatry in Azorean waters, both in space and time. Nonetheless, different environmental preferences were highlighted for each of them: colder areas for fin whales, high SST gradients for sei whales and, according to González García et al. (2018), waters further from the coast for blue whales.

Every year in the Azores, environmental conditions favour an explosion of life that increases primary productivity mainly in spring months. The high oceanographic dynamism of the area, which involve the presence of eddies, fronts, and other local features such as upwelling, enhances the effect of this spring bloom. This dynamism creates retention or convergence zones that trigger bottom-up processes that favour aggregation of life. Cetaceans, as highly mobile animals, can rapidly adapt to the dynamic ocean environment. Multiscale analyses, considering different temporal and spatial resolutions, provide a more robust understanding of the ecology of each species, and better capture both long term and short term oceanographic features largely responsible for marine life distribution.

## Author contribution

**Laura González García:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – Original draft, Writing - Reviewing & Editing, Visualization, Funding acquisition. **Graham J. Pierce:** Conceptualization, Methodology, Writing - Review & Editing. **Emmanuelle Autret:** Methodology, Resources, Data curation. **José M. Torres-Palenzuela:** Conceptualization, Methodology, Resources, Supervision, Project administration, Funding acquisition.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

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