

# Looking for the migratory whales: Routes of the baleen whales in the Macaronesia

Raul Fonseca Valente  
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MSC

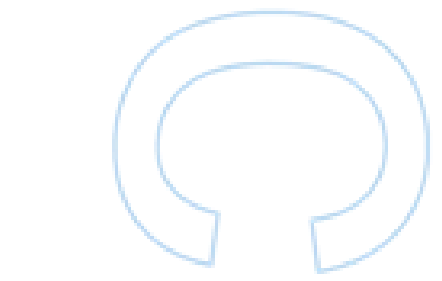
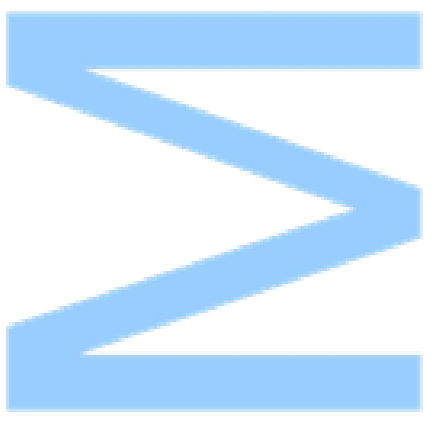
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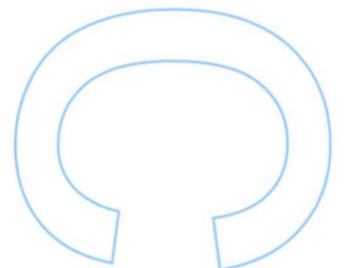
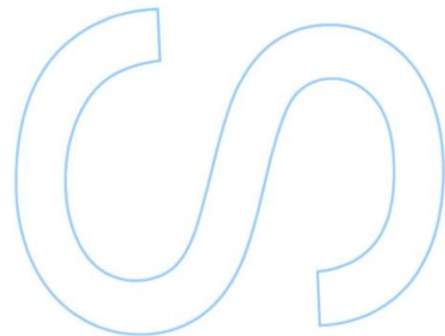
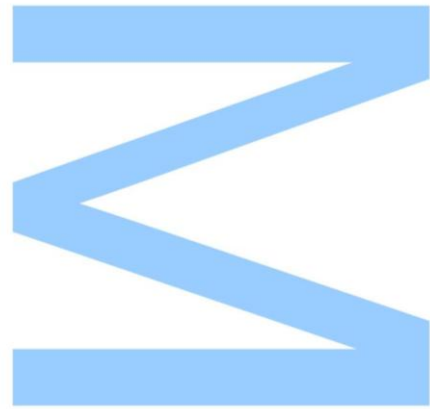
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## Supervisor

Prof. Dr. Isabel Sousa Pinto, Professor at Sciences Faculty, Porto University and Researcher at CIIMAR – Porto, Portugal



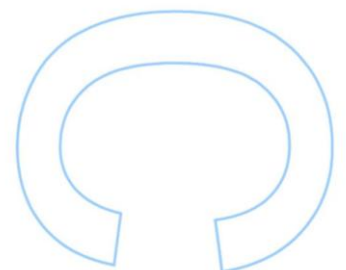
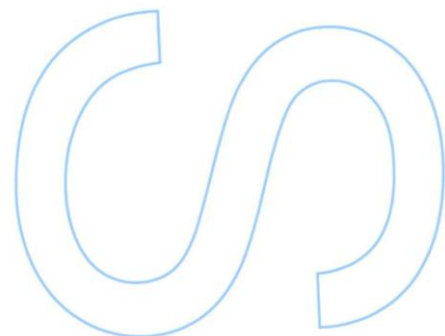
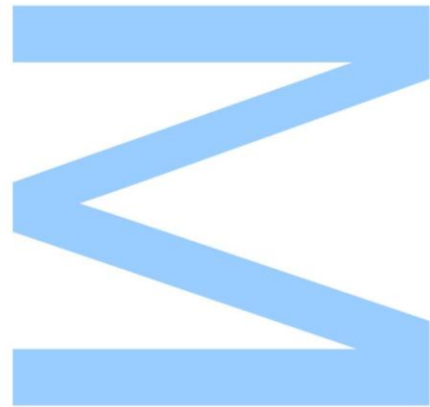




Todas as correções determinadas pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

Porto, \_\_\_\_/\_\_\_\_/\_\_\_\_





"So assured, indeed, is the fact concerning the periodicalness of the sperm whale's resorting to given waters, that many hunters believe that, could he be closely observed and studied throughout the world; were the logs for one voyage of the entire whale fleet carefully collated, then the migrations of the sperm whale would be found to correspond in invariability to those of the herring-shoals or the flights of swallows. On this hint, attempts have been made to construct elaborate migratory charts of the sperm whale."

Herman Melville, *Moby Dick*



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To CIIMAR,

To University of Porto.

Thank you very much!

# Resumo

As baleias de barbas têm um papel-chave nos ecossistemas marinhos. Sendo predadores de topo, este grupo de animais são fundamentais no controlo "top-down" e com isso na preservação da biodiversidade. Para além disto, são animais migratórios, atravessando largas distâncias entre as zonas de alimentação em latitudes superiores no verão e as zonas tropicais para acasalar e se reproduzirem no inverno. Sendo animais tão móveis, é fundamental conhecer a sua distribuição, de maneira a implementar as medidas necessárias para a conservação e proteção destes animais. No Nordeste Atlântico, são várias as espécies de baleias de barbas que atravessam a região da Macaronésia durante as suas migrações. No entanto, sabe-se muito pouco relativamente aos seus movimentos ao longo da área pois grande parte da informação relativamente à presença destes cetáceos é altamente fragmentada, restringindo-se maioritariamente a áreas junto à costa. Com tudo isto em consideração, este estudo visou perceber os padrões espaço-temporais das migrações de quatro espécies de baleias de barbas (baleia anã, comum, azul e de bossa), usando avistamentos de publicações e de bases de dados. Análises espaço-temporais foram realizadas com vista a obter uma ideia mais concreta relativamente a possíveis rotas migratórias na área. Posteriormente, com as ocorrências obtidas dos indivíduos, foram investigadas possíveis preferências de habitat. Finalmente, foi explorada uma possível correlação entre o geomagnetismo e as rotas migratórias. De um total de 15 artigos, 3 relatórios, 1 apresentação de conferência e 4 bases de dados, recolhemos 1797 avistamentos de baleias de barbas na Macaronésia. Os resultados mostram uma clara diferença na distribuição das baleias anãs e comuns comparativamente àquela observada para as baleias azuis e de bossa, muito provavelmente devido à existência de populações residentes para as primeiras duas. É também sugerida a existência de pelo menos 2 rotas migratórias na Macaronésia: ambas são em alto-mar, mas enquanto uma passa pelos Açores, a outra passará por águas "saharianas". A análise das preferências de habitat deu a entender que as baleias utilizam quer fenómenos oceanográficos quer a topografia dos oceanos para se alimentarem oportunisticamente durante as suas migrações. Relativamente ao geomagnetismo, embora não se tenha conseguido comprovar o seu uso durante as migrações, é demonstrado o potencial que determinados componentes magnéticos têm como possíveis meios de orientação das baleias quando elas estão em migração. Por último, este estudo demonstrou, mais uma vez, a necessidade de serem obtidos mais dados em áreas offshore para implementar medidas que protejam eficientemente este grupo de cetáceos.

Palavra-chave: Baleias de barbas, Migração, Macaronésia, Padrões espaço-temporais, Preferência de Habitat, Geomagnetismo

# Abstract

Baleen whales play a key role in marine ecosystems. Being top predators, this group of animals is fundamental in top-down regulation and thus in the preservation of biodiversity. In addition, they are migratory animals, crossing long distances between summer feeding grounds in upper latitudes and tropical winter grounds for mating and breeding. Being such mobile animals, it is fundamental to know their distribution, in order to implement the necessary measures for the conservation and protection of these animals. In the Northeast Atlantic, there are several species of baleen whales that cross the region of Macaronesia during their migrations. However, very little is known about their movements throughout the area because much of the information regarding the presence of these cetaceans is highly scattered and mainly restricted to areas near the coast. With all this in mind, this study aimed to understand spatio-temporal patterns in the migrations of four species of baleen whales (minke, fin, blue and humpback whales), using sightings from publication and databases. Spatio-temporal analysis were carried out in order to obtain a more concrete idea of possible migratory routes in the area. Posteriorly, with the occurrences of collected individuals, we investigate possible habitat preferences. Finally, a possible correlation between geomagnetism and migratory paths was explored. From a total of 15 articles, 3 reports, 1 conference proceeding and 4 databases, we gathered 1797 sightings of baleen whales in Macaronesia. The results show a clear difference in the distribution of minke and fin whales compared to the blue and humpback whales, most likely due to the existence of resident populations for the former two. It is also suggested the existence of at least 2 migratory routes in the Macaronesia: both are on the high seas, but while one passes through the Azores, the other will pass through "saharan" waters. The analysis of habitat preferences suggests that whales use both oceanographic phenomena and the topography of the oceans to feed opportunistically during their migrations. Regarding geomagnetism, although it has not been possible to demonstrate its use during migrations, it is definitely shown the potential of certain magnetic components as means of orienting the whales when they are migrating. Finally, this study demonstrated once again the need to obtain more data in offshore areas to implement measures that will effectively protect this group of cetaceans.

Key-words: Baleen whales, Migration, Macaronesia, Spatio-temporal patterns, Habitat Preference, Geomagnetism



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*Balaenoptera acutorostrata*; Bm - *Balaenoptera musculus*, Bp - *Balaenoptera physalus*; Mn - *Megaptera novaeangliae*. Below the x-axis, it is indicated the number of sightings used for each boxplot.

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# List of Abbreviations

**ABR** - Azores-Biscay Rise

**ACCOBAMS** - Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and contiguous Atlantic area

**AIC** - Akaike's Information Criterion

**Aper** - Annual periodically

**AUC** - Area Under the Curve

**ANOVA** - Analysis of Variance

**ASCOBANS** - Agreement on the Conservation of Small Cetaceans in the Baltic , North East Atlantic , Irish and North Seas

**AVISO** - Archiving, Validation and Interpretation of Satellite Oceanographic data

**AzC** - Azores Current

**CanC** - Canary Current

**CHLA** - Chlorophyll-a

**CMEMS** - Copernicus Marine and Environment Monitoring Service

**Co** - common

**DD** - Data Deficient

**e.d.f.** - effective degrees of freedom

**FC** - Flemish Cap

**GAM** - Generalized Additive Model

**GEBCO** - General Bathymetric Chart of the Oceans

**GLM** - Generalized Linear Model

**HSC** - Horseshoe Seamount Chain

**ICNF** - Instituto da Conservação da Natureza e das Florestas



**IUCN** - International Union for Conservation of Nature

**MAP** - Madeira Abyssal Plain

**MAR** - Mid-Atlantic Ridge

**MC** - Mauritania Current

**MGET** - Marine Geospatial Ecology Tools

**MODIS** - Moderate Resolution Imaging Spectrometer

**MPA** - Marine Protected Area

**n** - total number of points (available/used) considered in the model fitting

**NACW** - North Atlantic Central Water

**NEC** - North Equatorial Current

**NECC** - North Equatorial Counter-Current

**NS** - No sightings

**Oc** - occasional

**OPO** - Observation Platforms of Opportunity

**OSPAR** – Oslo and Paris Convention for the Protection of the Marine Environment of the North-East Atlantic

**Ra** - Rare

**ROC** - Receiving Operator Characteristic

**RSF** - Resource Selection Function

**SACW** - South Atlantic Central Water

**SD** - seasonally defined

**SI** - seasonally irregular

**s.e.** - standard error

**SLA** - Sea Level Anomaly

**SST** - Sea Surface Temperature

**UD** - Undefined

**VC** - very common in the region

**VIF** - Variance Inflation Factor

**WWF** - World Wildlife Fund



# 1. Introduction

## 1.1 Importance of baleen whales in marine ecosystems

Baleen whales (Order Cetacea, suborder Mysticeti), comprises a taxonomical group of 11 whales species, distributed across all-over the world. A common feature for all mysticetes is the presence of several hundred baleen in the mouth, with the number and type varying among species (Clapham *et al.*, 1999).

Currently, it is already demonstrated the key role of baleen whales in dynamic environments such as marine ecosystems (Roman *et al.*, 2014).

Baleen whales are commonly used as indicators of prey distribution and functioning of ecosystem processes as their abundance and distribution impacts on species interactions and community structures due to their position at the top of the trophic ladder (apex predators) (Berge *et al.*, 2011; Smith *et al.*, 2013).

Laws (1985) and Ballance (*et al.*, 2006a) studies in the Southern Ocean have shown that the brutal decline in populations of baleen and sperm whales due to whaling during the 20th century led to the availability of 150 million tones of krill to the remaining existing predators in the area. As a consequence, during the following decades, there was a significant increase in the number of seals, birds and remnant whales species that took advantage of the lack of competition for prey, with obvious consequences for the ecosystem equilibrium.

Baleen whales are widely known as having a seasonal cycle of migration between cold summer feeding grounds in high latitudes and winter tropical waters for mating and calving. Although there are different explanations for why these marine mammals show this behavior (Corkeron & Connor, 1999; Clapham, 2001; Avgar *et al.*, 2014), none of them is completely accepted. Notwithstanding, this migration is considered a response to spatial-temporal ecological patterns (Avgar *et al.*, 2013) and thus, a complete scrutiny of its characteristics is necessary to implement effective conservation measures for these species (e.g. Barnett *et al.*, 2009).

Depending on the populations of migratory whales being studied, migration patterns may vary: some are partially migrants (only a fraction of the population migrates) or

even non-migrants (e.g. *Megaptera novaeangliae* in Arabian Sea (Mikhalev, 1997)), while it has been documented individuals migrating large-distances from feeding grounds in productive high latitude waters to low latitudes for calving and mating (e.g. Rasmussen *et al.*, 2007).

Being migratory species, baleen whales are largely responsible for the horizontal transport of limiting nutrients and other essential materials during their migrations (Roman *et al.*, 2014). The "great whale conveyor belt" (Roman *et al.*, 2014) results in increased significant primary productivity in oligotrophic areas, due to the releasing of a considerable amount of nitrogen (in the form of urea) and other compounds, during their migrations from the poles to the tropical regions. Hence, baleen whales are keystone species (Roman *et al.*, 2014) given their impact on marine ecosystems.

With such influence on the ecosystems, whales are considered umbrella species (Zacharias & Roff, 2001) as they allow the natural order and function of food webs and trophic structures.

Lastly, it is undeniable the role of baleen whales as flagship species. Blue and humpback whales are constantly the target of campaigns to obtain funding from society in campaigns such as those carried out by WWF and Greenpeace (WWF, 2016; Greenpeace, 2016).

Species with this status are of utmost importance from a marine conservation perspective, since funding for conservation research and management is limited, and so focusing conservation efforts in this group allows a wider protection of marine ecosystems.

For all these reasons, the effective protection of baleen whales becomes increasingly urgent. The creation of protected areas on the basis of top predators existing in a given area, suggested by several authors (Hooker & Gerber, 2004; Sergio *et al.*, 2006; 2008), may be the optimal solution to address the lack of existing protection in offshore areas.

## 1.2 Threats and Protection Mechanisms

Marine pelagic areas are currently under threat due to the increasing of anthropogenic activities in this environment (Halpern *et al.*, 2008). More and more, the effects of overfishing, mining, pollution and climate change, lead us to believe that the structure and function of pelagic ecosystems are changing significantly (e.g. Fabry *et al.*, 2008; Hoegh-Guldberg & Bruno, 2010).

This problem is aggravated since there is almost no protection in these areas, due to the lack of data regarding information on the temporal and spatial distribution of oceanic species (Wood *et al.*, 2008).

For baleen whales, the main threats are the accidents related to entanglement in fishing gear (affecting mostly species known to travel by the coast as the humpback whales (Stockin & Burgess, 2005)) and ship collision (fin whales with reported higher number of accidents (Laist *et al.*, 2001)).

Global climate change is also a cause of concern in recent years. For migratory species, global climate change may cause changes in the length and / or timing of migrations between regions (Macleod, 2009), with unpredictable consequences for populations and the ecosystem in general.

With an annual distribution as large as an ocean basin (IUCN, 2016), it is necessary to identify priority areas potentially vulnerable to marine threats, both in feeding and breeding grounds but also in migratory corridors, to support effective conservation measures and assure the viability of populations (Geijer & Jones, 2015)

For the protection of highly-mobile vertebrates, as are baleen whales, the best solution to protect these species seems to be the creation of dynamic protected areas (Hyrenbach *et al.*, 2000; Hobday & Hartmann, 2006; Game *et al.*, 2009). Implementing these areas where it is predictable to exist critical habitat for certain species, is an effective mean of protection and conservation of marine biodiversity.

Therefore, it becomes increasingly imperative to study and understand migratory routes of baleen whales in order to support effective management and thereby ensure the balance of marine ecosystems.

### 1.3 Habitat preferences of baleen whales during migration

It is widely accepted that physiographic and oceanographic variables are proxies for prey abundance and availability that shape marine predators' distribution, including baleen whales (Cañadas *et al.*, 2002; Ballance *et al.*, 2006b).

Physiographic variables such as depth or sea floor bathymetry slope are known to limiting the distribution of benthic or demersal prey species (Cañadas *et al.*, 2002), whereas structures as seamounts chains are very important in a biological sense since they allow the formation of upwelling nutrient-rich waters into the photic zone and the occurrence of mixing water layers, resulting in an accumulation of primary and secondary producers (Genin, 2004).

Oceanographic features and processes (current systems, eddies...) also need to be considered when we try to infer habitat preference for these whales, since they are responsible to the aggregation of prey species with serious consequences in fitness, timing of migrations, and distribution of baleen whales (e.g. Friedlaender *et al.*, 2006).

Ballance (*et al.*, 2006b) suggests an important role of oceanographic processes in migratory patterns observed for the different species of baleen whales, since the selective forces created by these features act directly in their seasonal distribution.

The influence of these processes on the migration of baleen whales is demonstrated in several studies carried out in the Azores archipelago (Visser *et al.*, 2011; Prieto *et al.*, 2016). Those studies showed the influence of North Atlantic spring bloom on the migration timing by blue and fin whales, that arrive in the archipelago when there is a high prey abundance, using this zone as a mid-latitude feeding site. Therefore, oceanographic processes were influencing migration timing and baleen whales were presenting feeding behaviors during their migratory routes, as shown by several other studies (e.g. Stockin & Burgess, 2005; Silva *et al.*, 2013). Hence, the study of habitat

preferences through resource selection methods may suggest preferable areas for the migratory paths.

## 1.4 Descriptive and Modeling Techniques to study Habitat Preferences

Is designated as habitat preference the habitat most likely to be chosen by a species given the opportunity or which habitat the species is best suited for (Johnson, 1980). Within this definition, situations in which an animal has innate preferences for certain resources, but they are not actually available (Peek, 1986), are still encompassed.

These choices are fundamental to the survival of the individual since those decisions will allow a greater persistence of the species throughout its evolutionary history. For marine species living in a highly dynamic environment, we can consider habitat preferences in several scales, from large-broad scales (e.g. Kaschner *et al.*, 2006) to fine-scales (e.g. Johnston *et al.*, 2005), depending on the patch size of both predator and prey (Fauchald *et al.*, 2000).

Another factor that we have to take into account is the intra and inter-specific competition. Particularly important in heterogeneous environments, this interaction between different individuals will cause habitat partitioning, allowing the coexistence of different species within the same area (Amarasekare, 2003). Summing all these factors we may know the habitat use of a certain species, meaning, the set of physical and biological habitat components preferably chosen (Hall, 1997).

Describing habitat preferences of marine species, such as baleen whales, can be extremely challenging. Entirely pelagic with highly-mobility and elusive behavior, studying these whales require a huge financial cost (Kiszka *et al.*, 2007), making it difficult to improve our knowledge about their ecology.

Mathematical approaches use several environmental variables (dynamic and static), chosen as the most appropriate to characterize the habitat, and species occurrence to model distribution (Macleod *et al.*, 2008). Thus, we can predict both spatial and temporal patterns in species dispersion and know more about relationships between species and environment (Cañadas *et al.*, 2005).



When starting a preliminary analysis on cetacean-habitat relationships, descriptive analysis are useful tools to infer how cetaceans are affected by different habitat variables. These methods are based on hypothesis testing, allowing multiple comparisons between species occurrence and a single (or several) habitat variable(s) (Redfern *et al.*, 2006). However, these techniques have some limitations since they do not allow the quantification of cetacean-habitat relationships. Thus, this analysis are ideal for species whose knowledge about their habitat requirement is scarce, and baseline knowledge is needed (Redfern *et al.*, 2006).

As examples of descriptive analysis we can cite quantile analysis and overlay of sightings and maps of variables, techniques already used in several articles (e.g. Naud *et al.*, 2003; Rossi-Santos *et al.*, 2007).

Habitat modeling could be a good tool to predict cetaceans' distribution, particularly in cases where it is urgent to implement conservation measures and we have no ecological data that allow us to tell which marine areas need to be protected.

Modeling techniques are more complex analysis, which allow us to quantify large-scale relationships between cetacean distribution and habitat variables. These methods include Environmental Envelope Models, Regression Models and Classification/Regression trees (Redfern *et al.*, 2006).

Regarding Regression Models, they are widely used to model cetacean-habitat relationships. Examples of models included in this group are Generalized Linear Models (GLM's) and Generalized Additive Models (GAM's). While GLM's assume that the relationship between the response variable (or some linking function of the response variable) and the predictor variables is parametric, GAM's allow a data-driven approach by fitting smoothed non-linear functions of explanatory variables without imposing parametric constraints (Redfern *et al.*, 2006).

Modeling is a step-by-step process. In other words, this technique is composed of several phases that have to be performed so our model can give us a realistic explanation of the data. First, one has to choose the appropriate scale (based on the data able to be used and model purposes) and then model fitting and model evaluation (to assess the predictive accuracy of the model) need to be performed. Also, we can

either build an explanatory model (to see the effect of a specific variable in species distribution) or a predictive one (to foresee where the animals can be seen) depending on the aim and data availability (Redfern *et al.*, 2006).

## 1.5 The possible role of geomagnetism as a navigational cue in migrations

Migration as extensive as those reported by Rasmussen (*et al.*, 2007), suggest that there must be a mechanism of long-distance navigation allowing whales go from one place to another without getting lost. Moreover, humpback whales were reported as capable of maintaining constant courses over distances greater than 200 km, which demonstrates the need of a continually updated, directional orientation (Horton *et al.*, 2011).

Open-ocean is typically thought to be an environment lacking of any conventional navigation cues, so the external stimuli used by these animals to guide themselves remains a mystery until the present day.

If whales navigate to a particular destination in order to find the target from the place where they are, they must possess a system of "true navigation" (Bingman & Cheng, 2005), a system in which the animal navigates directly to the goal even if displaced or side-tracked. Otherwise, the influence of the currents (even a small deflection) could lead to a large error at the final destination.

Animals able to be guided by "true navigation" must have both "map" and "compass" senses, hypothesis presented by Kramer (1961), in which the "map sense" will allow the animal to know its position relative to its destination; and the "compass sense" to keep the direction to its destination as the animal migrates.

Since there are some possible cues that can be used by marine organisms during their migrations (several hypothesis were discussed by Lohmann (*et al.*, 2008)), and that these animals employ multiple sources of information while navigating and can switch between them as needed (Lohmann *et al.*, 2008), it is hard to know which means of orientation are used during their migrations in ocean.

The use of the earth's magnetic field as a means of orientation is a long placed hypothesis because unlike other cues sensory, this can be used for any period of time (no matter whether it is night or day), it is independent of the weather, sea state and depth (Lohmann *et al.*, 2012).

Furthermore, it is of the few navigational cues that form a bicoordinate magnetic "map", due to some components of the magnetic field (e.g. inclination and intensity of magnetic field) vary in a predictable manner both latitudinally and longitudinally, allowing the knowledge of its geographical position in any zone of the globe (Lohmann & Lohmann, 1996; Putman *et al.*, 2011).

It is already demonstrated that a number of animals, including some oceanic ones, such as the turtle (Lohmann *et al.*, 2004) and the salmon (Putman *et al.*, 2014), use the magnetic field as a cue for guidance during their annual migrations.

The hypothesis that baleen whales navigate using the earth's magnetic field is appealing, but lacks of experimental evidence, since studies of these organisms are mostly correlational (e.g. Klinowska, 1983; Kirschvink *et al.*, 1986).

However, there is already some evidence supporting the theory: Klinowska (1983) observed a relationship between stranding positions and areas where valleys in the geomagnetic field intersect the coast, and Kirschvink (*et al.*,1986) statistically demonstrated the same association.

In 1992, Walker (*et al.*,1992) corroborated the results, statistically demonstrating an association between fin whales migrating (south or north) and areas of low geomagnetic intensity.

Recently, Allen (2003), demonstrated a possible use of geomagnetic intensity and inclination as a navigational cue during migrations by tracking satellite-tagged humpback whales and using modeling techniques afterwards.

Also, the presence of ferromagnetic particles in cetaceans' bodies (Bauer *et al.*, 1985) (although due to the large amount of magnetic material, they could not correlate with a specific organ) can be a signal of a magnetite-based orientation system, hypothesis defended by Wiltschko & Wiltschko (1995).

Thus, there are no definitive conclusions on this issue, some strong indications point to the use of geomagnetic stimuli as an orientation cue to baleen whales' migrations.

## 1.6 The Macaronesia

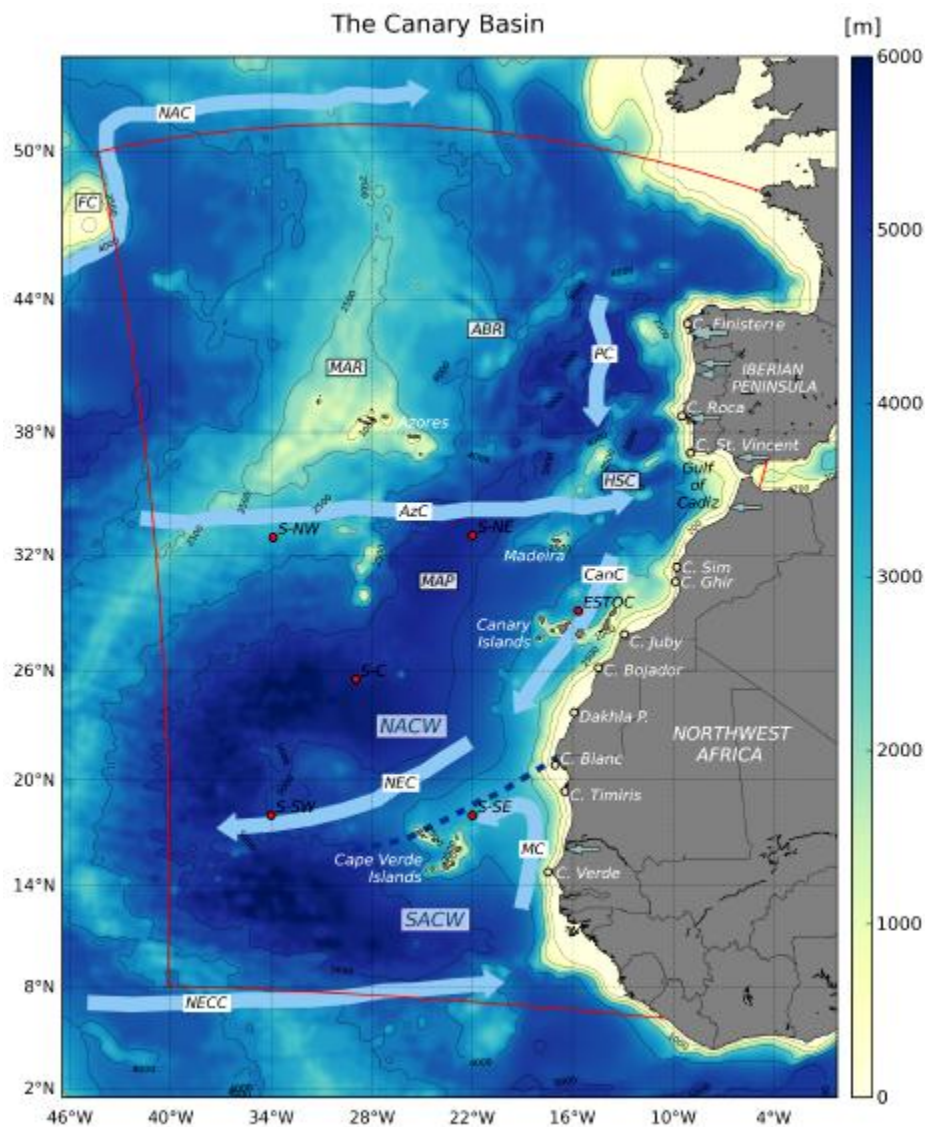
Macaronesia (figure 1) is an oceanic area of the Northeast Atlantic Ocean, encompassing the islands of Madeira, Azores, Canary and Cape Verde. It is latitudinally located between the meridians 10-44N, while longitudinally has as eastern limit the west of the Iberian Peninsula and Northwest Africa. The western boundary is approximately at 40 W (approximately the position of the mid-Atlantic ridge).

### 1.6.1 Topography and Oceanography

At the topographic level, this region contains a particularly rugged coastline, with numerous capes formed along the coast. The continental margin is known to contain numerous submarine canyons, whose role in eddies formation and deposition of sediments is well recognized (Allen & Durrieu de Madron , 2009) (e.g. Portimão Canyon in Gulf of Cádiz).

Other topographic structures, with an extremely relevant role at biological level, are the seamounts of volcanic origin. Among the possible effects of seamounts is the turbulence vertical mixing and the formation of jets where seamounts interact with ocean currents (White & Mohn, 2004). Moreover, currents can be created by amplified tides, and eddies may form and be trapped over seamounts in closed circulations cells known as Taylor columns (Boehlert & Genin, 1987).

At the biological level, the formation of upwelling phenomenon on seamounts, which bring nutrients to the surface, encourages primary production and possibly traps plankton in circulation cells (White *et al.*, 2007). These oceanographic processes lead to increased primary productivity , which in turn leads to formation of a complex food web that inevitably ends up in top predators, as are baleen whales.



**Figure 1:** Map of Macaronesia showing topographic and oceanographic features in the area. Original image from Mason (2009). Labels: AzC - Azores Current, CanC - Canary Current, MC - Mauritania Current, NEC - North Equatorial Current, NECC - North Equatorial Counter-Current; ABR - Azores-Biscay Rise, FC - Flemish Cap, HSC - Horseshoe Seamount Chain, MAP - Madeira Abyssal Plain, MAR - Mid-Atlantic Ridge, SACW - South Atlantic Central Water, NACW - North Atlantic Central Water. Five Subduction Experiment mooring locations are marked with red dots.

Regarding major oceanographic features, several currents are known to play an important role in this area. Marine currents have an important role in influencing species distribution. They are responsible for shaping highly dispersive species distribution, acting as a barrier to dispersal and promoting the transport of reproductive propagules to other areas (Lee *et al.*, 1992). The influence on prey distribution has consequences in pelagic species habitat preferences, with serious effects on migration timing and feeding patterns. Example of the important role in marine biodiversity can be seen at a mesoscale, with the formation of eddies that attract and aggregate schools of

marine pelagic species (Logerwell & Smith, 2001). In the area, as examples of these currents we can cite the North Atlantic Current, Azores Current, Canary Current and the North Equatorial Current and Counter-Current (Mason, 2009).

Another major feature is the Cape Verde Frontal Zone, that separates the South Center Atlantic Waters, cooler and richer in oxygen and nutrients, from the North Atlantic Central Waters (Mason, 2009).

Finally, the northeasterly trade winds running alongshore are responsible for the formation of an upwelling system along the Iberian and Northwest African coasts (Nykjaer & Van Camp, 1994). In close relationship with the Azores High (atmospheric high-pressure), this interaction leads to the seasonal formation of mesoscale oceanic eddies (Mason, 2009).

### 1.6.2 Species Diversity of Baleen whales

Six species of baleen whales were sighted crossing the Macaronesia waters during its inter-annual migrations (e.g. Hazevoet & Wenzel, 2000; Jann *et al.*, 2003). A seventh species, *Eubalaena glacialis*, although previously spotted, it has virtually disappeared in Macaronesian waters (Silva *et al.*, 2012).

For species such as Bryde's whale (*Balaenoptera edeni*) and Sei's whales (*Balaenoptera borealis*) information regarding their migration is scarce, and recent research efforts are being taken to achieve a better understanding of their migration (e.g. Prieto *et al.*, 2014).

For the other species, namely Minke whales (*Balaenoptera acutorostrata*), Fin whales (*Balaenoptera physalus*), Blue whales (*Balaenoptera musculus*) and Humpback whales (*Megaptera novaeangliae*), although more information is available, so far, this has not been compiled, and such work may be the key for a better understanding of their migratory routes in the Macaronesia.

.Humpback whales

Although humpback whales in the North Atlantic Ocean are the best ones studied worldwide (e.g. Palsbøll *et al.*, 1997; Smith *et al.*, 1999; Reeves *et al.*, 2004; Wenzel *et al.*, 2009;), lots of questions remain, specially considering offshore areas; and their migratory paths are still unknown.

Several studies described Cape Verde archipelago as breeding/mating area in winter and early spring (Hazevoet & Wenzel, 2000; Jann *et al.*, 2003; Wenzel *et al.*, 2009; Ryan *et al.*, 2013), and photo-ID studies showed they migrate to the high latitude feeding grounds (in Denmark Strait and Bear Island, in Norway) (Jann *et al.*, 2003; Wenzel *et al.*, 2009), where they stay during the summertime.

However, the migratory path from feeding to breeding ground remains largely unknown. It is suggested they have a "broad-band, diffuse migration that occurs over the course of several months" (Reeves *et al.*, 2004), and there is a single photo-ID registration from in the Azores Islands during their migrations (Wenzel *et al.*, 2009).

Moreover, a recent work performed by the team led by Professor Audun Rikardsen, in which satellite tags were placed on various humpback whales, allowed us to know that at least some individuals pass through the Azores when they go to breeding areas in the West Indies (Whaletrack, 2017).

#### . Blue whale (*Balaenoptera musculus*)

Blue whales, like the humpback whales, are known to undertake extensive north-south migrations, feeding at mid to high latitudes in summer and breeding in (sub)tropical regions during winter.

In the past they were widely distributed in the southern half of the North Atlantic in the late fall (Reeves *et al.*, 2004), while now there are many records in the African coast in December (Camphuysen *et al.*, 2012; Baines & Reichelt, 2014).

They have been tracked and seen in the Azores during spring and early summer (Silva *et al.*, 2013), suggesting the existence of a central migratory corridor in North Atlantic. However, there is also evidence of a migratory path along the European coast to reach the northern feeding grounds (Sears & Perrin, 2009), probably passing near Canary Islands (Ritter & Brederlau, 1998).

Azores have been demonstrated to constitute part of a regular pathway, an area considered stopover site during migration to the north, as whales were seen foraging for varying periods of time (Silva *et al.*, 2013). Hence, this archipelago is likely an important passage point during their inter-annual migrations. Moreover, mother-calf pairs have been seen in the islands, mainly in May (González, personal communication), suggesting that wintering breeding grounds can be near the islands, in agreement with the results observed by Nieukirk (*et al.*, 2004).

. Fin whale (*Balaenoptera physalus*)

Contrary to the blue and humpback whales, not all fin whales perform seasonal migrations (Edwards *et al.*, 2015). There are resident populations, knowing both at higher latitudes and lower latitudes, sometimes partially migrant (Edwards *et al.*, 2015).

The migration of fin whales is considered to be "incomplete" since they have an "equatorial hiatus", only migrating until 30° N in North Atlantic and 20° S in Southern Hemisphere (Edwards *et al.*, 2015). This "hiatus" means their breeding areas differ from those known for humpback or blue whales. Hain (*et al.*, 1992) suggested that fin whales' breeding areas are in open ocean, and therefore difficult to identify (although there are other explanations for this lack of knowledge - see Wild Whales b.c. sightings network (2016)).

In Macaronesia, Vighi (*et al.*, 2016) reported that there are at least 2 subpopulations of fin whales in the Northeast Atlantic and their results suggest that whales from Northwest Spain migrate to the breeding grounds located in low latitudes.

Moreover, it has been suggested that there is a breeding area near Azores (Silva *et al.*, 2011) based on acoustic data taken in November and December and also in Canaries where it is possible to observe calves with their mothers in April and May (Carrillo *et al.*, 2010; Pérez Vallazza, 2013).

Satellite-tracking data from Azores revealed the existence of a central migratory corridor in North Atlantic (Silva *et al.*, 2013) leading to eastern Greenland and western Iceland feeding grounds.

Finally, fin whales along the NW Iberian Peninsula are likely to be resident (Evans, 1987).

. Minke whale (*Balaenoptera acutorostrata*)

Like fin whales, minke whales seem to have both resident and migratory populations in Macaronesia (IUCN, 2016). Sightings confirm the presence of this species throughout the year (Correia *et al.*, 2015; Van Waerebeek *et al.*, 1999; ICNF, 2016), with the possibility of a breeding area on the West African shelf (Van Waerebeek *et al.*, 1999).



Even though it is a species associated with colder waters and areas near the coast, at least in Macaronesia, there is a lot of evidence pointing to a migration on the high seas. Telemetry data indicates that some minke whales make extensive migrations between high-latitude summer feeding grounds to wintering breeding areas in the offshore waters of the south of North Atlantic (Vikingsson & Heide-Jørgenssen, 2014), whereas acoustic data obtained with hydrophones placed parallel to the mid-atlantic ridge, point to the presence of individuals of this species in this area during the winter (Nieukirk *et al.*, 2004).

Records of minke whale both in the Azores and Madeira are relatively rare (Reiner *et al.*, 1993; Freitas *et al.*, 2012), suggesting an occasional presence of this species in these archipelagos.

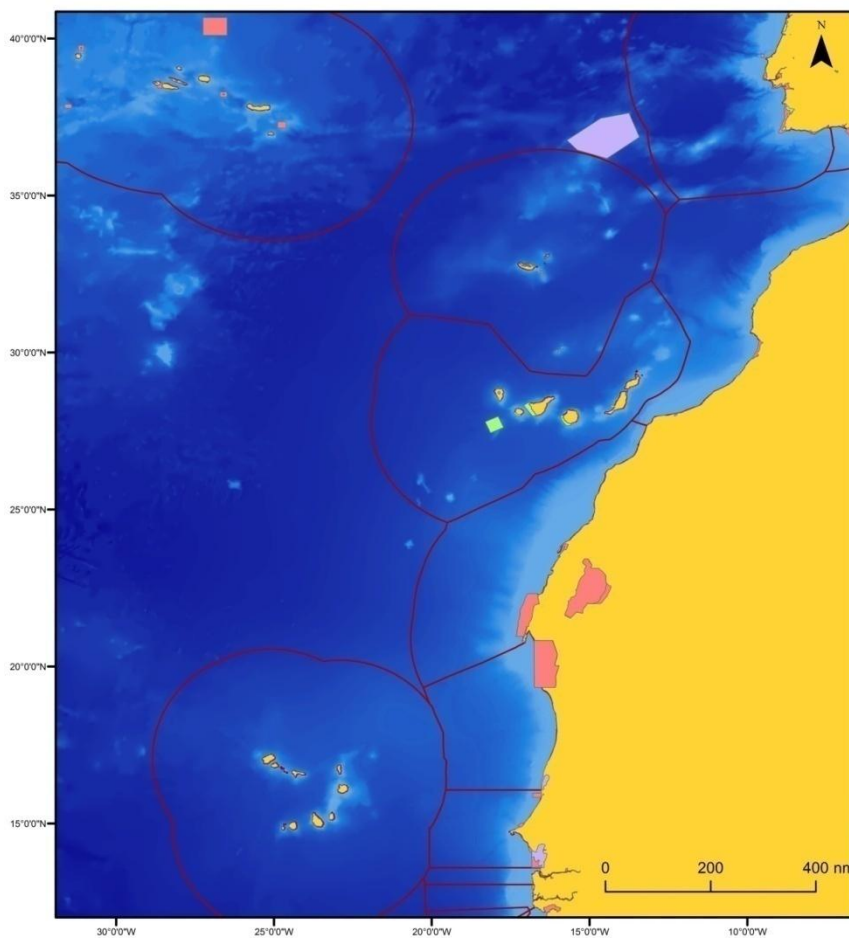
### 1.6.3 Conservation of Baleen whales

Macaronesia has roughly 150 marine/coastal areas in which some protection status has been given, most of which are managed at the regional level (figure 2). A large part of these areas are in the coast, with very few off-shore areas (generally seamounts) being used as places for biodiversity conservation (e.g. Josephine and Sedlo seamounts). Of all the areas in this Atlantic region, there are none whose implementation has served to specifically protect some species of cetaceans.

The European Union's Wild Birds and Habitats Directives are responsible for a network of marine and land-based protected areas in the European Community, while a number of conventions and agreements (e.g. OSPAR Convention for the Protection of the Marine Environment of the Northeast Atlantic, Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and contiguous Atlantic area (ACCOBAMS) and Agreement on the Conservation of Small Cetaceans in the Baltic , North East Atlantic , Irish and North Seas (ASCOBANS)) allows stakeholders to perceive what marine species, habitats and ecosystems need to be protected, conserved or restored in order to reduce threats to that are affecting them. Many protected areas (approximately 67 areas, (MPAtlas, 2017)) existing in this area arise from these legal mechanisms. Moreover in the area, there are several Wetlands of International Importance defined by Ramsar Convention (Ramsar Convention, 2017), some Biosphere Reserves within the Man and the Biosphere program (MAB

Programme, 2017) and a World Heritage Site (Banc d'Arguin National Park) in Mauritania (UNESCO World Heritage Center, 2017).

Likewise, in the Northwest Africa, The Convention for Cooperation in the Protection and Development of the Marine and Coastal Environment of the West and Central African Regions in conjunction with the protocol on Combating Pollution in Cases of Emergency (OPCW, 2016), are some of the few initiatives in the region, developed to control pollution and create infrastructures to manage the marine environment. A few protected areas along the African coast allow the protection of marine ecosystems.



**Level of Protection**

- International
- National
- Regional
- EEZ boundaries

**Figure 2:** Protected regions in the Macaronesia at the Regional, National and International level.

## 1.7 Aims

This study aims to provide a strong knowledge on spatial and temporal distribution on four species of migratory baleen whales in the Macaronesia, assess habitat preferences and the potential influence of the geomagnetism in the orientation mechanisms, with the final goal of better understanding migratory routes within the area.

More specifically, aims of the study are:

1. Create a database of the selected baleen whale occurrences in the Macaronesia gathered in literature over the past 26 years.
2. Provide a strong knowledge on spatial and temporal distribution.
3. Assess habitat preferences of selected baleen whales using topographic and oceanographic variables as proxies to characterize their preferred habitat.
4. Study the influence of the geomagnetism in migration.

Four species were selected for the research: blue and humpback whales, as charismatic and endangered species (Ducarme *et al.*, 2013), and minke and fin whales, as the species of baleen whales with more sightings gathered in the literature revision.

## 1.8 Limitations

Although this work is an important step in our understanding of baleen whales' migrations in the Macaronesia, some constraints need to be addressed.

Limitations of the work are presented below:

- Since our data were collected from several sources, levels and types of effort were distinct. Hence, there was a need to standardize effort for comparisons.
- High heterogeneity in the number of sightings per area. Our observations are largely concentrated along the coast and around the archipelagos due to fragmentation of research effort.
- No data regarding whether sightings are from migrating or resident individuals, specially considering the species that have known resident and migratory populations in the area (fin and minke whales (Silva *et al.*, 2013; Víkingsson & Heide-Jørgensen, 2014; ICNF, 2016)).

## 2. Material and Methods

For this study, besides a thorough literature revision, several analyses were performed on different softwares. All maps were produced with ArcGIS v10.3.1 (ESRI, 2016), from a WGS84 coordinate system (EPSG: 4326) projected to Mercator (EPSG: 3395), graphs and tables in Microsoft Excel (Microsoft, 2007) and boxplots and statistical analyses (descriptive, tests and models) in R Software (R Development Core Team, 2017).

### 2.1 Study area

For our study area we considered the following geographical limits: the upper limit at 42° N (north), lower limit at 12°N (south), eastern limit at 6°W and western limit at 32° (figure 2).

### 2.2 Data sampling

- Occurrence data

Sightings of baleen whales recorded in Macaronesia since 1990 were collected from several sources, comprising published data available from several sources (e.g., papers in peer-reviewed journals) to databases. For some sightings obtained, geographic coordinates are approximate positions (e.g. Hazevoet & Wenzel, 2000) since we did not have access to the exact geographical location.

#### 1. Published records

A deep bibliographic review was undertaken in order to obtain sightings of four baleen whale species (minke, fin, blue and humpback whales) recorded in Macaronesia since 1990. Several sources were considered, including peer-reviewed publications, conference proceedings and public reports. Occurrence data included sightings from different types of surveys: opportunistic, non-systematic, line-transect, and tagging and photo-identification studies.

## 2. Databases

Data on baleen whales sightings was searched in a number of databases from projects existing in this Atlantic region.

We collected data from OBIS-SEAMAP (Halpin *et al.*, 2009), an enormous online database providing distribution data on several marine species around the world, including cetaceans.

Also, we used data provided by MONICET Platform (Fernandez & Azevedo, 2017) that has been collecting information on cetacean presence in the Azores Archipelago from a whale watching companies since 2009. Data from Museu da Baleia was compiled from Visor Bio (Visor Bio, 2017; see Acknowledgments), an online database developed by the Observatório Oceânico da Madeira (OOM) with cetacean occurrence data collected mainly around Madeira archipelago.

Finally, another set of data was provided by CETUS Project (personal communication, Correia *et al.*, 2015) that collects cetacean occurrence in offshore areas of Macaronesia aboard cargo ships, used as Observation Platforms of Opportunity (OPOs), along the routes between mainland Portugal and the Portuguese islands, Canaries, Cape Verde and Mauritania.

### -Habitat data collection

To investigate habitat preferences, several topographic, oceanographic and geographical variables were accessed.

Bathymetric data was taken from “General Bathymetric Chart of the Oceans” (GEBCO) Digital Atlas (GEBCO, 2017) at 30 arc-second (to define seamounts and calculate slope) and at one arc-minute (for other habitat variables) and converted to ESRI compatible format (ASCII) with the “Grid display software”, downloaded from the British Oceanographic Data Centre website (BODC, 2017).

ArcGIS v10.3 (ESRI, 2016) was then used to generate the static variables used in the analyses. Slope was computed from bathymetry with the Surface Analysis tools. For rugosity we use Benthic Terrain Modeler toolbox (BTM) (Wright *et al.*, 2005),

incorporated in ArcGIS v10.3. The function "Terrain Ruggedness (VRM)" captures variability in slope and aspect into a single measure, based in vector analysis (measures how different it is the 3-D orientation of a specific cell compared with the neighborhood) (Sappington *et al.*, 2005). The topographic structures, namely seamounts, banks, hills, ridges and rises to compute the "distance to seamounts" variable, were obtained from GEBCO (GEBCO, 2017). A polygon shapefile was created to define polygons surrounding the structures with the limits around their base (whenever contour lines, created every 50m, started to be denser).

Three dynamic variables were collected with remotely sensed data: chlorophyll-*a* (as a proxy to primary production), sea-surface temperature and sea level anomaly. For these 3 variables, weekly data were collected from July 2002 until December 2016 (MODIS-satellite data only available since July 2002).

Chlorophyll-*a* and sea-surface temperature (measured at night) were obtained from the "Moderate Resolution Imaging Spectrometer" (MODIS) instrument on the Aqua satellite from the "National Aeronautics and Space Administration" agency (NASA), at 4km and weekly resolution.

Finally, maps of sea level anomaly were collected from global products of the "Archiving, Validation and Interpretation of Satellite Oceanographic data" agency (AVISO) (from satellites Jason-Envisat and Topex/Poseidon-ERS) (AVISO, 2017), with 25km of resolution. Copernicus Marine and Environment Monitoring Service (CMEMS) (CMEMS, 2017) was used to obtain the data. We use delayed time products from the period between July 2002 and May 2016, whereas data from May to December 2016 were from near-real-time products (as, up to the present moment, delayed products are not available yet).

All rasters for the three variables were extracted with the pack Marine Geospatial Ecology Tools (MGET) (Roberts *et al.*, 2010) from ArcGIS v10.3 (ESRI, 2016), more specifically in "Data Products" tools.

Habitat variables and its characteristics are presented in the table below (table 1).

**Table 1:** Characteristics of the habitat variables that will be collected.

Variable	Name used	Unit	Type	Spatial Resolution	Temporal Resolution	Source
Bathymetry	Bathymetry	M	Static	1 arc minute	-	GEBCO
Slope	Slope	Degree	Static	30 arc second	-	GEBCO
Distance to Seamounts	Dist. Sm.	Km	Static	30 arc second	-	GEBCO
Distance to Coast	Dist.coast	Km	Static	1 arc minute	-	GEBCO
Rugosity	Rug.		Static	1 arc minute	-	GEBCO
Latitude	Lat.	UTM northing (m)	Static	-	-	GPS
Longitude	Lon.	UTM northing (m)	Static	-	-	GPS
Chlorophyll-a	CHL	mg/m <sup>3</sup>	Dynamic	4 km	Weekly	MODIS (NASA)
Sea surface temperature	SST	°C	Dynamic	4 km	Weekly	MODIS (NASA)
Sea level anomalies	MSLA	Cm	Dynamic	1/3° or 1/4°	Weekly	AVISO

### - Geomagnetism

Regarding geomagnetism, for each sighting, the values of 7 magnetic components (total intensity, horizontal intensity, north component, east component, vertical intensity, geomagnetic inclination and geomagnetic declination) were obtained using Magnetic Calculator tool, available in ArcGIS v.10.3 (ESRI, 2016). For the geomagnetism analysis, only data since 2005 was available.

## 2.3 Data Analyses

### 2.3.1 Spatial and temporal analysis

#### - Spatial and seasonal distribution of the occurrence data

To access and analyze the spatial and seasonal distribution of the occurrence data collected in the bibliographic review, we split our study area in regions (figure 3), based on topography and political boundaries. These regions include areas with the continental platforms, the islands, ocean areas around archipelagos and the open-ocean between mainland and the islands.

Due to differences both in methodology and research platforms, survey effort was highly heterogeneous (as in Macleod *et al.*, 2006). Hence, we counted the number of articles or databases with records within each region to access research effort. Research effort includes from published data in journals, conference proceedings and reports.

For seasonal analysis, we divided the year as follows:

1. Winter: January–March;

2. Spring: April-June;
3. Summer: July-September;
4. Fall: October-December.

We characterized baleen whales occurrence according to number of records and months recorded, by area and season. The categories were defined according to the criteria used by Freitas (*et al.*, 2004):

.Presence in the region:

Very common - species sighted daily or almost in a daily basis, during the year or in a given period of the year. In our case, we consider a minimum of 40 sightings;

Common - species that is sighted quite frequently throughout the year or in a certain period of the year. In our case we consider a minimum of 10 sightings;

Occasional - sightings are summarized in a few observations per year. In our case we consider a minimum of 5 sightings;

Rare - with a very sporadic presence throughout the year. We consider as maximum limit to include in this category 4 sightings.

.Occurrence throughout the year:

Seasonally defined - most of the observations are made during a specific period of the year;

Seasonally irregular - observations are irregular over a specific period of the year. In our case we consider this category when there are few sightings practically only in one season;

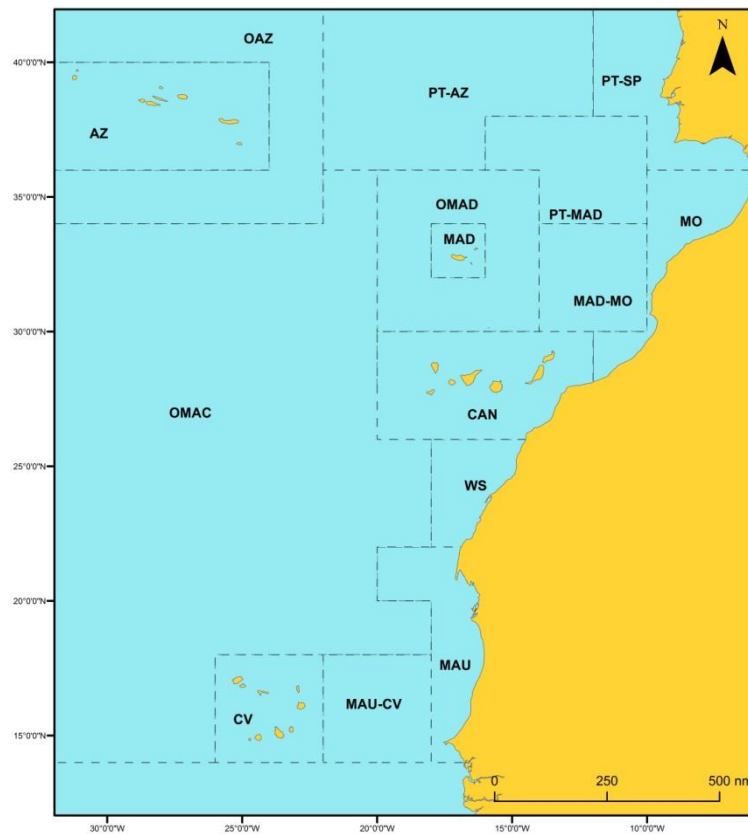
Annual periodically - observed throughout the year intermittently. In this category are included regions in which few sightings of a specific species were obtained throughout the year;

Undefined - when the low number of occurrences do not allow us to see any temporal patterns in the distribution of a species;

No sightings - when there is no sighting of a particular species in a region;

Data deficient - when the low number of sightings, due to the low survey effort carried out in these regions, does not allow to infer any spatial and temporal patterns in the distribution of a given species.





**Figure 3:** Map of the study area, divided by regions. Division is based on both topography and political boundaries. Labels: PT-SP - Portugal and Spain; AZ – Azores; OAZ- ocean around Azores; PT-AZ – ocean between Portugal and Azores; MO – Morocco; PT-MAD – ocean between Portugal and Madeira, OMAD- ocean around Madeira; MAD – Madeira; MAD-MO – ocean between Madeira and Morocco; CAN – Canaries; WS- Western Sahara; MAU – Mauritania; MAU-CV – ocean between Mauritania and Cape Verde; CV- Cape Verde; OMAC- ocean of Macaronesia.

For all the subsequent analyses, a measure of encounter rate was computed as follows:

(Number of sightings of species in study (humpback, blue, fin or minke) / Total number of sightings of cetaceans)

Hence, survey effort was being considered either in time and space by accounting for all encounters with cetacean species (Esteban *et al.*, 2013). The assumption is that for each sampling area, survey effort is proportional to the number of cetacean sightings recorded and is higher than zero if there is at least one record.,

For that, only databases were used (since, unlike other sources, they provide all records of cetacean occurrence), starting in July 2002. Moreover, sightings were the sampling

unit regardless the size of the group, minimizing the effect of population density on habitat selection patterns.

- Latitudinal variation

To evaluate latitudinal progression, we divided encounter rates by latitudinal ranges of 2 degrees and build graphs and maps to illustrate latitudinal progression across seasons in the area.

- Spatio-temporal models

We developed spatio-temporal models and we selected GAMs as they offer flexibility through smooth functions applied to each explanatory variable (Wood, 2003).

As explanatory variables, we selected the following geographic and temporal variables: Longitude, Latitude (lat), Year and Julian Days (Julian). The longitude was converted to its negative for ease of interpretation in the models' graphs, so the variable was designated as "neg\_lon". For geographical position, a grid of 2x2 degrees was generated in ArcGIS v10.3 (ESRI, 2016) and the latitude and longitude values of the centroid of the cell were given to the sightings.

We followed the approach by Esteban *et al.* (2013): a presence / pseudo-absence model, with all cetacean's sightings as "sampling stations". The rationale was the same as the one used to compute encounter rates: presences were the sightings of the species of interest and pseudo-absences the sightings of all other cetaceans. Also, sightings were the sampling unit regardless of the group size.

GAMs were fitted in package "mgcv" (Wood, 2006; Wood, 2011) of the statistics program R (R Development Core Team, 2017).

Before running the models, Correlation Analysis and Variance inflation factors (VIF) were used to assess the collinearity of the explanatory variables. Considering a threshold of  $VIF = 3$  (Zuur *et al.*, 2010) and a significant correlation as  $r > 0.80$ , explanatory variables that exceed these values were not used together in the same model.

A binomial distribution was chosen, with a logit link function (Hastie *et al.*, 2003) and predictors were considered statistical significant for the model with  $p\text{-value} < 0.05$ . All the other parameters were set to the default values in "mgcv".

Variable selection was performed through backward selection from an oversaturated model (e.g. Vilchis *et al.*, 2006) and using Akaike's Information Criterion (AIC) (Burnham & Anderson, 1998). For comparisons between AIC's values we used an ANOVA chi-square test. When we found significant differences, the model with the lowest AIC was selected. If there were no significant differences, the simplest model was maintained. A limit on the number of splines was defined, to modelling the data and not just fitting them (Quian, 2009).

For model evaluation we used the Area Under the Curve (AUC) metric of the Receiving Operator Characteristic (ROC) curve (Beck & Schultz, 1986). A ROC curve allows us to know the predictive power of the model, compared to a random model. Sensitivity values (in y-axis) represent true-positive sightings whereas Specificity values (in x-axis) represent false positive sightings. The AUC value varies between 0 and 1, with 0.5 meaning that our model performed the same way as a random model, whereas 1 means that our model has an excellent accuracy for what we want to find out. To evaluate these models, we had to create a set for fitting and another set for evaluation. The number of sightings used in both sets for each model are shown in table 2.

**Table 2:** Number of sightings for model fitting and model evaluation under the Receiving Operator Characteristic curve.

<i>Balaenoptera acutorostrata</i>	Presence	Pseudo-Absence
Fitting	63	15337
Evaluation	22	5261
<i>Balaenoptera physalus</i>		
Fitting	772	14628
Evaluation	263	5020
<i>Balaenoptera musculus</i>		
Fitting	276	15124
Evaluation	94	5189
<i>Megaptera novaeangliae</i>		
Fitting	90	15310
Evaluation	30	5253

In order to evaluate our model accuracy, we follow the criterion of Hosmer and Lemeshow (1989): 0.5 indicated no discrimination; 0.5 to 0.7 represented poor discrimination; 0.7 to 0.8 indicated an acceptable discrimination; 0.8 to 0.9 indicated an excellent discrimination; and over 0.9 represented outstanding discrimination.

### 2.3.2 Habitat preference analysis

First of all for each observation, data regarding topographic and oceanographic variables was extracted. Afterwards, as previous study area was divided in a grid of 2x2 degrees, and for each cell and topographic and oceanographic variable, we calculated several descriptive statistics, using "Zonal statistics as Table" tool incorporated in ArcGIS v10.3 (ESRI, 2016).

Boxplot graphs were used in order to establish the habitat range for the four baleen whale species, for each season. For variables such as chlorophyll-a, the boxplots were zoomed in to try to see if there were differences in preferences among the different species, since the boxplots were not being informative. For this reason some outliers will not be represented. Available habitat was defined as the range from all the cetacean sightings.

Mann-Whitney-Wilcoxon tests were performed for pairwise comparisons between the range of the available habitat and the habitat of each species, by season. Comparison tests were only performed with more than 30 sightings in each of the comparison group, for statistical representativity (e.g. van Belle & Millard, 1998).

### 2.3.3 Geomagnetism

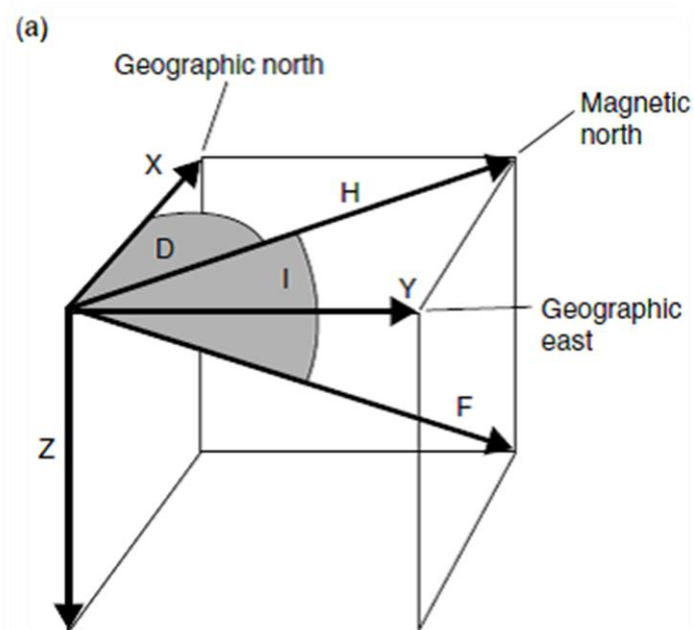
#### - Descriptive analysis

Firstly, we accessed how declination, inclination and total intensity of magnetic field varied with the geographic position (figure 25) using all sightings. Statistical significance of the correlation coefficients was inferred by using Student's t-test ( $P < 0,05$ ).

Declination is the angle between the magnetic north and the geographic north, whereas inclination is the angle between the horizontal plane and the magnetic field vector (figure 4).

Afterwards, we split our data in 2 groups: sightings from Azores and Madeira and the remaining sightings.

With the later, we build histograms and boxplots, by species of the declination, inclination and total intensity (see Appendix) and used descriptive statistics to confirm the patterns observed. Both histograms and descriptive statistics were computed in Microsoft Excel (Microsoft, 2007), whereas boxplots were computed in R Software (R Development Core Team, 2017).



**Figure 4:** Total magnetic field vector (F) and its components. Declination and Inclination are represented by the letters D and I, respectively. H represents the vector component in the horizontal plane. Original image from Walker (*et al.*, 2002).

If whales use geomagnetic field as an environmental cue for position determination, then different areas crossed must have magnetic fields with different characteristics. In order to test this idea, we use the sightings from Madeira and Azores islands to compare the magnetic field between the two. Only sightings of fin whales were used in this analysis, as it was the only species (of the four studied) with sightings in both islands.

Finally, we split occurrences into two datasets, according to the widely accepted periods of migration: spring (April, May and June) and fall (October, November and December); and magnetic field characteristics were compared. Humpback whales were not considered, as there were no sightings during the spring season. Comparisons among datasets were performed using histograms built in Microsoft Excel (Microsoft, 2007).

#### - Modeling of Magnetic Components

Generalized Additive Models (GAM) were used to investigate possible preferences of whales for a specific magnetic components. As explanatory variables we chose three magnetic components (declination, inclination, total intensity) and two geographic variables (latitude and longitude). As a response variable we consider the number of sightings in each cell of 2x2 degrees and as explanatory variables the mean of each component for that cell. The latitude and longitude of the centroid of the cell were used as geographical variables. To extract the values of the explanatory variables to the sightings, the tool "Magnetic Calculator" of the ArcGIS v10.3 (ESRI, 2016) was used. Moreover, season was computed as a factor in the model.

All models were fitted with the package 'mgcv' (Wood, 2006; Wood, 2011) in R 3.3.3. (R Development Core Team, 2017).

Since this is an exploratory study, we opted to use a negative binomial distribution, which is a very general distribution, so it can be used for almost all types of data and usually well fits overdispersed data (Zuur *et al.*, 2012). A log link function was chosen and predictors were considered statistical significant for the model with  $p\text{-value} < 0.05$ . All the other parameters were set to the default values in "mgcv".

Since variables were extremely correlated between them, models were fitted with only one variable at a time, allowing the analysis of each explanatory variable separately. Again, we defined a limit on the number of splines as suggested by Quian (2009).

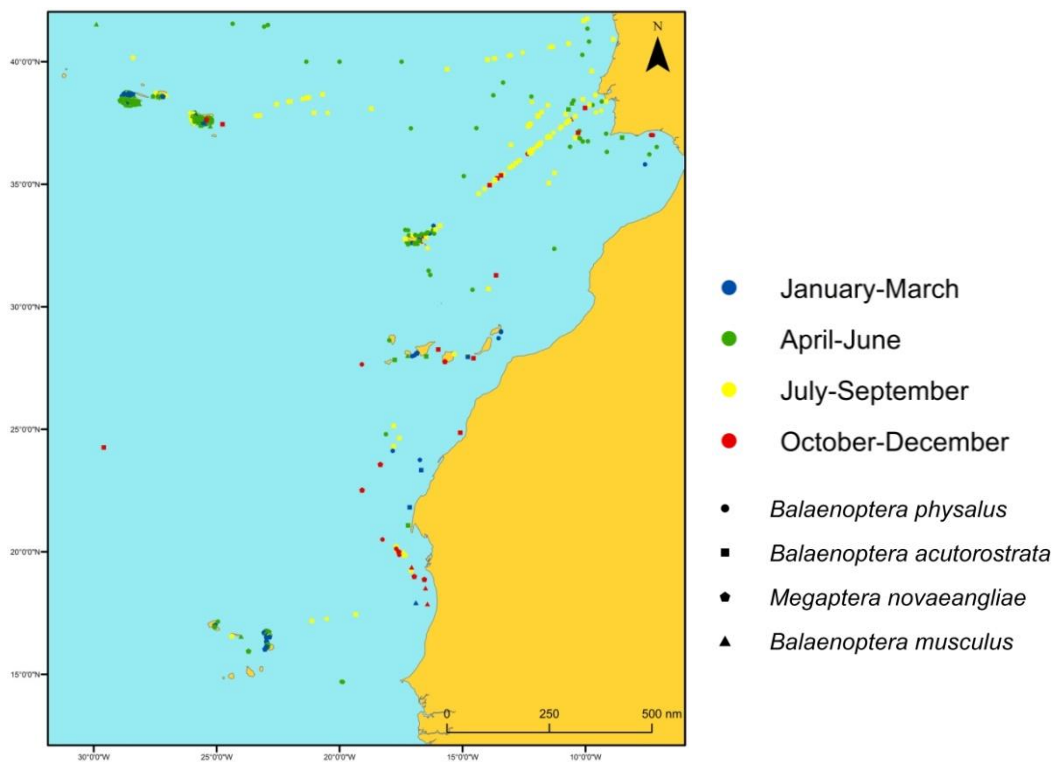
## 3. Results

### 3.1 Spatial-temporal analysis

- Spatial and seasonal distribution of the occurrence data

From a total of 15 articles, 3 reports, 1 conference proceeding and 4 databases, we gathered 1797 sightings of the four species of baleen whales in Macaronesia (121 minke, 1071 fin, 417 blue and 188 humpback whales).

In figure 5, distribution of the 4 species in the Macaronesia, by season, is represented. It is possible to observe differences in distribution among areas, seasons and species. While in Azores archipelago there are a lot of observations from all species, and in all seasons, for other regions there are only records for certain species and/or certain seasons. For example, in the Iberian Peninsula coast blue and humpback do not seem to be present in any season.

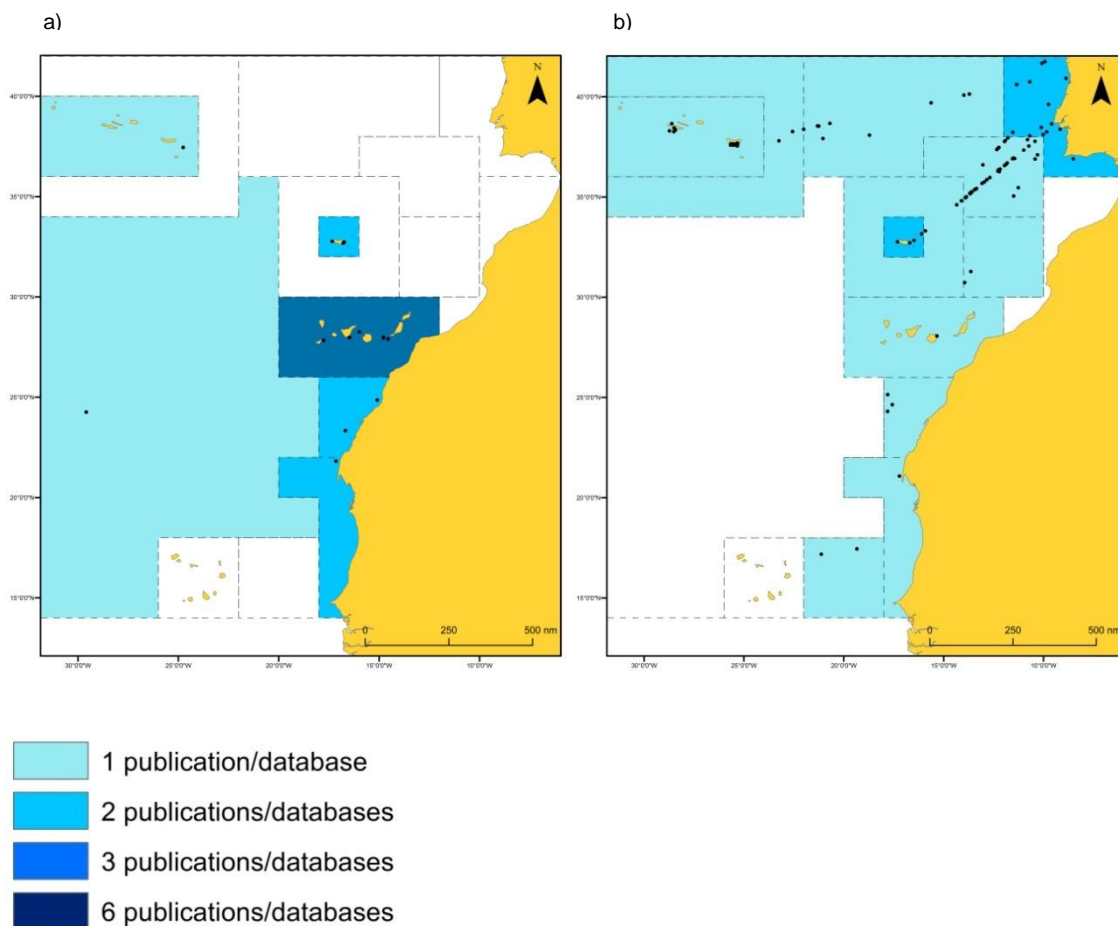


**Figure 5:** Sightings obtained seasonally for minke, fin, humpback and blue whales using information from databases and publications. Each color symbolizes a quarter of the year, while polygons represent the species of baleen whales.

## Looking for the migratory whales: Routes of the baleen whales in the Macaronesia

From figures 6-9, we can see that baleen whales were observed in the majority of the areas, with the exception of Morocco and the most offshore areas of Macaronesia, where sightings are limited. Having been collected information from only one database (CETUS, personal communication; Correia *et al.*, 2015), there is a lack of information for these areas regarding the presence of baleen whales during the year.

On the other hand, in regions such as the archipelagos of Madeira and the Canaries, many sightings were obtained even though from different data sources (Madeira - OOM and Canaries - publications).

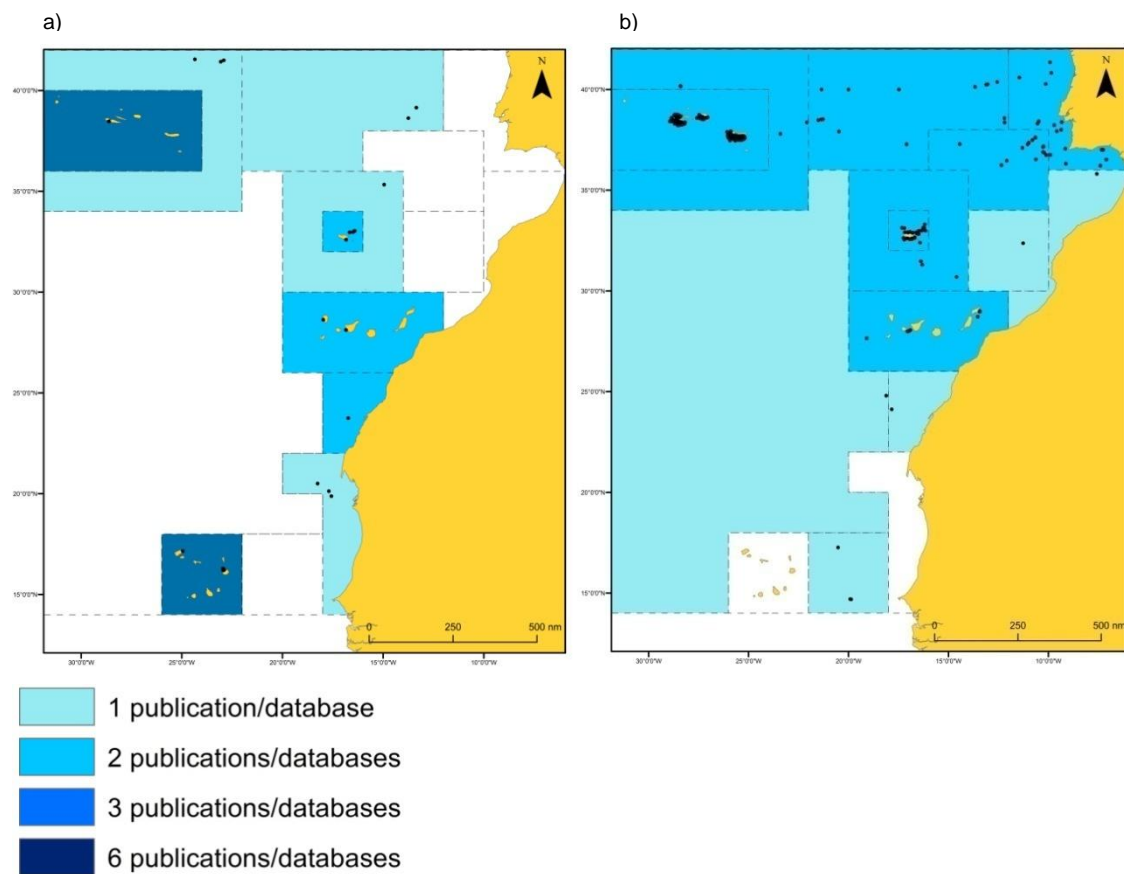


**Figure 6:** Global distribution of minke whales in Macaronesia, based on published data (a) and databases (b) information. Black circles represent sightings of minke whales. The color of the areas indicate the research effort according to the number of publications/databases providing records for the area.

Minke whales can be seen in both coastal and offshore areas (figure 6). It should be noted the many sightings obtained between mainland Portugal and Madeira

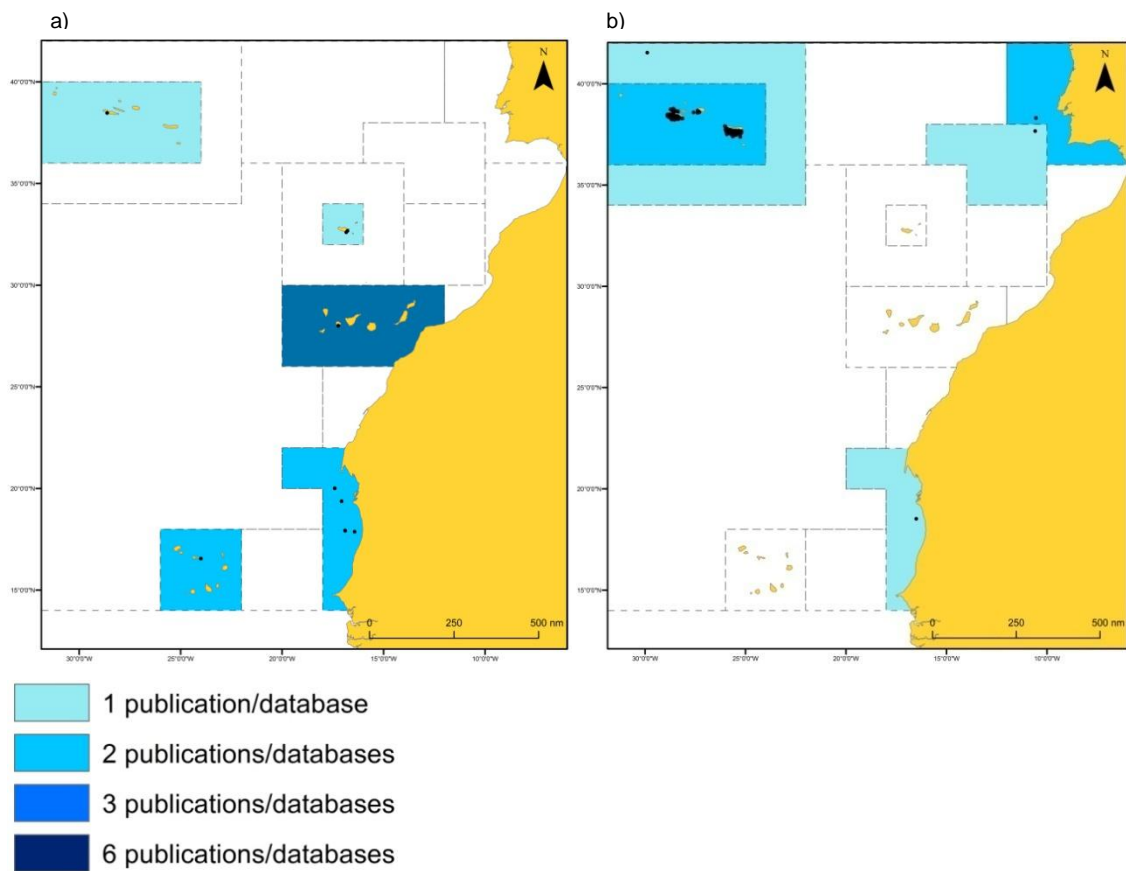


archipelago, even though they were taken only from a single database, this species was observed many times to frequent these waters.



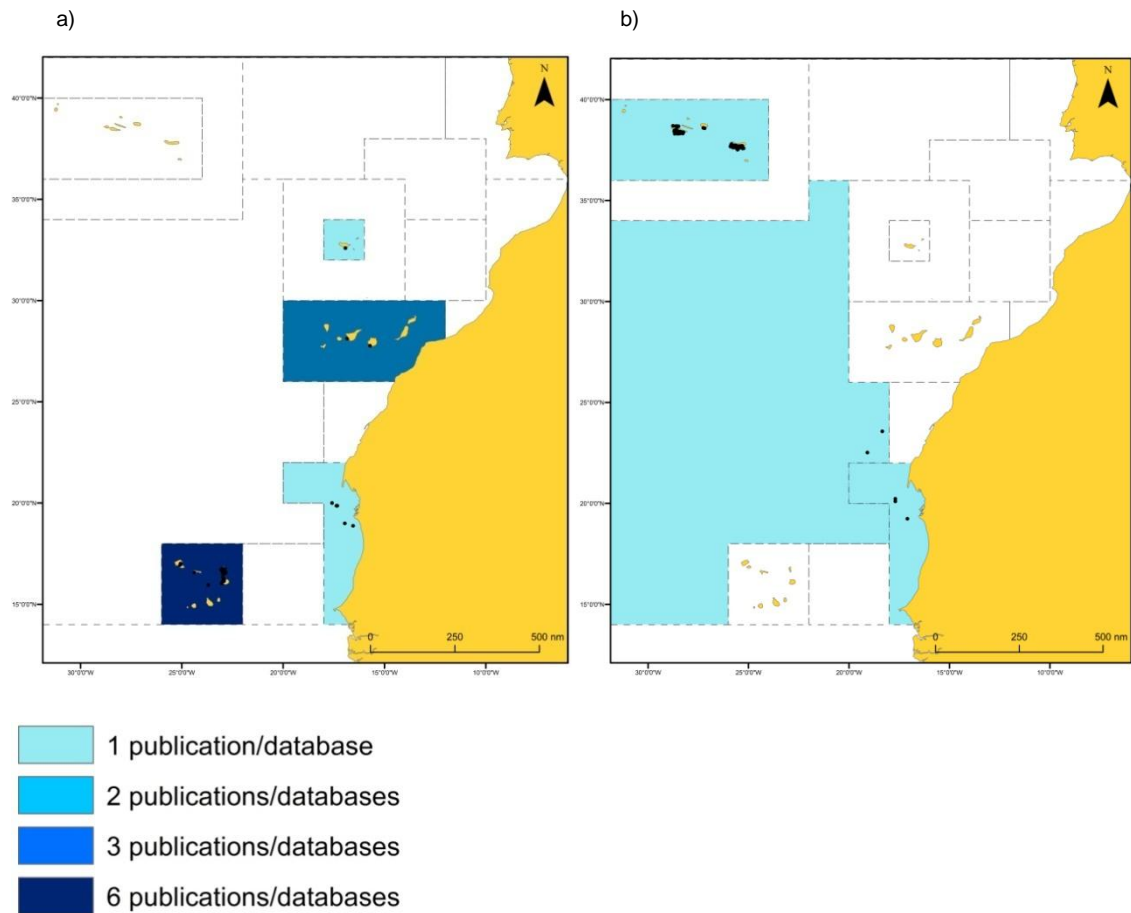
**Figure 7:** Global distribution of fin whales in Macaronesia, based on published data (a) and databases (b) information. Black circles represent sightings of fin whales. The color of the areas indicate the research effort according to the number of publications/databases providing records for the area.

Fin whales, like minke whales, can also be seen in both coastal and offshore areas (Figure 7). However, in areas such as the Madeira archipelago, with the same sampling effort, there is a greater presence of fin whales in the area compared to minke whales (Figures 6 and 7). Particularly noteworthy is the large number of sightings obtained in the archipelago of the Azores from the databases.



**Figure 8:** Global distribution of blue whales in Macaronesia, based on published data (a) and databases (b) information. Black circles represent sightings of blue whales. The color of the areas indicate the research effort according to the number of publications/databases providing records for the area.

The blue compared to the fin and minke, were not observed in many regions (figure 8), and in most of the areas, only one sighting was reported. Exception made to the Azores (with many sightings from the databases) and Mauritania where the species has been sighted several times.



**Figure 9:** Global distribution of humpback whales in Macaronesia, based on published data (a) and databases (b) information. Black circles represent sightings of humpback whales. The color of the areas indicate the research effort according to the number of publications/databases providing records for the area.

Humpback whales, like blue whales, were not seen in many regions (figure 9). The many sightings obtained in Cape Verde from the publications are the result of many studies in this known breeding area (hence the survey effort is very high). Moreover, and similarly to the blue whale, it should be noted the many sightings obtained in the region of the Azores, and the observations obtained in Mauritania, where this species was sighted frequently.

Seasonal distribution of records, according to the number of publications, is presented in figure 10.

Looking for the migratory whales: Routes of the baleen whales in the Macaronesia

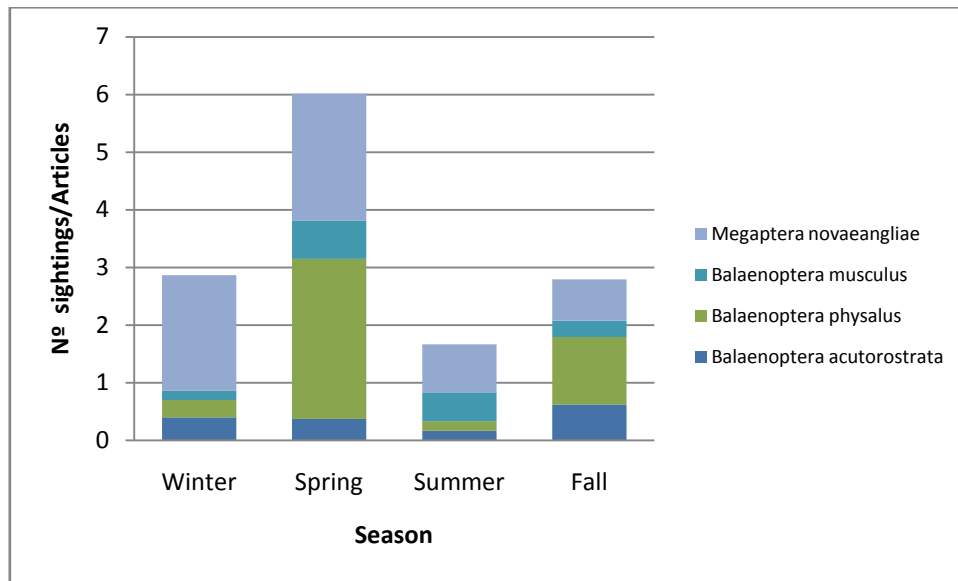


Figure 10: Seasonal abundance of four baleen whale species in Macaronesia, based in the number of publications.

Records considering research effort are higher during spring, with a big contribution of fin whale sightings. Records for blue and minke whales remain constant all over the year, while humpback whales have a greater number of records in winter and spring.

Tables 3-10 present the number of sightings, size of group and number of publications (tables 3, 5, 7 and 9) and databases (tables 4, 6, 8 and 10), by species, seasons and regions.

Tables 3 and 4: Records of minke whales and number of publications (table 3) and databases (table 4) by seasons and regions. Labels: PT-SP - Portugal and Spain; AZ – Azores; OAZ- ocean around Azores; PT-AZ – ocean between Portugal and Azores; MO – Morocco; PT-MAD – ocean between Portugal and Madeira, OMAD- ocean around Madeira; MAD – Madeira; MAD-MO – ocean between Madeira and Morocco; CAN – Canaries; WS- Western Sahara; MAU – Mauritania; MAU-CV – ocean between Mauritania and Cape Verde; CV- Cape Verde; OMAC- ocean of Macaronesia.

		Areas														
		PT-SP	AZ	OAZ	PT-AZ	MO	PT-MAD	OMAD	MAD	MAD-MO	CAN	WS	MAU	MAU-CV	CV	OMAC
Season	Winter	Sightings (Group size: min-max)	1 (1-1)													
		Research effort (Contributions to the records)	1 (1)													
	Spring	Sightings (Group size: min-max)	1 (1-1)													
		Research effort (Contributions to the records)	1 (1)													
	Summer	Sightings (Group size: min-max)	1 (1-1)													
		Research effort (Contributions to the records)	1 (1)													
	Fall	Sightings (Group size: min-max)	1 (1-1)													
		Research effort (Contributions to the records)	1 (1)													

		Areas															
		PT-SP	AZ	OAZ	PT-AZ	MO	PT-MAD	OMAD	MAD	MAD-MO	CAN	WS	MAU	MAU-CV	CV	OMAC	
Season	Winter	Sightings (Group size: min-max)	1 (1-1)														
		Research effort (Contributions to the records)	2	1 (1)	0	0	1	1	1	1	1	2	2	1	1	1	1
	Spring	Sightings (Group size: min-max)	2 (1-3)	19 (1-2)													
		Research effort (Contributions to the records)	2 (2)	3 (1)	2	2	1	2	2	2	2	2	1	1 (2-2)	2 (1)	1	1
	Summer	Sightings (Group size: min-max)	11 (1-2)	4 (1-1)	3 (1-1)	8 (1-2)											
		Research effort (Contributions to the records)	2 (2)	3 (1)	2 (1)	2 (1)	0	3 (1)	3 (1)	3 (2)	1 (1)	1 (3-3)	3 (1-3)	2 (1-1)	1 (1)	1 (1)	1
	Fall	Sightings (Group size: min-max)	1 (1-1)	1 (1-1)													
		Research effort (Contributions to the records)	2 (1)	3 (1)	1	1	0	2 (1)	3	3	2 (1)	2	2	1	1	1	2

Looking for the migratory whales: Routes of the baleen whales in the Macaronesia

Minke whales had a relatively low number of sightings. According to our literature review, they were recorded throughout the year in Canary Islands, whereas in more southern latitudes they were only found sighted in fall and in winter (table 3).

From databases, minke whales were recorded year-round in the waters of Azores, although the number of sightings is much greater in the spring compared to the other seasons. It is during the summer months that minke whales were most sighted (also due to the greater effort made), with observations in both coastal and offshore areas. Note the high number of sightings obtained for this species in the region between mainland Portugal and the Madeira archipelago.

**Tables 5 and 6:** Records of fin whales and number of publications (table 5) and databases (table 6) by seasons and regions. Labels: PT-SP - Portugal and Spain; AZ – Azores; OAZ- ocean around Azores; PT-AZ – ocean between Portugal and Azores; MO – Morocco; PT-MAD – ocean between Portugal and Madeira, OMAD- ocean around Madeira; MAD – Madeira; MAD-MO – ocean between Madeira and Morocco; CAN – Canaries; WS- Western Sahara; MAU – Mauritania; MAU-CV – ocean between Mauritania and Cape Verde; CV- Cape Verde; OMAC- ocean of Macaronesia.

		Fin whale	Areas													
			PT-SP	AZ	OAZ	PT-AZ	MO	PT-MAD	OMAD	MAD	MAD-MO	CAN	WS	MAU	MAU-CV	CV
Season	Winter	Sightings (Group size: min-max)	2 (1-1)											1 (6-6)		
		Research effort (Contributions to the records)	1 (1)											1 (1)		
	Spring	Sightings (Group size: min-max)	9 (1-1)	3 (1-2)	2 (1-2)				1 (3-3)	5 (1-10)	3 (1-2)		2 (1-1)			
		Research effort (Contributions to the records)	3 (1)	1 (1)	1 (1)				1 (1)	2 (2)	2 (2)		3 (2)			
Summer	Sightings (Group size: min-max)	1 (1-1)														
	Research effort (Contributions to the records)	1 (1)														
Fall	Sightings (Group size: min-max)												3 (1-2)		7 (1-12)	
	Research effort (Contributions to the records)												1 (1)		2 (1)	

		Fin whale	Areas													
			PT-SP	AZ	OAZ	PT-AZ	MO	PT-MAD	OMAD	MAD	MAD-MO	CAN	WS	MAU	MAU-CV	CV
Season	Winter	Sightings (Group size: min-max)	65 (1-5)				1 (1-1)		6 (1-2)		5 (1-1)		1 (1-1)			
		Research effort (Contributions to the records)	2	2 (1)	0	0	1 (1)	1	1	1 (1)	1	2 (1)	2 (1)	1	1	1
	Spring	Sightings (Group size: min-max)	11 (1-4)	735 (1-7)	5 (1-7)		7 (1-3)		3 (1-3)	16 (1-10)	1 (1-1)		2 (1-4)		1 (1-1)	
		Research effort (Contributions to the records)	2 (2)	3 (1)	2	2 (2)	1	2 (2)	2 (2)	2 (1)	2 (1)	2	1	2	1 (1)	1
	Summer	Sightings (Group size: min-max)	3 (1-4)	134 (1-5)	5 (1-2)	9 (1-3)	7 (1-1)		6 (1-2)				1 (2-2)			
		Research effort (Contributions to the records)	2 (2)	3 (1)	2 (1)	2 (1)	0	3 (1)	3	3 (2)	1	2	1	1	1 (1)	1
	Fall	Sightings (Group size: min-max)	2 (1-1)	5 (1-1)			1 (1-1)		2 (1-2)		2 (1-3)					
		Research effort (Contributions to the records)	2 (1)	3 (1)	1	1	0	2 (1)	3	3 (1)	2	2 (2)	2	1	1	1

Fin whales were mostly sighted throughout Macaronesia regions during spring and summer. In the Azores archipelago, they were sighted in all seasons, except in fall, while for Northwest Africa (Western Sahara and Mauritania) they were observed in the fall and winter. For Madeira and Canary islands, sightings were obtained in all seasons although there is a greater number in spring and winter, respectively.

This species was also recorded in low latitudes, including Cape Verde islands and waters between Cape Verde and Mauritania, during spring and summer.

Looking for the migratory whales: Routes of the baleen whales in the Macaronesia

**Tables 7 and 8:** Records of blue whales and number of publications (table 7) and databases (table 8) by seasons and regions. Labels: PT-SP - Portugal and Spain; AZ – Azores; OAZ- ocean around Azores; PT-AZ – ocean between Portugal and Azores; MO – Morocco; PT-MAD – ocean between Portugal and Madeira, OMAD- ocean around Madeira; MAD – Madeira; MAD-MO – ocean between Madeira and Morocco; CAN – Canaries; WS- Western Sahara; MAU – Mauritania; MAU-CV – ocean between Mauritania and Cape Verde; CV- Cape Verde; OMAC- ocean of Macaronesia.

		Blue whale																
		Areas																
		PT-SP	AZ	OAZ	PT-AZ	MO	PT-MAD	OMAD	MAD	MAD-MO	CAN	WS	MAU	MAU-CV	CV	OMAC		
Season	Winter	Sightings (Group size: min-max)	2 (2-2)															
		Research effort (Contributions to the records)	2 (1)															
	Spring	Sightings (Group size: min-max)	3 (1-1)														1 (1-1)	
		Research effort (Contributions to the records)	1 (1)														3 (1)	
	Summer	Sightings (Group size: min-max)	2 (1-1)															
		Research effort (Contributions to the records)	1 (1)															
	Fall	Sightings (Group size: min-max)	2 (1-2)															
		Research effort (Contributions to the records)	1 (1)															

		Blue whale														
		Areas														
		PT-SP	AZ	OAZ	PT-AZ	MO	PT-MAD	OMAD	MAD	MAD-MO	CAN	WS	MAU	MAU-CV	CV	OMAC
Season	Winter	Sightings (Group size: min-max)	40 (1-3)													
		Research effort (Contributions to the records)	2	2 (1)	0	0	1	1	1	1	1	2	2	1	1	1
	Spring	Sightings (Group size: min-max)	1 (1-1)	353 (1-6)	1 (1-1)											
		Research effort (Contributions to the records)	2 (1)	3 (1)	2 (1)	2	1	2	2	2	2	2	1	2	1	1
	Summer	Sightings (Group size: min-max)	5 (1-2)													
		Research effort (Contributions to the records)	2	3 (1)	2	2	0	3	3	3	1	2	1	1	1	1
	Fall	Sightings (Group size: min-max)	1 (1-1)													
		Research effort (Contributions to the records)	2	3	1	1	0	2 (1)	3	3	2	2	2	1 (1)	1	1

Regarding blue whales, although with few sightings, records are higher in spring, in several regions. During fall and winter, they were sighted near Western Sahara/Mauritania, whereas in Azores, they were present mainly in spring.

**Tables 9 and 10:** Records of humpback whales and number of publications (table 9) and databases (table 10) by seasons and regions. Labels: PT-SP - Portugal and Spain; AZ – Azores; OAZ- ocean around Azores; PT-AZ – ocean between Portugal and Azores; MO – Morocco; PT-MAD – ocean between Portugal and Madeira, OMAD- ocean around Madeira; MAD – Madeira; MAD-MO – ocean between Madeira and Morocco; CAN – Canaries; WS- Western Sahara; MAU – Mauritania; MAU-CV – ocean between Mauritania and Cape Verde; CV- Cape Verde; OMAC- ocean of Macaronesia.

		Humpback whale															
		Areas															
		PT-SP	AZ	OAZ	PT-AZ	MO	PT-MAD	OMAD	MAD	MAD-MO	CAN	WS	MAU	MAU-CV	CV	OMAC	
Season	Winter	Sightings (Group size: min-max)												1 (1-1)		21 (1-4)	
		Research effort (Contributions to the records)												3 (1)		5 (4)	
	Spring	Sightings (Group size: min-max)	2 (1-1)														
		Research effort (Contributions to the records)	1 (1)														
	Summer	Sightings (Group size: min-max)	1 (1-1)														
		Research effort (Contributions to the records)	1 (1)														
	Fall	Sightings (Group size: min-max)	1 (1-1)														
		Research effort (Contributions to the records)	1 (1)														

		Humpback whale														
		Areas														
		PT-SP	AZ	OAZ	PT-AZ	MO	PT-MAD	OMAD	MAD	MAD-MO	CAN	WS	MAU	MAU-CV	CV	OMAC
Season	Winter	Sightings (Group size: min-max)	17 (1-2)													
		Research effort (Contributions to the records)	2	2 (1)	0	0	1	1	1	1	1	2	2	1	1	1
	Spring	Sightings (Group size: min-max)	91 (1-2)													
		Research effort (Contributions to the records)	2	3 (1)	2	2	1	2	2	2	2	2	1	2	1	1
	Summer	Sightings (Group size: min-max)	14 (1-2)													
		Research effort (Contributions to the records)	2	3 (1)	2	2	0	3	3	3	1	2	1	3 (1-3)	1	1
	Fall	Sightings (Group size: min-max)	9 (1-1)													
		Research effort (Contributions to the records)	2	3 (1)	1	1	0	2	3	3	2	2	2	1	1	1

Humpback whales had lots of sightings in Cape Verde, mainly during fall and winter. They were spotted in Mauritania during the fall and summer, while in Madeira they were seen in spring, summer and fall. In Azores, they were recorded year-round, with the vast majority of sightings to be obtained in spring season.

Looking for the migratory whales: Routes of the baleen whales in the Macaronesia

Based on the previous tables with the distribution of records by species, regions and season, table 11 presents a summary of the temporal and spatial occurrence of the four species.

**Table 11:** Occurrence categorized by number of records and seasonality for minke, fin, blue and humpback whales, divided by regions of the Macaronesia and based on information collected in publications and databases. Occurrence categories: VC- very common in the region; Co- common; Oc-occasional; Ra- rare; SD – seasonally defined; SI – seasonally irregular; Aper- annual periodically; UD- undefined; NS- no sightings; DD – data deficient. Regions: PT-SP - Portugal and Spain; AZ – Azores; OAZ- ocean around Azores; PT-AZ – ocean between Portugal and Azores; MO – Morocco; PT-MAD – ocean between Portugal and Madeira, OMAD- ocean around Madeira; MAD – Madeira; MAD-MO – ocean between Madeira and Morocco; CAN – Canaries; WS- Western Sahara; MAU – Mauritania; MAU-CV – ocean between Mauritania and Cape Verde; CV- Cape Verde; OMAC- ocean of Macaronesia.

	Areas														
	PT-SP	AZ	OAZ	PT-AZ	MO	PT-MAD	OMAD	MAD	MAD-MO	CAN	WS	MAU	MAU-CV	CV	OMAC
<i>Balaenoptera acutorostrata</i>	Co (SD)	Co (SD)	Ra (SI)	Oc (SD)	DD	Co (SD)	Ra (SI)	Oc (SI)	Ra (UD)	Oc (Aper)	Oc (Aper)	Ra (UD)	Ra (UD)	NS	DD
<i>Balaenoptera physalus</i>	Co (SD)	VC (SD)	Oc (Aper)	Co (Aper)	DD	Co (Aper)	Oc (UD)	Co (SD)	Ra (UD)	Co (Aper)	Ra (UD)	Ra (UD)	Ra (UD)	Oc (UD)	DD
<i>Balaenoptera musculus</i>	Ra (UD)	VC (SD)	Ra (UD)	NS	DD	Ra(UD)	NS	Ra (UD)	NS	Ra (UD)	DD	Oc (Aper)	NS	Ra (UD)	DD
<i>Megaptera novaeangliae</i>	NS	VC (SD)	NS	NS	DD	NS	NS	Ra (UD)	NS	Ra (UD)	DD	Oc (Aper)	NS	VC (SD)	DD

From table 11 it is possible to verify that according to the region and the species of baleen whale studied, different patterns of presence can be observed. In areas such as the archipelagos of the Azores, Madeira and the Canaries and Mauritania one can see all the species of baleen whales under study. For species such as humpback whales and blue whales, in some regions between a given archipelago and a country (eg "PT-AZ" or "MAU-CV"), ie off-shore regions, no sightings were obtained.

Finally, regions such as Morocco and "OMAC", due to the lack of data collected, do not allow one to infer patterns of presence for these whales.

-Latitudinal variation across Macaronesia

Figures 11 to 14 show the latitudinal progression across Macaronesia through graphs complemented with spatial representation of the season with higher encounter rate for each latitudinal range.

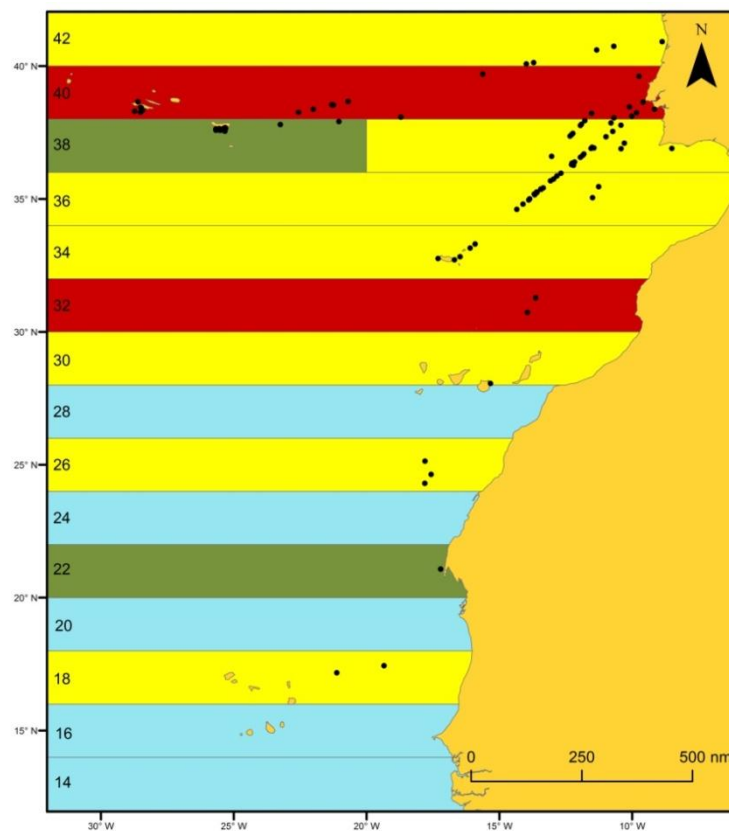
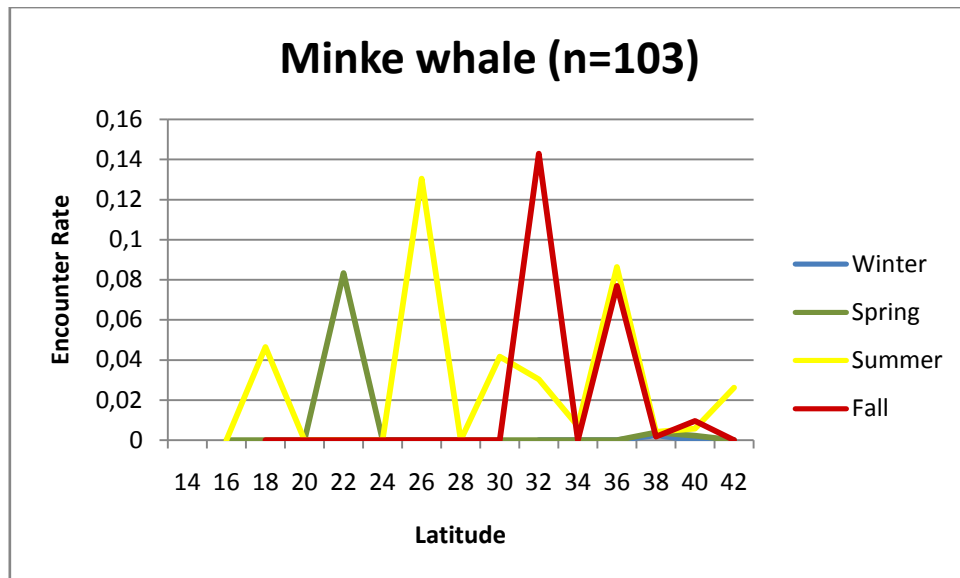


Figure 11: Latitudinal progression of minke whales throughout the year.



Looking for the migratory whales: Routes of the baleen whales in the Macaronesia

Minke whales have no notorious peak of encounter rate at any latitudinal range during winter and only one peak for spring, while for summer and fall, several peaks are observed. While summer was the season with a higher encounter rate in several latitudinal ranges, fall was only the season with a higher encounter rate in two latitudinal ranges (from 30°-32° and 38°-40°).

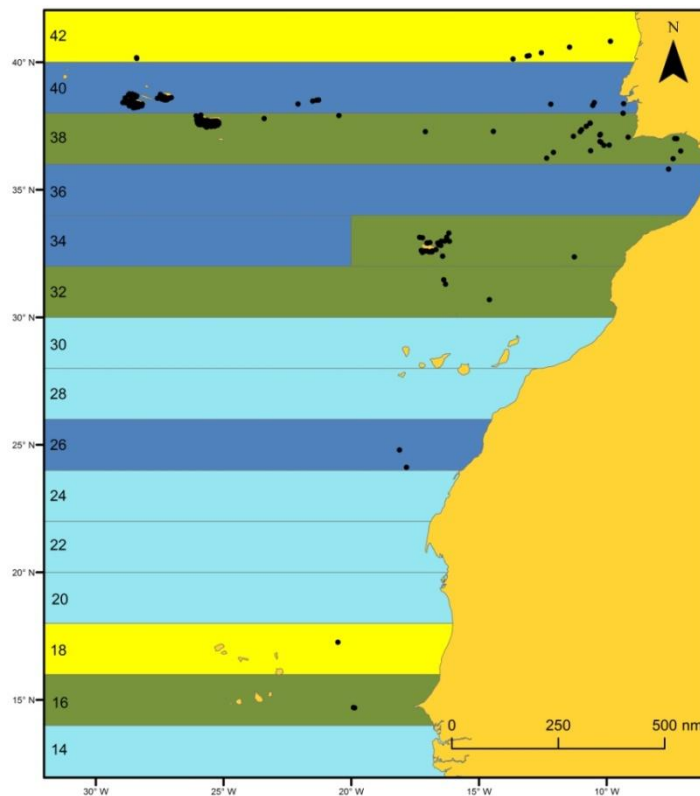
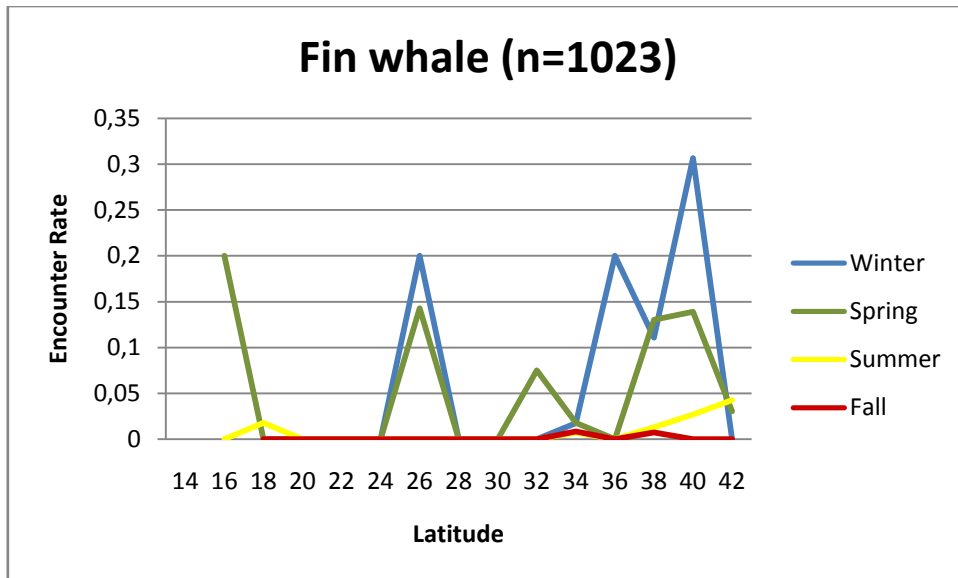


Figure 12: Latitudinal progression of fin whales throughout the year.

Fin whales had no notorious peaks in summer and fall, presenting several relative maximums of encounter rates for spring and winter. Both these seasons presented the higher encounter rate in several latitudinal ranges spread across the area.

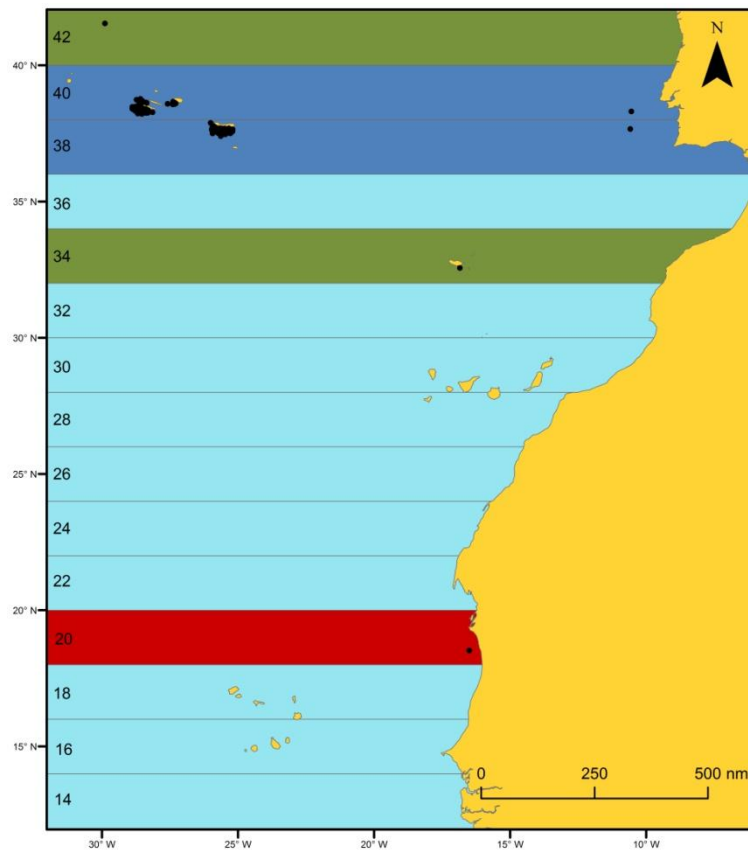
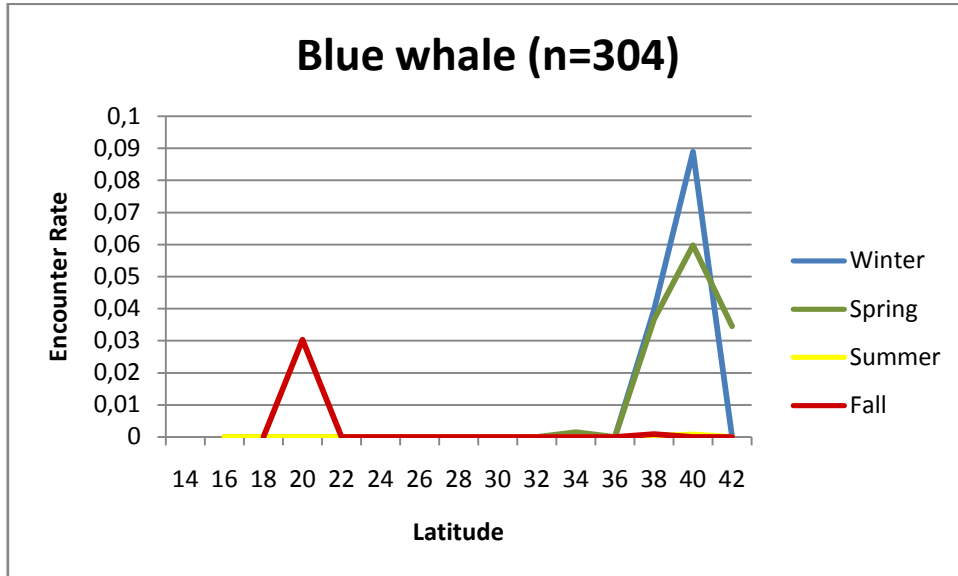


Figure 13: Latitudinal progression of blue whales throughout the year.

Blue whales had no peaks during summer. Winter and spring peaks occurred in the same latitudinal range (38°-40°) and both these seasons had the higher encounter rate in two different latitudinal ranges, all in northern areas (higher than 32°). As for the fall peak, this occurred at 18°-20°, latitudinal range were the encounter rate was also higher during this season.

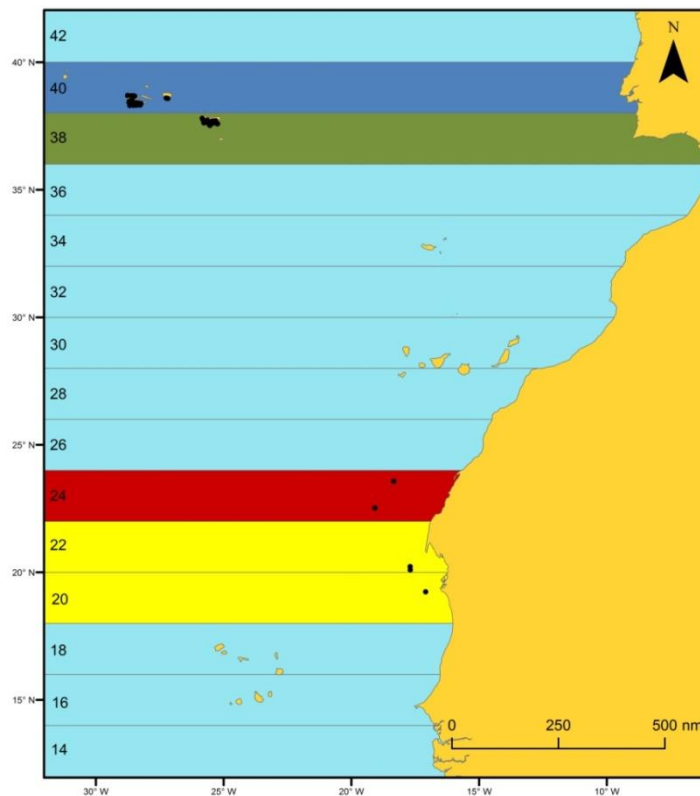
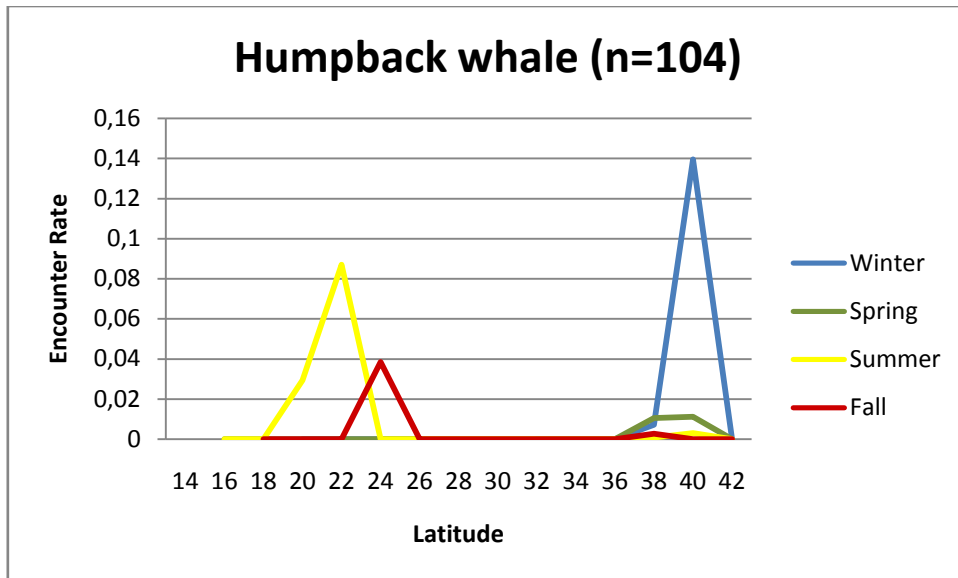


Figure 14: Latitudinal progression of humpback whales throughout the year.

For humpback whales, the spring peak was the lowest with more notorious peaks recorded for the other seasons. While summer and fall peaks were at southern latitudes, the winter peak had the higher encounter rate recorded in northern latitudes. The same pattern is visible for the seasons with higher encounter rates for each latitudinal range illustrated in the map.

- Spatio-temporal models

The results of the GAM models are presented in table 12, the respective plots in figure 15 and the associated ROC curves with AUC values in figure 16.

**Table 12:** Best GAM model results obtained. e.d.f. – effective degrees of freedom; s.e. – standard error; n – total number of points (available/used) considered in the model fitting.

Species and Parameter	Estimate	e.d.f.	s.e.	z-value	p-value	Deviance explained (%)	r <sup>2</sup>	AIC	Presences	Pseudo-Absences
<i>Balaenoptera acutorostrata</i>										
Intercept	-6.461		0.2307	-28.01	<0.001					
Smother Terms										
Lon			6.648		<0.001					
Year			3.710		0.00411					
Julain			6.572		0.02037					
Best final model: s(neg_lon) + s(Year)+s(Julian)						21.5	0.0338	1054.662	103	20580
<i>Balaenoptera physalus</i>										
Intercept	-4.25724		0.09739	-43.71	<0.001					
Smother Terms										
Lat,Lon			27.75		<0.001					
Year, Julian			24.83		<0.001					
Best final model: s(lat, neg_lon) + s(Year, Julian)						22.6	0.109	6415.943	1023	19660
<i>Balaenoptera musculus</i>										
Intercept	-757.6		157.9	-4.797	<0.001					
Smother Terms										
Lat,Lon			28.32		<0.001					
Year, Julian			28.00		<0.001					
Best final model: s(lat, neg_lon) + s(Year, Julian)						37	0.121	2112.017	304	20379
<i>Megaptera novaengliae</i>										
Intercept	-82.29		29.91	-2.751	0.00594					
Smother Terms										
Lat, Lon			7.28		0.00768					
Year, Julian			28.82		<0.001					
Best final model: s(lat, neg_lon) + s(Year, Julian)						25.6	0.0523	1047.628	104	20579

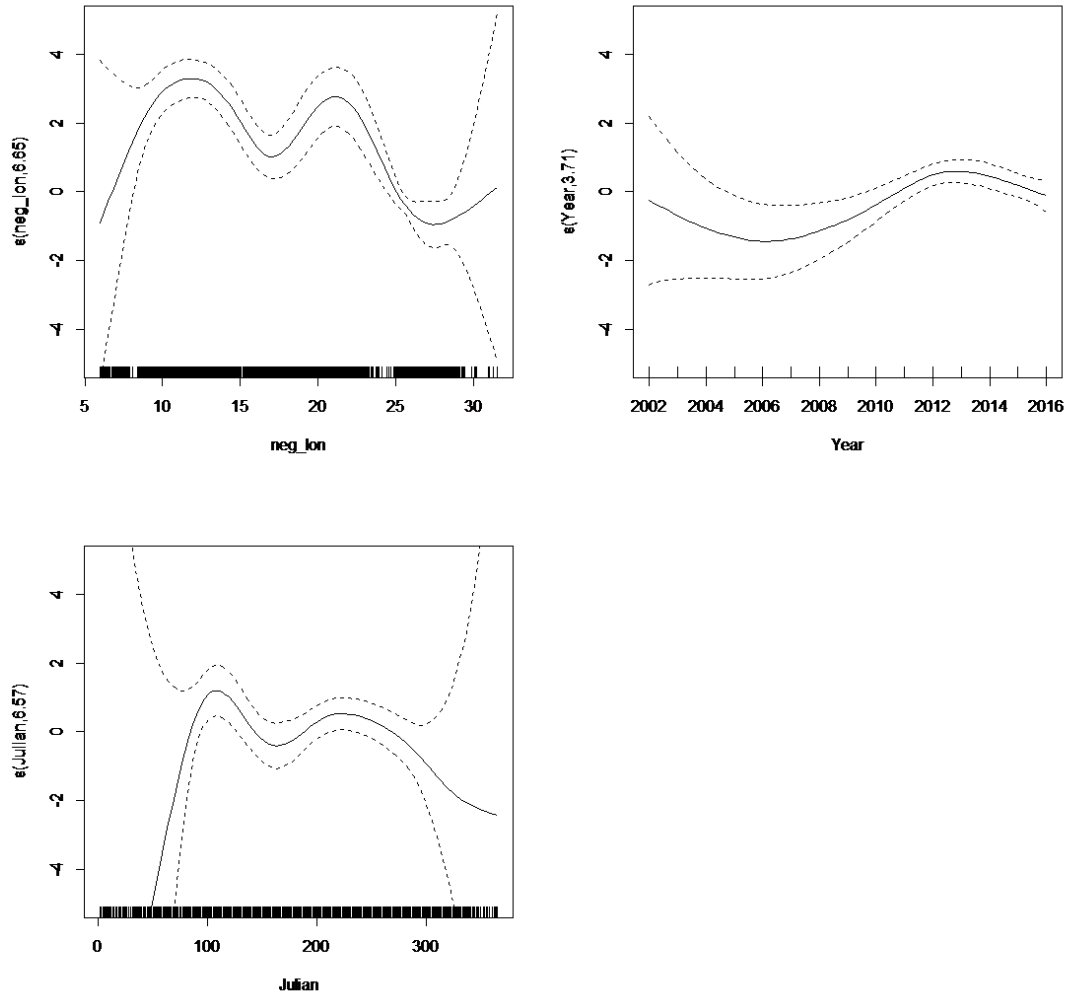
Best models included variables with no statistically significant p-value had to be kept in the models as their removal led to a model with a significantly worse AIC score. Blue whales had the model with the higher deviance explained (37%) while minke whale had the model with the lower deviance explained (21,5%) (table 12).

Blue whales had the highest deviance explained (37%) and AUC value (0,931 of predictive power), while minke whales had the lowest deviance explained (21.5%) and

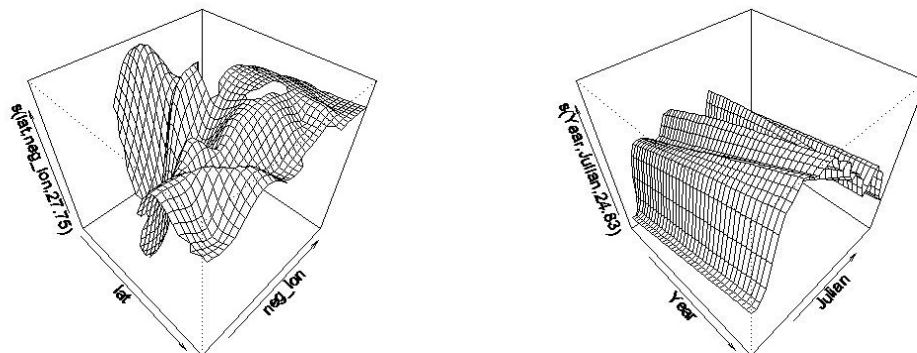
Looking for the migratory whales: Routes of the baleen whales in the Macaronesia

humpback whales the lowest AUC value (0,833 of predictive power) (table 12 and figure 16).

a) Minke whale

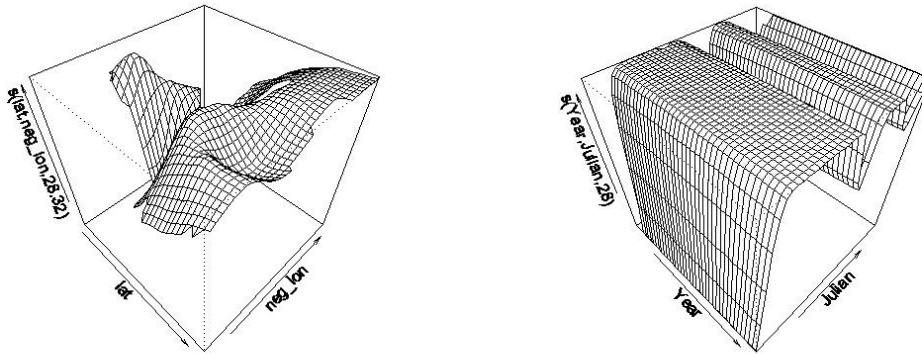


b) Fin whale

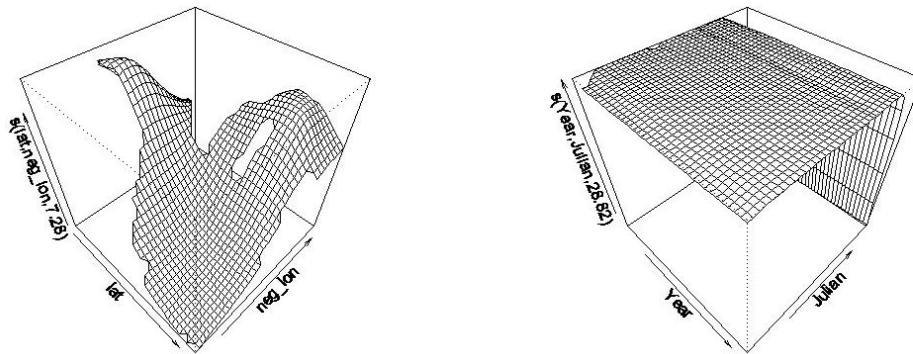


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c) Blue whale



d) Humpback whale



**Figure 15:** GAM predicted smooth splines of the response variable presence/pseudo-absence of the animals as a function of the explanatory variables. The effective degrees of freedom are in parenthesis on the y-axis. a) Minke whale; b) Fin whales; c) Blue whales; d) Humpback whales. Labels: neg\_lon- negative longitude, lat - latitude, Julian - julian days, Year - year of the sighting.

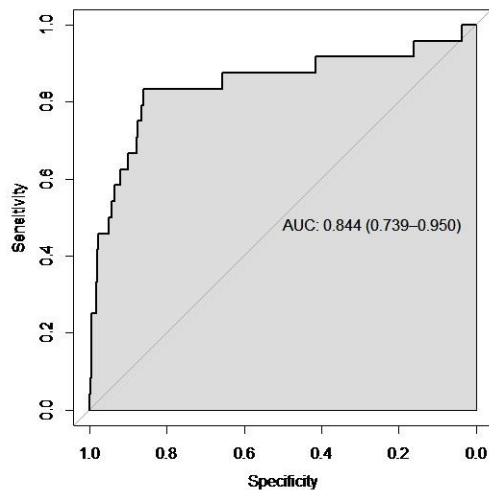
Minke whales' model was the only one that does not incorporate interactions between variables (table 12). The plot for longitude showed a possible preference of minke whales in areas next to the continents and waters next to the Azores (or off-shores areas) (figure 15 a)). Moreover, looking for julian days' plot, it is possible to see a general preference for early spring months and summer months (figure 15 a)) by these species.

The plots of the remaining baleen whales models show different preferences both spatially and temporally (figure 15 b), c) and d)). In areas such as the archipelago of

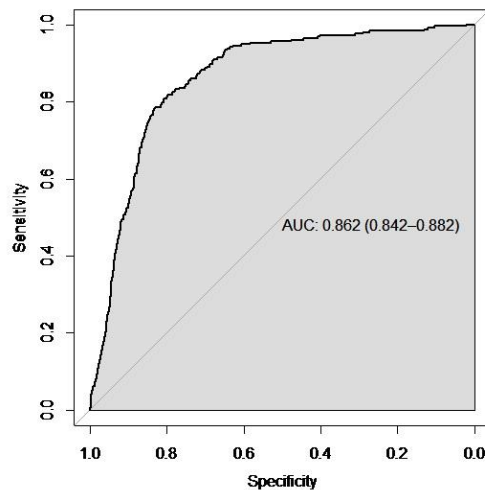
the Azores there is a preference for all species studied, while in areas such as Mauritania only blue whales and humpback whales have preference for these waters (figure 15 (b), (c) and (d)) .

The temporal plots are different depending on the species studied (figure 15 b), c) and d)). Fin whales have a preference for spring months, while blue whales also show preference for the early fall months. Humpback whales show no preference for any season.

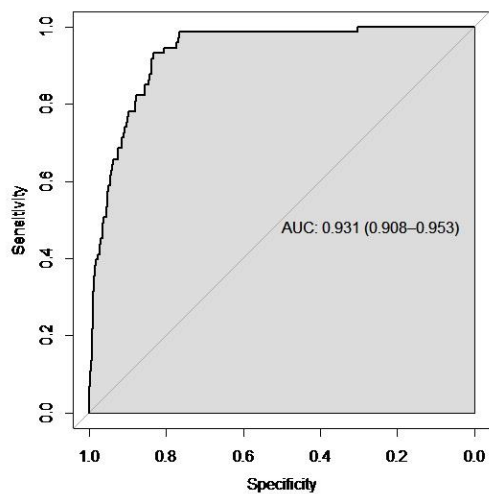
a) Minke whale



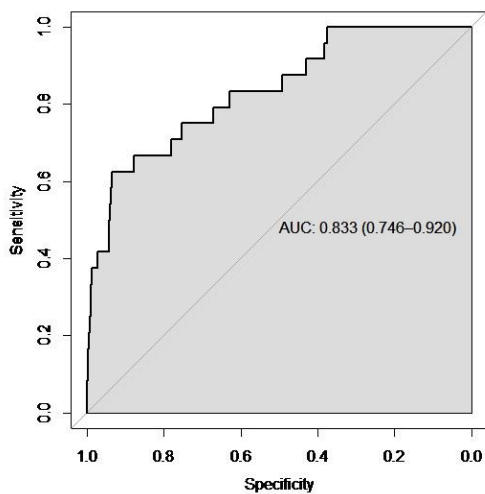
b) Fin whale



c) Blue whale



d) Humpback whale



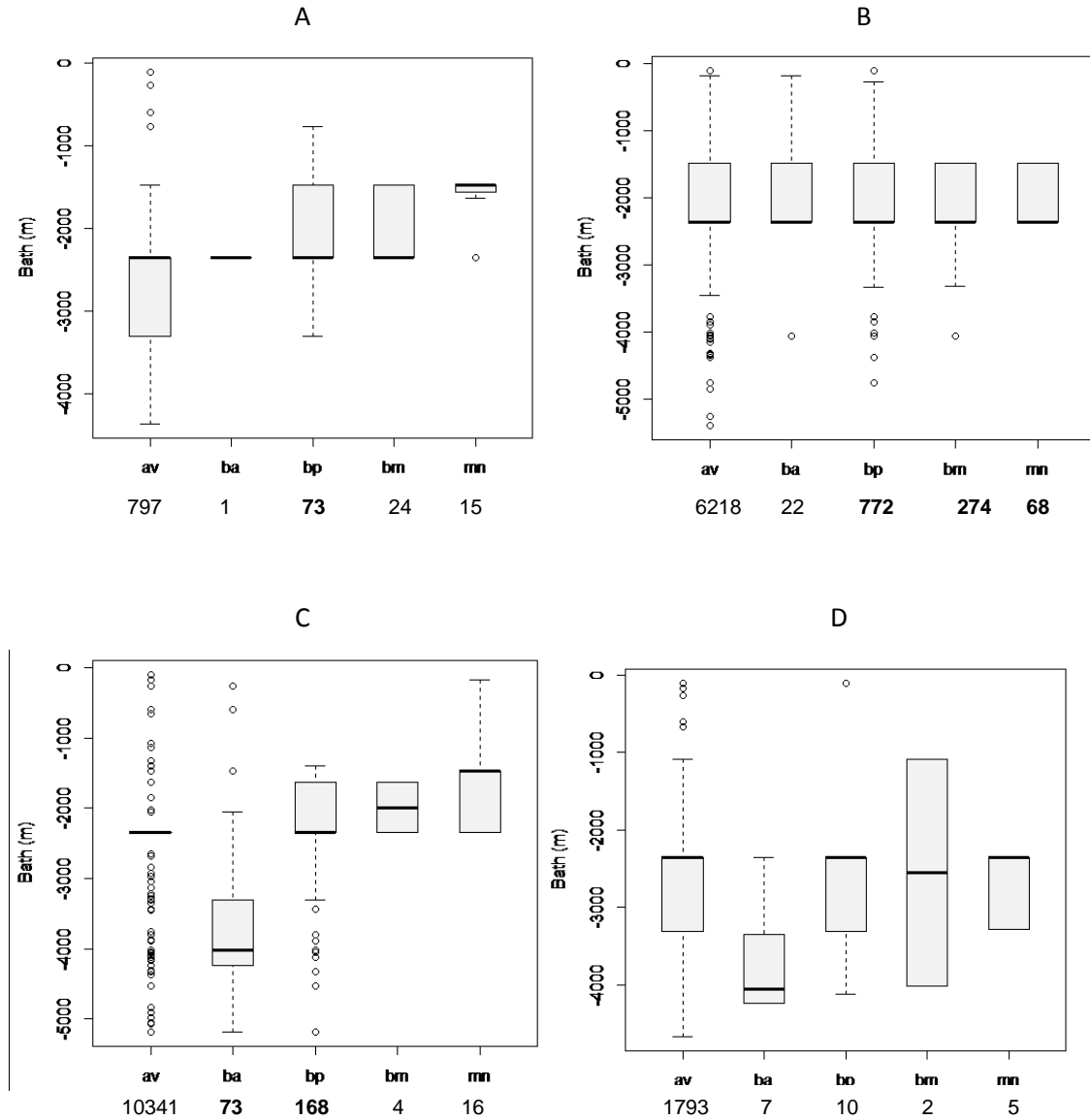
**Figure 16:** Receiver Operating Characteristic (ROC) curve and the values of the Area Under the Curve (AUC) for the GAM models of the four species: a) Minke whales; b) Fin whales; c) Blue whales; d) Humpback whales.

According to the criterion of Hosmer and Lemeshow (1989), all four models performed better than a random model ( $AUC > 0,5$ ) and all had an excellent ( $0,8 < AUC < 0,9$ ) or an outstanding discrimination ( $AUC > 0,9$ ) (figure 16).



### 3.2 Habitat preference analysis

Figures 17 to 24 illustrate the habitat range for the available habitat and the four species for each of the habitat variables selected.

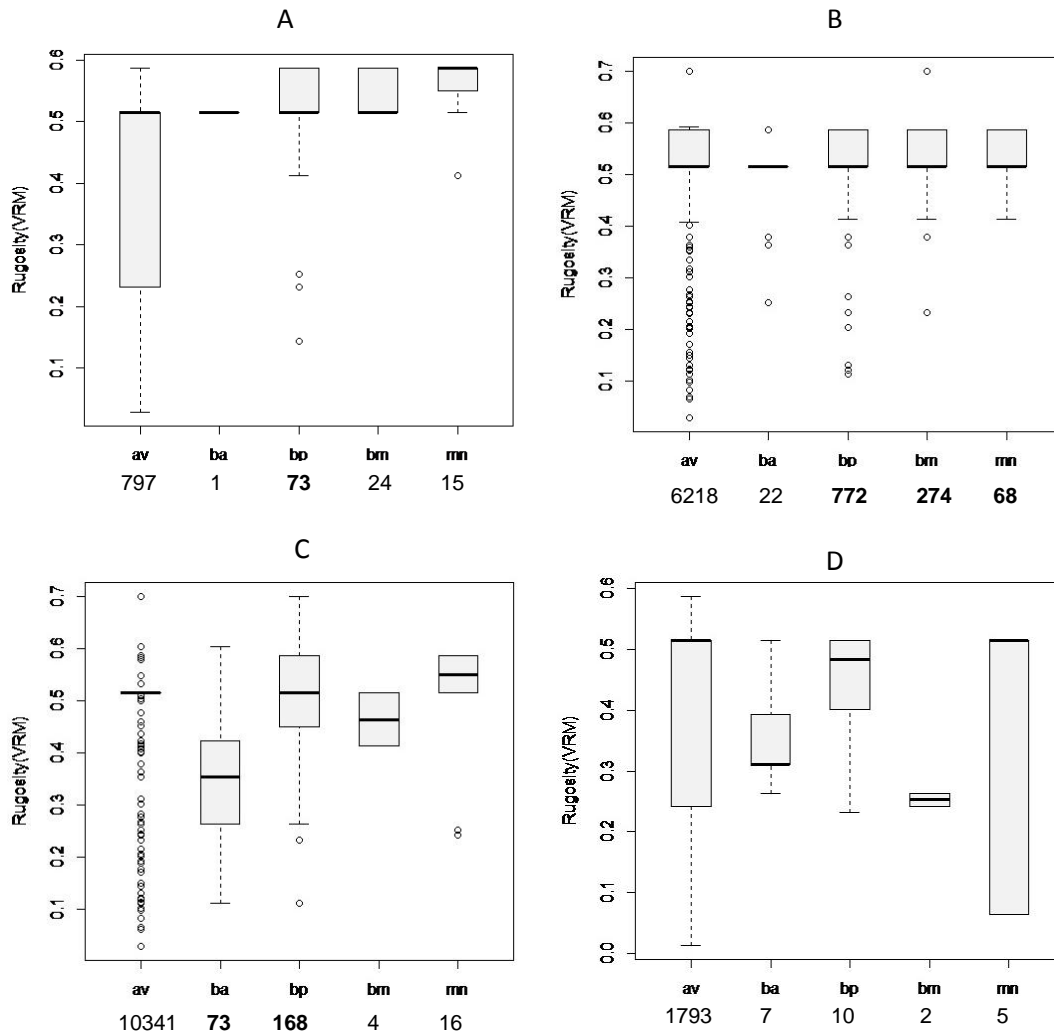


**Figure 17:** Habitat range regarding bathymetry (Bath) for four species of baleen whales by season. Whiskers represent the lower and upper 25% of the occurrences delimited by minimum and maximum, and the dashed line is the median (50% quartile). The box includes 50% of the occurrences. Labels: A- Winter, B- Spring, C- Summer and D- Fall. X-axis: av- available habitat, ba - *Balaneoptera acutorostrata*, bp - *Balaenoptera physalus*, bm - *Balaenoptera musculus* and mn - *Megaptera novaeangliae*. Below the x-axis, it is indicated the number of sightings used for each boxplot.

Regarding bathymetry, it is possible to observe that baleen whales prefer deeper areas, although there are also records in shallow areas (for example minke and fin whales in the spring). Minke whales highly change their range of depth depending on season: in winter / spring, median is roughly at 2300m, while in summer / fall, the median is roughly at 4000m. It should be noted that the minke whales observed in summer are at great depths, with significant differences in relation to the available habitat (table 15) which have a median of 2500 m depth.

It is in this season and this species where the lowest bathymetric values are found, with these whales frequenting waters with approximately 4000 m depth, and were sighted in waters with 5000 m depth (figure 17 c).

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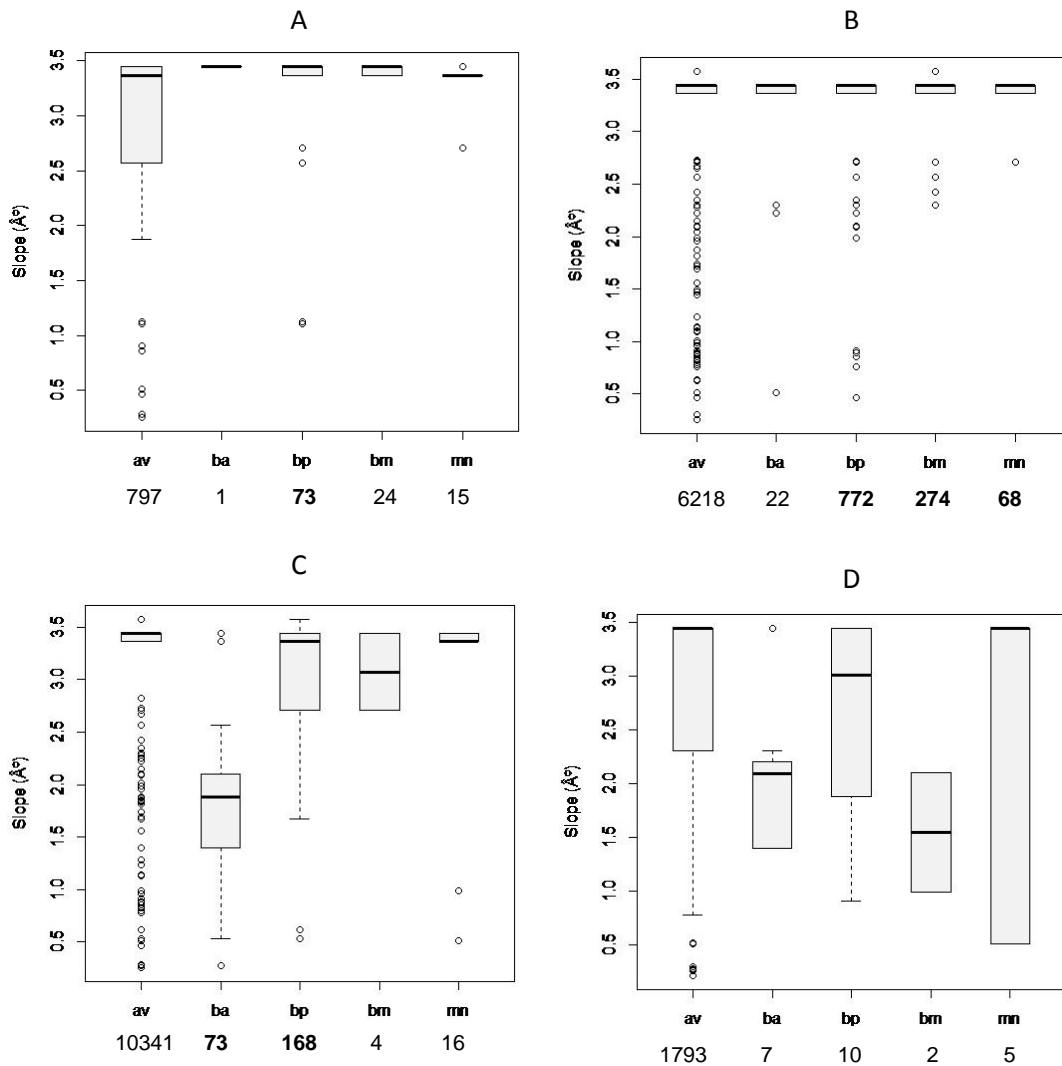


**Figure 18:** Habitat range regarding Rugosity for four species of baleen whales by season. Whiskers represent the lower and upper 25% of the occurrences delimited by minimum and maximum, and the dashed line is the median (50% quartile). The box includes 50% of the occurrences. Labels: A- Winter, B- Spring, C- Summer and D- Fall. X-axis: av - available habitat, ba - *Balaneoptera acutorostrata*, bp - *Balaenoptera physalus*, bm - *Balaenoptera musculus* and mn - *Megaptera novaeangliae*. Below the x-axis, it is indicated the number of sightings used for each boxplot.

Regarding rugosity, fin whales in summer were found in areas with a very rough surface (maximum of 0.7), although they did not statistically differ from available habitat (table 15), while humpback whales in fall frequented areas of very low rugosity (approximately 0.05).

Although they having been sighted in areas of low rugosity, humpback whales were also seen in very "rough" areas with the median reaching 0.6. Again, the minke whales in summer are found in areas with a lower rugosity compared to the available habitat, presenting in areas with a median of approximately 0.35.

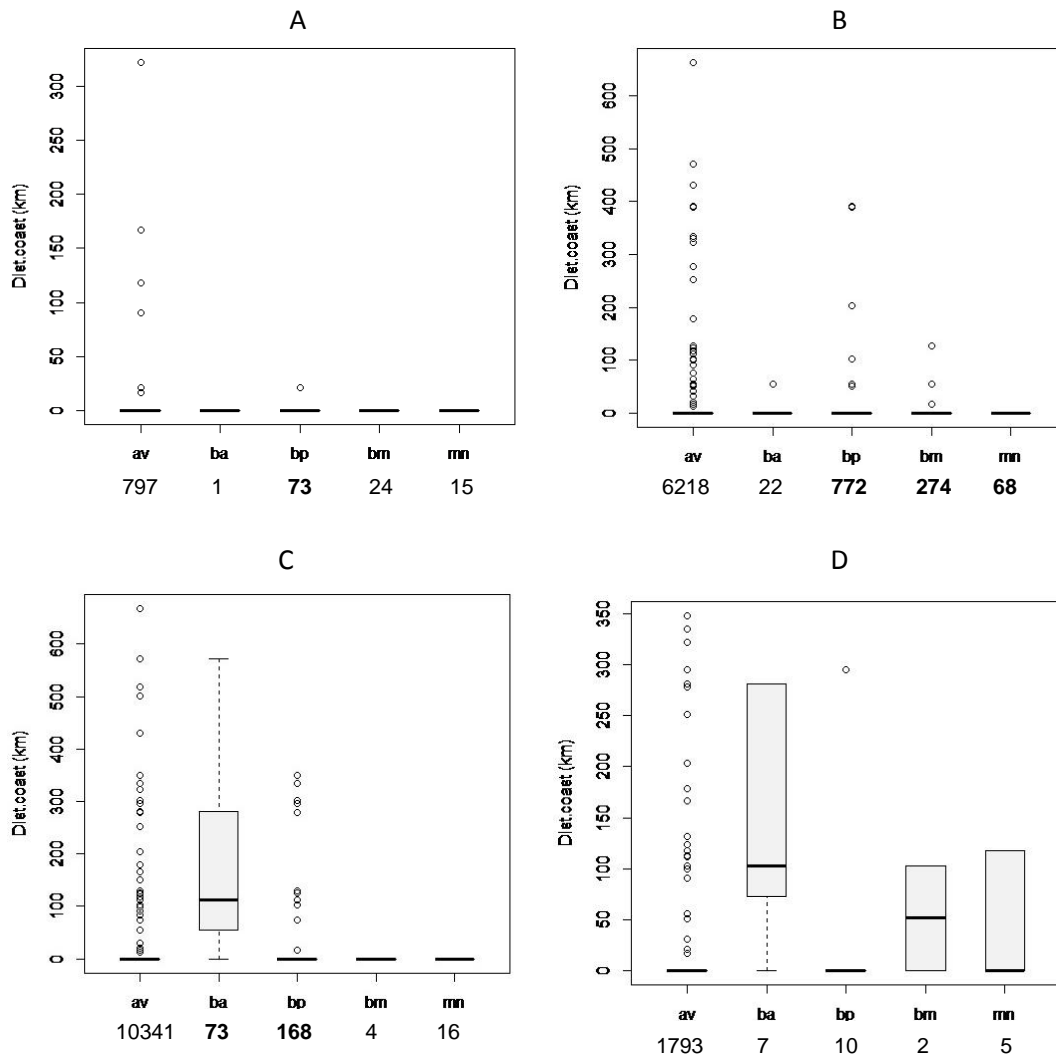
Even though there are not many sightings in the fall, all the balaenopterids have their median below that observed for the available habitat.



**Figure 19:** Habitat range regarding Slope for four species of baleen whales by season. Whiskers represent the lower and upper 25% of the occurrences delimited by minimum and maximum, and the dashed line is the median (50% quartile). The box includes 50% of the occurrences. Labels: A- Winter, B- Spring, C- Summer and D- Fall. X-axis: av- available habitat, ba - *Balaenoptera acutorostrata*, bp - *Balaenoptera physalus*, bm - *Balaenoptera musculus* and mn - *Megaptera novaeangliae*. Below the x-axis, it is indicated the number of sightings used for each boxplot.

For slope, the results observed, point to the presence of baleen whales in areas with a maximum slope of  $3.6^\circ$  (observed for blue whales in spring and fin whale in summer) and minimum slope of approximately  $0.2^\circ$  (for minke whales in the summer). Similar to the previous variables, the minke whales sighted in summer are statistically different from the available habitat, whereas all the balaenopterids found in fall have a median lower than that found in the available habitat.

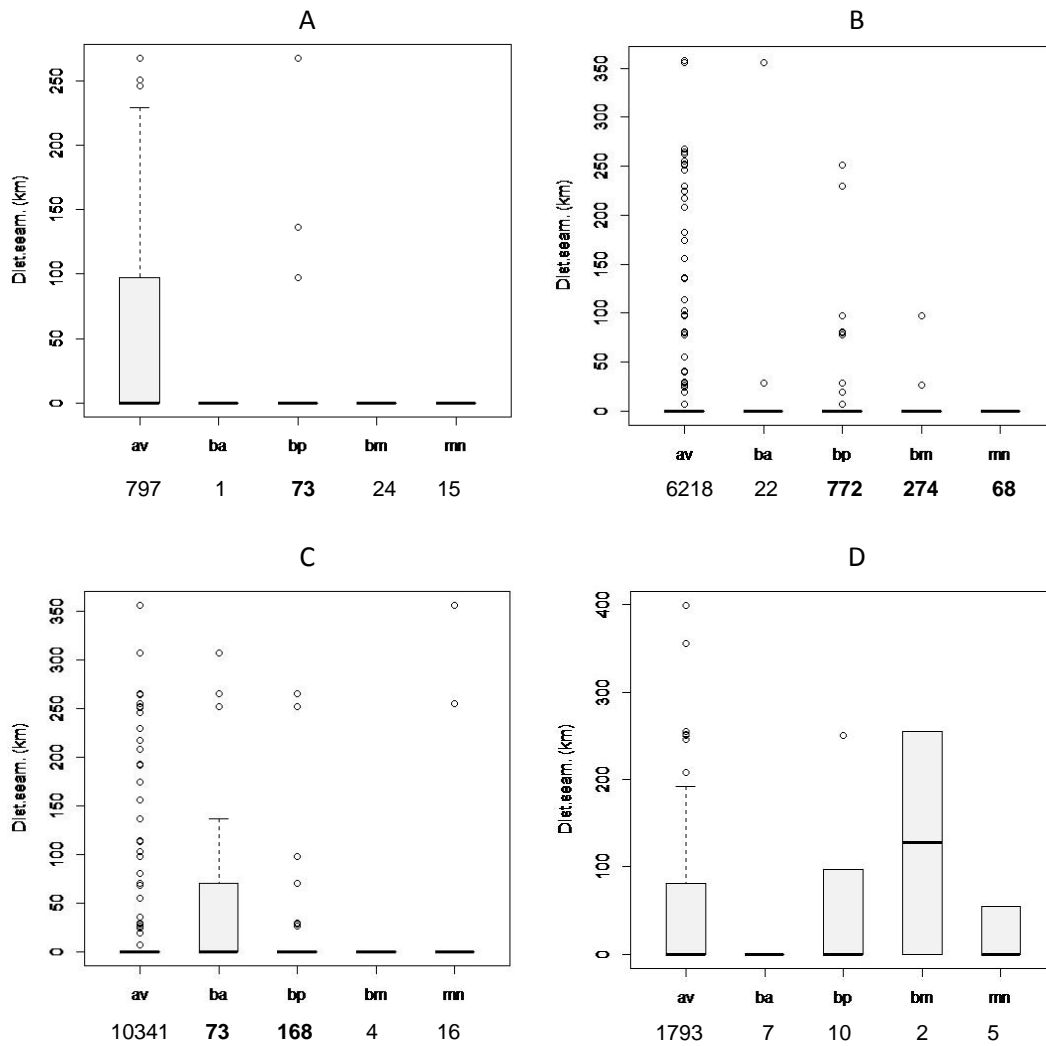
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**Figure 20:** Habitat range regarding distance to coast (Dist.coast) for four species of baleen whales by season. Whiskers represent the lower and upper 25% of the occurrences delimited by minimum and maximum, and the dashed line is the median (50% quartile). The box includes 50% of the occurrences. Labels: A- Winter, B- Spring, C- Summer and D- Fall. X-axis: av- available habitat, ba - *Balaenoptera acutorostrata*, bp - *Balaenoptera physalus*, bm - *Balaenoptera musculus* and mn - *Megaptera novaeangliae*. Below the x-axis, it is indicated the number of sightings used for each boxplot.

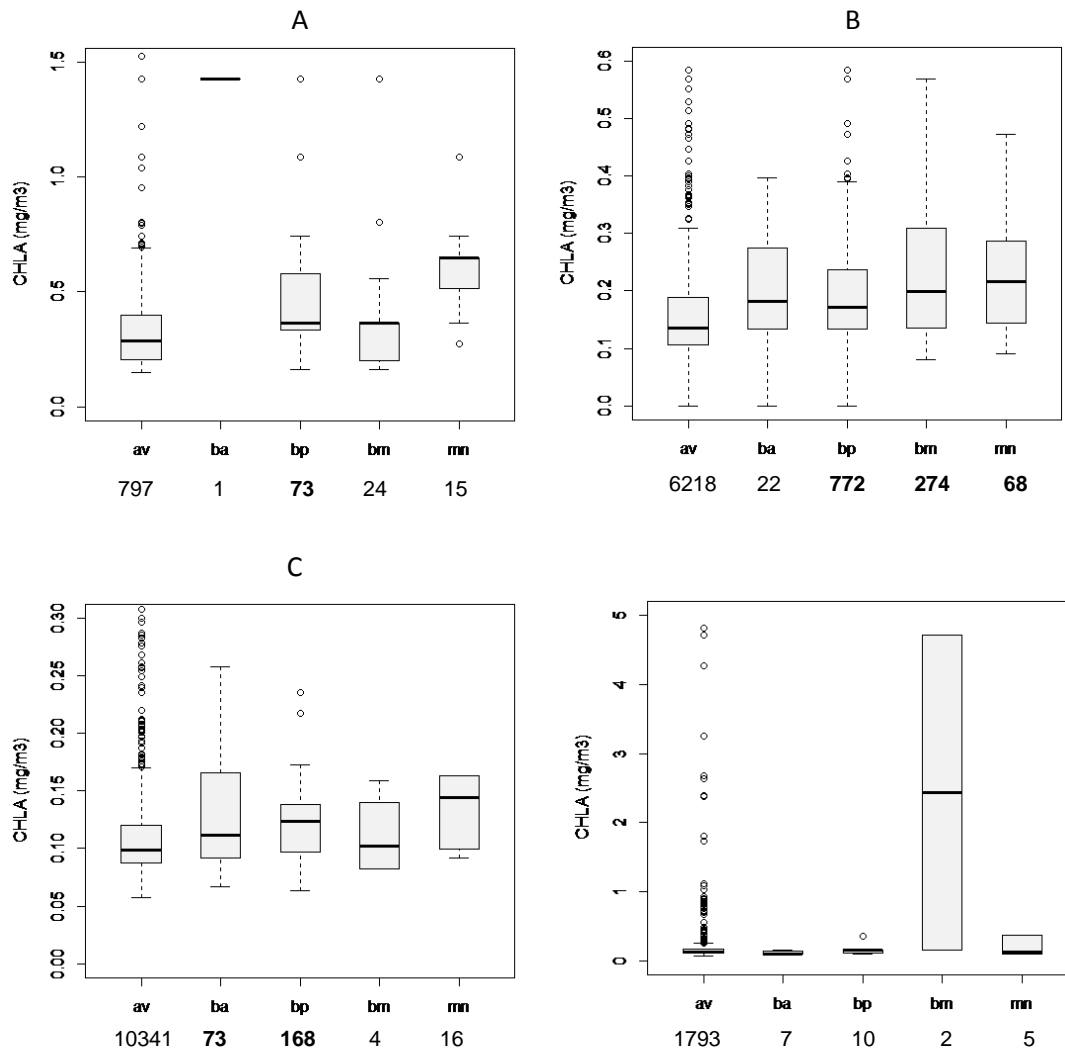
Looking at the distance to the coast (figure 20), we see that our available habitat was mostly in coastal areas, with only a few more off-shore areas having been surveyed. Most sightings far from the coast were obtained in summer and fall, in particular the minke whales sighted in summer and fall whose median (about 100 km from the coast) is much higher than the available habitat, with statistically significant differences between them (table 15).

The whale sighted farther off the coast was a fin whale found 400 km off the coast in the spring (figure 20 b)).



**Figure 21:** Habitat range regarding distance to seamounts (Dist.seam.) for four species of baleen whales by season. Whiskers represent the lower and upper 25% of the occurrences delimited by minimum and maximum, and the dashed line is the median (50% quartile). The box includes 50% of the occurrences. Labels: A- Winter, B- Spring, C- Summer and D- Fall. X-axis: av- available habitat, ba - *Balaeoptera acutorostrata*, bp - *Balaeoptera physalus*, bm - *Balaeoptera musculus* and mn - *Megaptera novaeangliae*. Below the x-axis, it is indicated the number of sightings used for each boxplot.

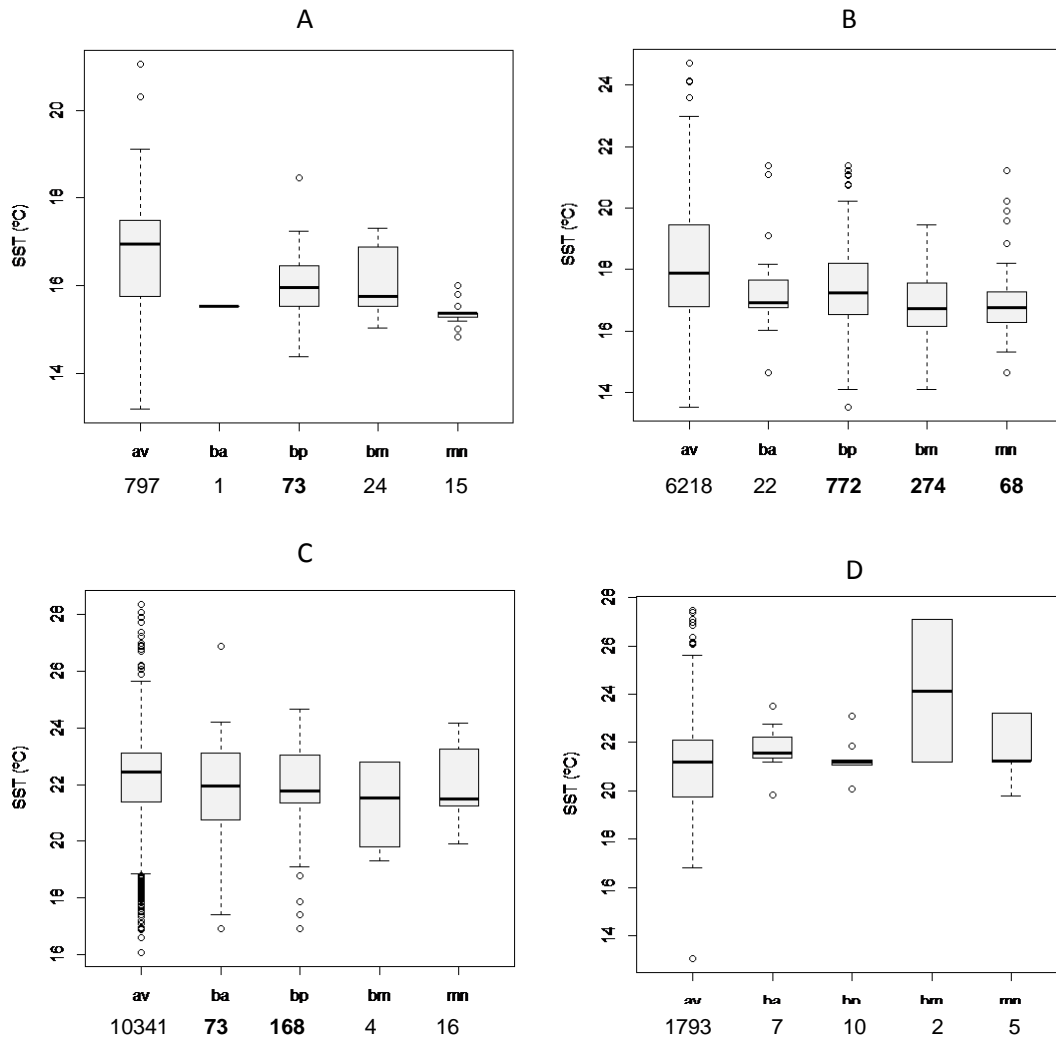
Similar to the distance to the coast (figure 20), our available habitat for the variable "distance to seamounts" was mostly in areas around undersea features (and coastal areas - hence mostly from the Azores), not allowing inferences regarding the habitat used by these whales. The whale found furthest from a undersea feature was a minke sighted in the spring (figure 21 b)) which was about 350 km from it. Having very few sightings, and not allowing the proper interpretation, the blue whales found in fall are the ones whose median is highest, lying at about 125 km.



**Figure 22:** Habitat range regarding chlorophyll-a (CHLA) for four species of baleen whales by season. Whiskers represent the lower and upper 25% of the occurrences delimited by minimum and maximum, and the dashed line is the median (50% quartile). The box includes 50% of the occurrences. Labels: A- Winter, B- Spring, C- Summer and D- Fall. X-axis: av- available habitat, ba - *Balaneoptera acutorostrata*, bp - *Balaenoptera physalus*, bm - *Balaenoptera musculus* and mn - *Megaptera novaeangliae*. Below the x-axis, it is indicated the number of sightings used for each boxplot.

For dynamic variables, in chlorophyll-a (CHLA) there is no great distinction between the different species of baleen whales, most of which have been observed in areas with a low concentration of chlorophyll (between 0.08 and 0.6 mg / m<sup>3</sup>). A blue whale sighting in fall was where there was a higher concentration of chlorophyll (about 4.8 mg / m<sup>3</sup>) (Figure 22d)).

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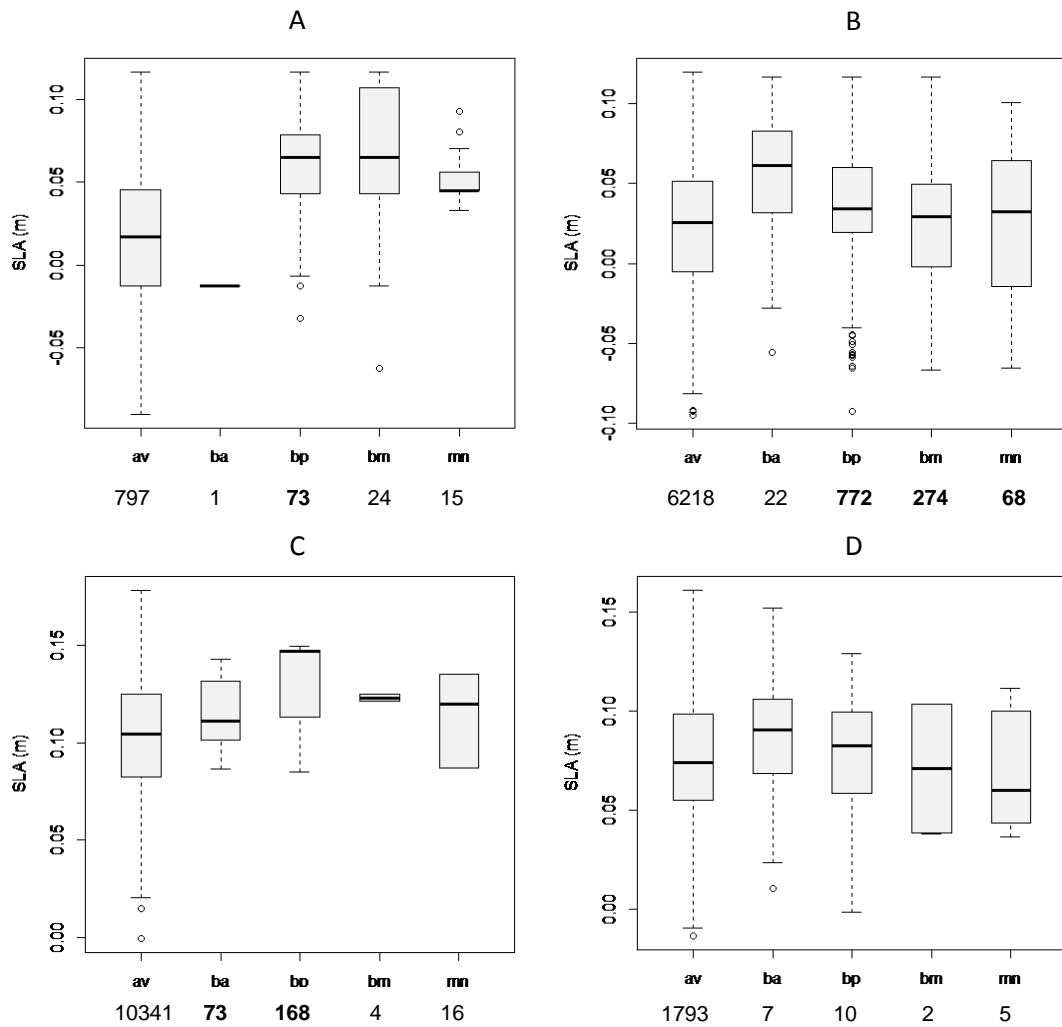


**Figure 23:** Habitat range regarding sea surface temperature (SST) for four species of baleen whales by season. Whiskers represent the lower and upper 25% of the occurrences delimited by minimum and maximum, and the dashed line is the median (50% quartile). The box includes 50% of the occurrences. Labels: A- Winter, B- Spring, C- Summer and D- Fall. X-axis: av- available habitat, ba - *Balaeoptera acutorostrata*, bp - *Balaenoptera physalus*, bm - *Balaenoptera musculus* and mn - *Megaptera novaeangliae*. Below the x-axis, it is indicated the number of sightings used for each boxplot.

Regarding SST (figure 23), baleen whales were observed in areas with temperatures around 17°C in winter and spring, and around 21°C in summer and fall. Both fin whales in winter and spring and blue and humpback whales in spring, compared to the available habitat, present significant differences (tables 13 and 14) in habitat use.

The highest temperature recorded was in the fall season, where blue whales occur in areas with a median of 24°C, and the lowest was found in winter when minke and humpback whales were sighted in areas with a median of about 15°C.





**Figure 24:** Habitat range regarding sea level anomaly (SLA) for four species of baleen whales by season. Whiskers represent the lower and upper 25% of the occurrences delimited by minimum and maximum, and the dashed line is the median (50% quartile). The box includes 50% of the occurrences. Labels: A- Winter, B- Spring, C- Summer and D- Fall. X-axis: av- available habitat, ba - *Balaenoptera acutorostrata*, bp - *Balaenoptera physalus*, bm - *Balaenoptera musculus* and mn - *Megaptera novaeangliae*. Below the x-axis, it is indicated the number of sightings used for each boxplot.

It should be noted that in winter, spring and summer, whales occur in areas with SLA values between 5 and 10 cm, whereas in the fall there is a preference for positive anomalies between 10 and 15 cm. Compared with the available habitat, baleen whales in winter, spring and summer are found in areas whose SLA is significantly higher. The maximum value of SLA obtained (15 cm) was in an area where baleen whales were found during the summer, while the minimum value was recorded in the waters frequented by baleen whales in the spring (-10 cm).

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Tables 13, 14 and 15 show the results of the Mann-Whitney-Wilcoxon tests comparing habitat variables between the available habitat and baleen whales species by season. No tests were performed for the fall season, as no species had more than 30 records.

**Table 13:** Mann-Whitney-Wilcoxon tests for pairwise comparisons between baleen whales species and the available habitat for the winter season. In bold are the p-values<0.05, indicating statistically significant differences.

Pairwise comparisons – Mann-Whitney-Wilcoxon test			
Winter	<i>Balaenoptera physalus</i>		
Available	CHLa	W = 19364	<b>p-value = 2.21e-06</b>
	SST	W = 39826	<b>p-value = 1.748e-07</b>
	SLA	W = 13912	<b>p-value = 1.501e-13</b>
	Bathymetry	W = 15354	<b>p-value = 3.356e-13</b>
	Rugosity	W = 15732	<b>p-value = 1.452e-12</b>
	Slope	W = 21058	<b>p-value = 2.076e-05</b>
	Dist.coast	W = 29798	p-value = 0.2837
	Dist.seamounts	W = 39640	<b>p-value = 5.178e-09</b>

**Table 14:** Mann-Whitney-Wilcoxon tests for pairwise comparisons between baleen whales species and the available habitat for the spring season. In bold are the p-values<0.05, indicating statistically significant differences.

Pairwise comparisons – Mann-Whitney-Wilcoxon test									
Spring	<i>Balaenoptera physalus</i>			<i>Balaenoptera musculus</i>			<i>Megaptera novaeangliae</i>		
Available	CHLa	W = 1753400	<b>p-value &lt; 2.2e-16</b>	CHLa	W = 537050	<b>p-value &lt; 2.2e-16</b>	CHLa	W = 123000	<b>p-value = 2.848e-09</b>
	SST	W = 2949500	<b>p-value &lt; 2.2e-16</b>	SST	W = 1238400	<b>p-value &lt; 2.2e-16</b>	SST	W = 288770	<b>p-value = 2.021e-07</b>
	SLA	W = 1925600	<b>p-value &lt; 2.2e-16</b>	SLA	W = 845250	p-value = 0.8274	SLA	W = 197620	p-value = 0.3542
	Bathymetry	W = 2149300	<b>p-value = 1.348e-07</b>	Bathymetry	W = 673720	<b>p-value = 8.337e-11</b>	Bathymetry	W = 181840	<b>p-value = 0.02785</b>
	Rugosity	W = 2132100	<b>p-value = 1.76e-08</b>	Rugosity	W = 636820	<b>p-value = 4.526e-15</b>	Rugosity	W = 172490	<b>p-value = 0.003791</b>
	Slope	W = 2144800	<b>p-value = 8.03e-08</b>	Slope	W = 794610	<b>p-value = 0.03688</b>	Slope	W = 177390	<b>p-value = 0.01139</b>
	Dist.coast	W = 2425400	p-value = 0.09315	Dist.coast	W = 864060	p-value = 0.1615	Dist.coast	W = 217500	p-value = 0.1559
	Dist.seamounts	W = 2683500	<b>p-value &lt; 2.2e-16</b>	Dist.seamounts	W = 971500	<b>p-value = 7.392e-11</b>	Dist.seamounts	W = 242560	<b>p-value = 0.0006382</b>

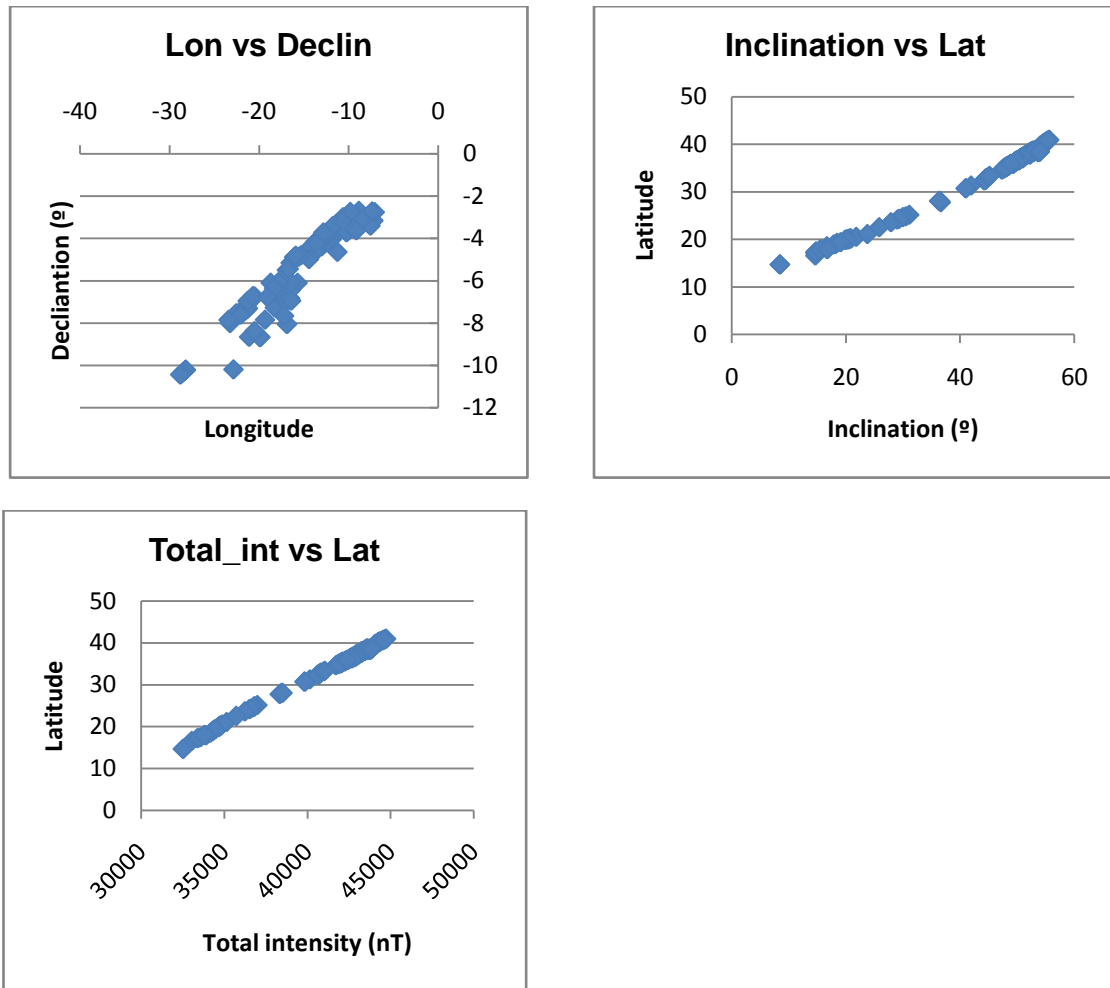
**Table 15:** Mann-Whitney-Wilcoxon tests for pairwise comparisons between baleen whales species and the available habitat for the summer season. In bold are the p-values<0.05, indicating statistically significant differences.

Pairwise comparisons – Mann-Whitney-Wilcoxon test						
Summer	<i>Balaenoptera acutorostrata</i>			<i>Balaenoptera physalus</i>		
Available	CHLa	W = 297740	<b>p-value = 0.001845</b>	CHLa	W = 547000	<b>p-value &lt; 2.2e-16</b>
	SST	W = 431260	<b>p-value = 0.03552</b>	SST	W = 942000	p-value = 0.06002
	SLA	W = 312280	<b>p-value = 0.0109</b>	SLA	W = 784910	<b>p-value = 0.03181</b>
	Bathymetry	W = 616950	<b>p-value &lt; 2.2e-16</b>	Bathymetry	W = 793160	<b>p-value = 0.02955</b>
	Rugosity	W = 600550	<b>p-value &lt; 2.2e-16</b>	Rugosity	W = 862700	<b>p-value = 0.8639</b>
	Slope	W = 686290	<b>p-value &lt; 2.2e-16</b>	Slope	W = 968490	<b>p-value = 0.003996</b>
	Dist.coast	W = 110220	<b>p-value &lt; 2.2e-16</b>	Dist.coast	W = 813860	<b>p-value = 0.004813</b>
	Dist.seamounts	W = 313360	<b>p-value = 8.217e-06</b>	Dist.seamounts	W = 894740	p-value = 0.2306

### 3.3 Geomagnetism

- Descriptive analysis

The correlation analysis (figure 25 and table 16) shows that both inclination and total intensity vary linearly with the latitude, whereas the declination is correlated with longitude.



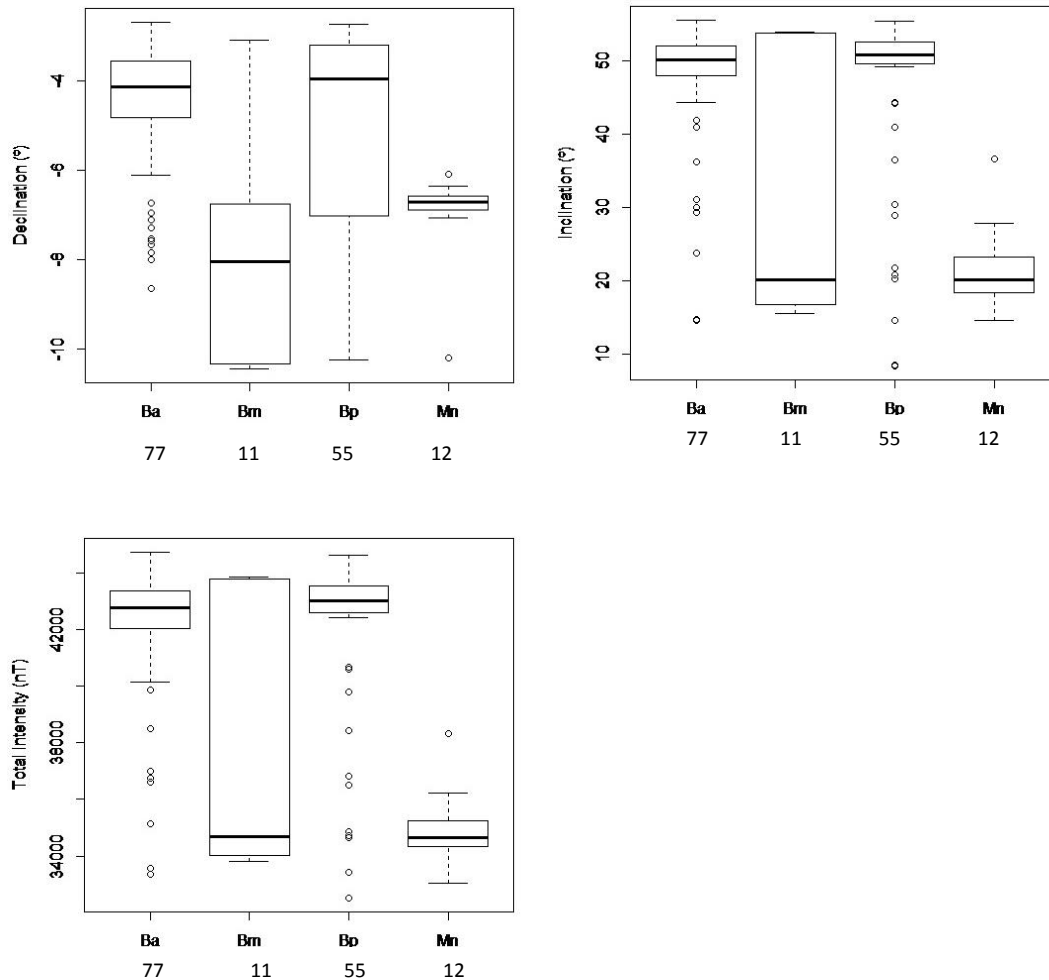
**Figure 25:** Correlation analysis between components of the magnetic field and geographic position. Longitude and latitude are in decimal degrees whereas values of declination and inclination are in degrees and total intensity in nanoTesla.

**Table 16:** Correlation analysis between components of the magnetic field and geographic position. Values above 0.8 (in bold) mean that variables are correlated.

	Longitude	Latitude	Declination	Inclination	Total intensity
Longitude	1				
Latitude	0,29319839	1			
Declination	<b>0,959021553*</b>	0,474204766	1		
Inclination	0,282470152	<b>0,99760174*</b>	0,466938072	1	
Total intensity	0,291133029	<b>0,999573546*</b>	0,469530848	<b>0,996858717</b>	1

\*P<0.05

From the boxplot graphs (figure 26) it is possible to observe baleen whales' ranges of the magnetic components.



**Figure 26:** Values of the magnetic components (declination, inclination and total intensity) for four species of baleen whales. Whiskers represent the lower and upper 25% of the occurrences delimited by minimum and maximum, and the dashed line is the median (50% quartile). The box includes 50% of the occurrences. Labels: Ba - *Balaenoptera acutorostrata*; Bm - *Balaenoptera musculus*, Bp - *Balaenoptera physalus*; Mn - *Megaptera novaeangliae*. Below the x-axis, it is indicated the number of sightings used for each boxplot.

For all the components, the median of values for blue and humpback whales is lower (approximately -7.5, 20 and 34500 for declination, inclination and total intensity, respectively) than for minke and fin whales (approximately -4, 50 and 43000 for declination, inclination and total intensity, respectively), even considering the low number of records for the former two species (tables 17-28 and figures 32-35 in Appendix).

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Using data of fin whale observations (21 in Madeira and 939 in Azores) from Azores and Madeira islands, there are no clear differences within the same archipelago, whereas differences among both are obvious (figure 27).

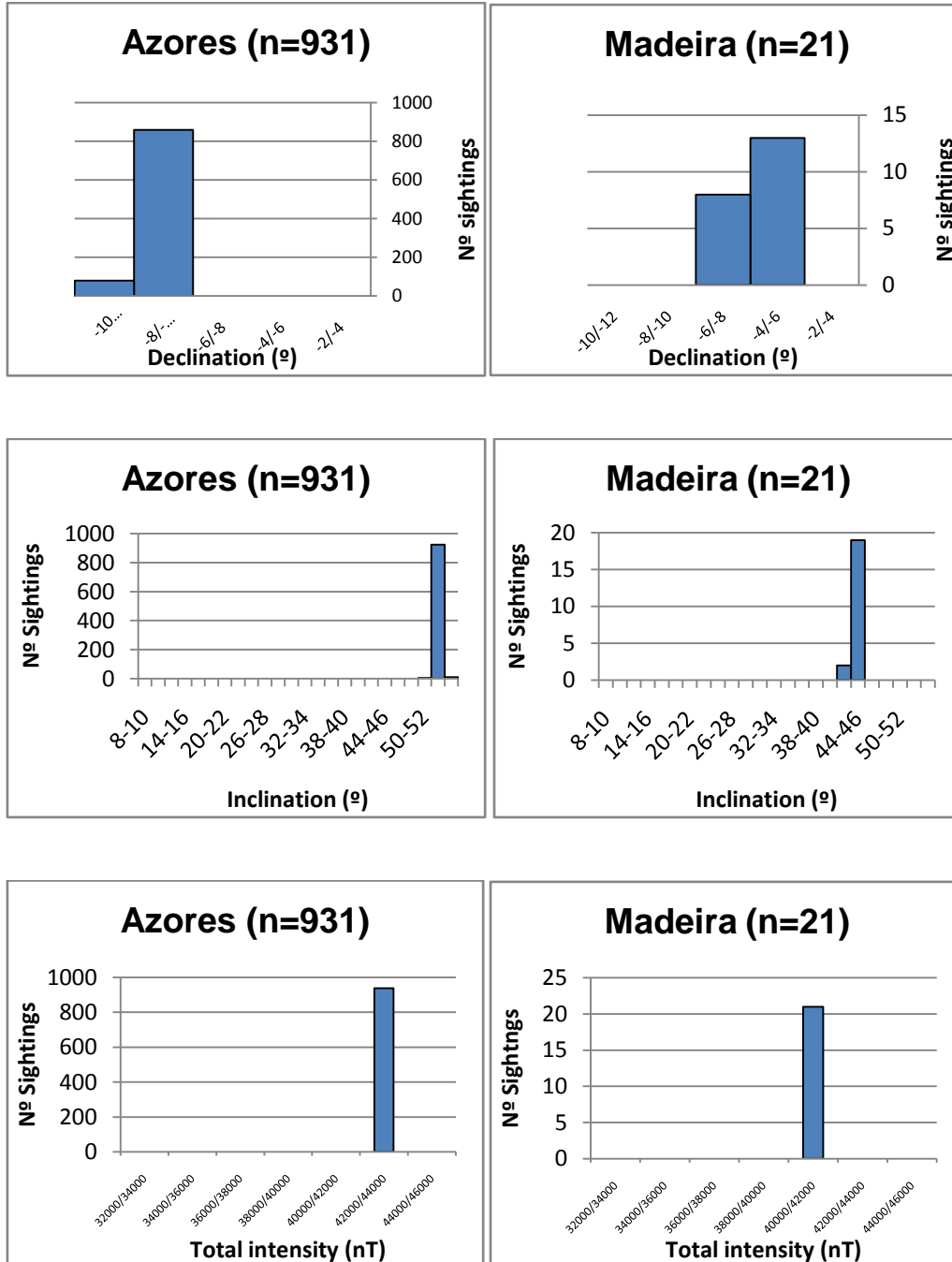


Figure 27: Values of the magnetic components at the position of the fin whales observations, for Madeira and Azores islands.

Splitting data by season, there are no evident patterns (figures 28, 29 and 30). For minke whales, values of the magnetic field components are similar in spring and fall, while for blue whales differences between both seasons are clear. Fin whales sightings

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are distributed along a wide range of values of the magnetic field components in both seasons.

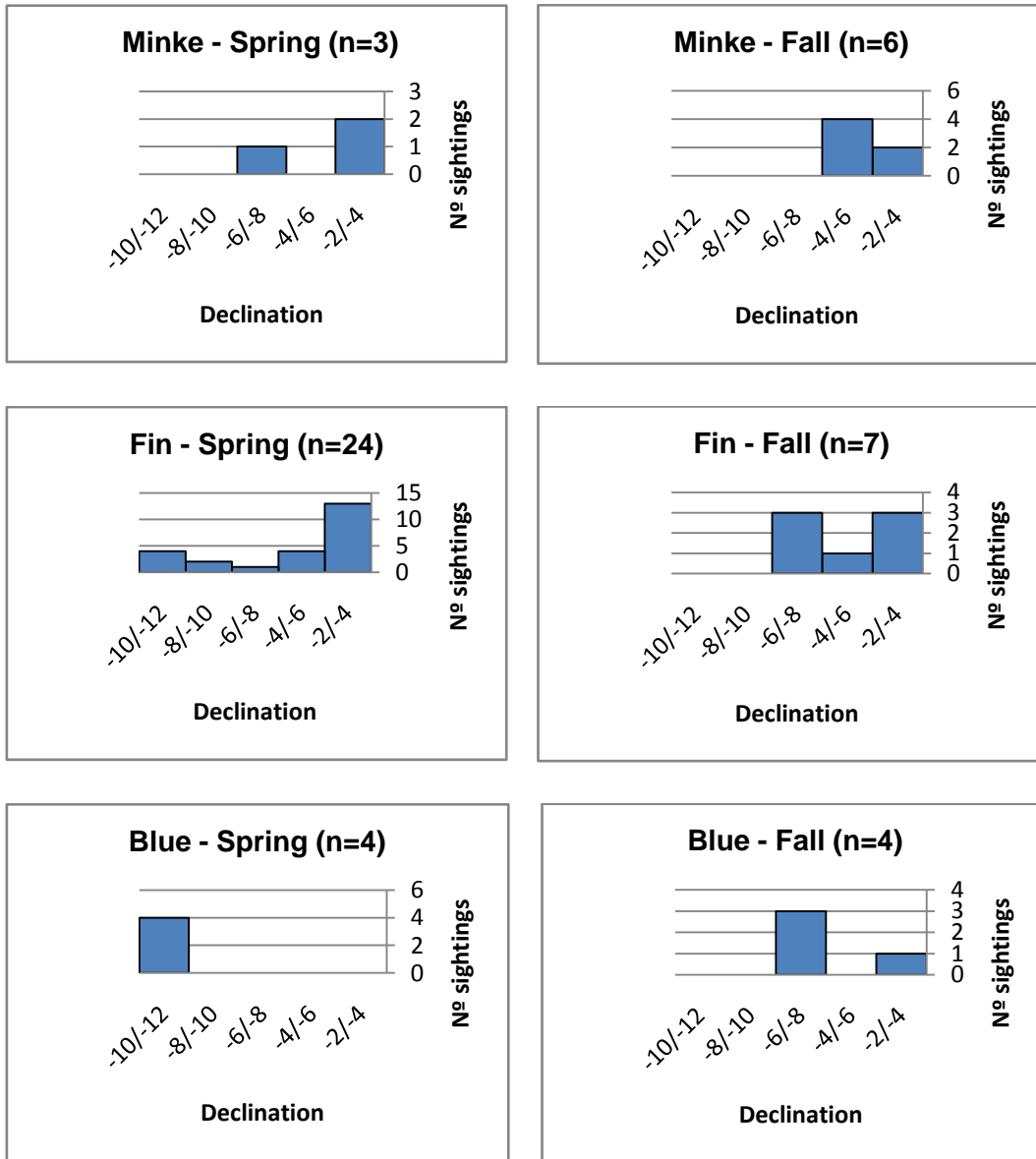


Figure 28: Values of declination, in two different seasons, using sightings of different baleen whale species.

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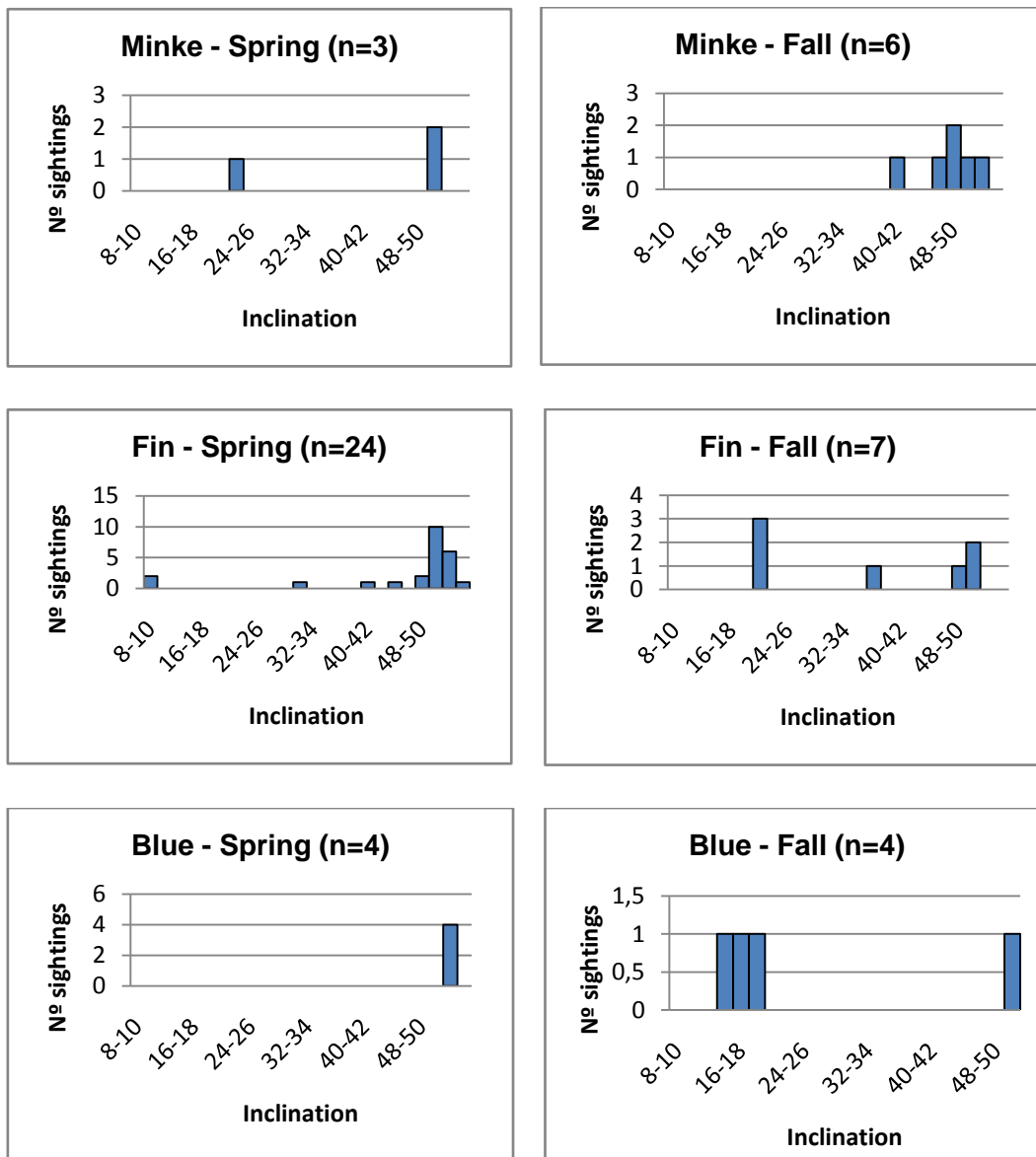


Figure 29: Values of inclination, in two different seasons, using sightings of different baleen whale species.

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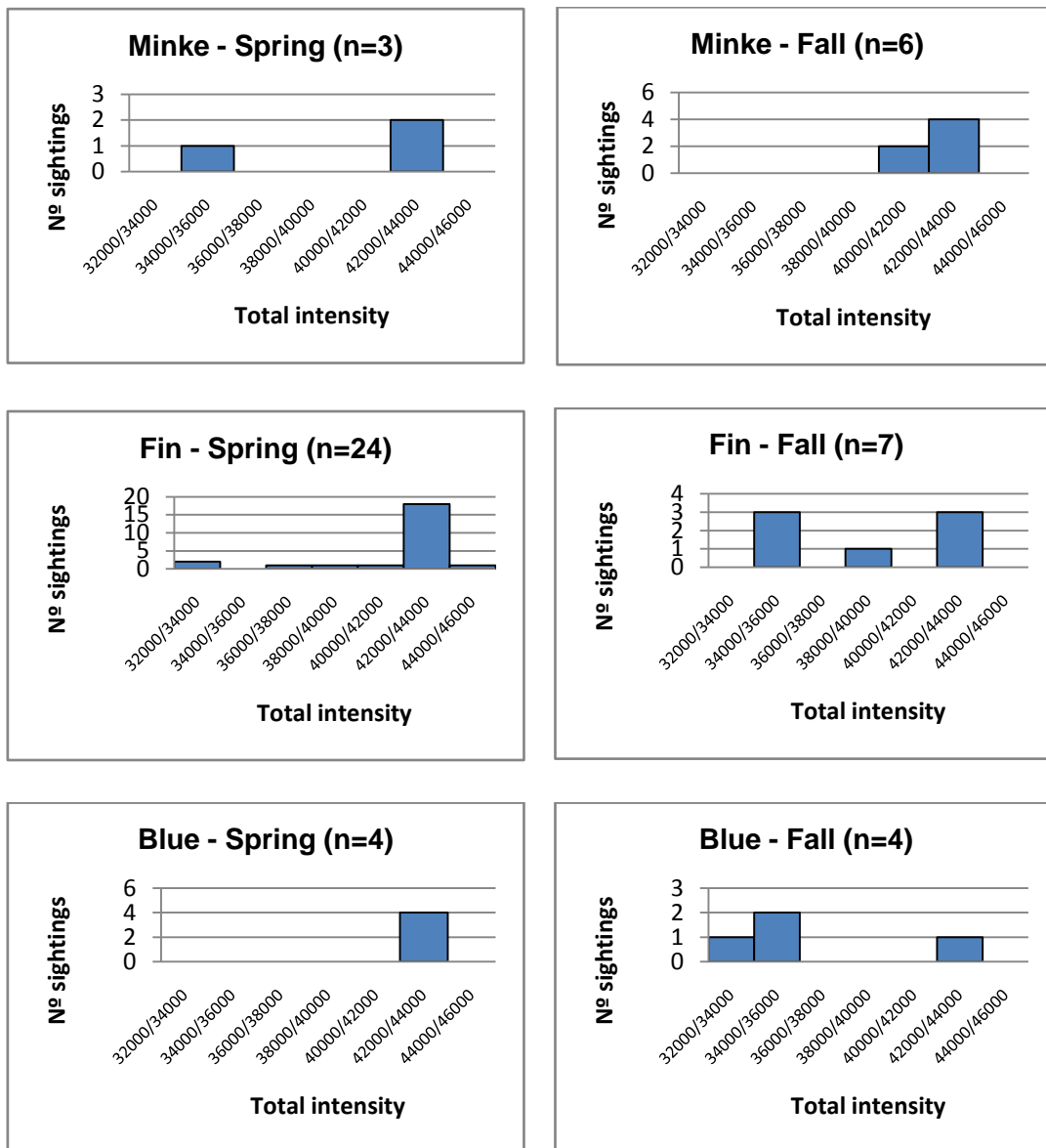


Figure 30: Values of total intensity, in two different seasons, using sightings of different baleen whale species.

Descriptive statistics (Appendix: Tables 30-47) complement results presented in the previous histograms.



-Modeling of Magnetic Components

Tables 17 and 18, show the results of the models for both minke and fin whales occurrences related with each of the explanatory variables. While for minke whales the percentage of deviance explained varies between 13.4 and 34.7%, for fin whales it varies between 35 and 75%. In fin whales, similar and high percentages are observed in declination and longitude (around 70-75%), while inclination, total intensity and latitude presented similar but with lower percentages (between 35-45%).

**Table 17:** Best GAM model results obtained for minke whales occurrences related with each of the explanatory variable used in this analysis.. e.d.f. – effective degrees of freedom; s.e. – standard error; n – total number of points. Labels: Lat - latitude, Lon - longitude.

Species and Parameter	Estimate	e.d.f.	s.e.	z-value	p-value	Deviance explained (%)	r <sup>2</sup>	n
Intercept	0.2900		0.5163	0.562	0.5743			
Spring	1.311		0.6625	1.979	0.0478			
Summer	0.7644		0.5505	1.388	0.1650			
Winter	-0.1024		1.4059	-0.073	0.9419			
Smother Terms								
mean_declination		1			0.505			
Model:s(mean_declination)						13.8	-0.0948	35
Intercept	0.2349		0.5031	0.467	0.6406			
Spring	1.2157		0.6409	1.897	0.0578			
Summer	0.8236		0.5373	1.533	0.1253			
Winter	-0.3403		1.3361	-0.255	0.7989			
Smother Terms								
mean_inclination		1.598			0.268			
Model:s(mean_inclination)						22.7	-0.0209	35
Intercept	0.1612		0.5019	0.321	0.7480			
Spring	1.2948		0.6385	2.028	0.0426			
Summer	0.8847		0.5345	1.655	0.0979			
Winter	-0.2888		1.3224	-0.218	0.8271			
Smother Terms								
mean_total_intensity		2.166			0.243			
Model:s(mean_total_intensity)						28.4	-9.22e-05	35
Intercept	0.1077		0.4984	0.216	0.8289			
Spring	1.2970		0.6297	2.060	0.0394			
Summer	0.9396		0.5306	1.771	0.0766			
Winter	-0.2784		1.3089	-0.213	0.8316			
Smother Terms								
Lat		2.436			0.155			
Model:s(Lat)						32.6	0.0307	35
Intercept	0.1096		0.5026	0.218	0.8274			
Spring	1.3095		0.6478	2.021	0.0432			
Summer	0.9449		0.5385	1.755	0.0793			
Winter	-0.3058		1.3612	-0.225	0.8222			
Smother Terms								
Lon		3.51			0.316			
Model:s(Lon)						34.7	0.0177	35

For minke whale, the model that explains the distribution is the one that incorporates longitude as an explanatory variable due to the higher percentage of deviance explained (34.7%). On the other hand, the model that explains least is the one in which declination is included, with only 13.4% deviance explained (table v). In all models, the

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smooth term is no significant ( $p > 0.05$ ), although when adding as a factor the season, the spring season is significant for all models, except for inclination.

**Table 18:** Best GAM model results obtained for fin whales occurrences related with each of the explanatory variable used in this analysis.. e.d.f. – effective degrees of freedom; s.e. – standard error; n – total number of points. Labels: Lat - latitude, Lon - longitude.

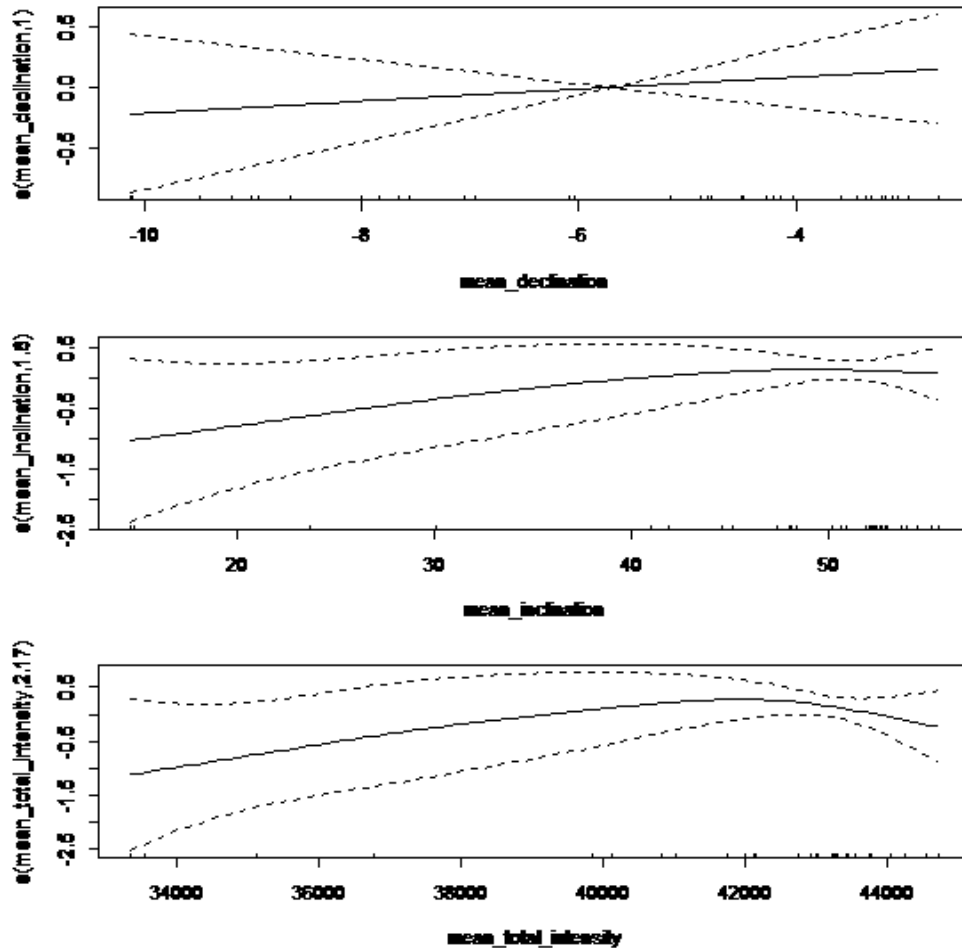
Species and Parameter	Estimate	e.d.f.	s.e.	z-value	p-value	Deviance	r <sup>2</sup>	n
Intercept	0.8418		0.4988	1.688	0.09150			
Spring	1.5665		0.5869	2.669	0.00761			
Summer	0.5396		0.5853	0.922	0.35655			
Winter	0.6074		0.7172	0.847	0.39706			
Smother Terms								
mean_declination		2.736			<0.001			
Model:s(mean_declination)						71.9	0.225	47
Intercept	1.4327		0.6261	2.288	0.0221			
Spring	1.7217		0.7296	2.360	0.0183			
Summer	0.1042		0.7725	0.135	0.8927			
Winter	0.7256		0.8846	0.820	0.4121			
Smother Terms								
mean_inclination		2.56			<0.001			
Model:s(mean_inclination)						45.2	-0.00538	47
Intercept	1.4015		0.6312	2.220	0.0264			
Spring	1.8522		0.7314	2.532	0.0113			
Summer	0.2569		0.7789	0.330	0.7416			
Winter	0.7917		0.8929	0.887	0.3753			
Smother Terms								
mean_total_intensity		2.133			<0.001			
Model:s(mean_total_intensity)						41	-0.0207	47
Intercept	1.2137		0.6405	1.895	0.05808			
Spring	2.2164		0.7433	2.982	0.00286			
Summer	0.6688		0.7853	0.852	0.39444			
Winter	0.9924		0.9075	1.094	0.27416			
Smother Terms								
Lat		1.201			<0.001			
Model:s(Lat)						35.2	-0.00416	47
Intercept	0.9230		0.4851	1.902	0.0571			
Spring	1.4344		0.5606	2.558	0.0105			
Summer	0.2995		0.5863	0.511	0.6095			
Winter	0.4386		0.6935	0.632	0.5271			
Smother Terms								
Lon		3.657			<0.001			
Model:s(Lon)						75.9	0.232	47

From table g, we can see that the model with the highest deviance explained is the one in which the longitude was used as an explanatory variable with 75.9%. The model with latitude was the one whose deviance explained was lower with 35.2%. Unlike the minke, all the variables used in the models are significant, and when adding the season as a factor, in spring the model was significant.

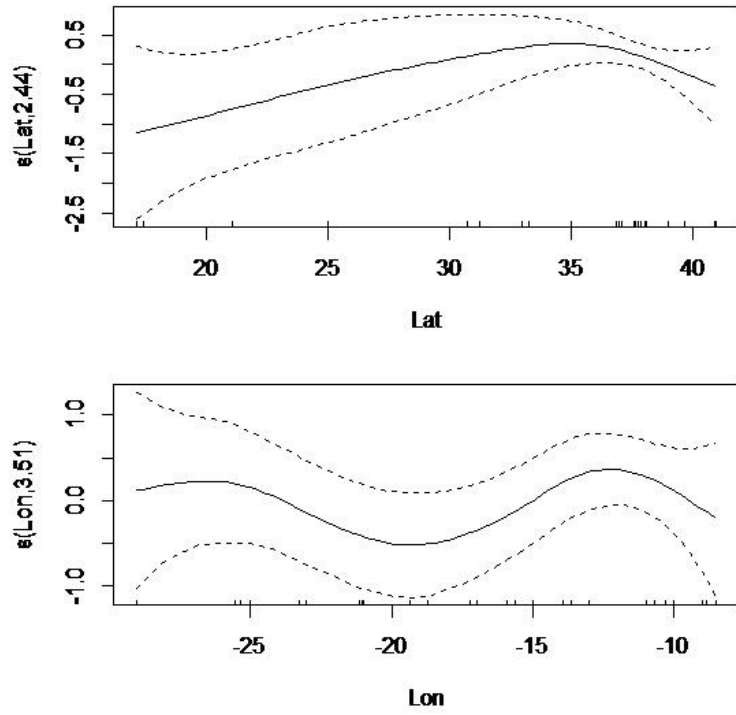
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GAM plots are presented in figure 31, allowing the visualization of the effect that each variable has in whales' distribution.

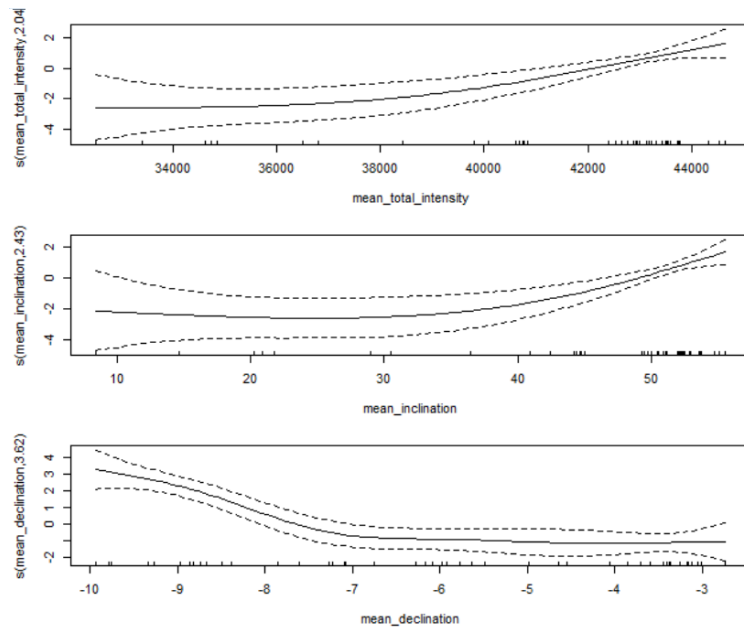
- *Balaenoptera acutorostrata*

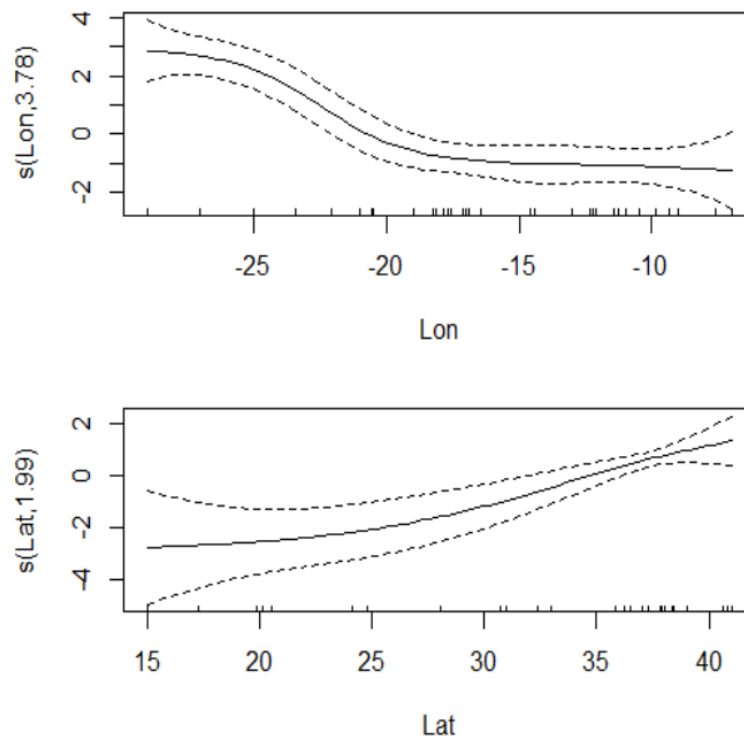


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- *Balaenoptera physalus*





**Figure 31:** Generalized Additive Models predicted smooth splines of the response variable as a function of the explanatory variables. The effective degrees of freedom are in parenthesis on the y-axis. Dashed lines represent the 95% confidence intervals and the tick marks above the x-axis indicate the distribution of points (used). Labels: Lat - latitude, Lon - longitude.

The plot for declination in minke whale was not informative, since in values where the confidence interval is reduced, there is no effect of declination on the response variable. The plots for inclination and total intensity show a positive effect of these variables at angles of approximately  $50^\circ$  (for inclination) and 43000 nT (for total intensity). Interestingly the plots for these variables are very similar to those found for latitude. The plot for longitude does not allow us to draw any conclusions since the confidence interval is very large over the entire range of values.

Similarly to minke whales, plots for fin whales show great similarity between the plots of inclination and total intensity with the plot of latitude, with a positive effect for the same values found in minke whales. However, and in contradiction to what is seen in minke whales' models, the plots for declination and longitude have a very similar pattern. For both models it was not possible to draw great conclusions because the confidence interval seems to be similar across all the range of values.

## 4. Discussion

### 4.1 Spatial and temporal distribution

- Distribution of Research Effort in the Macaronesia

Our results point to a lack of information at high-seas regarding the presence of baleen whales in Macaronesia, with very little knowledge about the distribution of these cetaceans in areas between different archipelagos and between archipelagos and continents. Example of this lack of data, is the small number of publications containing sightings in these off-shore areas (e.g. Gordon *et al.*, 1995; Correia *et al.*, 2015), contabilizing 18% of the total number of published records.

Furthermore, regions along the coast, in general, are better surveyed in comparison to the other areas. Areas such as the Iberian coast (e.g. Brito *et al.*, 2009; Goetz *et al.*, 2015) have been subject to several studies, allowing the knowledge regarding different patterns of presence for this baleen whales.

However, even being near the coast, there are certain areas that need more monitoring. The coast of Morocco is a major example of this lack of data, since it was very little explored and, to our knowledge, there was only one publication for the area (Notarbartolo-di-Sciara *et al.*, 1998).

It is also in coastal areas, but of the islands, that there is an enormous amount of information regarding the presence of cetaceans (e.g. Reiner *et al.*, 1996; Ritter, 2001; Freitas *et al.*, 2012; Silva *et al.*, 2014).

There are several reasons why there are much more data in coastal areas compared to the one obtained on high-seas:

- the lack of resources to monitor cetaceans in high-seas areas means that most of the studies (information collected) are carried out in areas near the coast (islands or mainland). An important platform for the obtainment of presence/absence data of cetacean species that occur relatively close to the coast are whale-watching boats, whose daily departures to the sea, lead to a obtention of a large amount of data, although very restricted in space (e.g. Ritter & Brederlau, 1998). In our case, the data obtained from MoniCet platform (Fernandez & Azevedo, 2017), makes the Azores one

of the areas in which we have a very clear idea of the occurrence of baleen whales throughout the year.

- the fact that a breeding area is known for a particular species (in our case for humpback whales) means that the number of studies in these areas is higher (Jann *et al.*, 2003; Wenzel *et al.*, 2009; Ryan *et al.*, 2013, 2014). The high number of humpback whales sighted in this archipelago is the result of this increased survey effort in the area.

Another interesting point of our results is the fact that there is a smaller research effort during the winter compared to the other seasons. The most likely explanation for this lower monitoring effort in winter may be due to the oceanic conditions of the area during this period, particularly difficult to monitor under the conditions required for a good sampling design. For other seasons, ocean conditions are significantly better, allowing for more survey effort at these months.

Finally, our results are consistent with a lack of data regarding the occurrence of blue whales and humpback whales in Macaronesia, compared to the number of sightings obtained for minke and fin whales. There are more blue whales and humpback whales sightings than minke whales sightings, but these are very concentrated in certain areas, preventing conclusions on the distribution of these species.

The fact that we see these species only in few places can be explained by the current abundance of these species in the Atlantic Ocean. Although much of the abundance estimates were made on feeding grounds located at higher latitudes, they are sufficiently enlightening regarding the discrepancy in the number of individuals existing for each species. Taking the data provided by IUCN (2016), we can see that the populations of fin and minke whales in the Northeast Atlantic are in the order of thousands of individuals (for example estimates for the population of minke whales in the Northeast Atlantic are approximately 80000 individuals), while populations of humpback and blue whales are just few thousand (estimates for the blue whales population in the central north Atlantic is approximately 1500 individuals, while for the breeding population of humpback whales in Cape Verde, it is estimated that there are about 160 individuals in this area (Ryan *et al.* , 2014)).

Another explanation for the difference in the spatial occupation of our sightings may be due to the resident "character" of fin and minke whales, contrasting with the migratory behavior normally associated with blue and humpback whales (Reeves *et al.*, 2004).

Evidences point to the existence of resident populations for minke whales and fin whales in the area (Van Waerebeek *et al.*, 1998; ICNF, 2016), confirmed by the sightings obtained during the summer (supposedly period in which they are on high-latitude feeding grounds). It is possible that the greater survey effort carried out in summer and having fewer individuals referring to the species considered "purely" migratory, could somehow "skew" the sightings obtained.

Lastly, the hypothesis for the fact that we only have very localized humpback and blue whales sightings, may be due to in Macaronesia these whales are mostly present in offshore areas. Little is known about the winter distribution of blue whales, presumably in this area in this season (Reeves *et al.*, 2004). Furthermore, they are thought to migrate in off-shore areas (Silva *et al.*, 2013; Nieukirk *et al.*, 2014), making it difficult to know their patterns of presence in the area. Humpback whales are known to migrate along the coast (Lockyer & Brown, 1981), though with notable exceptions to this "rule" (e.g. Kennedy *et al.*, 2013). As in Macaronesia only a single link between the Azores and Cape Verde was found (Wenzel *et al.*, 2009), we cannot discard the hypothesis of a migration along the coast.

#### - Spatial and Temporal Distribution of Baleen Whales Records in the Macaronesia

Our results, in general, support what is known about the distribution of these species in Macaronesia.

Minke whales are quite common along the coast of the Iberian Peninsula, confirming the results by the ICNF (2016). In addition, this species is not often observed in the islands, in agreement with the data present in several publications (Van Waerebeek *et al.*, 1998; Freitas *et al.*, 2012; Silva *et al.*, 2014). Along the African coast, few sightings of minke are collected, which may be a reflection of the little effort made in these areas, or may indicate a low presence of this species. When looking at the presence of minke whales in off-shore areas, we must point out the large number of sightings obtained in the region between Portugal and Madeira. This area is characterized by the presence of the Horseshoe seamount chain (which includes the MPA Josephine seamount). It is constituted by numerous topographic structures and it presents a great dynamism (due to the formation of eddies and upwelling phenomena) (Mason, 2009), being known for its great biological productivity (e.g. Xavier & van Soest, 2007). According to Van Waerebeek (*et al.*, 1998), in areas of high biological productivity it is possible that these



whales do not need to migrate to feed, having reported cases of minke whales that were observed exhibiting feeding behavior in lower latitudes. When we see many whales in the summer (supposedly when they should be in the high latitude feeding grounds (Mackintosh, 1965)), we can conclude that minke whales are very likely to be resident in this area.

Fin whales although they present some similarities in patterns of distribution with respect to minke whales, they have some differences mainly in their presence near the islands. In Azores it is the species of baleen whales with more sightings collected, with a clear peak of sightings in the spring months (April, May and June), confirming the results obtained in previous studies (González *et al.*, 2014; Silva *et al.*, 2014). In the archipelagos of Madeira and the Canaries, although it does not have such a significant presence compared to what is observed in Azores, there are also quite common in the areas mainly in the spring, confirming the data of several studies carried out in these archipelagos (Pérez-Vallazza *et al.*, 2008; Carrillo *et al.*, 2010; Pérez-Vallazza, 2013; Freitas *et al.*, 2014). Regarding their presence in tropical areas (African coast and Cape Verde archipelago) it is not common to see fin whales, in agreement with Edwards *et al.*, 2015) whose their results point to a gap in the distribution of fin whales between the 30° N in North Atlantic and 20° S in Southern Hemisphere. Finally, and in addition to the observations near the coast, a large number of sightings were obtained at high-seas (mostly in spring and summer), suggesting a ubiquitous distribution of this species in Macaronesia

Blue whales have very different patterns distribution compared to previous species, with rare sightings both along the coast and in off-shore areas. Exception to this pattern is the Azores archipelago where they are sighted in large numbers, mostly in the spring, supposedly towards the feeding grounds in the arctic (Silva *et al.*, 2013, 2014; González *et al.*, 2014). The Mauritanian region is one of the places where blue whales (Baines & Reichelt, 2014; Camphuysen *et al.*, 2012, 2015) were observed, mainly in fall and winter, and it has been suggested that this species uses the waters for feeding purposes. The remaining sightings are scattered throughout various regions, making it difficult to understand the patterns of distribution of this species.

Humpback whales follow a pattern of distribution very similar to that found in blue whales, but with some differences. Firstly, it is common to observe this species in the Cape Verde archipelago, since it is only known winter breeding area on the eastern margin of the North Atlantic basin, being mostly observed in winter and spring, when

they use these waters to breed and mate (Hazevoet & Wenzel, 2000; Wenzel *et al.*, 2009; Ryan *et al.*, 2013). In Azores this species was already seen in large numbers in the spring, not as expressive compared to those seen for blue and fin whales, although in the remaining seasons individuals are observed to swim through the waters. These results are in agreement (in part) with those obtained in several studies carried out in the Azores in which they point to a more occasional presence of this species in the waters of the archipelago (González *et al.*, 2014; Silva *et al.*, 2014), although the sightings obtained in the spring suggest that this area is not so little traveled by this species. With much fewer sightings for the Azores, the region of Mauritania, as in blue whales, is within the range of humpback whales, with some sightings in the summer and fall suggesting that this species passes through this area (Camphuysen *et al.*, 2012, 2015).

#### - Latitudinal progression of baleen whales in the Macaronesia

Minke whales had their greatest abundances in summer, mainly in the off-shore areas between mainland Portugal and the Madeira archipelago. This results reinforces the conclusions obtained previously, showing once again the importance that this off-shore region can have in the distribution patterns of this species of baleen whale.

Fin whales have the greatest encounter rates in winter and spring, between 30° N and 40° N. These peaks are in agreement with previously collected information on the biology of the species, since it is between January and June that migratory populations are in lower latitudes of Atlantic ocean to breed and mate (Nieukirk *et al.*, 2004). While peaks in the spring come from the presence of whales migrating to higher latitudes (Carrillo *et al.*, 2010; Silva *et al.*, 2013, González *et al.*, 2014), peaks in winter, being in higher latitudes in our study area, raise two hypothesis for this pattern: the possibility of these whales not making a complete migration (in this case it would be from feeding grounds to breeding grounds), a hypothesis posed by Mizroch (2009) and Aguilar (2009), not reaching the supposed breeding areas in lower latitudes (which is currently unknown (Vighi *et al.*, 2016) where they are) or the breeding areas are relatively close to the archipelagos where they were observed (in this case, the Azores and Madeira). The occurrence of singing behavior with a peak in the months of November-December in the Azores archipelago, lead to Silva (*et al.*, 2011) suggest that there is a possible North Atlantic Central breeding area for these species. In addition, mother-calf pairs have been observed in Madeira (Freitas *et al.*, 2004) indicating that there may be a

breeding area near the archipelago. Therefore, although much remains unknown, our results show how intricate is this species in terms of spatial and temporal patterns, probably related with the complex fin whale subpopulation structure in Northeast Atlantic (Vighi *et al.*, 2016).

Blue whales, have a peak in winter for the Azores area. As discussed earlier for fin whales, this peak is most likely to occur due to the existence of breeding grounds for this species in areas close of the archipelago. To support this hypothesis, the fact that all existing blue whale sightings in the winter were collected in March, the month in which blue whales are supposed to begin their journey to high latitude feeding grounds (Visser *et al.*, 2011 ) supports the possibility that the peak of presence may have been in the winter as it "caught" the onset of their migrations towards the north.

Humpback whales found in Azores archipelago have more records in the islands of the central group in winter, while in the eastern group they are more sighted in the spring. The reason may be the two different migrating populations passing in Azores: humpbacks found in winter may belong to populations in which their breeding areas are located on the western side of Atlantic Ocean (Whaletrack, 2017), migrating to Antilles /from Tromsø (as the population that reproduces in Cape Verde should be in lower latitudes in this period (Ryan *et al.*, 2014)), while those found next to the island of São Miguel may be from the eastern Atlantic, their northward migrations from Cape Verde towards the summer feeding grounds (Wenzel *et al.*, 2009). Although this hypothesis is not disposable, probably in both groups of islands there are individuals belonging to the two migrating populations. The only individual photo-identified in the Azores, re-sighted in Cape Verde islands some years later, was found around the island of Faial, which is in the central group (Wenzel *et al.*, 2009).

#### - Spatio-temporal models

The best model obtained for minke whales was highly different from all the other species. Besides not including variables interactions, latitude was not included in the final model, suggesting that records collected do not allow us to identify a north-south migration for this species. Most likely this is due to the fact that among the observations of minke whales obtained, a great amount is from resident populations (Van Waerebeek *et al.*, 1998; ICNF, 2016), whose existence was previously suggested. Since both longitude and time variables were considered in the model, it is possible

that minke whales (especially those pertaining to Macaronesia - resident populations) make horizontal migrations towards possible breeding off-shore areas. To our knowledge, there is no publication that has suggested this movement for minke whales, but the fact that minke whales vocalizations have already been recorded in areas near the mid-atlantic ridge (Nieukirk *et al.*, 2004; Risch *et al.*, 2014) confirm the hypothesis formulated by Sigurjónsson (1995) in which minke whales breed in open ocean areas.

For the remaining species, the best final models included interactions between latitude / longitude and year / julian days.

Fin whales models show us a possible preference for the areas of Azores, around the Iberian Peninsula and near the archipelago of Cape Verde. While for the first two areas, this species is frequently observed, in Cape Verde there are only a few records, and species was considered only as "Occasional", also in agreement with the results of Edwards (*et al.*, 2015) that pointed to an absence of fin whales between approximately 30 ° N in North Atlantic and 20 ° S in Southern Hemisphere. The preference for this area highlighted by the model can be due to the very little research effort in the area, which may lead to a poor prediction of the model. However, even the few sightings, considering the almost non-existing effort, may indicate to the presence of a resident population also (or coming from the South Atlantic) suggested by Moore *et al.* (2003). The sightings in these area may also be from South Atlantic populations, as they presented cookiecutter shark (*Isistius* sp.) bite lesions, lesions only reported for whales from South Atlantic. Moore (*et al.*, 2003) hypothesizes that this type of injury may allow the distinction between populations from the North Atlantic or the South Atlantic. Since whales have not yet been recorded in the North Atlantic with this lesion, it is very likely that these whales do not usually migrate to the north or west.

The spatial plot for the blue whales confirmed the maps of sightings that we had obtained previously. There is a positive effect of the model in areas such as the Azores (zone of passage during their migrations to the north) (Silva *et al.*, 2013; González *et al.*, 2014), in Mauritania (where they can find a possible feeding zone in lower latitudes (Baines & Reichelt, 2014)), in the zone of the archipelagos of Madeira and the Canaries (where spring sightings suggest the possibility of whales passing through this regions during their migrations to the feeding grounds in higher latitudes (Ritter & Brederlau, 1998; Freitas *et al.*, 2004)) and off the Iberian coast.

The blue whale temporal model indicated a positive effect on the occurrence of these whales in spring months (between march and june) and in the fall months (october and

november mainly), which is consistent with the existing information reporting the migration of blue whales during this period in the area (Silva *et al.*, 2013; Reeves *et al.*, 2004). The fact there is no effect in the winter months may relate to the limited research effort either in quantity and in space not allowing possible occurrences in the area, for example, in offshore areas. Blue whales are thought to be found in off-shore areas during winter to breed and mate (Nieukirk *et al.*, 2004). By being present in such inhospitable areas, almost impossible to be monitored, it becomes more difficult to obtain data, remaining its wintering distribution poorly understood.

The model for humpback whales highlights, once again, the importance of the Mauritania and the Azores for this species. It has been suggested that humpback whales have a resident population in the Northwest of Africa (Van Waerebeek *et al.*, 2013). This is supported by Papastavrou & Van Waerebeek (1997) that reported resident populations of humpback whales in several regions of the globe and by Mikhalev (1997) that studied the resident population of humpback whales in Arabian Sea. Both related humpback presence to strong upwelling phenomena. In fact, the coast of Mauritania is prone to the occurrence of these strong upwellings (Baines & Reichelt, 2014) that may support humpback populations year-round. However, there is another explanation for this pattern: sightings obtained from humpback whales in Macaronesia outside of the usual January-May occurrence led to Hazevoet (*et al.*, 2011) suggesting that these sightings were from individuals belonging to the populations of both hemispheres. Therefore, the sightings that we have in Mauritania during the summer season, can be explained by these hypothesis.

Temporally, the model shows there is no seasonal pattern, with the exception of a decrease in preference for the last months of the year, which may be explained, as in blue whales, by a lack of research effort during this period.

The overall dispersion of effort, the existence of data gaps and scattered records of occurrence may have lead to highly biased models, whose predictive power was different among regions and positively correlated with research effort and number of records (higher in Azores compared to offshore areas) and seasons (higher in summer compared to winter) (Cañadas *et al.*, 2005).

## 4.2 Habitat preference analysis

Habitat preference analyses have provided some insights into the environmental requirements for these four baleen whale species, allowing inferences about possible preferred habitats.

For the dynamic variables, all can be used as indicators of mesoscale eddies, although the SLA is the one that is most directly related to the ocean dynamics and patterns of circulation, and can be used in the calculation of geostrophic currents (e.g. Menkes *et al.*, 1996).

For CHLa and the SST, besides being able to be used as proxies of oceanic circulation, they also allow to know where there are located certain upwelling phenomena (e.g. Oliveira *et al.*, 2008), extremely important from a biological perspective.

In this study CHLa was found (almost always) at very low levels, when the whales were sighted (figure 22). This is most probably due to the fact that for the development of a trophic chain, it takes weeks for the individuals belonging to higher trophic levels begin to appear in the area where the phytoplankton bloom was formed (the so-called bottom-up control (Fredriksen *et al.*, 2006)). In addition, it is possible that in extremely dynamic environments, any prey for species belonging to the highest trophic levels are located in other areas than those found for phytoplankton (Grémillet *et al.*, 2008). A similar situation happens with other filter-feeding predators as whale sharks (Sleeman *et al.*, 2010), while for others as basking sharks there we have found short time between bloom and shark's occurrence (Sims & Quayle, 1998). Nevertheless, in the case of baleen whales, since the trophic chain in which they belong, does not contain many trophic levels (since they feed on either krill (zooplankton) or small fishes), it is possible that the lag between the bloom of phytoplankton and the presence of the baleen whales is not very large. Visser (*et al.*, 2011) for the area of the Azores estimated that the time between maximum bloom of phytoplankton in the spring and the presence of whales was one to fifteen weeks. On the other hand, Prieto (*et al.*, 2016), obtained more accurate models when using chlorophyll data with a lag of one month or two months before baleen whales' sightings. In any case, although it is not known which CHL data to be used in order to correctly characterize the distribution of baleen whales based on this variable, it is clear that only the use of data prior to whale sightings will inform us of their distribution.

The results for SST show that baleen whales are seen at increasingly higher temperatures throughout the year, following the increase in temperature in the area until autumn (seen in the habitat available and by the pattern found by Correia (2013)).

Baleen whales found in winter are found in areas with less temperature compared with the habitat available, since coastal upwelling (e.g. Baines & Reichelt, 2014) and cold tongue development in winter makes temperatures in this area not particularly high. At least in species where it was possible to make statistical comparisons with habitat available, the fact that these whales are in areas of lower temperature makes us to think that they take advantage of potential upwelling phenomena that occur either on the coast or near seamounts, to feed themselves and obtain energy for their migrations. In the spring the same phenomenon is observed, with whales preferring lower temperature areas, in agreement with the results obtained by Prieto (*et al.*, 2016) in Azores archipelago.

Analyzing habitat preferences with regard to SLA, the results suggest that whales prefer areas of positive sea level anomalies, as observed by Correia (*et al.*, 2015). These areas are associated with anti-cyclonic eddies and small upwelling phenomena, oceanic processes that may possibly be created by the effect of seamounts in the water bodies (White *et al.*, 2007).

Regarding static variables, these were little informative due to the high number of sightings collected in the Azores, which makes our results to show mostly the existing habitat in the region. However, it is possible to infer, some general preferences for these baleen whales.

Minke whales exhibit a great range of habitat preferences, and can be sighted in different environmental conditions both within the same season and between different seasons.

This ubiquitous presence corroborates the possible existence of resident and migratory populations in our study area, confirming the hypothesis formulated by Van Waerebeek and data from the ICNF in which a constant presence of this species is pointed out both on the Portuguese coast as well as on the coast of northwestern Africa (Van Waerebeek *et al.*, 1999; ICNF, 2016). Significant differences in minke whales habitat preferences in summer, where the sightings obtained are mostly outside the Azores, allow us to draw some conclusions regarding their preferences. Therefore, it seems that minke whales prefer areas far from the coast, of higher depth and with the

slope/rugosity relatively low, although in close relation with the seamounts, so in offshore areas. This result together with those presented for sea surface temperature and for sea level anomaly confirm a possible use of topographic structures as are the seamounts in the area, as feeding areas during the summer. The lower temperature and the presence of positive anomalies (significantly different from those sampled over the entire area), give more strength to this hypothesis because they are associated with an increase in primary productivity.

Fin whales, as minke whales, can also be found a little throughout Macaronesia region, being observed in different environmental conditions, confirming once again the possible presence of resident and migratory populations (ICNF, 2016; Silva *et al.*, 2013; González *et al.*, 2014). In almost all variables, fin whales have their median with the same values as the median of the available habitat, not being possible to know if this species has any preference for some specific habitat type.

Blue whales can only be found in areas of great depth. Moreover, almost all sightings in the spring and autumn collected outside the Azores were relatively far from the coast and seamounts in relatively low slope/rugosity areas. These results give more strength to the possibility of a migration in off-shore areas, in addition to a possible presence during the winter in high-sea regions. The few sightings obtained for this species in the Macaronesia region may be due to this preference for offshore areas, which as we have seen are much less surveyed compared to the coastal areas.

Humpback whales that pass through the Azores, unlike the other baleen whales, when they are passing through this archipelago they prefer shallower waters, compared with the other species, both in winter and in summer. In addition, in both seasons they are observed in rougher areas. The area of the Azores is characterized by a large diversity of habitats, including shallow seamounts (Silva *et al.*, 2014). It is possible that humpback whales during their migrations use these topographic structures to feed, taking advantage of the upwelling phenomena created by these structures (Genin & Dower, 2007) and the anti-cyclonic eddies (Taylor columns (White & Mohn, 2004)) formed there. Although our conclusions are lacking of evidence, other whale species have already been seen using this archipelago as a stop-over site to feed themselves during their migrations (Silva *et al.*, 2013), suggesting that humpback whales may have the same behavior in the area.



### 4.3 Geomagnetism

The possible use of the earth's magnetic field as a means of orienting baleen whales during their migrations has not yet been effectively demonstrated, largely due to the impossibility of carrying out laboratory studies to demonstrate the influence of the magnetic field on these cetaceans. The few studies that attempted to find a relation between the presence of cetaceans and a particular component of the magnetic field were mostly correlative (e.g. Kirschvink *et al.*, 1986; Walker *et al.*, 1992), with all their inherent limitations (Redfern *et al.*, 2006).

Despite the difficulties presented throughout this study, there are a number of results that give us a possible indication of the possibility of baleen whales, using this environmental stimulus as a navigational mechanism. The results of the correlation analysis between the three components of the magnetic field and the latitude and longitude, point to a quasi-linear relationship between declination / longitude and total intensity / inclination/ latitude. This relationship although does not tell us that whales orient themselves based on these stimuli, it indicates the potential of the use of these magnetic components to orient themselves, in agreement with what was suggested by Lohmann & Lohmann (1996). The gradients of these 3 components being not parallel they allow to form a large-scale bicoordinate "magnetic map", in which different oceanic regions are delineated by different combinations of declination, inclination and total intensity (Putman *et al.*, 2011). Furthermore, we have seen strong differences between different regions in the area (we can see it for the comparison between the Azores and Madeira archipelago) and that these stimuli remain relatively stable throughout the year. All these results give more strength to this hypothesis although they cannot confirm the use of this means of orientation by the whales.

The models created from the components of the magnetic field and geographic variables (latitude and longitude) have confirmed again the potential of declination to be used as proxy of the longitude, while total intensity and inclination as a proxy of latitude. However, there are models in which the percentage of deviance explained is very high, which leave us with some doubts regarding how these GAM's actually translate preferences. Generally, a higher deviance explained means that the variable is not the most appropriate to explain the distribution of a given sample, or that the data collected are either small or very concentrated in a specific area (which is mainly the case of fin whales).

Another interesting result is that in spring (almost) all models are significant. Although the limitations mentioned above do not allow us to go much further in our conclusions, it is suggested from these results that at least in the spring months (when whales are supposed to begin their migrations to the North) (e.g. Silva *et al.*, 2013) there is a possible preference of these whales for a given value in one (or several) magnetic field component (s).

Interestingly the models for declination and for longitude in minke whales are manifestly different. Although we do not know for certain why the models are different, probably the fact that we used the coordinates of the centroid as coordinates of our sightings (whenever we had more than one sighting per area), together with the fact that we do not have a large number of areas with sightings, may have make the models be so different.

Lastly, our results failed to be informative for us to say with confidence, that baleen whales use this orientation cue when they are migrating. There are a number of explanations for not having been as successful as we had hoped: firstly the data used for this analysis were not sufficiently distributed throughout our study area, with many sightings being found near the archipelagos and coast, while off-shore sightings were scarce. In addition, there were areas where the sampling effort was notoriously higher (for example in the Azores), with possible implications for the results obtained. With this bias in the data it is possible that our variable response (which was the number of sightings per season of two degree resolution) was not the most indicated, so there is the conviction that with another variable response (more adequate to the limitations of our data), the GAMs could explain more accurately the influence of each component of the magnetic field on the distribution (migration) of baleen whales.

Another reason why our results did not give us a convincing explanation regarding a possible preference in the magnetic field, may be due to the factor used in the GAMs. When considering the season as a factor, maybe we have not picked up all the existing variation within the preferences, since from information taken from several articles, apparently baleen whales, with the speed recorded during other migrations (Zerbini *et al.*, 2006; Horton *et al.*, 2011), can go through our study area in approximately one month. Thus, if we want to study possible differences in the preference for a particular magnetic component, probably with another temporal resolution, we have better answers about this topic.

Therefore, although our results are not sufficiently enlightening regarding the use of geomagnetism during their migrations, they allow us to believe that the hypothesis of a possible use cannot be ignored. Probably with a greater amount of data and with a greater spatial and temporal distribution in different areas, we can obtain results that will allow us to say with more certainty if these whales are guided by this environmental stimulus during one of the crucial phases within the life cycle of mysticetes.

#### **4.4 Possible migratory paths in Macaronesia for baleen whales**

Migratory phenomenon occur at both spatial and temporal scales (Dingle & Drake, 2007), therefore, seasonality is of major importance when studying migratory species.

Minke and Fin whales were recorded throughout the entire Macaronesia area, both in coastal and offshore areas. The existence of both migratory and resident populations in the area (Van Waerebeek *et al.*, 1998; Silva *et al.*, 2013; Víkingsson & Heide-Jørgensen, 2014; ICNF, 2016) may contribute to this fact, hence conclusions on migratory routes are hard to withdraw.

Minke whales were distributed throughout Macaronesia in different seasons of the year, which may relate to the presence of resident populations in the area (Van Waerebeek *et al.*, 1999). The possibility of resident populations becomes more credible when the greatest encounter rates were found in the summer (supposed season in which they would be in high latitude feeding grounds (Mackintosh, 1965)), in a region where environmental conditions (topographic and oceanographic) allow the maintenance of the necessary conditions for the survival of these whales throughout the year.

However, data also points out the migrations in high-seas. For example, the minke whale observed off the Azores in fall and later 1000 northwest from Cape Verde in fall (Víkingsson & Heidi-Jørgensen, 2014), suggests a migratory corridor parallel to the mid-Atlantic ridge, reinforced by the recordings obtained along the mid-Atlantic ridge (Nieukirk *et al.*, 04; Risch *et al.*, 2014). The idea of a horizontal migration (reinforced by the plot of longitude for minkes) although it cannot be demonstrated, is not an idea at all misleading. Both Nieukirk (*et al.*, 2004) and Risch (*et al.*, 2014) obtained no records for minke whales in hydrophones located further north, relatively close to the Azores archipelago. On the contrary, for the hydrophones placed at lower latitudes, vocalizations have already been obtained. When we thought of a vertical migration, we would supposedly to have recordings on all hydrophones because the whales would

come from the high latitudes to their breeding areas, unless they were not vocalizing at those latitudes or if they were far enough away from hydrophones to not record their vocalizations. Therefore, although this hypothesis has yet to be demonstrated, there is a great deal of evidence pointing to this type of behavior by this species.

Much like minke whales, fin whales were recorded year-round throughout almost in the entire study area, even if they are in higher numbers in spring and summer seasons. This pattern of distribution allow us to hypothesize a possible existence of resident and migratory populations, which is in line with the ideas of Evans (1987), at least in the West part of Iberian Peninsula, and in line with our results of habitat preferences. The migratory patterns of the fin whales are much more difficult to infer because in this area it is possible to see individuals belonging to several stocks, not knowing for sure how these whales move between the different feeding grounds existing in the Arctic (IWC, 2009; Vighi *et al.*, 2016). Furthermore, no breeding ground in the Northeast Atlantic is recorded, although it has been advocated by Hain (*et al.*, 1992) and by Nieu Kirk (*et al.*, 2004) that these areas are located in off-shore areas of Atlantic, possibly near the archipelago of the Azores (as our results suggest).

The large number of individuals sighted in the Azores archipelago during the spring months corroborates the idea that this region is a mandatory stopover site for fin whales during their migrations to feeding grounds in Northern Europe (Silva *et al.*, 2013). However, in autumn, these whales had very few records in this area, suggesting a different migratory route from the one used when heading for summer feeding grounds. This has been suggested before by González (*et al.*, 2014), after seeing that sightings of fin whales in fall are rare, in agreement with our results.

There is a lot of evidence pointing to a migratory route in "Saharan" waters. Sightings in Madeira and the Canaries obtained from databases, together with the observations taken from the various publications in the area (Freitas *et al.*, 2004, 2012; Pérez-Vallazza *et al.*, 2008; Carrillo *et al.*, 2010) suggest that these whales pass through these waters both during their northward migrations in spring, and their southward migrations in fall. Furthermore, recordings of fin whales vocalizations on the Gorringe bank during autumn and winter suggest a migratory or wintering habitat for this species in the area (Silva *et al.*, 2017). Thus, the possibility of having a migratory route in this area, is a hypothesis to be explored in the future.

Blue whales, like fin whales, are sighted in large numbers in the Azores during late winter (in March) and during spring, corroborating the existence of a off-shore

migratory route towards the summer feeding grounds in the area (Silva *et al.*, 2013; González *et al.*, 2014). In this archipelago there have been re-sightings of these whales in different years (González *et al.*, 2014), which suggests that Azores archipelago is a very common passage zone for the populations of blue whales existing in the eastern Atlantic.

However, few are the sightings in the remaining seasons, suggesting the possible existence of another migratory route. Like fin whales, this study suggests a route through "Saharan" waters for blue whales, a hypothesis confirmed by the various sightings in the Canary Islands, in Madeira archipelago and off the Iberian Peninsula during the spring and autumn, and defended by Ritter and Brederlau (1998). It is possible that when they arrive near the Iberian Peninsula, they begin to follow the waters along the European coast, an idea suggested by Sears and Perrin (2009).

Blue whale sightings in Mauritania, although they have not been obtained many times, may suggest that this area can be a regular pathway for some blue whales during their migrations (Baines & Reichelt, 2014; Camphuysen *et al.*, 2015). In fact, through a photo-ID study, it was possible to identify the same whale in Mauritania (in March) and in Iceland (in July) (Sears *et al.*, 2005), emphasizing once again the importance of Mauritania as an integral part of the migration of this species.

Humpback whales have a large number of sightings in Cape Verde, a region reported as a breeding area and where many research on breeding behaviors and seasonality is undertaken (e.g. Wenzel *et al.*, 2011; Ryan *et al.*, 2013). As for blue whales, our results suggest that humpback whales have 2 main routes. One of the routes passing through the Azores (meaning, they travel through offshore regions that have not been surveyed yet) as documented by Wenzel (*et al.*, 2009), while the other route passes through the waters between the African coast and the islands, as suggested by sightings off Western Sahara, Canaries and Madeira during the autumn months, idea defended by Carrillo (2002).

Although two routes are presented as hypotheses for both blue and humpback whales, a major difference exists: the number of blue whales found in Azores suggests that a large part of the population passes through this zone during their spring migrations, while only part of the humpback population in Northeast Atlantic is expected to pass by this archipelago (which suggests the use of the other route as an alternative).

Moreover, it is known that the humpback whales sighted in the Azores can be of 2 distinct populations: some individuals belong to the migratory populations that pass through this region during their migrations to the west side of the Atlantic Ocean (to the Antilles) (Whaletrack, 2017), whereas the others belong to the Cape Verde population which in spring migrate to high latitude feeding grounds (Wenzel *et al.*, 2009).

From the available data, it is possible to perceive that individuals from one population as well as from the other can "meet" in areas such as the Azores archipelago. Satellite tag data of whales migrating towards the Antilles point to their presence in the archipelago between March and April (Whaletrack, 2017), while the only photo-ID record that identified the same whale in the archipelagos of Cape Verde and the Azores indicates that the photo obtained in the Azores was taken on April 14 (Wenzel *et al.*, 2009).

#### 4.5 Future work

Today the oceans are increasingly threatened by anthropogenic activities whose impact on marine ecosystems has unpredictable consequences for the balance of the oceans (Fabry *et al.*, 2008). For this reason, it is increasingly urgent to know the distribution of the various populations of cetaceans in the oceans so that we can protect them and thereby protect all the ecosystems in which they are inserted (Hooker & Gerber, 2004). Being highly mobile species and often with their habitat in offshore areas, it is extremely difficult to obtain data that allows us to make an effective and increasingly necessary conservation. For baleen whales, the challenge is even greater. Making seasonal and extensive migrations from high latitude feeding grounds to low latitude breeding grounds, its distribution throughout the year is unclear, making very difficult to implement any protective measures for these cetaceans (Clapham *et al.*, 1999).

The region of Macaronesia is a clear case. The lack of data on the high seas, in contrast with those obtained in areas along the coast (of the archipelagos and the continents), makes knowledge about the migrations of these species scarce and does not allow to know where the conservation efforts should be allocated for these species. Therefore, efforts should be made to obtain more data in these areas, whose vital role in the survival of these species is clearly recognized (Agardy *et al.*, 2011).

## 5. Conclusion

This thesis aimed to study migratory routes of four species of baleen whales in the region of Macaronesia, analyzing spatio-temporal patterns, habitat preferences and the potential use of earth's magnetic field as a mean of orientation during their migrations. The main conclusions are:

- in the Macaronesia, the research effort is scattered, leading to data gaps, mainly in offshore area, directly affecting on existing knowledge regarding the distribution of these whales;
- fin and minke whales are present year-round throughout Macaronesia, specially near Horseshoe seamount chain and in west Iberian coast, pointing to the existence of resident populations in the area;
- records obtained suggest two potential migratory routes at least for fin, blue and humpback whales, one on the high seas passing through the Azores and the other on "saharan" waters occasionally passing near Madeira and the Canary Islands;
- habitat preference data suggest the opportunistic use of topographic and oceanographic features in the area to feed during their migrations;
- correlation between different components of the magnetic field and geographic variables show us the potential of this environmental stimulus to be used as a external cue to navigation during migrations.
- the work demonstrated that it is necessary to increase sampling effort in Macaronesia, especially in off-shore areas, if we want to obtain more concrete data regarding the possible migratory paths of baleen whales species and thereby promote the conservation of marine ecosystems.

This is the first study presenting a thorough bibliographic review of baleen whales in the Macaronesia. Moreover, besides the great effort on data collection and compilation, a spatial and temporal and habitat preferences analysis was undertaken, allowing, for the first time in the area, to take solid conclusions out of data from different research efforts and presenting an overall image and analysis on the knowledge collected and published so far. Furthermore, an approach on geomagnetic influence on migratory routes was done. The conclusions build on the knowledge about migratory species in

the area that supports the challenging task of an efficient management towards the conservation of marine ecosystems.



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## 7. Appendix

**Tables 19-22:** Descriptive statistics for declination for baleen whales. Labels: a) Fin whale, b) Blue whale, c) Minke whale and d) Humpback whales.

a) Fin whale	
Mean	-5,099778912
Standard-error	0,310728983
Median	-3,949290037
Standard deviation	2,304427816
Sample Variance	5,31038756
Kurtosis	-0,400058463
Skewness	-0,910914729
Range	7,519119501
Minimum	-10,24549961
Maximum	-2,72638011
Sum	-280,4878402
Count	55

b) Blue whale	
Mean	-7,967988058
Standard-error	0,696422833
Median	-8,043609619
Standard deviation	2,309773234
Sample Variance	5,335052391
Kurtosis	0,427864617
Skewness	0,675447599
Range	7,350149632
Minimum	-10,43929958
Maximum	-3,089149952
Sum	-87,64786863
Count	11

c) Minke whale	
Mean	-4,494184822
Standard-error	0,160963716
Median	-4,129710197
Standard deviation	1,412450871
Sample Variance	1,995017464
Kurtosis	0,908381204
Skewness	-1,289799799
Range	5,960919857
Minimum	-8,655509949
Maximum	-2,694590092
Sum	-346,0522313
Count	77

d) Humpback whale	
Mean	-6,956153313
Standard-error	0,303564576
Median	-6,703169823
Standard deviation	1,051578538
Sample Variance	1,105817423
Kurtosis	10,21011397
Skewness	-3,085174284
Range	4,093510151
Minimum	-10,19320011
Maximum	-6,09968996
Sum	-83,47383976
Count	12

Looking for the migratory whales: Routes of the baleen whales in the  
Macaronesia

**Tables 23-26:** Descriptive statistics for inclination for baleen whales. Labels: a) Fin whale, b) Blue whale, c) Minke whale and d) Humpback whales.

a) Fin whale	
Mean	46,39340727
Standard-error	1,635606982
Median	50,91799927
Standard deviation	12,12998602
Sample Variance	147,1365609
Kurtosis	3,184086308
Skewness	-2,065268326
Range	47,0753088
Minimum	8,421589851
Maximum	55,49689865
Sum	2551,6374
Count	55

b) Blue whale	
Mean	33,80091823
Standard-error	5,670771814
Median	20,18180084
Standard deviation	18,80782238
Sample Variance	353,7341827
Kurtosis	-2,413464219
Skewness	0,202456877
Range	38,42160034
Minimum	15,51720047
Maximum	53,93880081
Sum	371,8101006
Count	11

c) Minke whale	
Mean	48,01287014
Standard-error	0,909971305
Median	50,16889954
Standard deviation	7,984965798
Sample Variance	63,7596788
Kurtosis	7,965228015
Skewness	-2,7521893
Range	40,92980003
Minimum	14,64150047
Maximum	55,57130051
Sum	3696,991001
Count	77

d) Humpback whale	
Mean	21,74652505
Standard-error	1,685251285
Median	20,17884922
Standard deviation	5,837881697
Sample Variance	34,0808627
Kurtosis	3,212253618
Skewness	1,675315598
Range	21,95610142
Minimum	14,64070034
Maximum	36,59680176
Sum	260,9583006
Count	12

Looking for the migratory whales: Routes of the baleen whales in the  
Macaronesia

**Tables 27-30:** Descriptive statistics for declination for baleen whales. Labels: a) Fin whale, b) Blue whale, c) Minke whale and d) Humpback whales.

a) Fin whale	
Mean	41795,50533
Standard-error	440,4955836
Median	43028,10156
Standard deviation	3266,802681
Sample Variance	10671999,75
Kurtosis	2,114444859
Skewness	-1,835443442
Range	12112,69922
Minimum	32527,80078
Maximum	44640,5
Sum	2298752,793
Count	55

b) Blue whale	
Mean	38488,48189
Standard-error	1510,106206
Median	34694,10156
Standard deviation	5008,455679
Sample Variance	25084628,29
Kurtosis	-2,4237075
Skewness	0,206914122
Range	10031,69922
Minimum	33812,80078
Maximum	43844,5
Sum	423373,3008
Count	11

c) Minke whale	
Mean	42153,60395
Standard-error	259,9790818
Median	42762,60156
Standard deviation	2281,307184
Sample Variance	5204362,467
Kurtosis	5,746934364
Skewness	-2,361218056
Range	11370,19922
Minimum	33358
Maximum	44728,19922
Sum	3245827,504
Count	77

d) Humpback whale	
Mean	34982,05013
Standard-error	378,0173156
Median	34664,85156
Standard deviation	1309,490393
Sample Variance	1714765,09
Kurtosis	3,723378765
Skewness	1,553592318
Range	5297,5
Minimum	33043,39844
Maximum	38340,89844
Sum	419784,6016
Count	12



Looking for the migratory whales: Routes of the baleen whales in the Macaronesia

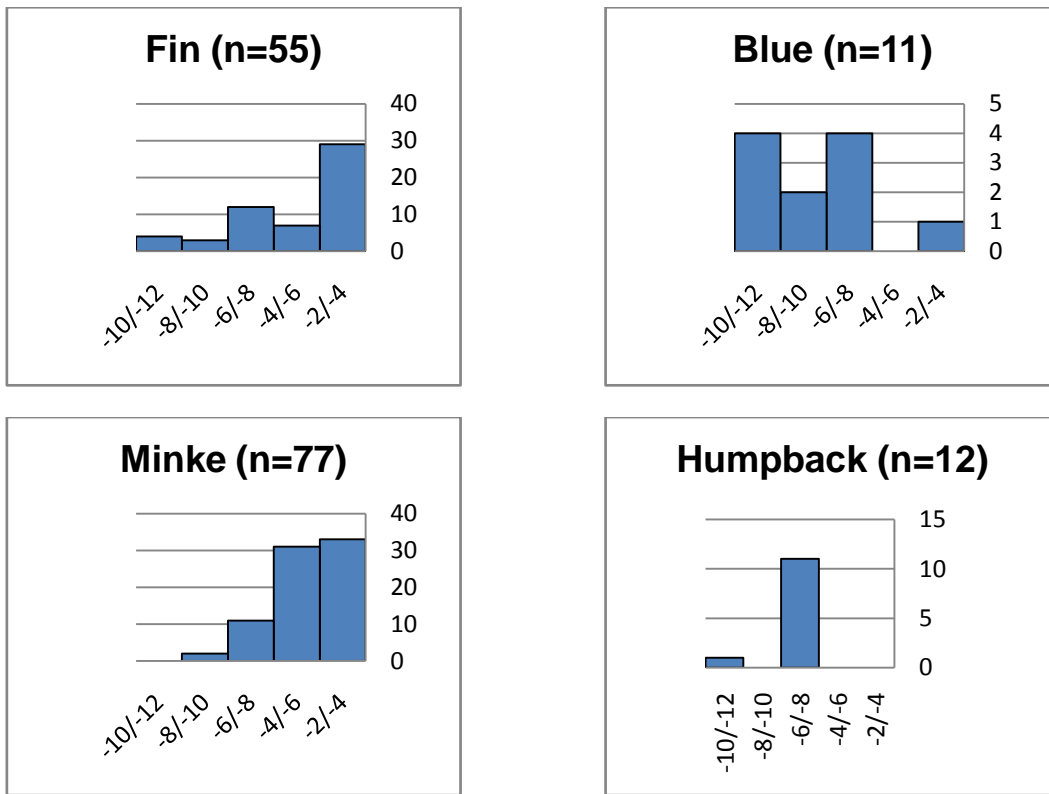


Figure 32: Values of declination using sightings of baleen whales in Macaronesia.

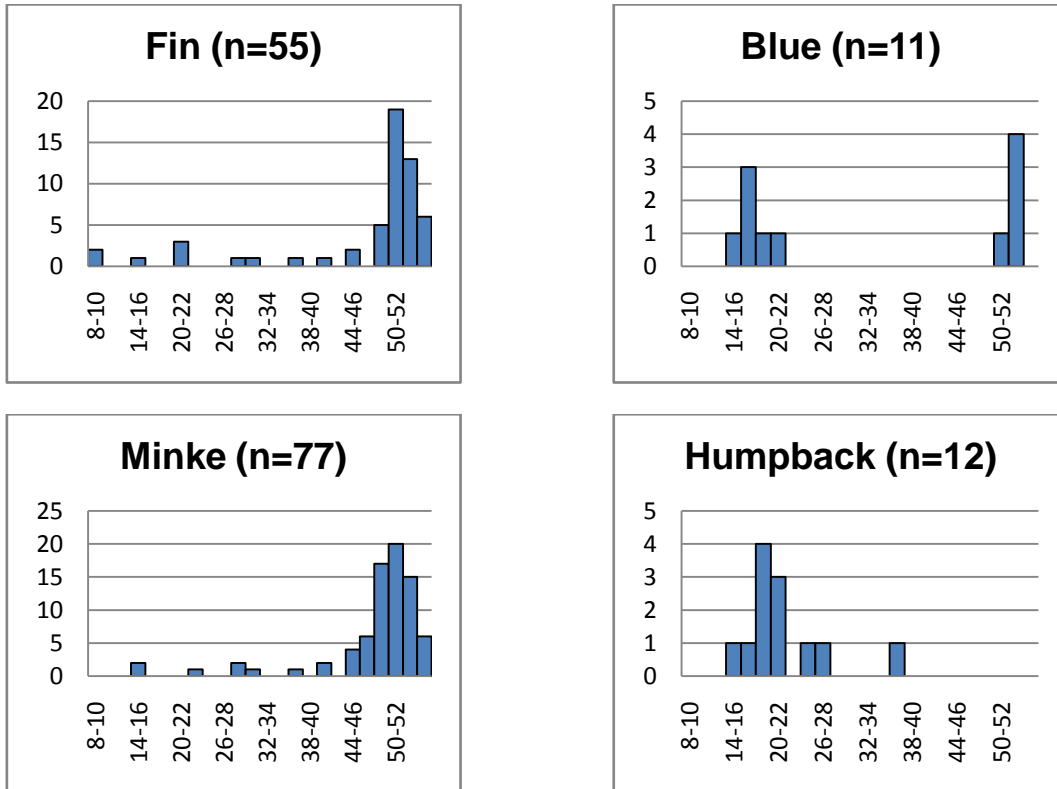


Figure 33: Values of inclination using sightings of baleen whales in Macaronesia

Looking for the migratory whales: Routes of the baleen whales in the Macaronesia

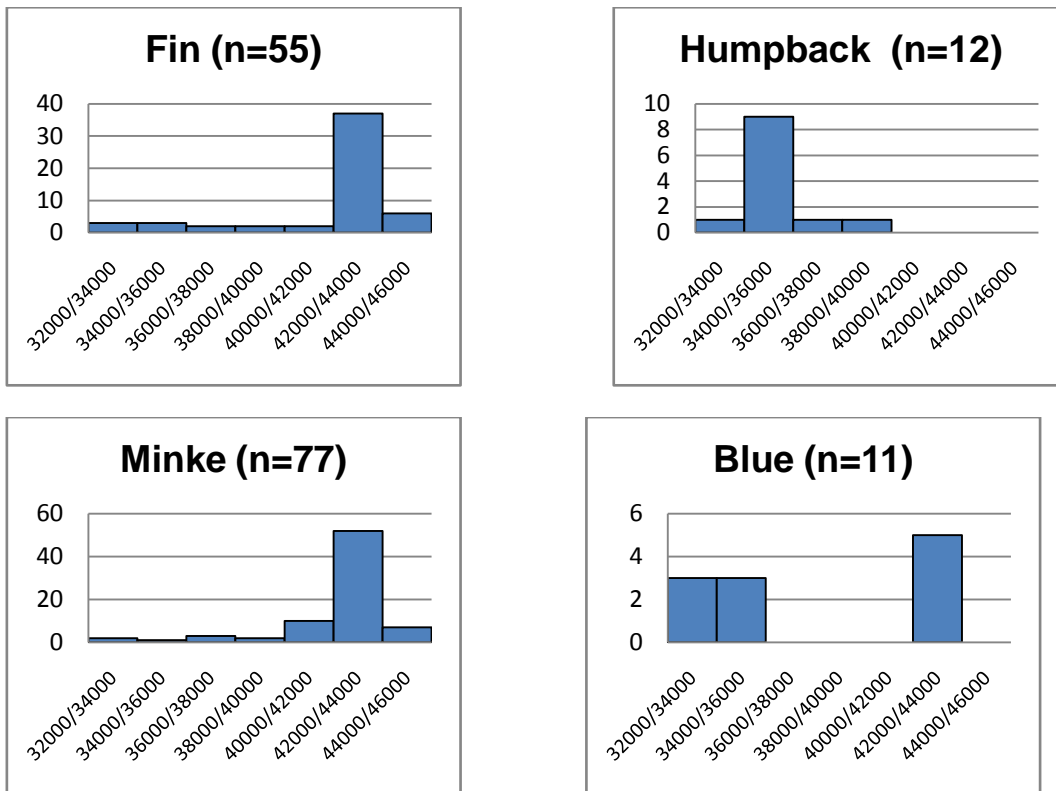


Figure 35: Values of total intensity using sightings of baleen whales in Macaronesia.

Looking for the migratory whales: Routes of the baleen whales in the Macaronesia

**Tables 31-36:** Descriptive statistics for declination, in spring and fall, using sightings of different baleen whale species. Labels: a) Minke whale, b) Fin whale, c) Blue whale.

a) Minke (Spring)	
Mean	-4,6491
Standard-error	1,5050
Median	-3,1792
Standard deviation	2,6068
Sample Variance	6,7952
Kurtosis	-
Skewness	-1,7306
Range	4,5496
Minimum	-7,6589
Maximum	-3,1093
Sum	-13,9473
Count	3

a) Minke (Fall)	
Mean	-3,9984
Standard-error	0,2767
Median	-4,2710
Standard deviation	0,6778
Sample Variance	0,4594
Kurtosis	-1,1679
Skewness	0,8706
Range	1,6660
Minimum	-4,6381
Maximum	-2,9721
Sum	-23,9904
Count	6

b) Fin (Spring)	
Mean	-5,2659
Standard-error	0,5715
Median	-3,7022
Standard deviation	2,8000
Sample Variance	7,8400
Kurtosis	-0,7238
Skewness	-0,9605
Range	7,5191
Minimum	-10,2455
Maximum	-2,7264
Sum	-126,3809
Count	24

b) Fin (Fall)	
Mean	-5,3017
Standard-error	0,7159
Median	-5,4928
Standard deviation	1,8942
Sample Variance	3,5880
Kurtosis	-2,4437
Skewness	0,1250
Range	4,1178
Minimum	-7,2668
Maximum	-3,1490
Sum	-37,1122
Count	7

c) Blue (Spring)	
Mean	-10,3800
Standard-error	0,0293
Median	-10,3778
Standard deviation	0,0585
Sample Variance	0,0034
Kurtosis	-5,4017
Skewness	-0,0612
Range	0,1141
Minimum	-10,4393
Maximum	-10,3252
Sum	-41,5201
Count	4

c) Blue (Fall)	
Mean	-5,8617
Standard-error	0,9315
Median	-6,7006
Standard deviation	1,8630
Sample Variance	3,4709
Kurtosis	3,6631
Skewness	1,9092
Range	3,8672
Minimum	-6,9563
Maximum	-3,0891
Sum	-23,4467
Count	4

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**Table 37-42:** Descriptive statistics for inclination, in spring and fall, using sightings of different baleen whale species. Labels: a) Minke whale, b) Fin whale, c) Blue whale.

a) Minke (Spring)	
Mean	42,0929
Standard-error	9,1824
Median	50,6039
Standard deviation	15,9043
Sample Variance	252,9471
Kurtosis	-
Skewness	-1,7185
Range	28,1865
Minimum	23,7442
Maximum	51,9307
Sum	126,2788
Count	3

a) Minke (Fall)	
Mean	48,1531
Standard-error	1,4299
Median	48,2432
Standard deviation	3,5025
Sample Variance	12,2678
Kurtosis	2,2447
Skewness	-1,1762
Range	10,2265
Minimum	41,8870
Maximum	52,1135
Sum	288,9187
Count	6

b) Fin (Spring)	
Mean	46,4007
Standard-error	2,6038
Median	50,6344
Standard deviation	12,7559
Sample Variance	162,7132
Kurtosis	5,6147
Skewness	-2,5148
Range	47,0753
Minimum	8,4216
Maximum	55,4969
Sum	1113,6170
Count	24

b) Fin (Fall)	
Mean	35,8185
Standard-error	5,5740
Median	36,4673
Standard deviation	14,7473
Sample Variance	217,4828
Kurtosis	-2,5799
Skewness	-0,0302
Range	30,6389
Minimum	20,2811
Maximum	50,9200
Sum	250,7298
Count	7

c) Blue (Spring)	
Mean	53,8848
Standard-error	0,0258
Median	53,8843
Standard deviation	0,0516
Sample Variance	0,0027
Kurtosis	-4,5745
Skewness	0,0241
Range	0,1070
Minimum	53,8318
Maximum	53,9388
Sum	215,5393
Count	4

c) Blue (Fall)	
Mean	25,6628
Standard-error	8,6115
Median	17,8660
Standard deviation	17,2230
Sample Variance	296,6311
Kurtosis	3,8485
Skewness	1,9564
Range	35,8847
Minimum	15,5172
Maximum	51,4019
Sum	102,6512
Count	4

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**Table 43-48:** Descriptive statistics for declination, in spring and fall, using sightings of different baleen whale species.  
Labels: a) Minke whale, b) Fin whale, c) Blue whale.

a) Minke (Spring)	
Mean	40497,5339
Standard-error	2688,6512
Median	42940,5000
Standard deviation	4656,8805
Sample Variance	21686536,2769
Kurtosis	-
Skewness	-1,7110
Range	8297,1016
Minimum	35127,5000
Maximum	43424,6016
Sum	121492,6016
Count	3

a) Minke (Fall)	
Mean	42103,1999
Standard-error	468,6289
Median	42062,3496
Standard deviation	1147,9016
Sample Variance	1317678,1951
Kurtosis	1,4331
Skewness	-0,8745
Range	3320,1016
Minimum	40134,5000
Maximum	43454,6016
Sum	252619,1992
Count	6

b) Fin (Spring)	
Mean	41823,7876
Standard-error	667,4869
Median	42901,0000
Standard deviation	3270,0044
Sample Variance	10692928,8212
Kurtosis	4,3365
Skewness	-2,2595
Range	12112,6992
Minimum	32527,8008
Maximum	44640,5000
Sum	1003770,9023
Count	24

b) Fin (Fall)	
Mean	38742,1283
Standard-error	1532,2527
Median	38429,1992
Standard deviation	4053,9595
Sample Variance	16434587,9814
Kurtosis	-2,5858
Skewness	0,0582
Range	8356,1016
Minimum	34635,5000
Maximum	42991,6016
Sum	271194,8984
Count	7

c) Blue (Spring)	
Mean	43822,7998
Standard-error	10,3433
Median	43822,5996
Standard deviation	20,6866
Sample Variance	427,9338
Kurtosis	-4,5418
Skewness	0,0256
Range	43,0000
Minimum	43801,5000
Maximum	43844,5000
Sum	175291,1992
Count	4

c) Blue (Fall)	
Mean	36439,7500
Standard-error	2275,7134
Median	34302,2500
Standard deviation	4551,4268
Sample Variance	20715485,9861
Kurtosis	3,9495
Skewness	1,9850
Range	9362,1016
Minimum	33896,1992
Maximum	43258,3008
Sum	145759,0000
Count	4