Inês Afonso Teixeira Coelho

HABITAT PREFERENCES OF SPERM WHALES (*PHYSETER MACROCEPHALUS*) OFF SÃO MIGUEL ISLAND, AZORES

UNIVERSIDADE DO ALGARVE

Faculdade de Ciências e Tecnologia

2021

Inês Afonso Teixeira Coelho

HABITAT PREFERENCES OF SPERM WHALES (*PHYSETER MACROCEPHALUS*) OFF SÃO MIGUEL ISLAND, AZORES

Mestrado em Biologia Marinha

Supervisor:

Prof. Dr. David Abecasis

Co-supervisor

PhD Laura González García

UNIVERSIDADE DO ALGARVE

Faculdade de Ciências e Tecnologia

2021

Declaração de autoria de trabalho

HABITAT PREFERENCES OF SPERM WHALES (*PHYSETER MACROCEPHALUS*) OFF SÃO MIGUEL ISLAND, AZORES

Declaro ser a autora deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída,

____

Inês Afonso Teixeira Coelho

Acknowledgements

First of all, I would like to thank my supervisor, Professor David Abecasis, for accepting me as his student, for all the suggestions and advices and for guiding me throughout this thesis process. He always managed to help me, when I needed it, despite the distance.

I cannot begin to express my thanks to Laura González García, for all the infinite patience to my infinite questions, for all the motivational speeches through these two long years, for all her knowledge and expertise and for all her time spent with me because of this thesis. If we hadn't cross paths, I know I would not be here (with my thesis finally done!!!).

Four years ago, I got the opportunity to work for Futurismo Azores Adventures which I am truly grateful for. Here I learned everything I know about cetaceans and the sea, not only with the amazing biologist team but also with the skippers that can read the ocean like nobody. My first professional experience was to go to the sea and watch whales and dolphins in one of the most amazing places in the world, I could not be any more luck.

Two special thanks, from the Futurismo family, go to Cristina Montoya and Víctor Ojeda for being the best companions I could ever ask for during the long hours spent on sea (and also on land!). Thank you for all the good laughs and moments that we've shared.

To André and Carolina thank you for making all this journey unforgettable, much more fun and for all the mutual support through this last three years. To Maria Ernesto and Maria Ferrer Aguilar (that are as much as whale nerds as me!) for the endless conversations and friendship.

Finally, I especially want to thank my family. To my brothers that teach me everyday the meaning of being patient and calm (sometimes is hard) but always supported me in all my decisions. To my parents for all the sacrifices, for all the opportunities that they allowed me to have, for always being there when I needed it the most and for all the love and support. Muito obrigada por tudo!

Resumo

A complexidade batimétrica e as características oceanográficas que rodeiam o arquipélago dos Açores, fazem deste local um *hotspot* para a megafauna marinha. O cachalote (*Physeter machrocephalus*), classificado como "Vulnerável" pela IUCN, é uma espécie residente nos Açores, observados durante todo o ano no arquipélago, maioritariamente em grupos familiares compostos por fêmeas e indivíduos jovens, e ocasionalmente machos adultos, que usam esta área para reprodução. O extremo dimorfismo sexual e a segregação social, entre machos e fêmeas, desta espécie levou a uma diferenciação nas respetivas necessidades ecológicas de ambos os géneros. No século passado esta espécie era amplamente caçada na região fazendo da baleação uma das principais atividades económicas do arquipélago, sendo que em 1986 proclamou-se o fim à baleação comercial em escala mundial. Hoje em dia os cachalotes continuam a ter um grande peso para a região uma vez que a observação de cetáceos é a principal atividade do setor de turismo. Este estudo, tem como objetivo principal dar ênfase às diferenças de preferências de habitats por unidades familiares, machos solitários e o único macho (conhecido até hoje) e avistado regularmente na área de estudo, muito provavelmente residente, Mr. Liable. Os dados de presença de cachalotes foram obtidos através de uma empresa de observação de cetáceos que opera maioritariamente na costa sul de São Miguel, durante todo o ano, no período de 2009 a 2019. Os pontos das pseudo-ausências (necessários devido à natureza binomial dos dados) foram considerados a presença das outras espécies avistadas, assim, os dados das presenças e pseudo-ausências foram recolhidos sobre o mesmo esforço. Modelos generalizados aditivos (GAMs), com distribuição binomial, foram usados para explorar as relações entre as diferentes classes de cachalotes (grupos familiares, machos e Mr. Liable), em comportamentos distintos (*foraging* – à procura de alimento; ou noutro comportamento, sem ter consideração o primeiro, como por exemplo socialização ou a descansar), e as variáveis ambientais, tais como fatores oceanográficos (temperatura superficial da água; profundidade da camada homogénea da água; anomalia do nível da água; desvio padrão da temperatura superficial da água; gradiente da temperatura da superfície da água) e batimétricos (profundidade). Três modelos distintos foram desenvolvidos para cada classe de cachalotes (grupos familiares, machos e Mr. Liable): (i) modelo geral, onde todos os avistamentos da classe são considerados, (ii) modelo em *foraging*, onde apenas avistamentos da classe neste comportamento são considerados, (iii) modelo de outros comportamentos, onde apenas

os avistamentos que não em *foraging* são considerados. Durante os onze anos usados para a análise, a temperatura média mensal da superfície da água (SST) na área de estudo tem vindo a aumentar assim como o valor médio mensal da anomalia do nível da água (SLA), sendo que desde 2013 não se regista valores negativos de SLA. Os grupos familiares correspondem a 79% das nossas observações, os machos a 11% e o Mr. Liable aos restantes 10%. *Foraging* foi o comportamento observado mais frequentemente para as três classes, sendo que os machos foram avistados neste comportamento 55% das vezes, os grupos familiares 66% e o Mr. Liable 94%. Devido ao facto de o Mr. Liable apenas ter sido visto raramente em outros comportamentos (9 avistamentos em 11 anos), apenas se desenvolveu um modelo para Mr. Liable em *foraging*, uma vez que o universo amostral seria muito reduzido. A taxa de observação de grupos familiares seguiu a sazonalidade do esforço (número de saídas) onde o valor mais alto foi observado em julho e o mais baixo em fevereiro. A relação entre o esforço e a taxa de observação de machos e Mr. Liable não mostrou ser tão evidente, com os picos a ocorrer em agosto e em novembro, respetivamente. Todas as classes de cachalotes mostraram ter distintas preferências de habitats entre elas, sendo que as fêmeas também demonstraram ter em consideração diferentes variáveis oceanográficas quando em *foraging* ou noutro comportamento. A profundidade foi a única variável retida por todos os modelos, mostrando uma correlação positiva entre esta variável e presença de cachalotes, sendo que os machos e os grupos familiares mostraram uma maior preferência por águas mais profundas e o Mr. Liable pela zona entre os 500 e os 700 m. Os grupos familiares em *foraging* mostraram uma maior preferência por águas quentes, valores altos da profundidade da camada homogénea da água (MixLayer), valores altos para o desvio padrão de SST e valores negativos de SLA. Quando em outros comportamentos (que não *foraging*) os grupos não consideraram relevante a MixLayer nem a SLA. O Mr. Liable, em *foraging*, mostra maior afinidade por águas mais frias (entre os 20ºC aos 22ºC), valores da MixLayer mais restritos (aproximadamente aos 80 m), valores baixos de gradiente de SST e valores nos dois extremos de SLA (negativos e positivos mostrando pouca afinidade por valores intermédios). Os machos apenas apresentaram preferência pela profundidade, tanto em *foraging* como noutros comportamentos, sendo que as restantes variáveis ambientais não mostraram qualquer tipo de relevância para esta classe. Os valores negativos de SLA estão associados a *eddies* ciclónicos enquanto valores positivos estão associados a *eddies* anticiclónicos, isto representa áreas de *upwelling* e *downwelling* que parece influenciar a presença de diferentes classes de cachalotes. A variável MixLayer está diretamente

relacionada com maior ou menor produção primária. Todas estas diferenças entre Mr. Liable e grupos familiares poderão estar associadas à exploração de diferentes tamanhos de presas, que se traduz por diferentes necessidades ecológicas, o que também é ilustrado pela diferenciação no uso de diferentes profundidades. O facto de o Mr. Liable estar presente durante todo o ano na mesma área do que grupos familiares poderá ter criado uma diferenciação nas preferências de variáveis oceanográficas que resultará numa diminuição de competição entre as duas classes. As diferenças entre machos e Mr. Liable poderá ser devido ao facto de estas duas classes usarem a área de estudo para propósitos diferentes, o primeiro maioritariamente para acasalamento e o segundo também para *foraging* (uma vez que é avistado durante todo o ano na área). Neste estudo mostramos que existem divergências na preferência de habitats de cachalotes não só considerando o género/estrutura social e comportamento, mas também a individualidade. Estes resultados poderão ajudar a delinear planos de conservação, tendo em consideração necessidades de habitats de cachalotes locais, em vez de abordar de uma maneira generalista, e fornecer informação necessária para entender os potenciais efeitos do impacto antropogénico nos oceanos.

Palavras-chave: Preferência de habitats, variáveis ambientais, cachalotes, Açores, GAM

Abstract

Sperm whales (*Physeter machrocephalus*), classified as "Vulnerable" by the IUCN, are sighted year-round in the Azores, often in known family groups composed of females and immatures, and occasionally adult males for mating purposes. This study highlights differences in the habitat preference of family units (79% of our sightings), solitary males (11%) and the only known male sighted regularly and throughout the year in the study area, Mr. Liable (10%). Sperm whale occurrence data was obtained from whale watching platforms operating in the south of São Miguel Island from 2009 to 2019. Generalized Additive Models with binomial distribution were used to assess the relationship between the occurrence of the different behaviours and classes of sperm whales and topographic and oceanographic variables at the surface and in the water column. Depth was the only variable retained by all models, always showing higher suitability in waters deeper than 500 m. Groups preferred negative values of altimetry (SLA) and high standard deviation of the sea surface temperature (SST) while males only retained depth as a relevant variable. However, Mr. Liable presented a higher affinity for more extreme SLA values, lower SST gradients and avoided intermediate values of SLA. This contrast of habitat preference might be related to the exploitation of different prey sizes of males and females and because males and Mr. Liable might use the study area for different purposes. Mixed layer thickness was only significant for foraging behaviour. We highlight divergences on habitat preference of sperm whales, both regarding different behaviours and social structure, but also individual preferences. These results may help to delineate appropriate management plans, by accounting habitat needs of local sperm whales rather than a general approach and providing information to understand potential effects of anthropogenic and natural changes in the ocean.

Key-words: Habitat preference, environmental variables, sperm whales, Azores, GAM

Table of Contents

Indices of Figures

Chapter 1: Introduction

Indices of tables

List of abbreviations and acronyms

SST – Sea Surface Temperature

SD_SST – Standard Deviation of Sea Surface Temperature

Grad_SST – Gradient of the Sea Surface Temperature

SSH – Sea Surface Height

SLA – Sea Level Anomaly

MixLayer – Thickness of the Mixed Layer

ST500 – Sea Temperature at 500 m depth

ST1000 – Sea Temperature at 1000 m depth

STBottom – Sea Temperature at the bottom of the ocean

GAM – Generalized Additive Models

AIC – Akaike Information Criterion

AUC – Area Under the receiving-operator Curve

FB – Foraging Behaviour

OB – Other Behaviours

Chapter 1: Introduction

1.1 Whaling

The history between sperm whales (*Physeter macrocephalus*, Linnaeus 1758) and the Azorean people goes back to the 18th century when the American whalers began to explore the Azorean waters, also known as the "western islands", and recruiting the islanders for their crews (Clarke, 1954; Reeves & Smith, 2003). During the Yankee whaling era (between 17th century to 1924; Reeves & Smith, 2003) sperm whales were the most important target around Azores and shortly after the first exploration in 1765, it was already seen as a profitable area (Clarke, 1954).

In the 19th century, land-based whaling started to develop in the archipelago, emerging from the experience of the Azorean people that had been on board the American ships (Clarke, 1954; Vieira, 1996). This activity became present in all the islands of the archipelago, apart from Corvo (Clarke, 1956). Traditional methods were always used by the local population (Figure 1.1): a 12-meter open boat, occupied by seven men, would chase the sperm whale (sometimes bigger than the boat itself) using only hand-held harpoons and lances (Clarke, 1954). After the hunt, the whale was towed to shore where almost all the whale carcase was used and transformed into the most diverse products: the bones and meat were transformed into flours; the occasional ambergris, found in the intestine of sperm whales, could be used in the cosmetic industry; the teeth were used for decorative objects ("scrimshaw"); the skin was transformed into leather; the tendons and connective tissue fibers were used as cables (Clarke, 1954); the blubber oil was transformed into lamp fuel (Rice, 2009). But the whales were hunted for one product in particularly, the spermaceti oil that was used for machinery lubricant, essential for the industrial revolution, and First and Second World Wars (Neves-Graça, 2004; Vieira, 2009). Whaling become the core economic activity for some islands (Clarke, 1954; Neves-Graça, 2004; Vieira, 2009) and peaked in the 1950's regarding the number of catches (Brito, 2008) and biomass removal (Prieto et al., 2013). In the middle of the 20th century, around 200 boats were hunting sperm whales in the archipelago, all of this promoted the transformation of the small land-based whaling activity into commercial whaling (Santos et al., 1995).

Figure 1.1. Azorean whaler getting ready to harpoon the sperm whale. Retrieved from: https://bit.ly/39NNmOq

The fame and success of the activity started to fade away during the 1960's (Martin & Melo, 1983) due to the decrease of whale stocks, the increase of economic costs and the discovery/development of the abundant petroleum oil that eventually led to the inevitable extinction of the whaling industry (Coleman, 1995). The whalers laid down their harpoons permanently with the proclamation of the global "moratorium" on all commercial whaling in 1986 by the IWC (International Whaling Commission), and with the implementation of the national Decreto-Lei 316/89, 22 of September. In the Azores, whaling decreased the amount of sperm whales in the region (Vieira & Brito, 2009) and between the year of 1991-1994 (nine years after the global moratorium) around 1600-2200 individuals were estimated for the regional population (Matthews et al., 2001). However, the high genetic diversity and absence of inbreeding observed in recent years using microsatellite markers, suggests that the population is recovering (Pinela et al., 2009).

1.2 Whale watching

The shift of cultural perception regarding cetaceans (Lawrence & Phillips, 2004), from "edible commodities" to "symbols of nature" (van Ginkel, 2007) catapulted the whale watching industry as one of the fastest growing (from 9 million USD in 1998 to 2.1 billion USD in 2008) touristic activities worldwide (Hoyt, 2001; O'Connor et al., 2009). In the 1980's (the same decade of the global moratorium) whale watching industry is viewed as the new sustainable "use" for whales by the IWC and, if managed properly, it is capable to generate educational, scientific, ecological, and socio-economic benefits regionally

(Hoyt, 2001; Cisneros-Montemayor et al., 2010). The transition period between whaling to whale watching in the Azores embraced both the whaling heritage and the scientific perspective by combining practical knowledge of the whalers and the ecological perspectives of scientists (Neves-Graça, 2006). Former employers of the whaling industry adapted to the new reality by becoming “vigias”, land-based lookouts that scanned the ocean with binoculars searching for cetaceans, for the new whale watching companies (Neves-Graça, 2006, Sequeira et al., 2009).

Since 2015 that tourism has been growing sharply in the Archipelago of the Azores transforming it into a promising sector for the region (Vieira et al., 2019). Wildlife and natural beauty are tourists’ main reasons when choosing the Azores, with whale watching being the most relevant activity (Queiroz et al., 2014). Around 27 species of cetaceans have been recorded in Azorean waters (Borges et al., 2016) with sperm whale being one of the most sighted species all year round (Silva et al., 2013; González García, 2018). This hotspot of megafauna transformed the Azores into a famous destiny for whale watchers worldwide, especially for those following the big whales (O’Connor et al., 2009). A very low percentage (from 1% to 5%) of whale watching trips with zero sightings of cetaceans is the result of the high biodiversity combined with the use of the lookout technique (Sequeira et al., 2009).

Within the objective of maintaining a sustainable growth the Autonomous Region of the Azores established a strict regulation of conduct for whale and dolphin watching (DLR 10/2003/A) and a restrict number of licensed vessels (Portaria Nº 5/2004 of 29 of January). The development of the whale watching industry allowed sperm whales to continue to be an iconic symbol for the region.

1.3 Sperm whale biology and ecology

1.3.1 Sperm whale taxonomy and anatomy

It is believed that sperm whales, phylogenetically, are close to the root odontocetes (suborder Odontoceti) retaining some primitive characteristics (Mchedlidze, 2009). The Physeteridae family presents a very diverse fossil record that goes back at least to the Miocene (~21 Ma) but nowadays, *Physeter macrocephalus* is the only surviving species

(Berta et al., 2015). This species, together with the two closest related species, pygmy sperm whale (*Kogia breviceps*, Blainville, 1838) and dwarf sperm whale (*Kogia simus*, Owen, 1866), both belonging to Kogiidae, comprise de extant members of the superfamily Physeteroidea (Fordyce & Muizon, 2001).

This species is considered the largest of the toothed whales (Gosho et al., 1984) and the cetacean with the highest level of sexual dimorphism regarding length and weight (Best, 1979; Whitehead, 2018). Mature males can reach up to, approximately, 18 m while females up to 12 m, weighing 57 t and 24 t, respectively (Elwen et al., 2016).

A very evident trait of sperm whales is the huge square nasal complex (Figure 1.2) that can exceed one third and one quarter of the total weight and length, respectively (Clarke, 1978a; Gosho et al., 1984). Most of the nasal complex is occupied by two structures (i) the spermaceti organ, enclosed in a muscular case (Clarke, 1978a), consists in a spongy tissue impregnated with spermaceti oil, a waxy composition oil (Wellendorf, 1963; Morris, 1973; Clarke, 1978a; Rice, 2009), that is limited by air sacs in both edges (Whitehead, 2018); (ii) the "junk", which is homologous to the melon of other odontocetes (Heyning & Mead, 1990), placed right below the first one and above the rostrum of the skull, is divided in segments of fibrous connective tissues ("lenses"-like) and this structure is also saturated with spermaceti oil (Clarke, 1978a). Surrounding the spermaceti organ there is an asymmetric arrangement or air passages which is externally detected by the position of the blowhole, in the left end of the sperm whale head (Figure 1.2; Raven & Gregory, 1933).

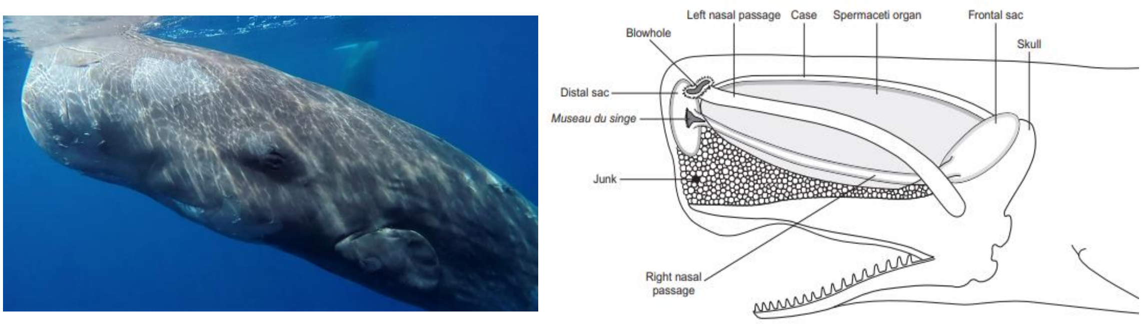


Figure 1.2: Sperm whale breathing at the surface. Photo by: Inês Coelho (Left). Anatomy of sperm whale head. Retrieved from: Whitehead, 2018 (Right).

The hypertrophy of the nasal complex suggests a vital function and for many years its purpose was debated. It is now widely accepted that this structure is responsible for the production of clicks with the purpose of communication and echolocation (Norris &

Harvey 1972; Cranford et al., 1996; Møhl, 2001; Madsen et. al., 2002). These clicks can reach the intensity of 235 dB, the loudest sound ever recorded in the animal kingdom (Møhl et al., 2003). Other hypothesis suggests buoyancy control (Clark, 1970), a specialization for male-male aggression interaction (Carrier et al., 2002; Panagiotopoulou et al., 2016), a response to sexual selection (Cranford, 1999) and prey debilitation using powerful sounds (Norris & Møhl, 1983). Sperm whales are unique and peculiar looking cetaceans but these odd characteristics are the perfect tools to thrive in their surroundings, the deep ocean (Cantor et al., 2019).

1.3.2 Social structure and behaviour

Sperm whales are K-selected species meaning that the efficient exploitation of resources and mortality avoidance becomes fundamental, therefore, social relationships might be the answer for cooperative foraging, vigilance, and defence against predators, especially for calves (Whitehead, 2003). Female sperm whales are extremely social animals that spend all their lives in the company of their social "units", the basic element of sperm whale society, that consists in mature females, immature offspring, and calves (Best, 1979; Whitehead et al., 1991; Whitehead, 2003; Gero et al., 2014). This units can come together to form "groups" during variable periods of time (Best, 1979; Whitehead et al., 1991). At a certain point, immature males abandon their original units to start their solitary lives (Best, 1979) although, on some occasions, males can form aggregations called bachelor groups (Best, 1979; Lettevall et al., 2002). In the Azores, the social units are comprised by up to 12 sperm whales (Antunes, 2009; van der Linde & Eriksson, 2020), mainly composed by individuals of the same family, and the dispersal age of males is around 16.6 years (Pinela et al., 2009). The social system of sperm whales differs from any other odontocete and due to a "colossal convergence" it is only comparable to the largest terrestrial animal, the elephant (Weilgart et al., 1996).

The behaviour of sperm whales can be divided into two categories: foraging (1.3.3) and socializing/resting (Whitehead & Weilgart, 1991). Due to the importance of the social society for females and immatures, 25% of the day is spent on socializing while the rest of the time is dedicated to forage (Whitehead & Weilgart, 1991). During this active time on the surface many behaviours can be observed (Figure 1.3) like lobtailing, breaching, spy-hopping, side-fluke, rolling and touching each other (Whitehead, 2018; Whitehead &

Weilgart, 1991). In addition to visual behaviour, vocal exchange between individuals can also be heard during the socialization periods at or near the surface (Watkins & Schvill, 1977; Whitehead & Weilgart, 1991). This "sequences of clicks which are repeated several times", are called codas (Watkins & Schvill, 1977) and many different types of codas have been registered worldwide (e.g, Pavan et al., 2000; Rendell & Whitehead, 2003; Antunes, 2009). The use of the different types of codas by different units vary regionally (Weilgart & Whitehead, 1997) and the set of units with similar coda repertories (dialects) can be organized into acoustic "clans" (Rendell & Whitehead, 2003).

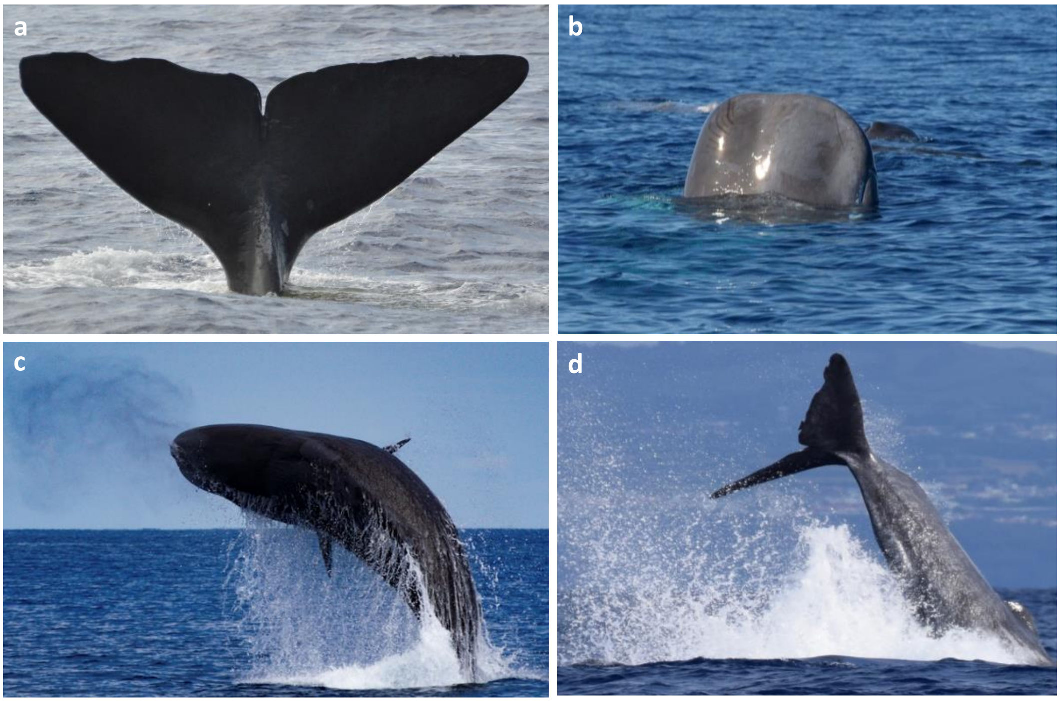


Figure 1.3: Sperm whale behaviour at the surface of the water. Fluke (a), beginning of spy-hopping (b), Breaching (c), lobtailing (d). Photos: by Rafael Martins.

Although little is known about the resting behaviour of cetaceans in the wild Miller et al. (2008) observed that sperm whales worldwide rest in a vertical posture just below the surface while drifting.

1.3.3 Foraging

Sperm whales play an important role as the largest and one of the most significant predators in the global mesopelagic ecosystems (Smith & Whitehead, 2000; Whitehead et al., 2003). Several thousand stomachs contents of sperm whales have been analysed around the world, mostly during the whaling era, and it was clear that cephalopods, particularly squids, were the principal item (Kawakami, 1980). Nevertheless, in some regions, fishes (teleosts and elasmobranchii) also play an important role in sperm whales' diet (Kawakami, 1980) and in Iceland are the principal prey (Martin & Clark, 1986). Clarke et al. (1993) analysed the stomach content of 17 sperm whales in the Azores and the cephalopod families Octopoteuthidae, Histioteuthidae and Architeuthidae (the giant squid) seemed to be sperm whales' main food resource (regarding mass), with different sized whales choosing different size preys. They also found out that 77% of sperm whale food (mass) was derived from species possessing bioluminescent features and neutral buoyance. However, there might be an over or under representation of some taxa due to associated bias to this sampling method (Whitehead, 2003).

Even though sperm whales are the biggest predators in the world there is no visual record of a sperm whale hunting, making the question of how sperm whales locate and capture their prey a very debatable topic along the years. There is a general consensus that echolocation plays a vital role to forage in the deep ocean (e.g., Norris & Harvey 1972; Madsen et al., 2002; Miller et al., 2004; Drouot et al., 2004). The foraging dive starts with a fluke-up, when the whale raises the tail above the surface of the water and begins the descent almost vertical (Whitehead & Weilgart, 1991; Drouot et al., 2004). The descendent phase of the sperm whale dive is dedicated to search for prey, by producing regular clicks that work as a long-range biosonar (Watwood et al., 2006). The foraging phase is defined by the starting of buzzes, high frequency clicks, that mark the encounter and active hunt of the prey and will update the position of the prey in the last seconds before capture. This is the longest phase, and the feeding occurs throughout this time (Madsen et al., 2002; Drouot et al., 2004; Miller et al., 2004; Watwood et al., 2006; Fais et al., 2016). Finally, the whale starts the ascend back to the surface where will stay for some minutes for an aerobic recovery (Watwood et al., 2006). Normally the whole dive cycle lasts 45 min (Drouot et al., 2004; Watwood et al., 2006; Teloni et al., 2008) and can go up to 1860 m of depth (Teloni et al., 2008). Groups of females when foraging can be spread out over 1 km while males, generally, forage independently (Whitehead, 2018).

Clarke (1977) estimated that sperm whales alone consume more than 110 million tonnes of oceanic squid annually which exceeds the total capture fisheries of 90 million tonnes worldwide (FAO, 2018). The foraging efficiency of the sperm whale is higher than any other air-breather mesopelagic predator, this is due to a combination of long-range echolocation of prey patches, efficient locomotion, and a large aerobic capacity (Watwood et al., 2006).

1.3.4 Distribution and habitat preferences

Sperm whales are one of the most globally distributed species on Earth, it can be found in both hemispheres from the edge of the ice packs to the warm tropical waters (Whitehead, 2003; Whitehead, 2018). Due to different ecological requirements of both sexes (Pace et al., 2018), there is a sex related segregation in terms of social organization (1.3.2) and geographical distribution (Jaquet et al., 2000). While the social units of females and immature individuals are found in latitudes lower than 40º, the solitary males can be found up to the edge of polar ice packs in both hemispheres (Figure 1.4; Gosho et al., 1984; Rice, 1989). The overlap of both sexes happens when males migrate from the polar waters to the lower latitudes breeding areas (Gosho et al., 1984), like at the Azores (Clarke, 1956; Silva et al., 2014), but little is known about these migrations. During the commercial whaling era, traditional harpoons were recovered which led to the association of sperm whale's movements between Azores, Iceland and Spain (Martin, 1982; Aguilar, 1985). In more recent years, using photo identification methods, three adult males were matched between the Azores (Pico Island) and Norway (Tromsø; Steiner et al., 2012), different sperm whale groups between the different group islands of the Azores within and between years (Magalhães et al., 2005) and between the Azores and the Gulf of Mexico (Mullin et al., in press).

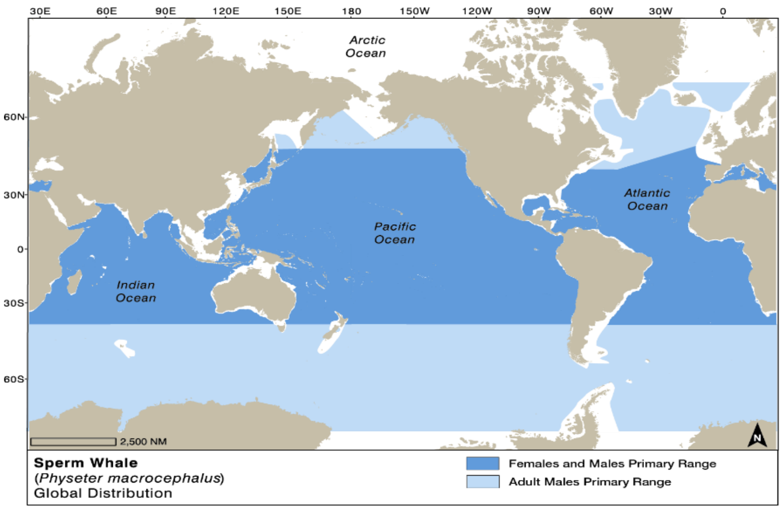


Figure 1.4: Sperm whale global distribution. Retrieved from Whitehead 2018.

Understanding the movements and habitat preferences of a species is essential to understand more about their ecology, to identify critical areas (e.g., breeding areas), to know the degree of overlap with human activities and finally to implement possible conservation measures (Redfern et al. 2006; Cañadas et al., 2005). The habitat preferences of various species of cetaceans have already been studied worldwide and they are often related with topographic factors like depth and slope (Cañadas et al., 2002; Cañadas et al., 2005; Azzellino et al., 2008), but also with group size, behaviour, seasonality (Azzellino et al., 2008), presence or absence of calves (Ersts & Rosenbaum, 2003) and chlorophyll concentration (Correia et al., 2015, González García, 2018). For sperm whales some of these factors can also be applied. Topographic characteristics, as depth, slope and direction of slope, often seem to be an important factor for sperm whales (e.g., Seabra et al., 2005; Priotta et al., 2011; Tepsich et al., 2014; Skov et al., 2008). Specific types of habitats like submarine canyons (Moors-Murphy, 2014; Johnson et al., 2016; Guerra et al., 2017), seamounts (Wong et al., 2014) and ridges (Skov et al., 2008) appear to be crucial for sperm whales. In an oceanographic perspective, the presence of SST-fronts (Gannier & Praca, 2007) and high eddy kinetic energy (Wong et al., 2014) appear to favour the sperm whale presence in some cases. All these features combined might be related with upwellings and higher productivity, ultimately creating more feeding opportunities for sperm whales (Moors-Murphy, 2014). Although Azores is considered an important area for sperm whales, very few habitat preference/selection studies are focused on this archipelago. It is known that the offshore and deeper waters (1000 – 1500 m; Silva et al., 2003) are usually preferred by this species and that there is a positive relationship with sea surface temperature and sperm whales' sightings (Seabra et al., 2005). Tobeña et al. (2016) presents the most extensive study regarding this subject in the Azores. The authors shows that the most relevant variable is the time-lagged (two months) variance of the chlorophyll-a concentration, that is related with high primary production areas and that there seems to be a preference for areas with high density of seamounts, that can be related with prey aggregation.

When studying the habitat preference of sperm whales, it is important to take into consideration their social aggregation since the different ecological requirements of groups and solitary animals are related with different behaviours such as foraging or socializing (Pace et al., 2018). Whitehead & Rendell (2004) observed that different vocal clans, in the South Pacific, had different preferences for depth and movements which resulted into different feeding successes. In the Balearic Islands, Pirotta et al. (2011) demonstrated that the probability to encounter solitary individuals in warm waters would be higher when compared to social groups.

1.4 Azores

Rising from the ocean base of the North Atlantic of 4000 m (Sala et al., 2016), the archipelago of the Azores, composed by nine volcanic islands, are distributed along 600 km (Pacheco et al., 2013) within 36°55’-39°43’ N and 24°46’-31°16’ W. The Azores is the most remote archipelago of the North Atlantic, distancing approximately 1400 km from Lisbon and 4000 km from the east coast of North America. Although the small land cover, Azores represents a big portion of the Portugal’s Exclusive Economic Zone (EEZ) with around 1 million km^2, one of the biggest in the European Union. The islands are divided into three groups: (i) western group composed by Flores and Corvo islands; (ii) central group composed by Faial, Pico, São Jorge, Graciosa and Terceira islands; (iii) eastern group composed by São Miguel and Santa Maria islands (Figure 1.5). From a tectonic point of view, Azores is situated in the triple junction of the North American, Eurasian and African plate, with the Mid Atlantic Ridge dividing the first two (Pacheco et al., 2013). In an oceanographic perspective the Azores are within the northern boundaries of the North Atlantic Subtropical Gyre. It is influenced by the Gulf Stream, which crosses from the northwest of the archipelago, and it is divided into two branches: the North Atlantic Current in the north of the archipelago that continues to continental Europe; and the Azores Current that crosses the southeast of the islands (Käse & Siedler, 1982). While the western and central groups of islands are mostly influenced by the North Atlantic Current and associated eddies, the eastern group of islands are more influenced by the Azores Current and associated eddies (Caldeira & Reis, 2017). The Azores current is characterized by a high Eddy Kinetic Energy that is related with the complexity of the mesoscale eddy system, generated eastward of the archipelago and with a western propagation (Caldeira & Reis, 2017). The archipelago is, therefore, considered a confluence zone of eddies, meanders and filaments originating mostly from the Gulf Stream and the Azores Current. These confluence zones are often presented as major carbon sinks (Caldeira & Reis, 2017). The Azores is also influenced by warm sub-tropical waters (22ºC – 24ºC) during the summer/autumn and colder temperate waters (15ºC – 18ºC) during winter/spring (Caldeira & Reis, 2017). The colder periods coincide with the peaks of the chlorophyll concentration due to the fact that the nutrient rich waters are associated with lower temperatures. This seasonality is directly linked with the phytoplankton spring bloom of the North Atlantic (Caldeira & Reis, 2017).

The oceanographic dynamic complexity of the region combined with the numerous seamounts in the area (37% of the Azorean EEZ is covered by seamounts; Morato et al., 2008), and high particle retaining/capturing capacity of the island, (Sala et al., 2016), creates a variety of essential megafauna habitats making the Azores one of the places in the world with the highest cetacean biodiversity (Afonso et al., 2020).

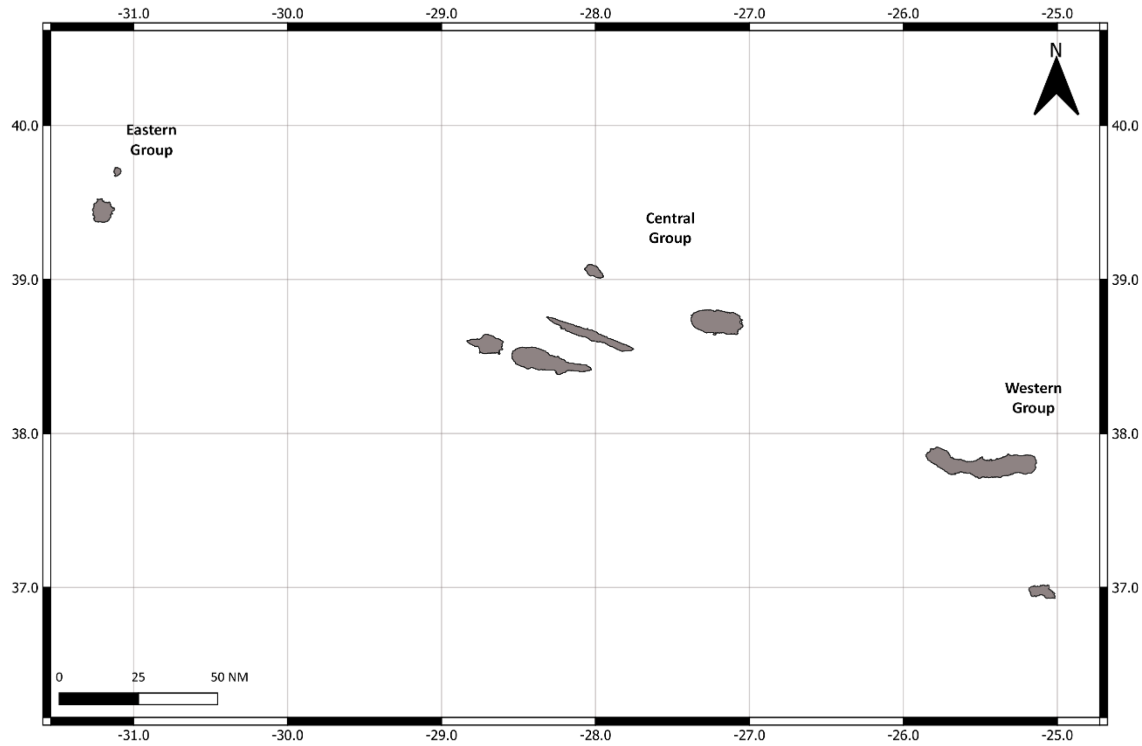


Figure 1.5: Nine islands of the archipelago of the Azores and respective groups.

In fact, 28 species of cetaceans have been recorded in Azorean waters (Silva et al., 2014) corresponding around to 1/3 of all cetacean species in the world. Sperm whales, common dolphis (*Delphinus delphis*), bottlenose dolphins (*Tursiops truncatus*), Risso's dolphins (*Grampus griseus*) and Atlantic spotted dolphins (*Stenella frontalis*) are the most sighted species year-round in the whole archipelago (Silva et al., 2003; Silva et al., 2014; Tobeña et al., 2016, González García, 2019). For some baleen whales, like the blue whales (*Balaenoptera musculus*), fin whales (*Balaenoptera physalus*) and sei whale (*Balaenoptera borealais*) this region serves as a seasonal foraging and/or passing area during their migrations (Silva et al., 2013; Prieto et al., 2013; González Garcia et al., 2018). Even the enigmatic beaked whales (Ziphiidae), one of the least known group of mammals in the world, are often sighted in the archipelago (Silva et al., 2014; Tobeña et al., 2016, González García et al., 2018) providing an opportunity to know more about this family (e.g., Pereira et al., 2011; Visser, 2012).

The Regional Government is responsible for the classification, management and administration of the protected areas of the Autonomous Region of Azores (Decreto Legislativo Regional nº 15/2007/A, 25 of June). With this, the Regional Network of Protected Areas of the Autonomous Region of the Azores was created, and it is divided into two different types: Island Natural Park (PNI), responsible for the MPA's of each island (9 PNI's) and the Azores Marine Park (PMA) responsible for MPA's outside the EEZ and beyond national jurisdiction.

1.5 Objectives

The goal of this study is to assess the environmental preferences of sperm whales recorded off São Miguel Island, taking into consideration different group and behaviour conditions of these animals, using Generalized Additive Models (GAMs).

(i) Environmental variables – depth; slope; monthly sea surface temperature; sea temperature at different depths (500 m, 1000 m, at the sea bottom); standard deviation of the sea surface temperature (as a measure of ocean variability); gradient of the sea surface temperature (as a proxy for oceanographic fronts); thickness of the mixed layer; sea surface height; sea level anomaly.

(ii) Different group conditions – Behaviour (foraging vs. other behaviours); group composition (solitary males vs. family groups).

1.5 Bibliography

Afonso, P., Fontes, J., Giacomello, E., Magalhães, M. C., Martins, H. R., Morato, T., ... & Vandeperre, F. (2020). The Azores: a mid-Atlantic hotspot for marine megafauna research and conservation. Frontiers in Marine Science, 6, 826.

Aguilar A. (1985) Further information on the movements of the sperm whale (*Physeter macrocephalus*) in the North Atlantic. Mammalia, 49, 421–424.

Antunes, R. N. C. (2009). Variation in sperm whale (*Physeter macrocephalus*) coda vocalizations and social structure in the North Atlantic Ocean (Doctoral Dissertation). Retrieved from: http://hdl.handle.net/10023/827.

Azzellino, A., Gaspari, S., Airoldi, S., & Nani, B. (2008). Habitat use and preferences of cetaceans along the continental slope and the adjacent pelagic waters in the western Ligurian Sea. Deep Sea Research Part I: Oceanographic Research Papers, 55(3), 296–323.

Berta, A., Sumich, J. L., & Kovacs, K., M. (2015). Cetacean evolution and systematics. *Marine Mammals: Evolutionary Biology* (pp. 63-98). Elsevier.

Best, P. B. (1979). Social Organization in Sperm Whales, Physeter macrocephalus. Behavior of Marine Animals, 227–289.

Best, B. D., Halpin, P. N., Read, A. J., Fujioka, E., Good, C. P., LaBrecque, E. A., Schick R. S., Roberts, J. J., Hazen, L. J., Qian, S. S., Palka D. L., Garrison, L. P., & McLellan W. A. (2012). Online cetacean habitat modeling system for the US east coast and Gulf of Mexico. Endangered Species Research, 18, 1-15.

Borges, P.A.V., Costa, A., Cunha, R., Gabriel, R., Gonçalves, V., Martins, A.F., Melo, I., Parente, M., Raposeiro, P., Rodrigues, P., Santos, R.S., Silva, L., Vieira, P. & Vieira, V. (Eds.) (2016): A list of the terrestrial and marine biota from the Azores. v1.1. Universidade dos Açores. Dataset/Checklist.

Brito, C. (2008). Assessment of catch statistics during the land-based whaling in Portugal. Marine Biodiversity Records, 1.

Cañadas, A., Sagarminaga, R., & García-Tiscar, S. (2002). Cetacean distribution related with depth and slope in the Mediterranean waters off southern Spain. Deep Sea Research Part I: Oceanographic Research Papers, 49(11), 2053–2073.

Cañadas, A., Sagarminaga, R., De Stephanis, R., Urquiola, E., & Hammond, P. S. (2005). Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. Aquatic Conserv: Mar. Freshw. Ecosyst, 15(5), 495–521.

Cantor, M., Gero, S., Whitehead, H., & Rendell, L. (2019). Sperm Whale: The Largest Toothed Creature on Earth. Ethology and Behavioral Ecology of Marine Mammals, 261–280.

Carrier, D. R., Deban, S. M., & Otterstrom, J. (2002). The face that sank the Essex: potential function of the spermaceti organ in aggression. The Journal of Experimental Biology, 205, 1755–1763.

Cisneros-Montemayor AM, et al. The global potential for whale watching. Marine Policy (2010), doi:10.1016/ j.marpol.2010.05.005

Clarke, M. R. (1954). Open boat whaling in the Azores: the history and present methods of a relic industry. Discovery Reports, 26, 281–354.

Clarke, M. R. (1956). Sperm whales of the Azores. Discovery Reports 28, 237-98.

Clarke, M. R. (1970). Function of the Spermaceti Organ of the Sperm Whale. Nature, 228 (5274), 873–874.

Clarke, M. R. (1977). Beaks, nets and numbers. Symposium of the Zoological Society of London, 38, 89-126.

Clarke, M. R. (1978a). Structure and proportions of the spermaceti organ in the sperm whales. Journal of Marine Biology Association, 58, 1-17.

Clarke, M. R., Martins, H. R., & Pascoe, P. (1993). The Diet of Sperm Whales (Physeter macrocephalus Linnaeus 1758) off the Azores. Philosophical Transactions: Biological Sciences, 339(1287), 67-82.

Coleman, J. L. (1995). The American whale oil industry: A look back to the future of the American petroleum industry? Nonrenewable resources 4(3), 273–288.

Correia, A. M., Tepsich, P., Rosso, M., Caldeira, R., & Sousa-Pinto, I. (2015). Cetacean occurence and spatial distribution: Habitat modelling for offshore waters in the Portuguese EEZ (NE Atlantic). Journal of Marine Systems, 143, 73-85.

Cranford, T. W., Amundin, M., & Norris, K. S. (1996). Functional morphology and homology in the odontocete nasal complex: Implications for sound generation. Journal of Morphology, 228(3), 223–285.

Cranford, T. W. (1999). The sperm whale’s nose: sexual selection on a grand scale?. Marine Mammal Science, 15(4), 1133–1157.

Cunningham, P. A., Huijbens, E. H., & Wearing, S. L. (2011). From whaling to whale watching: examining sustainability and cultural rhetoric, Journal of Sustainable Tourism, 1-19.

Drouot,V., Gannier, A., & Goold, J. C. (2004). Diving and Feeding Behaviour of Sperm Whales (Physeter macrocephalus) in the Northwestern Mediterranean Sea. Aquatic Mammals, 30(3), 419-426.

Elwen S., Findlay K., Meÿer M., Oosthuizen H., & Plön S. (2016). A conservation assessment of Physeter macrocephalus. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Ersts, P. J., & Rosenbaum, H. C. (2003). Habitat preference reflects social organization of humpback whales (Megaptera novaeangliae) on a wintering ground. Journal of Zoology, 260(4), 337–345.

Fais, A., Johnson, M., Wilson, M., Aguilar Soto, N., & Madsen, P. T. (2016). Sperm whale predator-prey interactions involve chasing and buzzing, but no acoustic stunning. Scientific Reports, 6, 28562.

Fordyce, R. E., & Muizon, C. (2001). Evolutionary history of cetaceans: a review. In: Mazin J-M de Buffrénil V, eds. *Secondary adaptation of tetrapods to life in water*. München: Verlag Dr. Friedrich Pfeil. (169–233).

Forney, K. A. (2000). Environmental Models of Cetacean Abundance: Reducing Uncertainty in Population Trends. Conservation Biology, 14(5), 1271–1286.

Gannier, A., & Praca, E. (2007). SST fronts and the summer sperm whale distribution in the north-west Mediterranean Sea. Journal of the Marine Biological Association of the United Kingdom, 87, 187–193.

Gero, S., Gordon, J., & Whitehead, H. (2015). Individualized social preferences and long-term social fidelity between social units of sperm whales. Animal Behaviour, 102(2015), 15–23.

González García, L. (2018). Cetacean distribution in São Miguel (Azores): influence of environmental variables at different spatial and temporal scales (Doctoral Dissertation).

González García, L., Pierce, G. J., Autret, E., & Torres-Palenzuela, J. M. (2018). Multi-scale habitat preference analyses for Azorean blue whales. Plos one, 13(9).

Gosho, M. E., Rice D. W., & Breiwick J. M. (1984). The Sperm Whale Physeter macrocephalus. Mar Fish Rev, 46(4), 54–64.

Guerra, M., Hickmott, L., van der Hoop, J., Rayment, W., Leunissen, E., Slooten, E., & Moore, M. (2017). Diverse foraging strategies by a marine top predator: Sperm whales exploit pelagic and demersal habitats in the Kaikōura submarine canyon. Deep Sea Research Part I: Oceanographic Research Papers, 128, 98–108.

Hastie, T., & Tibshirani, R. (1986). Generalized Additive Models. Statistical Science, 1(3), 297-318.

Heyning, J. E., & Mead, J. G. (1990). Evolution of the Nasal Anatomy of Cetaceans. Sensory Abilities of Cetaceans, 67–79.

Hoyt, E. (2001). Whale watching 2001: Worldwide Tourism Numbers, Expenditures, and Expanding Socioeconomic Benefits. International Fund for Animal Welfare, Yarmouth Port, MA, USA, 1-158.

Johnson, C. M., Beckley, L. E., Kobryn, H., Johnson, G. E., Kerr, I., & Payne, R. (2016). Crowdsourcing Modern and Historical Data Identifies Sperm Whale (Physeter macrocephalus) Habitat Offshore of South-Western Australia. Frontiers in Marine Science, 3.

Kawakami, T. (1980) A review of sperm whale food. Sci Rep Whales Res Inst, 32,199–218.

Keller, C. A., Garrison, L., Baumstark, R., Ward-Geiger, L. I., & Hines, E. (2012). Application of a habitat model to define calving habitat of the North Atlantic right whale in the southeastern United States. Endagered Species Research, 18, 73-87.

Lambert, C., S. Laran, L. David, G. Dorémus, E. Pettex, O. Van Canneyt and V. Ridoux (2016). How does ocean seasonality drive habitat preferences of highly mobile top predators? Part II: The eastern North-Atlantic. Deep-Sea Research Part II: Topical Studies in Oceanography, 141, 115–132.

Lawrence, T., & Phillips, N. (2004). From Moby Dick to Free Willy: macrocultural discourse and institutional entrepreneurship in emerging institutional fields. Organization, 11 (5), 689-711.

Lettevall, E., Richter, C., Jaquet, N., Slooten, E., Dawson, S., Whitehead, H., Christal, J., & Howard, P. C. (2002). Social structure and residency in aggregations of male sperm whales. Canadian Journal of Zoology, 80(7), 1189–1196.

Madsen, P. T., Payne, R., Kristiansen, N. U., Wahlberg, M., Kerr, I., & Møhl, B. (2002). Sperm whale sound production studied with ultrasound time/depth-recording tags. The Journal of Experimental Biology, 205, 1899-1906.

Madsen, P., Wahlberg, M., B., & Møhl, B. (2002). Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: implications for echolocation and communication. Behavioral Ecology and Sociobiology, 53(1), 31–41.

Magalhães, S., Silva, M. A., Prieto, R., Quérouil, S., Pinela, A., & Santos, R. S. (2005). Spatial and temporal patterns of sperm whale groups in the Azores archipelago. In Proceedings of the Nineteenth Annual Conference of the European Cetacean Society, La-Rochelle, France (pp. 2-7).

Martin A.R. (1982) A link between the sperm whales occurring off Iceland and the Azores. Mammalia 46, 259–260.

Martin, A. R., & Melo, A. M. A. (1983). The Azorean sperm whale fishery: a relic industry in decline. Report of the International Whaling Commission, 33, 283-286.

Martin, A. R., & Clarke, M. R. (1986). The Diet of Sperm Whales (Physeter Macrocephalus) Captured Between Iceland and Greenland. Journal of the Marine Biological Association of the United Kingdom, 66(4), 779-790.

Matthews, J. N., Steiner, L., & Gordon, J. (2001). Mark-recapture analysis of sperm whale (*Physeter macrocephalus*) photo-id data from the Azores (1987-1995). Journal of cetacean research and management, 3(3), 219-226.

Mchedlidze, G. A. (2009). Sperm Whales, Evolution. *Encyclopedia of Marine Mammals*, 1097–1098.

Miller, P. J. O., Johnson, M. P., & Tyack, P. L. (2004). Sperm whale behaviour indicates the use of echolocation click buzzes ‘creaks’ in prey capture. Proceedings of the Royal Society of London, 271, 2239–2247.

Miller, P. J. O., Aoki, K., Rendell, L. E., & Amano, M. (2008). Stereotypical resting behaviour of the sperm whale. Current Biology, 18(1), 21–23.

Møhl, B. (2001). Sound transmission in the nose of the sperm whale *Physeter catodon*. A post mortem study. J. Comp. Physiol. A ,187, 335–340.

Møhl, B., Wahlberg, M., Madsen, P. T., Heerfordt, A., & Lund, A. (2003). The monopulsed nature of sperm whale clicks. Journal of the Acoustical Society of America, 114(2), 1143-1154.

Moors-Murphy, H. B. (2014). Submarine canyons as important habitat for cetaceans, with special reference to the Gully: A review. Deep. Res. Part II Top. Stud. Oceanogr., 104, 6–19.

Morato, T., Machete, M., Kitchingman, A., Tempera, F., Lai, S., Menezes, G., Pitcher, T., J., & Santos, R. S. (2008). Abundance and distribution of seamounts in the Azores. Marine Ecology Progress Series, 357, 17-21.

Morris, R. J. (1973). The lipid structure of the spermaceti organ of the sperm whale (*Physeter catodon*). Deep Sea Research and Oceanographic Abstracts, 20(10), 911–916.

Mullin, K., D., Steiner, L., Dunn, C., Claridge, D., González García, L., Gordon, J. & Lewis, T. Long-Range Longitudinal Movements of Sperm Whales (*Physeter macrocephalus*) in the North Atlantic Ocean Revealed by Photo-Identification. In Press.

Neves-Graça K. (2004). Revisiting the Tragedy of the Commons: Ecological Dilemmas of Whale Watching in the Azores. Human Organization, 63, 3.

Neves-Graça, K. (2006). Politics of Environmentalism and Ecological Knowledge at the Intersection of Local and Global Processes. Journal of Ecological Anthropology, 10 (1), 19-32.

Norris, K. S., & Harvey, G. W. (1972). A Theory for the Function of the Spermaceti Organ of the Sperm Whale (*Physeter Catodon L.*). Animal Orientation and Navigation, 397-417.

Norris, K. S., & Mohl, B. (1983). Can Odontocetes Debilitate Prey with Sound?. The American Naturalist, 122(1), 85–104.

O'Connor, S., Campbell, R., Cortez, H., & Knowles, T. (2009). Whale-watching Worldwide: Tourism Numbers, Expenditures and Expanding Economic Benefits. Yarmouth, MA: IFAW.

Pace, D. S., Arcangeli, A., Mussi, B., Vivaldi, C., Ledon, C., Lagorio, S., Giacomini, G., Pavan, G., & Ardizzone, G. (2018). Habitat suitability modeling in different sperm whale social groups. The Journal of Wildlife Management, 82(5), 1062–1073.

Panagiotopoulou, O., Spyridis, P., Mehari Abraha, H., Carrier, D. R., & Pataky, T. C. (2016). Architecture of the sperm whale forehead facilitates ramming combat. PeerJ 4:e1895

Pavan, G., Hayward, T. J., Borsani, J. F., Priano, M., Manghi, M., Fossati, C., & Gordon, J. (2000). Time patterns of sperm whale codas recorded in the Mediterranean Sea 1985–1996. The Journal of the Acoustical Society of America, 107(6), 3487–3495.

Pinela, A., Quérouil, S., Magalhães, S., Silva, M. A., Prieto, R., Matos, J., & Santos, R. S. (2009). Population genetics and social organization of the sperm whale (*Physeter macrocephalus*) in the Azores inferred by microsatellite analyses. Canadian Journal of Zoology, 87, 802-813.

Pereira, J. N., Neves, V. C., Prieto, R., Silva, M. A., Cascão, I., Oliveira, C., Cruz, M. J., Medeiros, J. V., Barreiros, J. P., Porteiro, F. M., & Clarke, D. (2011). Diet of mid-Atlantic Sowerby's beaked whales Mesoplondon bidens. Deep Sea Research Part I: Oceanographic Research Papers, 58(11), 1084-1090.

Prieto, R., Pham, C. K., Brito, C., & Morato, T. (2013). Biomass removal from shore-based whaling in the Azores. Fisheries Research, 143, 98–101.

Prieto, R., Silva, M. A., Waring, G. T., & Gonçalves, J. M. (2014). Sei whale movements and behaviour in the North Atlantic inferred from satellite telemetry. Endangered Species Research, 26(2), 103-113.

Pirotta, E., Matthiopoulos, J., Mackenzie, M., Scott-Hayward, L., & Rendell L. (2011). Modelling sperm whale habitat preference: a novel approach combining transect and follow data. Marine Ecology Progress Series, 436: 257-272.

Queiroz, R. E., Guerreiro, J., & Ventura, M. A. (2014) Demand of the tourists visiting protected areas in small oceanic islands: the Azores case-study (Portugal). Environ Dev Sustain 16, 1119–1135.

Raven, H. C., & Gregory, W. K. (1933). The spermaceti organ and nasal passages of the sperm whale (*Physeter catodon*) and other odontocetes. America museum novitates, 677.

Redfern, J.V., Ferguson, M.C., Becker, E.A., Hyrenbach, K.D., Barlow, C. G. J., Kaschner, K., Baumgartner, M. F., Forney, K. A., Balance L. T., Fauchald, P., Halpin, P., Hamazaki, T., Pershing, A. J., Qian, S. S., Read, A., Reilly, S. B., Torres, L. & Wener, F. (2006) Techniques for cetacean–habitat modeling. Mar Ecol Prog Ser, 310, 271–295.

Reeves R. R., & Smith T. D. (2003). A taxonomy of world whaling: Operations, Eras and Data Sources. Northeast Fisheries Science Center Reference Document 03-12.

Rendell, L. E., Whitehead, H. (2003). Vocal clans in sperm whales (*Physeter macrocephalus*). Proceedings of the Royal Society of London B: Biological Sciences, 270(1512), 225–231.

Rice, D.W. (1989). Sperm whale. *Physeter macrocephalus* Linnaeus, 1758. In Handbook of marine mammals. Vol. 4. Edited by S.H. Ridgway and R. Harrison. Academic Press, London. pp. 177–233.

Rice, D. W. (2009). Spermaceti. Encyclopedia of Marine Mammals, 1098–1099.

Sala, I., Harrison, C. S., & Caldeira, R. M. (2016). The role of the Azores Archipelago in capturing and retaining incoming particles. Journal of Marine Systems, 154, 146-156.

Santos, R. S., Hawkins, S., Monteiro, L. R., Alves, M., & Isidro, E. J. (1995). Marine research, resources and conservation in the Azores. Aquatic Conservation: Marine and Freshwater Ecosystems, 5(4), 311–354.

Seabra, M.I., Silva, M., Magalhães, S., Prieto, R., August, P., Vigness-Raposa, K., Lafon, V., and Santos, R.S. (2005) Distribution and habitat preferences of bottlenose dolphins (*Tursiops truncatus*) and Sperm Whales (*Physeter macrocephalus*) with respect to physiographic and oceanographic factors in the waters around the Azores (Portugal). In: Proceedings of the 19th Annual Conference of the European Cetacean Society (ed. Evans, P.G.H.). ECS, La Rochelle.

Sequeira, M., Elejabeitia, C., Silva, M. A., Dinis, A., de Stephanis, R., Urquiola, E., Nicolau, C., Prieto, R., Oliveira, C., Cruz, M. J., Freitas, L. (2009). Review of whalewatching activities in mainland Portugal, the Azores, Madeira and Canary archipelagos and the Strait of Gibraltar. J Cetacean Res Manage, SC61/WW11.

Silva, M. A., Prieto, R., Magalhães, S., Cabecinhas, R., Cruz, A., & Gonçalves, J. M. (2003). Azores (Portugal), Summer and Autumn 1999–2000. Aquatic Mammals, 29, 77-83.

Silva, M. A., Prieto, R., Jonsen, I., Baumgartner, M. F., & Santos, R. S. (2013). North Atlantic blue and fin whales suspend their spring migration to forage in middle latitudes: building up energy reserves for the journey?. PLoS One, 8(10).

Silva, M. A., Prieto, R., Cascão, I., Seabra, M. I., Machete, M., Baumgartner, M. F., & Santos, R. S. (2014). Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. Marine Biology Research, 10(2), 123–137.

Skov, H., Gunnlaugsson, T., Budgell, W. P., Horne, J., Nøttestad, L., Olsen, E., Søiland, H., Víkingsson G., & Waring, G. (2008). Small-scale spatial variability of sperm and sei whales in relation to oceanographic and topographic features along the Mid-Atlantic Ridge. Deep Sea Research Part II: Topical Studies in Oceanography, 55(1-2), 254–268.

Steiner, L., Lamoni, L., Plata, M. A., Jensen, S. K., Lettevall, E., & Gordon, J. (2012). A link between male sperm whales, *Physeter macrocephalus*, of the Azores and Norway. Journal of the Marine Biological Association of the United Kingdom, 92(8), 1751-1756.

Teloni, V., Johnson P. Mark; Miller J.O. Patrick; Madsen T. Peter (2008). Shallow food for deep divers: Dynamic foraging behavior of male sperm whales in a high latitude habitat. Journal of Experimental Marine Biology and Ecology , 354(1), 119–131.

Tepsich, P., Rosso, M., Halpin, P. N., & Moulins, A. (2014). Habitat preference of two deep diving cetacean species in the northern Ligurian Sea. Marine Ecology Progress Series, 508, 247-260.

Tobeña, M., Prieto, R., Machete, M., & Silva, M. A. (2016). Modeling the potential distribution and richness of cetaceans in the Azores from fisheries observer program data. Frontiers in Marine Science, 3, 202.

van der Linde, & M., Eriksson, I. K. (2019). An assessment of sperm whale occurrence and social structure off São Miguel Island, Azores using fluke and dorsal identification photographs. Marine Mammal Science, 2019, 1-19.

Vieira J. A. G. (2009). A baleação e a identidade cultural duma ilha: o projecto de recuperação da Fábrica Baleeira do Boqueirão - um modelo museológico inserido em realidades locais. Cadernos de Sociomuseologia. Centro de Estudos de Sociomuseologia.

Vieira, N., & Brito, C. (2009). Past and recent sperm whales sightings in the Azores based on catches and whale watching information. Journal of the Marine Biological Association of the United Kingdom, 89(5), 1067-1070.

Vieira, J., Câmara, G., Silva, F., & Santos, C. (2019). Airline choice and tourism growth in the Azores. Journal of Air Transport Management, 77, 1–6.

Visser, F. (2012). Diving behavior of Sowerby's beaked whale in the Azores. KELP MARINE RESEARCH HOORN (NETHERLANDS).

Watkins, W. A., & Schevill, W. E. (1977). Sperm whale codas. The Journal of the Acoustical Society of America, 62(6), 1485-1490.

Watwood, S. L., Miller, P. J. O., Johnson, M., Madsen, P. T., & Tyack, P. L. (2006). Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). Journal of Animal Ecology, 75(3), 814–825.

Weilgart, L., Whitehead, H., & Payne, K. (1996). A colossal convergence. American Scientist, 84(3), 278-287.

Weilgart, L., Whitehead, H. (1997). Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. Behaviour Ecology and Sociobiology, 40(5), 277–285.

Wellendorf, M. (1963). Composition of Spermaceti. Nature, 198 (4885), 1086–1087.

Whitehead, H., & Arnbom, T. (1987). Social organization of sperm whales off the Galapagos Islands, February-April 1985. Can. J. Zool., 65, 913-919.

Whitehead, H., & Weilgart, L. (1991). Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. Behaviour, 118 (3/4), 275-296.

Whitehead, H., Waters, S., & Lyrholm, T. (1991). Social organization of female sperm whales and their offspring: constant companions and casual acquaintances. Behavioral Ecology and Sociobiology, 29(5), 385–389.

Whitehead, H. (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales. Behavioral Ecology and Sociobiology, 38(4), 237–244.

Whitehead, H. (2000). The diet of Galápagos sperm whales *Physeter macrocephalus* as indicated by fecal sample analysis. Marine Mammal Science, 16, 315–325.

Whitehead, H., MacLeod, C. D., & Rodhouse, P. (2003). Differences in niche breadth among some teuthivorous mesopelagic marine mammals. Marine Mammal Science, 19 (2), 400-406.

Whitehead, H. Sperm whales: social evolution in the ocean. University of Chicago Press, 2003.

Whitehead, H. (2018). Sperm Whale: Physeter macrocephalus. Encyclopedia of Marine Mammals, 3 ,919–925.

Wong, S. N. P., & Whitehead, H. (2014). Seasonal occurrence of sperm whales (Physeter macrocephalus) around Kelvin Seamount in the Sargasso Sea in relation to oceanographic processes. Deep Sea Research Part I: Oceanographic Research Papers, 91, 10–16.

Chapter 2: Habitat preferences of sperm whales (*Physeter macrocephalus*) off São Miguel Island, Azores

Inês Coelho[1, 2], David Abecasis[1, 3], Laura González García[2, 4]

[1] University of Algarve, 8005-139, Faro, Portugal.

[2] Futurismo Azores Adventures, Portas do Mar, loja 24-26, 9500-771. Ponta Delgada, São Miguel, Azores, Portugal

[3] Centre of Marine Sciences (CCMAR), University of Algarve, 8005-139, Faro, Portugal.

[4] Azores Biodiversity Group and Centre for Ecology, Evolution and Environmental Changes (cE3c), University of the Azores, Rua Mãe de Deus, 9500-321 Ponta Delgada, Portugal.

2.1 Abstract

For many decades whaling was a popular and profitable activity in the Azores with the main target being the sperm whale (*Physeter macrocephalus*). Nowadays this species continues to be very attractive for the region, since it is a charismatic species possible to observe all year round by the whale watching companies, the main touristic activity in archipelago. Sperm whales use the Azores both as feeding and reproductive grounds, but little is known about their habitat preferences in the region. The objective of this study is to investigate the relationship between different classes of sperm whales (family groups, males and Mr. Liable, a possible resident male sperm whale in the study area) and environmental variables taking into consideration the observable behaviour (foraging or other behaviour). Generalized Additive Models (GAMs), with binomial distribution, were used for the habitat preference analysis and remotely sensed environmental variables were extracted. The occurrence sperm whale data was collected from 2009 to 2019 during whale watching tours mostly in the south coast of São Miguel Island. All classes presented differences in the habitat preference, with depth being the only relevant variable common to all classes and behaviours, showing a preference for waters deeper than 500 m. Family groups (79% of our observations), when in foraging, seemed to prefer deep and warm waters, negative values of sea level anomaly and deeper mixed layers. During other behaviours the family groups discarded sea level anomaly and mixed layer depth as relevant variables. Mr. Liable (10% of our observations) showed a bigger affinity for colder and less deep waters, specific values of mixed layer depths and extreme positive and negative values of the sea level anomaly. Males (11% of our observations) only considered deep waters to be a relevant factor. These differences might be related with the exploitation of different prey sized items that is known to exist between male and female sperm whales. Mr. Liable uses the same area of family groups throughout the year, this might have created a divergence in habitat preferences in order to decrease intraspecific competition. The differences between males and Mr. Liable can be explained by the fact that these two classes use the region for different purposes, the first one manly for reproducing and the second also for foraging. Understanding the relationship between environmental variables and local populations of sperm whales is crucial for the management and conservation of this species, especially in an unpredictable changing ocean.

Key-words: Sperm whales, Azores, Habitat preference, GAM's

2.2 Introduction

The complex relationship between the oceanographic conditions and bathymetric features that describe the Azores, creates a unique hotspot for cetaceans (Afonso et al., 2020), with 28 species being registered in the area up until now (Silva et al., 2014). Since the whaling era that Azores archipelago is known to be an important area for sperm whales (*Physeter macrocephalus*, Linnaeus 1758) as a breeding and foraging grounds (Clarke, 1956; Silva et al., 2014), with groups of females, immatures and mature males being sighted throughout the year (van der Linde & Eriksson, 2019).

Sperm whale is the largest odontocete (Gosho et al., 1984) and the cetacean with the highest sexual dimorphism, with males reaching 18 m and females up to 12 m (Best, 1979). The differences between males and females are also noticeable regarding their social life. Female sperm whales are social animals that spend their lives with their social units, composed by adult females, immatures and calves (Whitehead, 2003; Gero et al., 2014) and most of the times, all these individuals belong to the same family (Pinela et al., 2009). At a certain point, the juvenile males abandon their social unit to become solitary males as they grow older (Best, 1979). Social units are distributed in lower latitude areas (below 40º) and males are found up to the edges of ice packs in both hemispheres (Gosho et al., 1984; Rice, 1989). The overlap of distribution of the two sexes happens in breeding areas, when the males migrate from the poles to lower latitudes (Gosho et al., 1984).

In a changing ocean it is vital to understand the relationship between the wild populations and the environment surrounding them, in order to apply successful conservation measures, like for example marine protected areas. Habitat preference modelling represents a strong conservation tool in the way that determines the distribution of cetaceans based on the on the influences of the environmental variables on the species (Cañadas et al., 2005; Redfern et al., 2006). Previous studies already demonstrated that sperm whales take some environmental variables into considerations when choosing their habitats. Most studies, shows that bathymetric features, like depth always seems to be a vital variable in their distribution patterns (Davis et al., 1998; Azzellino et al., 2008; Pirotta et al., 2011; Fais et al., 2016; Pace et al., 2018). Chlorophyll concentration with an associated temporal lag (Jaquet et al., 1996; Wong & Whitehead, 2014), sea surface temperatures (Jaquet, 1996; Pirotta et al., 2011; Praca & Gannier, 2008; Rendell et al., 2004), presence of thermal fronts (Griffin, 1999; Gannier & Praca, 2007), eddy kinetic energy (Wong & Whitehead, 2014; Diogou et al., 2019) and nearby mesoscale eddies (Davis et al., 2002; Pirotta et al., 2020) are just some of the variables that seem to have positive influence in the presence of sperm whales. Although the tight relationships of sperm whales with the environmental conditions around them, social organization structure of this species will differentiate their habitat preference. Differences of habitat use between males and groups of females have been reported in the Mediterranean (Pirotta et al., 2011; Pace et al., 2018) and between different social units have been shown in the Caribbean (Milligan, 2013). In the south pacific Whitehead & Rendell (2004) demonstrated that social clans have distinct habitat preferences that results in different feeding successes and ultimately different fitness. In the end, all this differences between different classes of sperm whale organizations can be related with distinct ecological requirements (Pirotta et al., 2011) but also cultural factors (Whitehead & Rendell 2004). Regarding the Azores, very few studies exist that relate the distribution of sperm whales with the environmental conditions available to them. To this date it is known that there seems to be a preference for deep waters (Silva et al., 2003; Seabra et al., 2005; Magalhães; Silva et al., 2014; et al., 2016) and that there is a positive relationship between sperm whales and sea surface temperature (Seabra et al., 2005). According with Tobeña et al. (2016) the most important environmental variable for sperm whales is the time-lagged (two months) chlorophyll-a local variation, associating this species with oceanographic characteristics that enhance local primary production.

The goal of this study is to assess the environmental preferences of groups of females and solitary males using opportunistic data from a whale watching company. Behaviour conditions of the individuals will also be taken into consideration, by comparing foraging conditions and other behaviours (all behaviour that are not considered foraging) conditions. The environmental variables considered for this study are: depth, slope, monthly sea surface temperature, standard deviation of the sea surface temperature, gradient of the sea surface temperature, sea temperature at different depths (500 m, 1000 m and at the sea bottom), depth of the mixed layer, sea surface heigh and sea level anomaly.

2.3 Materials and Methods

2.3.1 Study Area

This study is focused on São Miguel, the largest island of the Azores archipelago located at 37.3-38.1ºN and 25-26.2ºW. A range of depths and steep slopes surround the island, from shallower water along the small continental shelf (the same characteristic for the rest of the islands) to waters with more than 1000 m close to shore. In the southwestern tip of the island, Mar da Prata, a large seamount of volcanic origins that extends for 60 km south, reaches a minimum depth of 169m (Santos et al., 2020). The Azores archipelago, in the Mid-Atlantic, is located within the North Atlantic Subtropical Gyre and designates as a confluence region between the west and east North Atlantic (Caldeira & Reis, 2017). The North Atlantic Current (a branch from the Gulf Stream) crosses the north of the archipelago and influences it with colder waters intrusions, while the Azores Current passes south of the archipelago and brings warm subtropical waters for the region (Silva et al., 2013).

2.3.2 Field data collection

For this study, all the cetacean occurrence data was collected aboard whale watching vessels by the biologist staff of Futurismo Azores Whale Watching from January 2009 to June 2019. Tours are conducted throughout the year if there is a minimum number of tourists and if the sea and/or meteorological conditions allow it. Most of the tours are conducted in the south coast of the island (operating from Ponta Delgada), but since 2015 in the summer months, occasionally in the north coast as well (operating from Rabo de Peixe). The tours last approximately 3 hours, our sampling period, and it is conducted twice a day (09h-12h and 13h-16h). Three different kinds of vessels were used for these tours: (i) two catamarans around 18 m each (ii) rigid-hulled inflatable boats between 8 m to 11 m, and (iii) one fiberglass boat with 12 m. Before and during each tour, cetaceans were spotted by experience land-based “vigias” (lookouts) located in strategic points along the coast of São Miguel Island (Figure 2.1) using Steiner 20 x 80 mm binoculars, that allows a visible range of 40 km in perfect visibility conditions. The lookouts’ location could vary according to the visibility conditions throughout the day, with the location in Caloura (lookout point known as “Quarenta”) being the preferred one (Figure 2.1). When the lookouts spotted any evidence of cetaceans’ presence, the location was transmitted to the vessels (using VHF radio) and the animals were approached following the regional legislation (DLR 10/2003/A). During the observation the collected data included: beginning and end time of the encounter and respective GPS coordinates; sea state; visibility; species observed; the size and composition of the group; behaviour of the animals; presence/absence of other boats. When possible, photos (for photo-ID purpose) were taken as well as some additional data like known individuals, gender of the animals and diving times (especially for sperm whales). Duplicates of the same individual and/or group observations may bias the results, leading to an overestimation of the number of real observations. To avoid this situation, when observing sperm whales over shorter periods of time and space, only one sighting was retained. Most of the times only one sighting per sampling period (morning or afternoon trip) was used. All data was compiled in an Excel database.

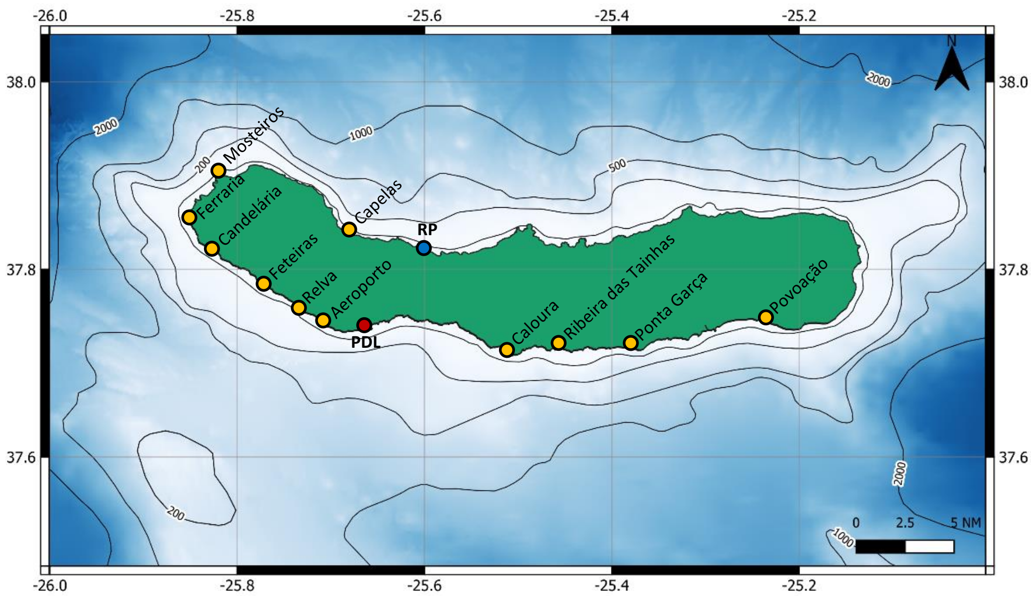


Figure 2.1: São Miguel Island showing the main lookouts (yellow circles), the location of Ponta Delgada (red circle; PDL), the location of Rabo de Peixe (blue circle; RP) and the bathymetric representation around the island.

The classification of the age classes, gender, behaviour and group size of sperm whales in the field are not always straightforward, especially when dealing with opportunistic data collected by numerous observers. Therefore, in this study we use the following definitions:

Solitary Males: Sperm whales larger than 13m with a prominent head (van der Linde & Eriksson, 2020) with no other sperm whale visible by the crew and/or lookout in the same area (hereafter as males).

Groups: When we are observing females and immatures sperm whales smaller than 13m (van der Linde & Eriksson, 2020), apparently moving together in a coordinated fashion and sometimes spread out in hundreds or thousands of meters (Whitehead, 2003).

Foraging: The foraging behaviour is considered when the sperm whale flukes-up, the tail is raised above the water surface to start a deep dive.

Other Behaviours: All observational behaviours that are not foraging (socializing, travelling, resting, etc.).

2.3.3 Temporal and Spatial distribution

The encounter rate of each class of sperm whales was calculated as the number of observations of each class divided by the number of tours per month. Afterwards, an arithmetic mean was calculated, to obtain a mean encounter rate per month during the 11 years. Because the main goal of the whale watching company is tourism, the route of the tours (spatial effort) was not recorded, to interfere as less as possible with the activity, therefore the effort was considered as the number of tours per month. For the spatial distribution analysis, we used the heatmap tools of the open-source geographic information system QGIS 3.16.1 "Hannover" to obtain the heatmaps of the sightings of the distinct classes of sperm whales.

2.3.4 Environmental Data

Two types of variables were used in this study to predict the presence of sperm whales (i) static variables: depth and slope (ii) dynamic variables: sea surface temperature (SST), standard deviation of the sea surface temperature (as a measurement for ocean variability; SD_SST), gradient of the sea surface temperature (as a proxy for SST fronts; Grad_SST), sea surface height (SSH), sea level anomaly (SLA), thickness of the mixed layer (MixLayer), sea temperature at different depths (ST500, ST1000), potential temperature at the sea floor (STBottom; Table 2.1).

Table 2.1: Description of the environmental variables used for the habitat preference models with respective units, spatial and temporal scales.

Variables	Units	Description	Spatial Scale	Temporal Scale
Depth	m	Depth of the sea bottom	1 km	-
Slope	Degrees (º)	Depth slope of the sea bottom	1 km	-
SST	ºC	Sea surface temperature	4 km	Monthly
SD_SST	ºC	Standard deviation of the monthly SST	4 km	Daily and Monthly
Grad_SST	ºC/km	Rate of change in the SST	4 km	Monthly
SSH	cm	Sea surface height above geoid	8 km	Monthly
SLA	cm	Sea surface heigh above sea level mean (1993-2012)	8 km	Monthly
MixLayer	m	Thickness of the surface mixed layer	8 km	Monthly
ST500; ST1000; STBottom	ºC	Potential sea temperature at different depths (500 m, 1000 m and at the bottom)	8 km	Monthly

The depth data was obtained from the General Bathymetric Chart of the Oceans (GEBCO; www.gebco.net, 2020) and the values were extracted using QGIS tools from a raster file. The same raster file was used to calculate the slopes for each observation using the Raster Terrain Analysis tools from QGIS.

For the SST (monthly and daily) we used the Level-3 product SST (daytime) Moderate Resolution Imaging Spectroradiometer (MODIS) data from NASA's Aqua satellite (https://oceancolor.gsfc.nasa.gov, 2020). Daily SST data was used to estimate the SD_SST by calculating the standard deviation of each cell for all the days of each month. A discrete numerical gradient (function gradient from the package "pracma" in R) was calculated for the central cell in between two neighbouring cells (one in the latitude direction and another in the longitude direction), corresponding to 4 km, and afterwards the following formula was used to estimate the Grad_SST:

$$\text{Grad\_SST} = \text{SQRT}(gx^2 + gy^2)$$

Where gx and gy corresponds to the longitude and latitude matrixes originated from the last step, respectively. While SD_SST is a measure of temperature variability over time, Grad_SST is a measure of temperature variability over space (SST fronts).

The SSH, MixLayer, ST500, ST1000 and STBottom derived from the same product (GLOBAL_REANALYSIS_001_030) using the Sentinel satellites from E.U Copernicus Marine Services Information (CMEMS; http://marine.copernicus.eu, 2020).

The values of all dynamic variables were extracted for each observation (presences and pseudo-absences) by using the "ncdf4" and "raster" libraries from the open-source software R.

2.3.5 Habitat preference analyses

Generalized additive models (GAMs) with a binomial distribution and a logit function were used to investigate the relationship between environmental variables and the presence of the different classes of sperm whales (males and groups) when in foraging or other behaviour. This method is being extensively adopted for cetacean habitat-modelling studies (e.g. Forney, 2000; Best et al., 2012; Keller et al., 2012; Tepsich et al., 2014; Correia et al., 2020; Lambert et al., 2016; González García, 2019). GAMs are non-parametric extension of the more usually used GLM (Generalized Linear models; Hastie & Tibshirani, 1990) that add non-linear forms to the model, giving the chance for more flexible patterns to stand out, what normally corresponds to the reality of the data (Forney, 2000). Because there is no data from the real absences of sperm whales, the distribution of other species (that were also collected during the study time) will be used as pseudo-absences (Esteban et al., 2013, González Garcia, 2019), this will reduce the sampling bias since the presence/pseudo-absence was registered under the same effort. Using the open-source software RStudio (R Development Core Team, 2012) with the "mgcv" library (Wood, 2011), GAMs were applied to the different datasets: general model of the family groups; family groups foraging; family groups in other behaviour; general model of males; males foraging; males in other behaviours.

Pearson collinearity was tested for the environmental variables to investigate possible correlation between them, if there was a dependence between two variables (≥ 0,8), the variable with the larger dataset would be used (the dataset with less missing values). To choose the best fitted model, we used a general backwards selection method based on the Akaike Information Criterion (AIC) scores. This consists of sequentially dropping a single term with the least significant p-value (normally corresponds to the highest p-value) from the saturated first model where all the variables are considered. Every time this led to a lower score of the AIC, the model was retained. The final model retained all variables significant at p-value <0,01, with a minimum AIC score and the deviance explained value was retained. The model validation was performed by applying a temporal k-fold cross validation, using the sightings from all years but one to train the model, and the remaining one for validation (in this case 11 years of studying), obtaining then an AUC value for each of the years validated, and calculating the mean and standard deviation for each final model. The Area Under the receiving-operator Curve (AUC) measures the performance of our models by telling us how well our models can distinguish between a presence and a pseudo-absence (Wiley et al. 2003). The AUC values vary between 0-1, with 0,5 indicating the model did not perform better than random (Wiley et al. 2003). After calculating the AUC for each year of each dataset, an arithmetic mean, and respective standard deviation, was calculated to obtain the final AUC value for each model.

2.4. Results

A total of 4093 tours were performed in the study area between January 2009 and June 2019. During this time, 1402 observations of sperm whales were registered, from which 1269 (presence points) were used for the statistical analysis, the excluded ones were due to errors in the field (ex. missing coordinates or missing behaviours associated with the observation). There were 9539 observations of other species, during the study time, that correspond to the pseudo-absences. The seasonality of the effort, here considered as the number of tours, is quite evident throughout the months of the year reaching the maximum point in July and the minimum point in December. In general, the effort has been slightly increasing over time and the total number of encounters with sperm whales shows a close relationship with the effort (Figure 2.2).

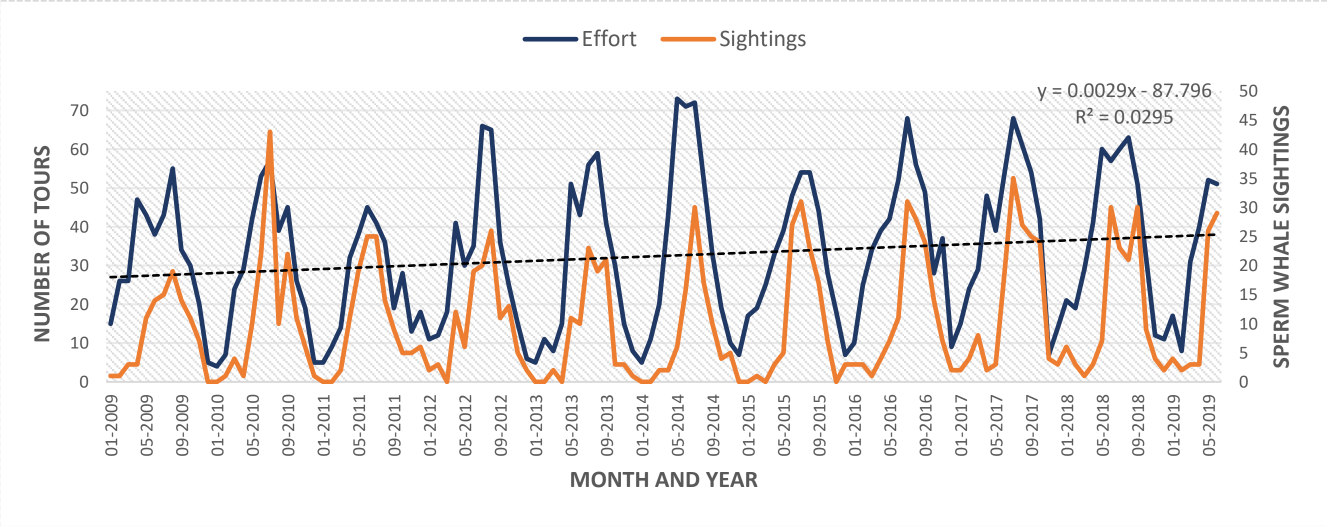


Figure 2.2: Total effort and total observations of the study period with the linear predictor of the effort (dashed line).

Approximately 79% of the analysed sightings were groups of females and immatures with calves being present in almost half of the sightings (Figure 2.3a). Solitary males represent the remaining 21% (Figure 2.3a), with one specific individual, called Mr. Liable, comprising 10% of the males' sightings (Figure 2.3a). Because of the big representation of this individual in this class, Mr. Liable was considered as a different class from all the other males (from now on Mr. Liable referred as such and the other males referred as males) to investigate possible disparities between these two classes. Foraging seems to be the most sighted behaviour for all different classes of sperm whales in the study area, when compared to other behaviours. Males revealed to be the class with the lowest percentage of foraging sightings (55%; Figure 2.3c), followed by the groups of females (66%; Figure 2.3b) and finally Mr. Liable (94%; Figure 2.3d).

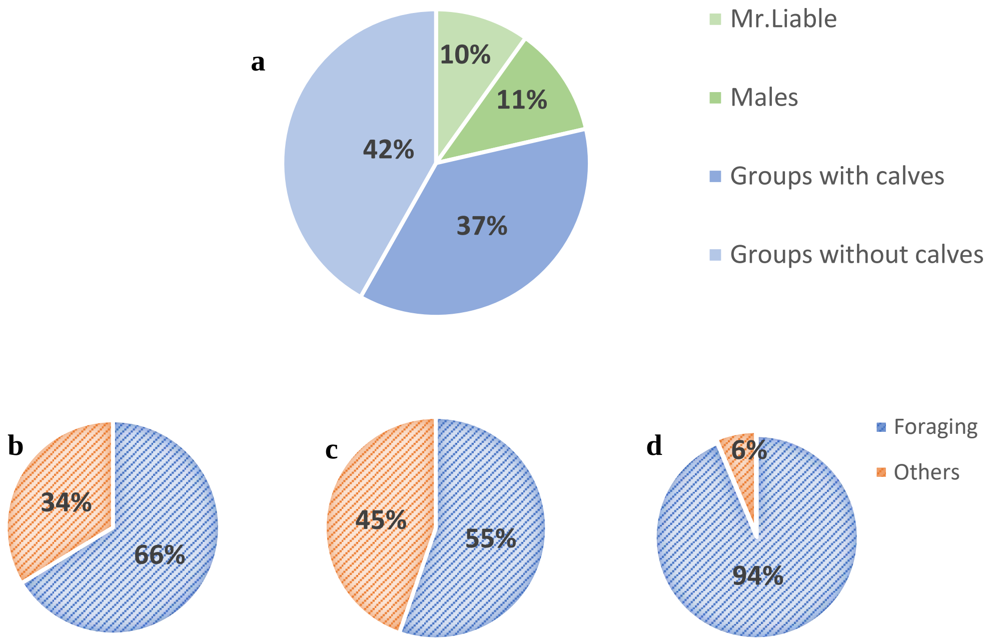


Figure 2.3: (a) Percentage of sightings representing each class. Behaviour observed during the study period for (b) Groups, (c) Males and (d) Mr. Liable.

2.4.1 Dynamic oceanographic variables

Variances of the sea surface temperature throughout the years and space were visible in the study area. The seasonality of the SST (Figure 2.4a) is well defined with the highest mean temperatures being recorded in the months of August and September and the lowest ones being verified in February and March. In March of 2011 and September of 2018, the SST reached respectively the lowest (14.9 ºC) and highest (24.3 ºC) recorded values, during the study period and for the study area (Appendix A). Considering the evolution of the yearly and monthly means of the SST throughout time, an increasing trend of the mean SST for the study area is observed in a period of just 11 years (Figure 2.4b). In most of the months, a latitudinal SST gradient was observed with warmer waters in the south region of S. Miguel and colder waters in the northern coast of the island, like for example in March of 2013 (Figure 2.5). Occasionally, a distinct west-east SST asymmetry was also detected, where warmer waters are found in the southwest of the island and cold waters are found in the northeast of the island, like for example in November of 2015 (Figure 2.5).

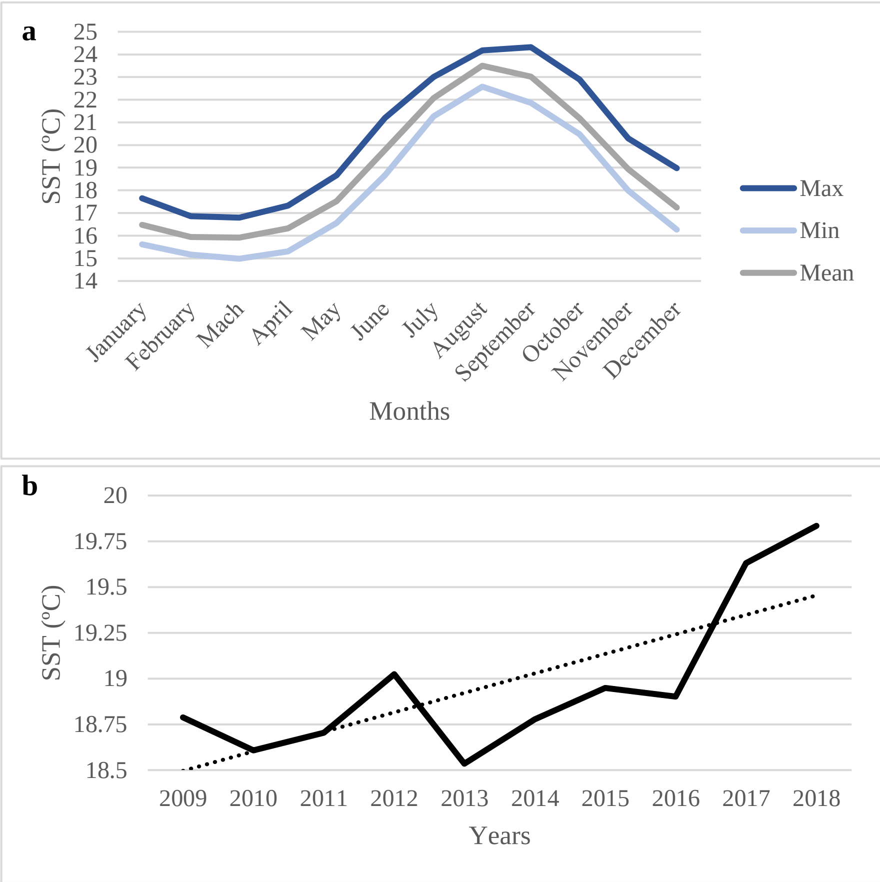


Figure 2.4: Sea surface temperature (SST) variability throughout the seasons (a) and annual mean sea surface temperature with the linear predictor (dashed line; b).

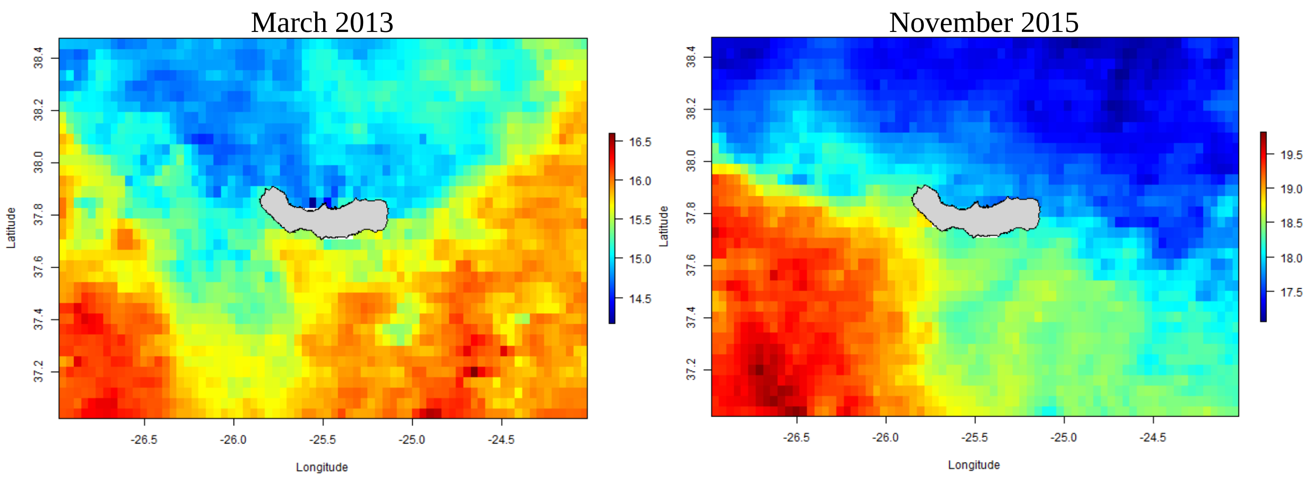


Figure 2.5: Spatial variability of the sea surface temperature (SST in ºC) showing the latitudinal gradient of warm waters in the south to cold waters in the north (March 2013) and the gradient of warm waters in the southwest to cold waters in the northeast (November 2015).

The mixed layer thickness also demonstrated a marked seasonality in the study area (Figure 2.6). It reaches deeper waters always in the winter months (December, January and February) ranging between 70.7 m (December 2013) and 94.8 m (February 2014). In the summer months (June, July and August) the thinnest MixLayer are registered, ranging from 10.7 m (July 2010) and 11.1 m (July 2012), showing almost no variance in the 11 years of study (Figure 2.6).

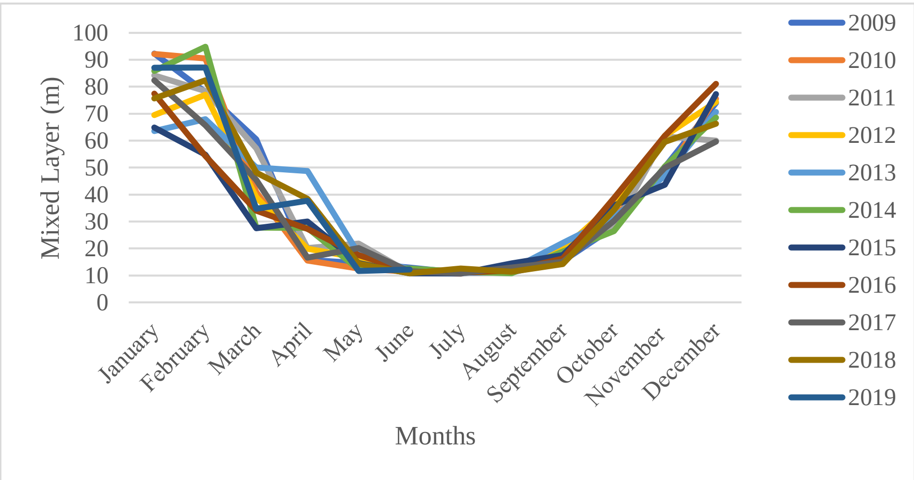


Figure 2.6: Temporal variability of the mixed layer depth (m) throughout the months for each year.

During the study period, sea level anomaly was the oceanographic variable that revealed the highest increase of mean values (Figure 2.7). The lowest value recorded was -6.2 m in March of 2011 and the highest value was 18.2 m in October of 2018. Important to notice is the fact that negative values of SLA are not recorded in the study area since March of 2013 (Figure 2.7). Like the other variables, SLA follows a seasonal pattern reaching the lowest mean values in spring (March and April) and the highest values in autumn (September and October) (Appendix B).

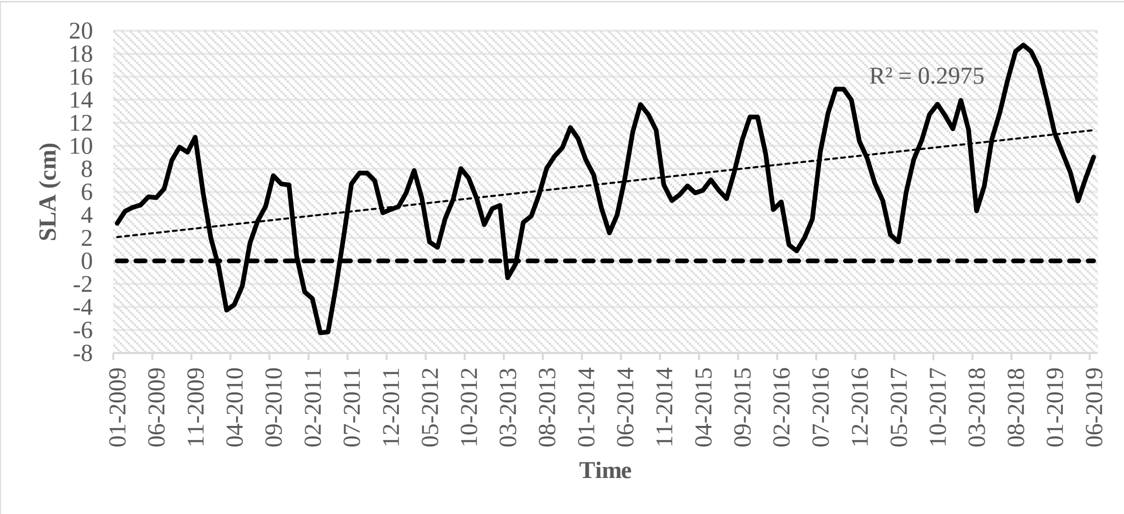


Figure 2.7: Temporal variability of the sea level anomaly (SLA) throughout the months of the year with the respective linear predictor (dashed line).

2.4.2 Spatial and temporal distribution of sperm whales

All classes of sperm whales were sighted throughout the years from January to December, except for Mr. Liable, who was never spotted in March (Figure 2.8). The family groups were the most frequently sighted class of sperm whales every month and every year, reaching the maximum encounter rate in July, where the effort was also the highest (Figure 2.8). In the months of spring and summer (from March to August) males had higher encounter rates than Mr. Liable, however in the winter and autumn (from September from February) the opposite happened (Figure 2.8). Although it is quite evident that the encounter rate of groups tends to follow the effort, the same is not so clear for Mr. Liable, with the highest encounter rates from September to December, where the tendency of the effort is to decrease.

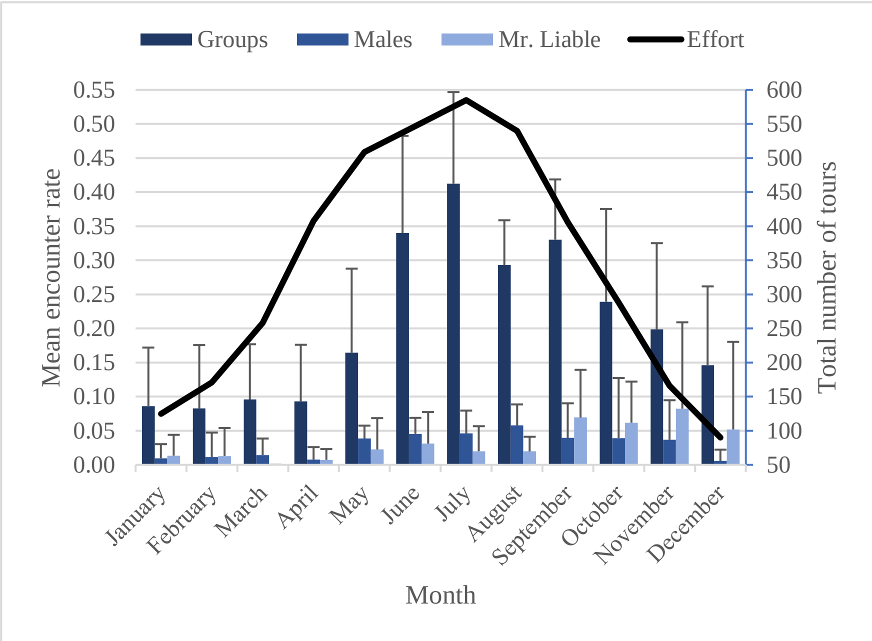


Figure 2.8: Monthly mean encounter rate of the different classes of sperm whales throughout the study period, with the associated standard deviations (lines on top of the bars) and the effort during the same period, number of tours per month.

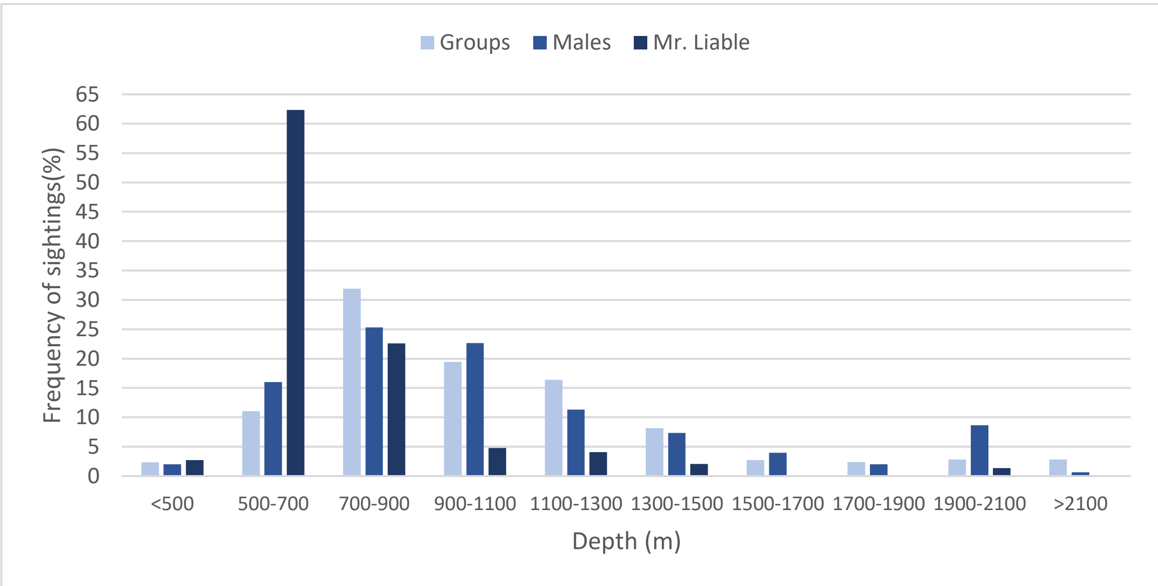


Figure 2.9: Distribution of the different classes of sperm whales according to the depth of the area where they were sighted.

Sperm whales where found distributed along the area where the whale watching tours were conducted, in the south, west and sometime in the north coast of São Miguel, with a higher incidence in the south (area with the highest effort). Occurrences in waters shallower than 200 m were extremely rare and the most frequent depth for sperm whale encounters range from 500 to 1000 m (Figure 2.9). Differences between classes are evident. While Mr. Liable was seen 62% of the times in waters between 500 m to 700 m, whereas males and groups did not reveal such a strong affinity towards any depth interval. Groups and males were sighted frequently between the 700 m to 900 m (32% and 25%, respectively; Figure 2.9). Groups show two different areas with highest incidence in the south coast of S. Miguel, one being in front of Ponta Delgada and the other being in front of Vila Franca do Campo, most commonly in the 500 m-1000 m bathymetric corridor (Figure 2.10a). The males' incident area overlaps the groups however males appear to have a wider dispersion (Figure 2.10b). Mr. Liable shows a higher preference for a more delimited area, around the southwest part of the island near a very known fishing ground called Mar da Prata (Figure 2.10c).

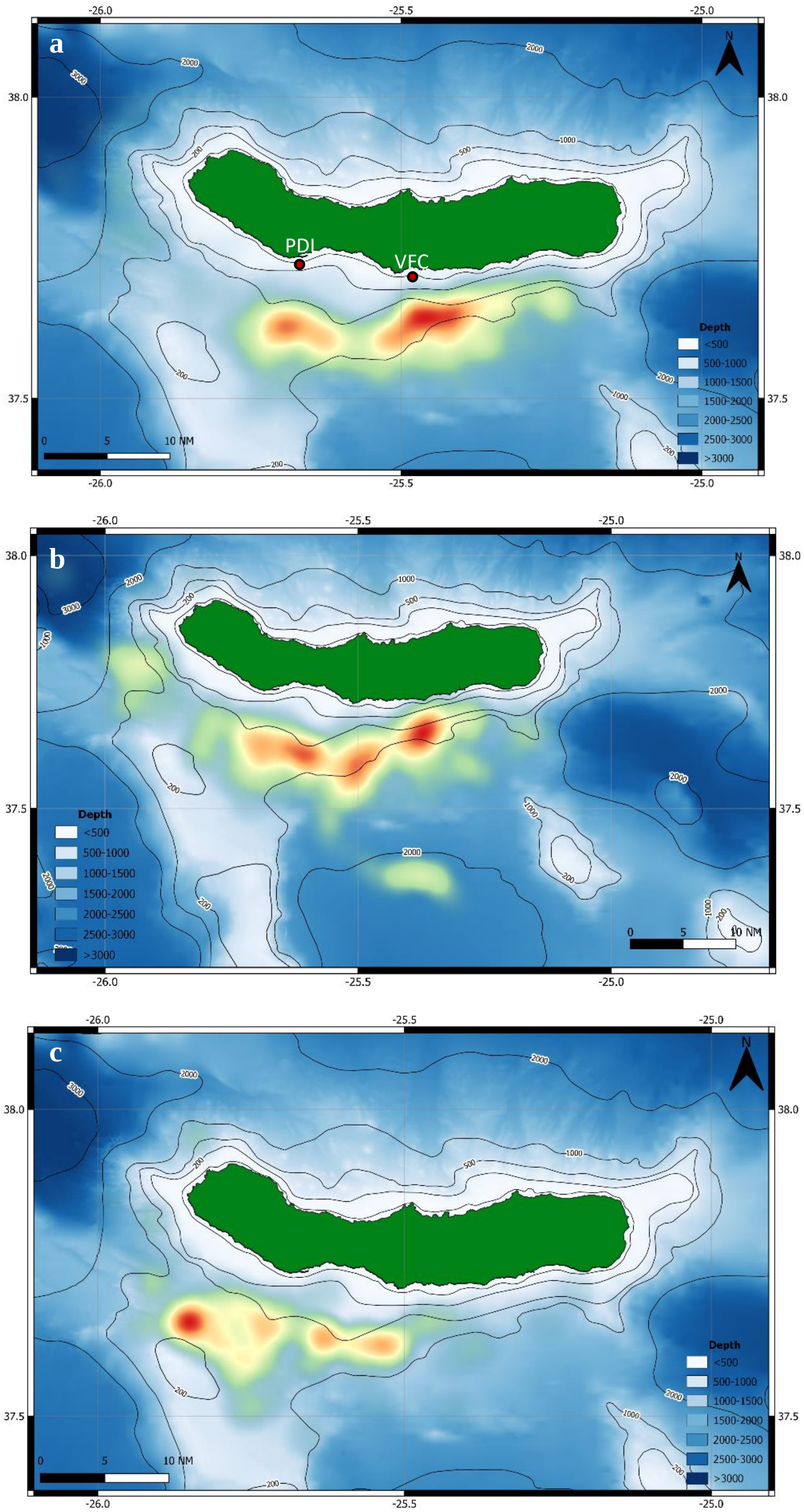


Figure 2.10: Heatmaps showing areas with higher concentration of sightings of (a) groups, (b) males and (c) Mr. Liable in the study area. Green to red colours gradient correspond to high to low occurrence, respectively. PDL – Ponta Delgada; VFC – Vila Franca do Campo

2.4.3 Habitat models

Collinearity was observed between Depth and STBottom; and between SLA and SSH. To avoid misinterpretation of the models, due to the correlation among some variables, one of the variables will be exclude from the analysis. STBottom was discarded due to the high percentage of missing values (17%) compared with Depth. Because SLA represents relative values of sea surface height (sea surface height anomaly over a period of 20 years) and SSH represents absolute values (sea surface height above geoid), SLA was the retained variable in order to see the response of whale presence to these anomalies. ST500 and ST1000 were not used in the models because of the high percentage of missing values (44,4% and 77,3% respectively), which would result in the reduction of the sampling data. Three different models were estimated for each class of sperm whales (family groups, males and Mr. Liable) i) the general model that englobes all sightings of that particular class (not taking into consideration any specific behaviour), ii) the foraging behaviour model where only observations of foraging behaviour of that class were considered, and iii) the other behaviours model that englobes the remaining sightings of that class (when foraging is not observed). Since Mr. Liable, was only observed 9 times not foraging, the model for other behaviours was not performed due to the low number of presences.

Table 2.2: Summary of the models and preferred environmental variables of the different classes of sperm whales performing different behaviours (G – General model; F – Foraging Behaviour; OB – Other behaviour). Deviance explained (D. Explained) and AUC (Area Under the Curve (standard deviation)) are represented to illustrate the performance of the models.

	Depth	SST	SD_SST	GradSST	MixLayer	SLA	D. Explained	AUC (SD)
Groups G	x	x	x		x	x	23.2%	0.83 (0.05)
Groups F	x	x	x		x	x	19.4%	0.83 (0.05)
Groups OB	x	x	x				24.5%	0.86 (0.05)
Males G	x						18.6%	0.82 (0.06)
Males F	x						15.4%	0.82 (0.05)
Males OB	x						18.7%	0.82 (0.1)
Mr. Liable G	x	x		x	x	x	19.3%	0.84 (0.07)
Mr. Liable F	x	x		x	x	x	21.9%	0.86 (0.06)

2.4.3.1 Family Groups

The general model for the groups performed very similar to the foraging model because of the highest representation of the foraging behaviour in the overall sighting of groups (see Appendix C). The foraging model for family groups retained Depth, MSST, SD_SST, and SLA all as smooth variables and MixLayer as a linear variable. The model for other behaviours only retained Depth, MSST and SD_SST. The family groups show a similar response for deeper and warmer waters, for both foraging and other behaviours (Figure 2.11). Family groups always show a preference for waters deeper than 500 m and warmer than 19ºC, approximately (Figure 2.11). However, when foraging, there seems to be a preference for waters around 700 m and/or deeper than 1500 m (Figure 2.11). For other behaviours, family groups show a higher affinity for extreme values of SD_SST, avoiding intermediate values, (although the interpretation of the model should be cautious due to the big confidence intervals) but when foraging only high values of this variable are relevant (Figure 2.11). Additionally, for the foraging behaviour, MixLayer performs as linear covariate with higher values of MixLayer being preferred by the family groups as well as negative values of SLA (Figure 2.11). The foraging and other behaviours models explained 19.4% and 24.5% respectively. The AUC was 0.83 (SD = 0.05) and 0.86 (SD = 0.05), respectively showing a good model performance, despite the low values of deviance explained (Table 2.2).

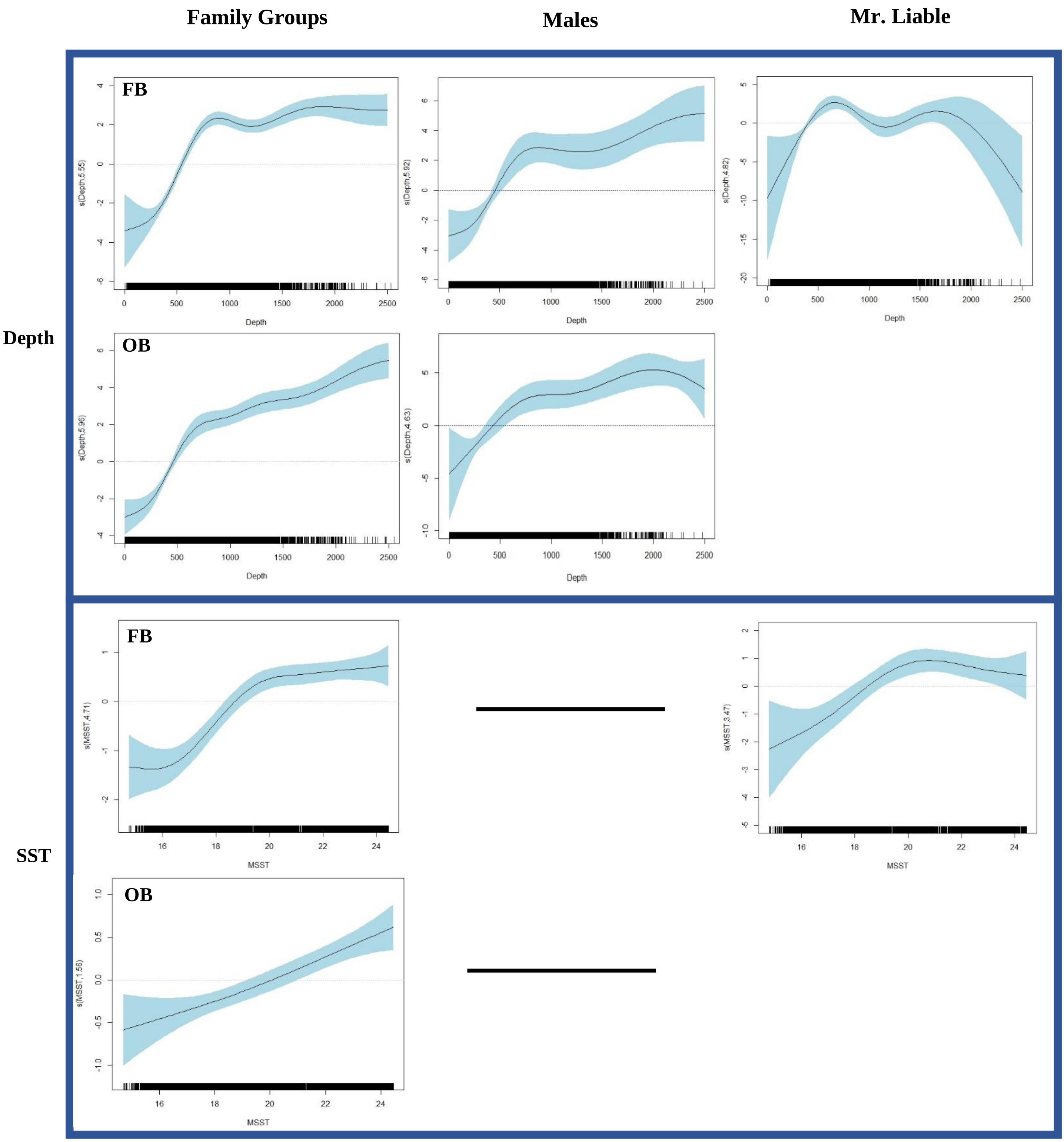
2.4.3.2 Males

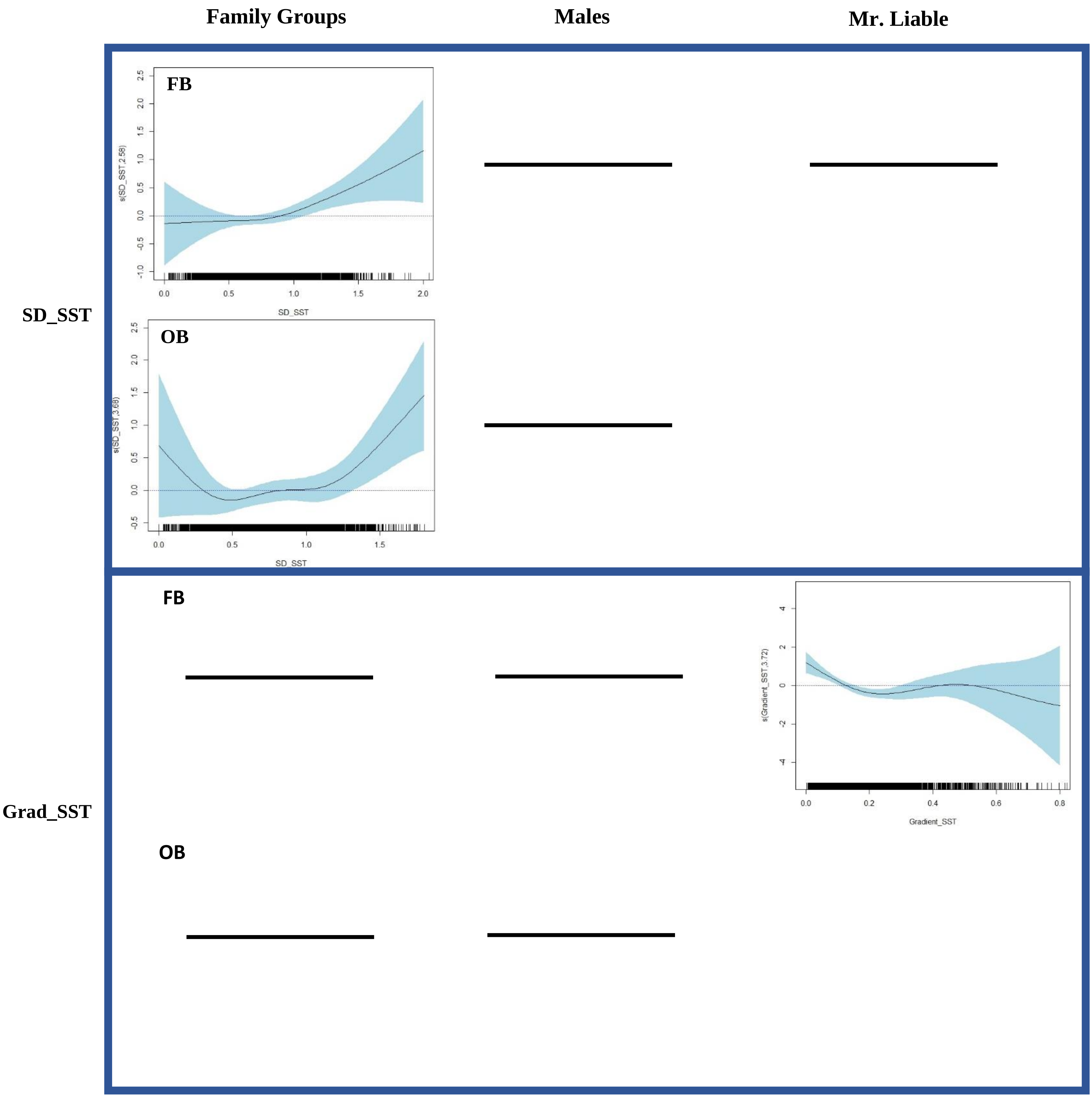
The three models for this class (general model, foraging behaviour model and other behaviours model) only retained depth as a relevant variable and they all behaved similar, showing a preference for waters always deeper than 500 m (Figure 2.11), like the family groups. Males and family groups show a similar response to depth with an increasing preference for deeper waters and, males when in other behaviour, appear to slightly decrease the preference for waters deeper than 2000 m (Figure 2.11). The deviance explained is higher for the other behaviours model (18.7%) when compared with the foraging model (15.4%) and both present the same AUC value (0.82; Table 2.2).

2.4.3.3 Mr. Liable:

Mr. Liable, Pm31 in the photo-ID catalogue of Futurismo Azores Adventures is the only known male spotted year-round in São Miguel Island and has been resighted since 2004 by the same company. This individual is the most photographed and the most sighted sperm whale in the study area (Gardoki et al., 2018; van der Linde & Eriksson, 2020).

Because 91% of Mr. Liable sightings were foraging behaviour, the general model for Mr. Liable (foraging and/or other behaviours) had similar outputs to the Mr. Liable foraging model (see Appendix C). Mr. Liable represents 47.6% of all sightings of solitary males and was spotted 21 times interacting with groups of females. In this case, these sightings were classified as a group sighting and not considered for the models of Mr. Liable. Depth, MSST, Grad_SST, MixLayer and SLA were retained as important variables for the foraging model of Mr. Liable. As the family groups and the males, Mr. Liable also shows a preference for waters above 500 m depth (Figure 2.11). While family groups show a preference for higher values of depth, MSST and MixLayer, Mr. Liable foraging model shows a decrease of occurrence after a peak of 500 and 1800 m for depth, a peak around 21°C for MSST and a peak of 80 m for the MixLayer (Figure 2.11). Although Grad_SST revealed to be a relevant environmental variable for Mr. Liable, only very low values of this variable seems to be preferred (Figure 2.11). Regarding SLA, there seem to be a preference for negative and higher values of SLA and lower occurrence in intermediate values (Figure 2.11). Mr. Liable foraging was the only class that considered Grad_SST as a significant variable, despite the preference for lower values. The explained variance is around 21.9% with an AUC of 0.86 (SD = 0.06) indicating a good model performance (Table 2.2).


Family Groups
Males
Mr. Liable
Depth
SST
FB
OB
FB
OB
s(Depth,5.55)
s(Depth,5.92)
s(Depth,4.82)
s(Depth,5.96)
s(Depth,4.63)
Depth
s(MSST,4.71)
s(MSST,3.47)
s(MSST,1.56)
MSST


Family Groups
Males
Mr. Liable
SD_SST
FB
s(SD_SST,2.58)
SD_SST
OB
s(SD_SST,3.68)
SD_SST
Grad_SST
FB
OB
s(Gradient_SST,3.72)
Gradient_SST

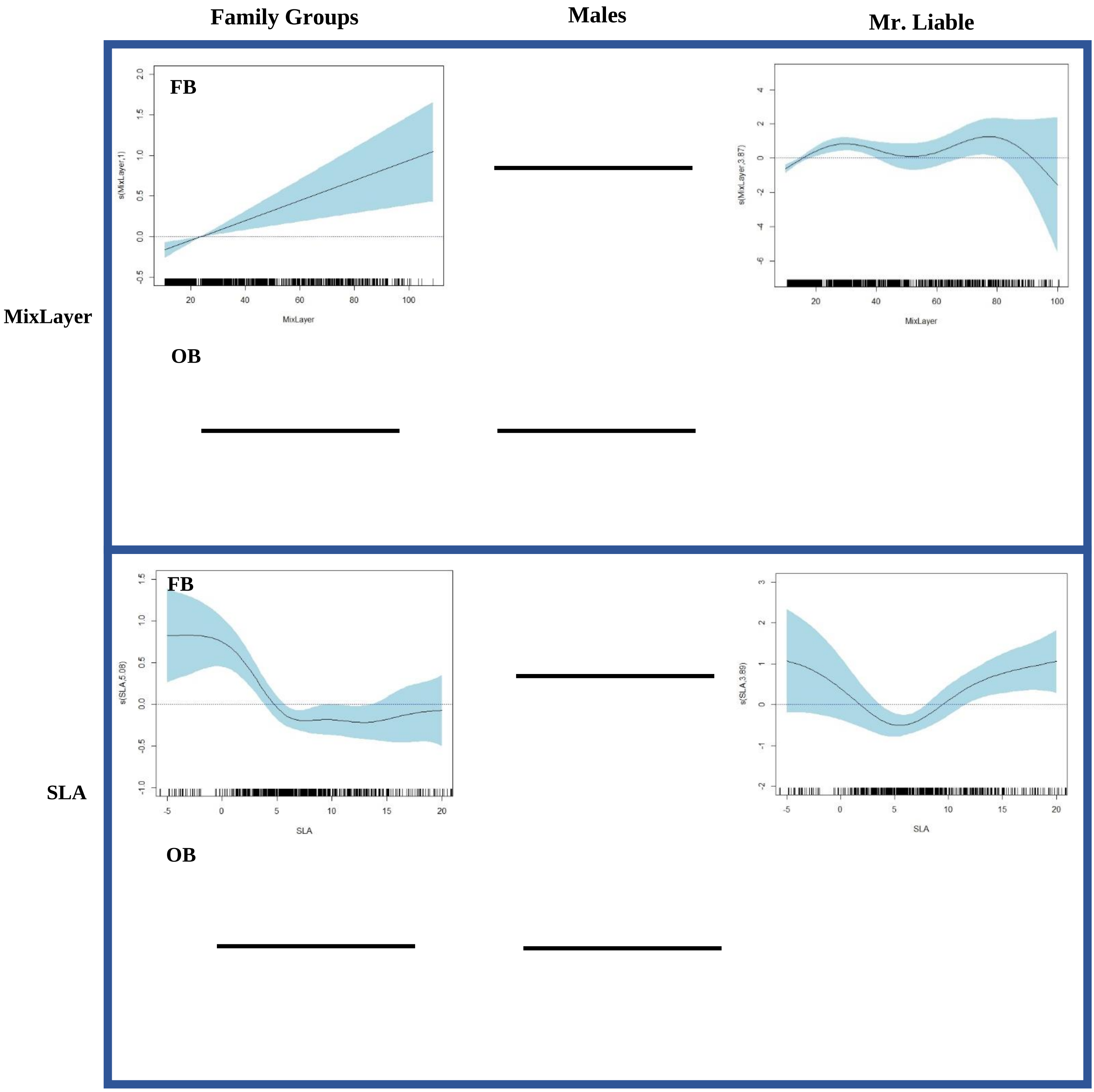


Figure 2.11: Smoothers representing the relationship between the presence of the groups, males and Mr. Liable (columns) and the environmental variables ((blue boxes): Depth; SST – Sea surface temperature; SD_SST – Standard deviation of the sea surface temperature; Grad_SST – Gradient of the sea surface temperature; MixLayer – Thickness of the mixed layer; SLA – Sea level anomaly) taking into consideration different behaviours, Foraging (F) and Other Behaviours (OB) (lines). The blue shades represent 95% confidence intervals.

2.5 Discussion

To the best of our knowledge this was the first research studying the correlation between oceanographic variables and the presence of sperm whales focused on São Miguel Island, one of the busiest coastal areas of the Azores. The complex relationship among bathymetric features and oceanographic parameters seems to influence the distributions and habitat use of sperm whales around São Miguel Island. The divergences between different classes of sperm whales have already been shown by other studies (Pirotta et al., 2011; Pirotta et al., 2020). Sperm whales' behaviour also demonstrated to be a factor that influences the preference for the different environmental variables for females.

2.5.1 Opportunistic Data

The main challenge of this study was regarding the opportunist nature of our data collected by a whale watching company. The lack of real quantification of the effort (land-based surveys plus the time spent on the sea) and the fact that the effort in areas closer to shore and in summer months (better weather conditions) is higher can generate bias. To minimize this problem, we used the presence of other species as the pseudo-absence's points for our models, that were collected under the same effort, this methodology was used by other authors (e.g Esteban et al., 2013; González Garcia et al., 2019). Despite this obstacle, this research shows the value of whale watching companies that provide opportunistic distribution cetacean data in a unexpensive way and year-round.

2.5.2 Environmental preferences of sperm whales:

2.5.2.1 Depth

Depth was the only variable that influenced the presence of sperm whales, regardless of classes or behaviours, with all sperm whales preferring waters deeper than 500 m. The relationship between sperm whale occurrence and deep waters has been consistently shown throughout the world using various methodologies (ex: Hooker et al., 1999; Seabra et al., 2005; Pirotta et al., 2011; Firori et al., 2014; Johnson et al., 2016; Sahri et al., 2020). The spatial distribution of all sperm whales in the 500-1000 m corridor was visible on this study in accordance with what has been described for the Mediterranean by Pirotta et al. (2011) and also in the Azores, during foraging dives by Oliveira et al. (2016). These results can be explained by the vertical distribution of different sized prey species (Roper & Young, 1975) that are preferred by different sized sperm whales (Clarke et al., 1993). Mr. Liable distribution shows a higher concentration of sightings close to Mar da Prata bank, an area with high fishing activity due to high marine life concentration (Santos et al., 2021) and where pronounced thermo-, halo- and picnocline are known to exist (Lafon et al., 2004). The presence of this topographic structures was already demonstrated to be preferred habitats for sperm whales (Wong et al., 2014; Tobeña et al., 2016).

2.5.2.2 Sea surface temperature (SST, SD_SST, Grad_SST)

While in high latitude places the occurrence of sperm whales is related with high values of SST (Diogou et al., 2019) in lower latitudinal areas, including the Mediterranean, colder waters are preferred by the species (Jaquet, 1996; Pirotta et al., 2011; Praca and Gannier, 2008; Rendell et al., 2004). In the study area Mr. Liable shows a preference for waters around 20ºC while family groups seem to prefer warmer waters (foraging and other behaviour), the preference of females for warmer waters when compared with males was also shown in the Mediterranean by Pirotta et al. (2020). The only study that investigated the relationships between sperm whales and environmental variables in the Azores showed that sperm whales in general tend to prefer warmer waters (Seabra et al., 2005). Nevertheless, our results might be biased because of the higher effort incidence during the summer months, a problem that comes inevitably with opportunist whale watching data. Both Grad_SST and SD_SST variables were used in the models to explore the relationship of sperm whales to relative values of SST (anomalies of SST values over time and space) rather than absolute. While the first can be used as a proxy of thermal fronts, the second is a measure of temporal SST variability in the ocean. It was already demonstrated that sperm whales can take advantage of oceanographic thermal fronts, that can provide positive conditions for sperm whale prey (Gannier & Praca, 2007; Diogou et al., 2019). In our study, this correlation was not observable for any class of sperm whales. Although the models considered Grad_SST as an important variable for, Mr. Liable, he revealed a preference for lower thermal gradients. Families preferred areas where SST variability (SD_SST) is more pronounced over a period of time (one month in this case), results also shown by previous studies (Pirotta et al., 2020). The relationship of the sperm whales with SST features should be further studied to better understand the preferences and habitat use of the species. The importance of these studies becomes essential due to the obvious increase of SST in the study area over time.

2.5.2.3 Mixed Layer Depth (MixLayer)

The turbulence in the ocean surface caused by the direct contact with the atmosphere causes a homogenous mixed layer regarding temperature, salinity, and density (Polovina et al., 1995; de Boyer Montégut et al., 2004). In areas with lower nutrient concentrations (like the Azores), deeper mixed layers will supply the scarce deeper nutrients to phytoplankton in the surface and therefore, increase the primary production; the opposite happens in low light regions, where deeper mixed layers will decrease the primary production by sending the phytoplankton to deeper waters (Polovina et al., 1995). Because of this correlation, the mixed layer depth is also used as a proxy for primary production. In our study, the linear relationship of MixLayer values and the occurrence of family groups sperm whales foraging seems to follow the idea of preference for high primary production areas related with the mixed layer depth (Diogou et al., 2019b; Cauchy et al., 2020). Mr. Liable shows a more restrict preference when compared with the females, with a preference for two specific MixLayer peaks (one peak around 30 m and the other around 80 m). Once again, the differences in these two classes might be related with different prey requirements and therefore to reduce conspecific competition.

2.5.2.4 Sea level anomaly (SLA)

Sea level anomaly measurements can be used as a proxy for mesoscale oceanographic processes like eddies. Cold core, cyclonic eddies are related with negative values of SLA; warm core, anti-cyclonic eddies are characterized by positive values of SLA (Zimmerman & Biggs, 1999). Positives values of SLA are associated with downwelling movements which can influence the diversity and density of mesopelagic communities and eventually transform these areas into feeding habitats for higher trophic level (Godø et al., 2012; Della Penna & Gaube, 2020). The preference for negative values of SLA have been shown for sperm whales in general (ex: Davis et al., 2002) but also for females in particular (Pirotta et al., 2020) that can be the result of preferences for nutrient rich, high productivity, and upwelling zones (Caldeira et al., 2002, Davis et al., 2002). Waters with these specifications can aggregate more preys and eventually more feeding opportunities for females (Moors-Murphy, 2014) that prefer exploitation of prey patches (Whitehead, 2003). Mr. Liable shows a preference for low values of SLA (like family groups) but also for higher values. These results suggests that female sperm whales might be losing preferred habitat conditions given the increasing trend of mean SLA values throughout the last eleven years, as demonstrated in this study.

2.5.3 Comparisons of the sperm whale classes

Mature male sperm whales, present a lower feeding success compared with females, immatures, and smaller males, when in the same area together (Whitehead, 2003). This can happen because the females might auto-compete the males in lower latitudes (females are more adapted to lower latitude habitats) and/or the males might give priority to other factors, besides foraging, when with females (Whitehead, 2003). In our study both hypothesis fit in. Mr. Liable affinity for the area creates an unique case of a mature male sperm whale being resighted very often in this latitudinal range (van der Linde & Eriksson, 2020). The fact that Mr. Liable is sighted year-round in the same location as family groups, might have created a necessary divergence regarding oceanographic and bathymetric preferences. This can be translated in exploitation of different food resources and ultimately reduction of competition. Mr. Liable can explore more diverse habitats that might increase his feeding opportunities and therefore his feeding success. The fact that female sperm whales tend to feed mostly on cephalopods while males have a more diverse diet including large demersal fishes (Whitehead, 2009), might explain the divergence in habitat preference between these two classes.

The other mature males, sighted in the Azores are most likely to be aiming for mating, since the Azores is a known breeding ground since the whaling era (Clarke, 1956; Silva et al., 2014). The idea of males giving priority to other factors rather foraging when with females, is reinforced by the absence of significant variables, related with prey presence in their models, as well as a lower percentage of foraging sightings in comparison with family groups. When comparing the time dedicated to foraging by family groups and Mr. Liable, it is evident that for both classes that use the same area year-round, Mr. Liable spends much more of his time foraging. This happens because females and their young must balance their time between socializing, to maintain strong social bonds between their unit individuals, and foraging (Whitehead & Weilgart, 1991). Not foraging family groups did not had any preferences for Grad_SST, MixLayer or SLA, what turned out to be the opposite when foraging. This could happen because the groups might not give importance to oceanographic variables that can be related with prey presence/abundance when performing other behaviours.

The deviance explained by the final models (Table 2.2) demonstrated relatively low explanation for all classes in any specific behaviour, especially for males. When comparing other behaviour models (Groups OB and Males OB in Table 2.2) with foraging models (Groups F and Males F in Table 2.2) we can see that the deviance explained is always higher when the sperm whales are not foraging. Because not foraging sperm whales, do not take into consideration as many environmental variables related with prey occurrence and distribution, modelling habitat preference of this species in these conditions might be more straightforward. To improve the deviance explained of the models, other bathymetric and oceanographic variables must be explored, but also other variables regarding behaviour and social structure characteristics of the sperm whales (e.g. presence of calves and size of the groups). The fact that the AUC values are all above 0.75 (Table 2.2) indicates that, models present a high performance and have the potential to be useful (Elith, Burgman, & Regan, 2002).

2.6 Conclusions

This study gives us the first insight in the different environmental preferences of sperm whales in such a relevant area. Differences in habitat preferences were observed during this study between family groups and males and a possible resident male (Mr. Liable) in the area. The differences in the environmental preferences were demonstrated among gender, behaviour and individuality, because physical characteristics of each sperm whale may influence their capacity to move, forage and even rest (Oliveira, 2014), highlighting the complex societies and ecological requirements of sperm whales:

- Family groups prefer waters characterized to be warm, deep, with high values of mixed layer thickness and negative values of sea level anomaly.

- Mr. Liable demonstrated a preference for wates characterized to be colder, less deep, lower mixed layer thickness values and extreme values for sea level anomaly (high and low).
- Males only showed a preference for deeper waters without any of the other variables being relevant.
- Family groups demonstrated that less environmental variables are relevant when not foraging (excluding mixed layers thickness and sea level anomaly).

Whale watching companies demonstrated to be a valuable platform (when following the correct guidelines for whale and dolphin observation) for long run, and year-round studies that are essential to understand cetacean distribution and habitat use. Habitat preference studies are a fundamental tool for the adequate management of conservation measures for the species and for correct implementation of human activities legislation. Climate change is known to impact all marine life, cetaceans are no exception, in just eleven years of study the variances in SST and SLA are clear, while some species might benefit from it, others will be put under dangerous pressure (van Weelden et al., 2021). Forty years ago, sperm whales faced extinction due to whaling, nowadays the unpredictability of climate change threats them again. Conservation actions are needed to ensure the perpetuation of healthy megafauna in our oceans.

2.7 Bibliography

Azzellino, A., Gaspari, S., Airoldi, S., & Nani, B. (2008). Habitat use and preferences of cetaceans along the continental slope and the adjacent pelagic waters in the western Ligurian Sea. Deep Sea Research Part I: Oceanographic Research Papers, 55(3), 296–32.

Best, P. B. (1979). Social Organization in Sperm Whales, Physeter macrocephalus. Behavior of Marine Animals, 227–289.

Best, B. D., Halpin, P. N., Read, A. J., Fujioka, E., Good, C. P., LaBrecque, E. A., Schick R. S., Roberts, J. J., Hazen, L. J., Qian, S. S., Palka D. L., Garrison, L. P., & McLellan W. A. (2012). Online cetacean habitat modeling system for the US east coast and Gulf of Mexico. Endangered Species Research, 18, 1-15.

Caldeira, R. M. A., Groom, S., Miller, P., Pilgrim, D., & Nezlin, N. P. (2002). Sea-surface signatures of the island mass effect phenomena around Madeira Island, Northeast Atlantic. Remote Sensing of Environment, 80(2), 336-360.

Caldeira, R., & Reis, J. C. (2017). The Azores confluence zone. Frontiers in Marine Science, 4, 37.

Cañadas, A., Sagarminaga, R., De Stephanis, R., Urquiola, E., & Hammond, P. S. (2005). Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. Aquatic conservation: marine and Freshwater Ecosystems, 15(5), 495-521.

Cauchy, P., Heywood, K. J., Risch, D., Merchant, N. D., Queste, B. Y., & Testor, P. (2020). Sperm whale presence observed using passive acoustic monitoring from gliders of opportunity. Endangered Species Research, 42, 133-149.

Clarke, M. R. (1956). Sperm whales of the Azores. Discovery Reports 28, 237-98.

Clarke, M. R., Martins, H. R., & Pascoe, P. (1993). The diet of sperm whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 339(1287), 67-82.

Correia, A. M. (2020). Distribution and habitat modelling for cetacean species in the eastern north Atlantic Ocean.

Davis, R. W., Fargion, G. S., May, N., Leming, T. D., Baumgartner, M., Evans, W. E., ... & Mullin, K. (1998). Physical habitat of cetaceans along the continental slope in the northcentral and western Gulf of Mexico. Marine Mammal Science, 14(3), 490-507.

Davis, R.W., Ortega-Ortiz, J.G., Ribic, C., Evans, W.E., Biggs, D.C., Ressler, P.H., Cady, R.B., Leben, R.R., Mullin, K.D., & Würsig, B. (2002). Cetacean habitat in the northern oceanic Gulf of Mexico. Deep Sea Res. Part I Oceanogr. Res. Pap. 49, 121–142.

de Boyer Montégut, C., Madec, G., Fischer, A. S., Lazar, A., & Iudicone, D. (2004). Mixed layer depth over the global ocean: An examination of profile data and a profile-based climatology. Journal of Geophysical Research: Oceans, 109(C12).

Diogou, N., Palacios, D. M., Nieukirk, S. L., Nystuen, J. A., Papathanassiou, E., Katsanevakis, S., & Klinck, H. (2019). Sperm whale (Physeter macrocephalus) acoustic ecology at Ocean Station PAPA in the Gulf of Alaska–Part 1: Detectability and seasonality. Deep Sea Research Part I: Oceanographic Research Papers, 150, 103047.

Diogou, N., Palacios, D. M., Nystuen, J. A., Papathanassiou, E., Katsanevakis, S., & Klinck, H. (2019). Sperm whale (Physeter macrocephalus) acoustic ecology at Ocean Station PAPA in the Gulf of Alaska–Part 2: oceanographic drivers of interannual variability. Deep Sea Research Part I: Oceanographic Research Papers, 150, 103044.

Della Penna, A., & Gaube, P. (2020). Mesoscale eddies structure mesopelagic communities. Frontiers in Marine Science, 7, 454.

Elith, J., Burgman, M. A., & Regan, H. M. (2002). Mapping epistemic uncertainties and vague concepts in predictions of species distribution. Ecological Modelling, 157(2–3), 313–329.

Esteban, R., Verborgh, P., Gauffier, P., Giménez, J., Afán, I., Cañadas, A., ... & de Stephanis, R. (2014). Identifying key habitat and seasonal patterns of a critically endangered population of killer whales. Journal of the Marine Biological Association of the United Kingdom, 94(6), 1317-1325.

Fais, A., Lewis, T. P., Zitterbart, D. P., Álvarez, O., Tejedor, A., & Aguilar Soto, N. (2016). Abundance and distribution of sperm whales in the Canary Islands: Can sperm whales in the archipelago sustain the current level of ship-strike mortalities?. PLoS One, 11(3), e0150660.

Fiori, C., Giancardo, L., Aissi, M., Alessi, J., & Vassallo, P. (2014). Geostatistical modelling of spatial distribution of sperm whales in the Pelagos Sanctuary based on sparse count data and heterogeneous observations. Aquatic conservation: Marine and freshwater ecosystems, 24, 41-49.

Forney, K. A. (2000). Environmental Models of Cetacean Abundance: Reducing Uncertainty in Population Trends. Conservation Biology, 14(5), 1271–1286.

Gannier, A., & Praca, E. (2007). SST fronts and the summer sperm whale distribution in the north-west Mediterranean Sea. Journal of the Marine Biological Association of the United Kingdom, 87(1), 187-193.

Gardoki, M., González, L., van der Linde, M., Fernández, M., & Azevedo, J., M., N. (2018). Mister Liable, a resident male sperm whale in the Azores?. 32nd conference of the European cetacean society, La Spezia, Italy.

Godø, O. R., Samuelsen, A., Macaulay, G. J., Patel, R., Hjøllo, S. S., Horne, J., ... & Johannessen, J. A. (2012). Mesoscale eddies are oases for higher trophic marine life. PloS one, 7(1) e30161.

González García, L. (2018). Cetacean distribution in São Miguel (Azores): influence of environmental variables at different spatial and temporal scales (Doctoral Dissertation). Retrieved from: http://hdl.handle.net/11093/1218

Gosho, M. E., Rice D. W., & Breiwick J. M. (1984). The Sperm Whale Physeter macrocephalus. Mar Fish Rev, 46(4), 54–64.

Griffin, R. B. (1999). Sperm whale distributions and community ecology associated with a warm-core ring off Georges Bank. Marine Mammal Science, 15(1), 33-51.

Hastie, T., & Tibshirani, R. (1990). Exploring the nature of covariate effects in the proportional hazards model. Biometrics, 1005-1016.

Hooker, S. K., Whitehead, H., & Gowans, S. (1999). Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. Conservation biology, 13(3), 592-602.

Jaquet, N., Whitehead, H., & Lewis, M. (1996). Coherence between 19th century sperm whale distributions and satellite-derived pigments in the tropical Pacific. Marine Ecology Progress Series, 145, 1-10.

Johnson, C. M., Beckley, L. E., Kobryn, H., Johnson, G. E., Kerr, I., & Payne, R. (2016). Crowdsourcing modern and historical data identifies sperm whale (*Physeter macrocephalus*) habitat offshore of South-Western Australia. Frontiers in Marine Science, 3, 167.

Keller, C. A., Garrison, L., Baumstark, R., Ward-Geiger, L. I., & Hines, E. (2012). Application of a habitat model to define calving habitat of the North Atlantic right whale in the southeastern United States. Endagered Species Research, 18, 73-87.

Lafon, V. M., Martins, A. M., Bashmachnikov, I. L., Jose, F., Melo-Rodrigues, M., Figueiredo, M. P., ... & Macedo, L. M. (2004). SST variability in the Azores region using AVHRR imagery: regional to local scale study. In Remote Sensing of the Ocean and Sea Ice 2004 (Vol. 5569, pp. 130-139). International Society for Optics and Photonics.

Lambert, C., Virgili, A., Pettex, E., Delavenne, J., Toison, V., Blanck, A., & Ridoux, V. (2017). Habitat modelling predictions highlight seasonal relevance of Marine Protected Areas for marine megafauna. Deep Sea Research Part II: Topical Studies in Oceanography, 141, 262-274.

Magalhães, S., Silva, M. A., Prieto, R., Quérouil, S., Pinela, A., & Santos, R. S. (2005). Spatial and temporal patterns of sperm whale groups in the Azores archipelago. In Proceedings of the Nineteenth Annual Conference of the European Cetacean Society, La-Rochelle, France (pp. 2-7).

Milligan, M. (2013). Fine-scale distribution, habitat use, and movements of sperm whales (Doctoral dissertation).

Oliveira, C. I. (2014). Behavioural ecology of the sperm whale (Physeter macrocephalus in the North Atlantic Ocean.

Oliveira, C., Wahlberg, M., Silva, M. A., Johnson, M., Prieto, R., Wisniewska, D. M., ... & Madsen, P. T. (2016). Foraging behaviour of the sperm whale in the Azores. 30th conference of the European cetacean society, Madeira, Portugal.

Pace, D. S., Arcangeli, A., Mussi, B., Vivaldi, C., Ledon, C., Lagorio, S., ... & Ardizzone, G. (2018). Habitat suitability modeling in different sperm whale social groups. The Journal of Wildlife Management, 82(5), 1062-1073.

Pinela, A., Quérouil, S., Magalhães, S., Silva, M. A., Prieto, R., Matos, J., & Santos, R. S. (2009). Population genetics and social organization of the sperm whale (*Physeter macrocephalus*) in the Azores inferred by microsatellite analyses. Canadian Journal of Zoology, 87, 802-813.

Pirotta, E., Matthiopoulos, J., MacKenzie, M., Scott-Hayward, L., & Rendell, L. (2011). Modelling sperm whale habitat preference: a novel approach combining transect and follow data. Marine Ecology Progress Series, 436, 257-272.

Pirotta, E., Brotons, J. M., Cerdà, M., Bakkers, S., & Rendell, L. E. (2020). Multi-scale analysis reveals changing distribution patterns and the influence of social structure on the habitat use of an endangered marine predator, the sperm whale Physeter macrocephalus in the Western Mediterranean Sea. Deep Sea Research Part I: Oceanographic Research Papers, 155, 103169.

Praca, E., & Gannier, A. (2008). Ecological niches of three teuthophageous odontocetes in the northwestern Mediterranean Sea. Ocean Science, 4(1), 49-59.

Polovina, J. J., Mitchum, G. T., & Evans, G. T. (1995). Decadal and basin-scale variation in mixed layer depth and the impact on biological production in the Central and North Pacific, 1960-88. Deep Sea Research Part I: Oceanographic Research Papers, 42(10), 1701-1716.

Redfern, J. V., Ferguson, M. C., Becker, E. A., Hyrenbach, K. D., Good, C., Barlow, J., ... & Werner, F. (2006). Techniques for cetacean–habitat modeling. Marine Ecology Progress Series, 310, 271-295.

Rendell, L., Whitehead, H., & Escribano, R. (2004). Sperm whale habitat use and foraging success off northern Chile: evidence of ecological links between coastal and pelagic systems. Marine Ecology Progress Series, 275, 289-295.

Rice, D.W. (1989). Sperm whale. *Physeter macrocephalus* Linnaeus, 1758. In Handbook of marine mammals. Vol. 4. Edited by S.H. Ridgway and R. Harrison. Academic Press, London. pp. 177–233.

Roper, C. F., & Young, R. E. (1975). Vertical distribution of pelagic cephalopods. Smithsonian contributions to zoology.

Sahri, A., Putra, M. I. H., Mustika, P. L. K., & Murk, A. J. (2020). A treasure from the past: Former sperm whale distribution in Indonesian waters unveiled using distribution models and historical whaling data. Journal of Biogeography, 47, 2102–2116.

Santos, R., Medeiros-Leal, W., Novoa-Pabon, A., Silva, H., & Pinho, M. (2021). Demersal fish assemblages on seamounts exploited by fishing in the Azores (NE Atlantic). Journal of Applied Ichthyology, 37(2), 198-215.

Seabra, M.I., Silva, M., Magalhães, S., Prieto, R., August, P., Vigness-Raposa, K., Lafon, V. and Santos, R.S. (2005) Distribution and habitat preferences of bottlenose dolphins (*Tursiops truncatus*) and Sperm Whales (*Physeter macrocephalus*) with respect to physiographic and oceanographic factors in the waters around the Azores (Portugal). In: Proceedings of the 19th Annual Conference of the European Cetacean Society (ed. Evans, P.G.H.). ECS, La Rochelle.

Silva, M. A., Prieto, R., Magalhães, S., Cabecinhas, R., Cruz, A., & Gonçalves, J. M. (2003). Azores (Portugal), Summer and Autumn 1999–2000. Aquatic Mammals, 29, 77-83.

Silva, M., A., Prieto, R., Jonsen, I., Baumgartner, M. F., & Santos, R. S. (2013). North Atlantic Blue and Fin Whales Suspend Their Spring Migration to Forage in Middle Latitudes: Building up Energy Reserves for the Journey?. Plos One, 8(10).

Silva, M. A., Prieto, R., Cascão, I., Seabra, M. I., Machete, M., Baumgartner, M. F., & Santos, R. S. (2014). Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. Marine Biology Research, 10(2), 123–137.

Tepsich, P., Rosso, M., Halpin, P. N., & Moulins, A. (2014). Habitat preference of two deep diving cetacean species in the northern Ligurian Sea. Marine Ecology Progress Series, 508, 247-260.

Tobeña, M., Prieto, R., Machete, M., & Silva, M. A. (2016). Modeling the potential distribution and richness of cetaceans in the Azores from fisheries observer program data. Frontiers in Marine Science, 3, 202.

van Weelden, C., Towers, J. R., & Bosker, T. (2021). Impacts of climate change on cetacean distribution, habitat and migration. Climate Change Ecology, 100009.

van der Linde, & M., Eriksson, I. K. (2019). An assessment of sperm whale occurrence and social structure off São Miguel Island, Azores using fluke and dorsal identification photographs. Marine Mammal Science, 2019, 1-19.

Whitehead, H., & Weilgart, L. (1991). Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. Behaviour, 118 (3/4), 275-296.

Whitehead, H. Sperm whales: social evolution in the ocean. University of Chicago Press, 2003.

Whitehead, H., & Rendell, L. (2004). Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. Journal of Animal Ecology, 73(1), 190-196.

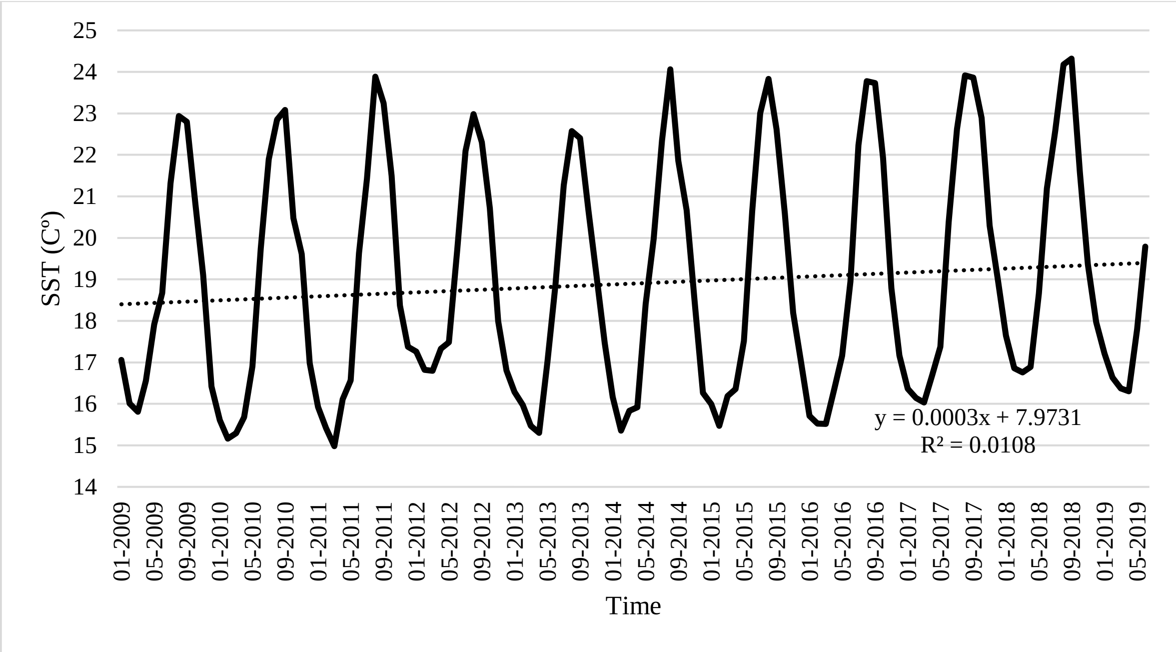
Whitehead, H. (2009). "Sperm whale *Physeter macrocephalus*" in Encyclopedia of Marine Mammals, 2nd Edn., eds W. F. Perrin, B. Würsig and J. G. M. Thewissen (New York, NY: Academic Press), 1091–1097.

Wiley, E. O., McNyset, K. M., Peterson, A. T., Robins, C. R. & Stewart, A. M. (2003) Niche modeling and geographic range predictions in the marine environment using a machine-learning algorithm. Oceanography 16(3):120–127.

Wong, S. N., & Whitehead, H. (2014). Seasonal occurrence of sperm whales (*Physeter macrocephalus*) around Kelvin Seamount in the Sargasso Sea in relation to oceanographic processes. Deep Sea Research Part I: Oceanographic Research Papers, 91, 10-16.

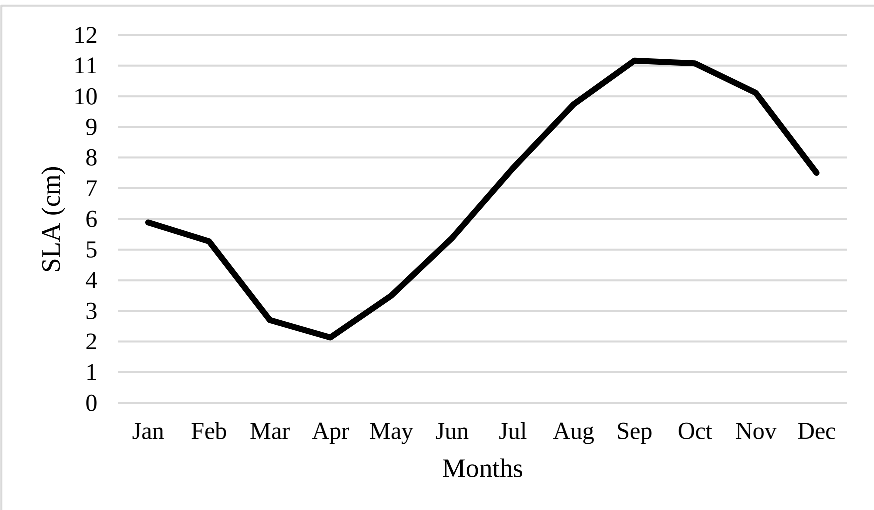
Zimmerman, R. A., & Biggs, D. C. (1999). Patterns of distribution of sound-scattering zooplankton in warm-and cold-core eddies in the Gulf of Mexico, from a narrowband acoustic Doppler current profiler survey. Journal of Geophysical Research: Oceans, 104(C3), 5251-5262.

Appendix A



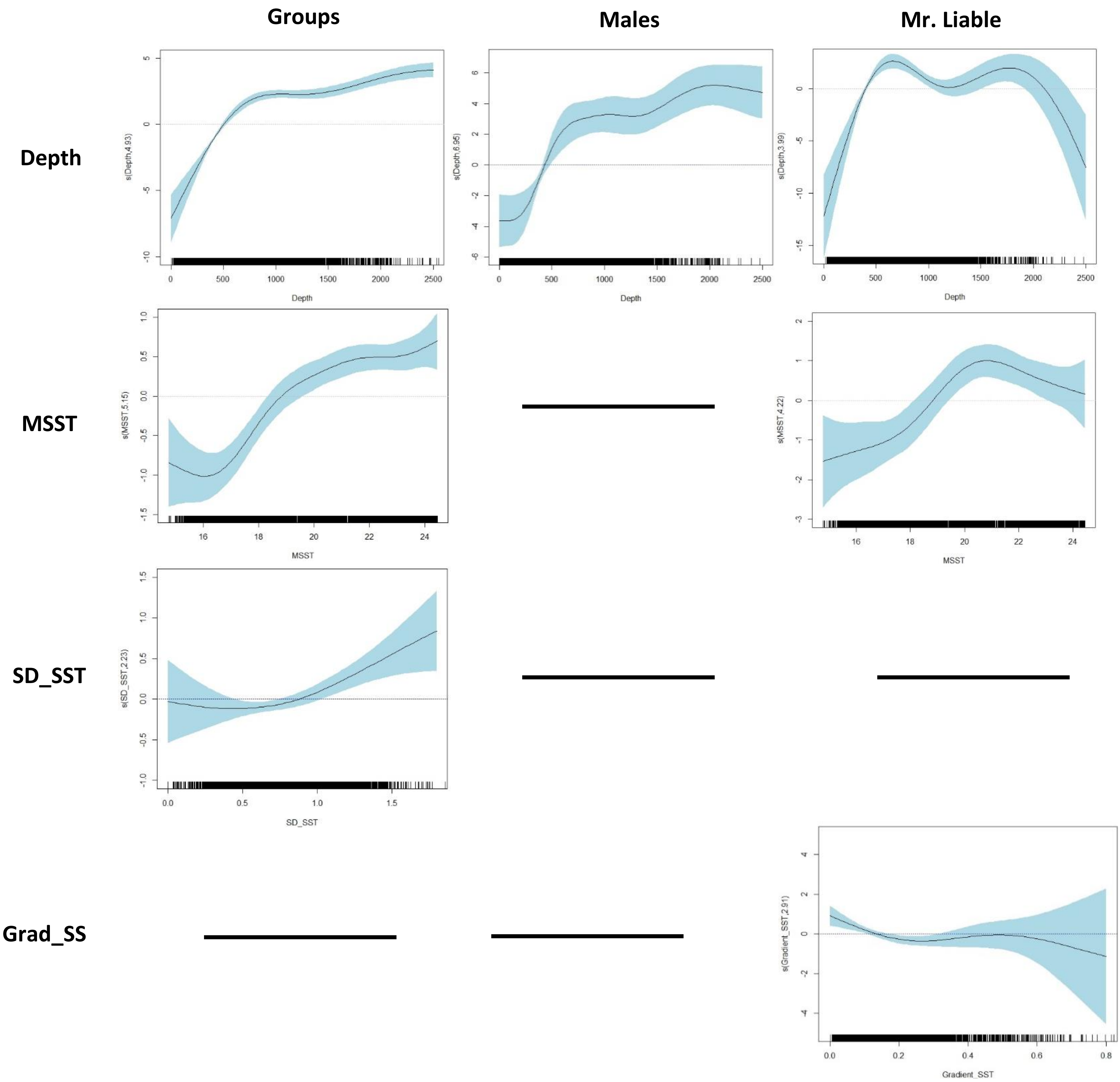
Variation of the sea surface temperature (SST) throughout the study period and the linear tendency (dashed line) with the respective linear predictors.

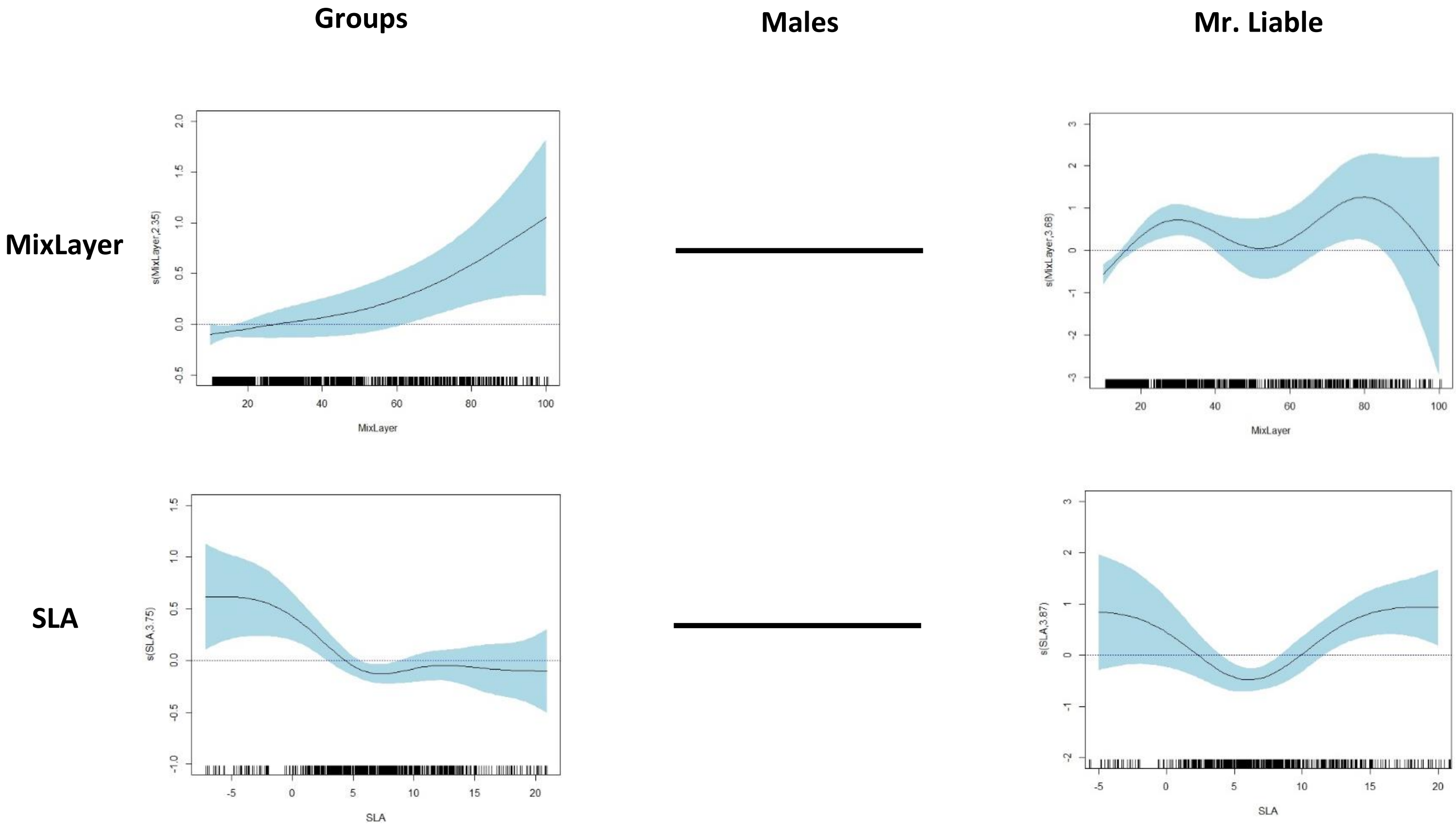
Appendix B



Seasonality of the sea level anomaly (SLA) showing the monthly mean throughout the study period.

Appendix C


Groups
Males
Mr. Liable
Depth
MSST
SD_SST
Grad_SS
s(Depth,4.93)
s(Depth,6.95)
s(Depth,3.99)
Depth
s(MSST,5.15)
s(MSST,4.22)
MSST
s(SD_SST,2.23)
SD_SST
s(Gradient_SST,2.91)
Gradient_SST



Smoothers representing the relationship between the presence of the family groups, males and Mr. Liable and the environmental variables (Depth; SST – Sea Surface Temperature; SD_SST – Standard deviation of the sea surface temperature; Grad_SST – Gradient of the sea surface temperature; MixLayer – thickness of the mixed layer; SLA – sea level anomaly). The blue shades represent 95% confidence intervals.