Gerard Subiron Moreso

Understanding sperm whale (*Physeter macrocephalus*) in Pico Island, Azores

UNIVERSIDADE DO ALGARVE

Faculdade de Ciências e Tecnologia

2021

Gerard Subiron Moreso

Understanding sperm whale (*Physeter macrocephalus*) in Pico Island, Azores

Mestrado em Biologia Marinha

Supervisors:

Dr. Rita Castilho

Co-supervisor

Rui Peres dos Santos

UNIVERSIDADE DO ALGARVE

Faculdade de Ciências e Tecnologia

2021

Declaração de autoria de trabalho

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

Gerard Subiron Moreso

Gerard Subiron Moreso

ABSTRACT

Photo-identification has proven a reliable tool to study cetacean species such as the sperm whale (*Physeter macrocephalus*). Sperm whales have a worldwide distribution that differs between females and males. Females and immature social units are mostly found in tropical and subtropical waters such as the Azores, and males more frequently in higher latitudes. In this study, the use of whale watching as an opportunistic platform to acquire almost year-round data, allowed to assess the sperm whale occurrence, distribution, social structure, and behaviours displayed around Pico Island, Azores during a seven-year period (2012 to 2018). Individuals were photo-identified, and a database of 4851 fluke photographs were visually analysed by three independent researchers, which yielded a sperm whale catalogue for Pico (n = 516). From all catalogued whales, most were sighted only one time in the study period (78%). However, for some individuals it was found a pattern of seasonal residency, with times of individual permanence up to 72 days. Most sightings accounted for females and immature individuals, including calves, which appeared more abundant in summer. Sperm whales off the Azores presented a similar unit size displayed in other regions of the Atlantic Ocean. Male sperm whales, despite the small sample size, were more abundant in summer, and presented different foraging diving times than females. Spatial distribution analysis was performed by calculating the encounter rates for the study area using the sightings and effort. We observed homogeneous distribution, although additional research should be made in some areas. Environmental variables such as depth, distance to coast and sea surface temperature appeared to be a factor influencing the sperm whale occurrence in the area, and more research is needed to provide conclusive answers. Opportunistic platforms such as whale watching, despite some limitations, have proven helpful to obtain cost-efficient and reliable data for research purposes.

RESUMO

O cachalote (*Physeter macrocephalus*) é considerado, por muitas razões, um animal de extremos: grandes dimensões corporais, dimorfismo sexual, mergulhos profundos e longos, ampla distribuição, entre muitas outras. São as espécies mais icónicas do mar dos Açores, fundamental para o desenvolvimento do Arquipélago durante o período da "Caça à Baleia", sendo atualmente o principal alvo da atividade de observação de cetáceos, e de diversos trabalhos de investigação.

É uma espécie presente em todos os Oceanos, mas a sua distribuição difere substancialmente entre as fêmeas e machos. As fêmeas habitam águas tropicais e subtropicais como os Açores, e os machos habitam latitudes mais elevadas, inclusive zonas polares, e só regressam a latitudes mais baixas, presumivelmente para reprodução.

O cachalote é um animal extremamente social. Pequenos grupos de fêmeas e imaturos constituem o nível fundamental da estrutura social, a "unidade", onde os indivíduos são geneticamente próximos, e com uma filiação parcialmente matrilinear ao longo de vários anos. Agregações de nível superior, tais como "grupos" e "clãs", existem temporariamente em certas áreas. Os cachalotes machos, quando se dispersam dos seus grupos natais, formam grupos de machos jovens, que à medida que atingem a fase adulta, os grupos tendem a ser menores, até se tornarem animais solitários quando sexualmente maturos, migrando para latitudes mais elevadas durante este processo.

O cachalote é o maior predador do mundo, alimentando-se predominantemente de cefalópodes, especialmente de lulas, geralmente a profundidades de pelo menos 500 m, podendo inclusive alimentar-se de lulas gigantes. Os peixes representam a segunda presa mais abundante nos estômagos do cachalote, e a frequência e importância desta presa varia de região para região. Estudos revelaram a presença de apenas 13% de peixe nos estômagos desta espécie em águas açorianas.

O Arquipélago dos Açores é constituído por nove ilhas vulcânicas divididas em três regiões (ocidental, central e oriental) espalhadas ao longo da Crista Médio-Atlântica, entre 37º a 40ºN e 25º a 32ºW. A estreita plataforma continental caracteriza esta área, proporcionando um ambiente adequado para muitas espécies de cetáceos, inclusive o cachalote, permitindo avistar estes animais muito perto da costa.

O cachalote sempre foi uma espécie de interesse, primeiro pelas embarcações baleeiras americanas que as caçaram em águas açorianas e depois com o desenvolvimento de uma atividade mais tradicional durante cerca de 90 anos, terminando a mesma em 1986. Nas últimas décadas desenvolveu-se muitos estudos científicos e uma crescente indústria de observação de baleias, que começou três anos após o fim da atividade baleeira. O principal foco da investigação tem sido a estrutura social, o comportamento, a dieta e a acústica. Nos Açores, a maior parte dos estudos são realizados nas águas da ilha de São Miguel. Mas, no presente estudo quisemos analisar a população em redor da ilha do Pico para aumentar o conhecimento de outra zona do Arquipélago, com base em dados de foto-identificação e usando uma plataforma oportunista como a observação de baleias.

A foto-identificação, em embarcações de observação de cetáceos, provou ser uma ferramenta fiável para a investigação de espécies de cetáceos, tais como o cachalote. Nesta espécie, são utilizadas principalmente fotografias da barbatana caudal para sua identificação, em que os principais elementos para diferenciar os indivíduos é o contorno da barbatana que pode apresentar cortes e cicatrizes, por vezes também se utiliza a pigmentação presente na barbatana. Recentemente, foi testada positivamente a viabilidade da utilização da barbatana dorsal como uma potencial ajuda para a identificação.

O principal objetivo do estudo foi avaliar a população do Pico, com especial enfoque na ocorrência, estrutura social e comportamento, bem como padrões ambientais que pudessem definir a sua distribuição na área de estudo. Queríamos testar a hipótese de que os cachalotes no Pico têm a mesma organização social e padrões de comportamento exibidos noutras regiões do mundo. Além disso, compreender se a distribuição dos cachalotes está ligada a certos parâmetros ambientais.

Os dados de avistamentos de cachalotes utilizados para este projeto foram recolhidos oportunisticamente de 2012 até 2018 durante 1452 viagens comerciais de observação de cetáceos em duas empresas que operam a partir das Lajes do Pico (Espaço Talassa e Futurismo). Como a investigação não era o objetivo principal da atividade, a recolha de dados padronizados, sempre registados manualmente, foi restringida para interferir o menos possível com o objetivo principal, o turismo. Além disso, a observação de baleias opera no Pico principalmente de Abril a Outubro, excluindo o Inverno do estudo. O resultado destas viagens foram 4851 fotografias de foto-identificação de cachalotes, dados de posição, hora de observação, tamanho e composição do grupo, comportamento, e outras observações quando possível (por exemplo, tamanho, sexo, e ciclo de mergulho).

Todas as fotografias foram analisadas visualmente por três investigadores independentes, o que deu origem a um catálogo de cachalotes para o Pico (n = 516). De todos os indivíduos catalogados, a maioria foi avistada apenas uma vez durante o período de estudo (78%). No entanto, para alguns indivíduos, foi encontrado um padrão de residência sazonal, com períodos de permanência até 72 dias. A maioria dos avistamentos foram de fêmeas e indivíduos imaturos, incluindo crias, que foram mais abundantes no Verão. Os cachalotes machos, embora escassos neste estudo, os seus avistamentos também atingiram o auge durante o Verão, especialmente em Julho. Apesar do pequeno tamanho da amostra, os machos apresentavam tempos de mergulho significativamente diferentes dos das fêmeas (77 min de machos Vs 54 min de fêmeas).

Os grupos de fêmeas neste estudo apresentaram tamanhos "unitários" de 5,18, semelhantes a outras regiões do Oceano Atlântico. No Oceano Pacífico, os tamanhos "unitários" são normalmente maiores, possivelmente devido à presença em maior abundância nestas águas dos seus predadores naturais, as orcas, uma vez que o cachalote se defende social e comunitariamente. No entanto, um método padronizado deve ser utilizado em estudos futuros para confirmar a organização social exibida no Pico.

A busca de alimento foi o comportamento primário observado no estudo (43,15%). Este resultado, embora inferior ao da literatura, deve-se possivelmente à metodologia de recolha de dados e um resultado do tempo limitado disponível para observações em atividades de observação de cetáceos (30 min).

A análise da distribuição espacial foi realizada através do cálculo das taxas de encontro para a área de estudo, utilizando os avistamentos e o esforço. Observámos uma distribuição homogénea, embora devesse ser feita investigação adicional em algumas áreas dispersas que apresentavam taxas de encontro mais elevadas. As variáveis ambientais tais como profundidade, distância à costa e temperatura da superfície do mar foram obtidas de diferentes fontes e parecem fatores que influenciam a ocorrência de cachalotes na área. Por exemplo, observámos um claro intervalo de profundidade dos cachalotes ao largo do Pico, variando entre 600 e 1700 m. Também, a maioria dos cachalotes avistados (75%) foram registados com uma temperatura à superfície do mar acima dos 19ºC. No entanto, são necessários mais estudos para fornecer respostas conclusivas. Plataformas oportunísticas como a observação de cetáceos, apesar de algumas limitações, revelaram-se úteis para a obtenção de dados, economicamente muito pouco dispendiosas e fiáveis para fins de investigação.

STATE OF THE ART

Cetaceans are one of the most iconic and charismatic components of ocean biodiversity (Braulik et al., 2017). This charisma gives them a flagship status, which helps to achieve conservation goals and outreach. Classified as megafauna, they have a vital role in maintaining the structure of marine ecosystems and their functions, both by bottom up- and top-down forcing (Bowen, 1997; Roman & McCarthy, 2010, Roman et al., 2014; Kiszka et al., 2015; Ballance, 2018). Some of the functions include to promote nutrient flux from the bottom to the surface through the whale pump, and from high productivity, high latitude feeding areas to low latitude calving areas; to be important consumers due to large body sizes and high metabolic rates; to provide habitat and food to bottom communities when animals die (Bowen, 1997; Roman et al., 2014; Ballance, 2018).

Whaling was the main threat for cetaceans in past centuries, especially after the appearance of industrial whaling. The most valuable item was the spermaceti oil, extracted from sperm whales (*Physeter macrocephalus*), but almost everything was used: their blubber, rendered into oil and used for fuel, lubrication and the manufacture of nitroglycerine; meat, and whalebone, used to create flour to fertilize the fields; and ambergris, used as a fixative for perfumes (Roman et al., 2014). Commercial whaling induced many cetaceans to be endangered, leading to declines of the populations ranging from 66% to 90%, and an estimated total whale biomass reduction of 85% (Branch & Williams 2006; Christensen 2006).

Nowadays, the main pressures and stressors the cetaceans face in offshore waters are the intense shipping traffic, plastics, military exercises, seismic surveys for oil and gas exploration, and marine research (Silva et al., 2013), which could lead to further declines in the populations (Lewison et al., 2004; Heithaus et al., 2008). More information about habitat use and population size is needed to properly assess the magnitude of the impact, and offer solutions (Jewell *et al.*, 2012; Kaschner et al., 2012; Silva et al., 2013; Braulik et al., 2017). The great whale populations continue to recover from whaling, but it is difficult to know the original numbers due to the scarce and bad quality data available (Christensen, 2006). Also, it is uncertain whether they will be able to ever reach the pre-whaling densities, because of the many anthropogenic impacts in the oceans (Christensen, 2006). The loss of these animals could have severe ecological consequences, such as an impact in the ecosystem services or destabilization of food webs (Katona & Whitehead, 1988; Bowen, 1997; Roman et al., 2014).

The distribution and relative abundance of cetaceans in offshore North Atlantic waters are still relatively unknown, and the current information from European Atlantic waters comes from large-scale international surveys. The least area covered is the Mid-Atlantic ridge (Silva et al., 2013). Most baleen whales migrate throughout the year, going from low latitudes, where they breed, to high latitudes, where they feed (Simon et al., 2010). Mid-latitude areas such as the Azores Islands, offer the possibility to forage during the migrations towards summer feeding grounds, and therefore we can spot annually the species in such places (Visser et al., 2011).

The Archipelago of the Azores is in the middle of the North Atlantic, spread along the Mid-Atlantic Ridge, approximately 1500 km from Europe and 3000 km from the US (Silva et al., 2013). The Azores are a group of nine volcanic islands, which results in a very narrow continental shelf. This condition, among others, provides a suitable environment for many cetacean species, and makes the Azores a perfect place to sight these animals close to the shore (Santos et al., 1995). The Azorean archipelago is strongly influenced by the Gulf Stream, which efficiently transports warm water of equatorial and tropical origin into colder northern waters. The Gulf stream splits at about 40” N into the North Atlantic Current, which influences the northern part of the Azores, and the Azores Current, which influences the southern part. This pattern results in the high salinity, high temperature, and low nutrient regime that typifies the Azores (Santos et al., 1995). The Azores current, later, is the main feeder of the Madeira Current and Canaries Current.

A total of 28 cetacean species have been documented in Azores (Borges et al., 2010; Silva et al., 2013), some of them, *Physeter macrocephalus*, *Delphinus delphis*, *Tursiops truncates*, and *Grampus griseus*, inhabiting those waters year-round. Some other species, including *Balaenoptera physalus*, *Balaenoptera musculus*, *Balaenoptera borealis*, or *Stenella frontalis* are regular seasonal visitors (Silva et al., 2013). Sperm whale is the main target species for whale watching activity in the Azores Islands. South of Pico Island is a concurred area for this activity (Magalhães et al., 2002). The season in this island spans at least from April to October while in São Miguel it is year-round.

The sperm whale (*Physeter macrocephalus*) is defined as an animal of extremes (Whitehead, 2018). Belongs to the odontocetes, or toothed whales, and went its own way shortly after the odontocete-mysticete division with an anagenesis evolution (Fordyce, 2018), making it the most phylogenetically distinct of all living species in this group (Whitehead, 2003). Its closest relatives are the Kogiids: pygmy sperm whale (*Kogia breviceps*) and dwarf sperm whale (*Kogia simus*), much smaller than its predecessor. Kogiids separated from the sperm whale lineage at least 8 Ma (Berta & sumich, 1999).

Morphologically, sperm whales are characterized by the prominent head that covers between a quarter and a third of the body (Whitehead, 2003). Inside the head resides the spermaceti organ, – spermaceti oil is the reason behind the common name of "sperm whale", because the substance has some resemblance to semen and its function was misinterpreted – involved in the production of sound (Clarke, 1956; Norris & Harvey, 1972; Cranford, 1999). The blowhole is also unusual, located in the left side of the head and with an S-shape. The lower jaw is outlined in white, and the only jaw that develops teeth (Whitehead, 2003). Moving from the head and following the back, we reach the dorsal fin, which is low and rounded, and is usually followed by a series of knuckles (Whitehead, 2003). Finally, the fluke, very important for research, has a pattern of marks and scars in the trailing edge that can be used to identify individuals by photo-identification (Whitehead, 2003).

Sperm whales are the largest among the odontocetes and the most sexually dimorphic cetaceans, together with killer whales (*Orcinus orca*) (Whitehead, 2018). Adult males can reach lengths close to 20 m, whereas in females the maximum is 12 m (Rice, 1989). Also, males have a more prominent head with a characteristic bump at the end of the spermaceti, that only some mature females develop in a less pronounced way.

They have the most global distribution of all marine mammal species, only rivalled by the killer whale (Whitehead, 2018), one of the reasons that explains their anagenesis evolution (Fordyce, 2018). The distribution ranges from the equator to the edges of the pack ice, through all deep oceans of the world (Rice, 1989), although it is completely different between sexes. Females inhabit latitudes less than 40º, with few exceptions, and with water deeper than 1000 m (Rice, 1989). When young males separate from female groups, something between 4 and 21 years of age, migrate gradually to high latitudes (Whitehead, 2018). Larger males are found until the edge of the pack ice in both hemispheres, and contrary to females, are regularly sighted at less than 1000 m depth. They only return to lower latitudes, where females inhabit, for breeding (Whitehead, 2018).

Current population of sperm whales was estimated by Whitehead (2002) extrapolating from surveys that covered 24% of their habitat. His results suggest a population of 360.000 animals and a pre-whaling number of 1.110.000 (Whitehead, 2002). Nowadays, after the impact of whaling, IUCN Red List of Threatened species classifies sperm whale globally as vulnerable (Taylor et al., 2019), except for the Mediterranean population, considered endangered due to having less than 2.500 individuals (Notarbartolo di Sciara et al., 2012). Traditional whaling accounted for 23.557 sperm whale catches between 1896 and 1987 in the Azores (Prieto et al., 2013). A recent study detected 393 different individuals in São Miguel during the period from 2010 to 2017 (Linde & Eriksson, 2019), from which we can observe a large decline in the abundance.

Sperm whales are social animals; their social structure was first studied in Sri Lanka (Gordon, 1987) and then developed in other areas, such as the Caribbean (Gordon et al., 1998; Gero et al., 2015) or Galapagos (Whitehead & Kahn, 1992; Christal et al., 1998; Cantor & Whitehead, 2015). The studies have shown that sperm whale social structure is based on a hierarchy of levels (Whitehead et al., 2012). The fundamental level is the "unit", corresponding to a small group of females and immature whales that have a stable and partially matrilineal membership over several years (Whitehead et al., 1991; Christal et al., 1998; Whitehead et al., 2012; Gero et al., 2014) and with the individuals often being related (Richard et al., 1996; Christal et al., 1998; Mesnick, 2001; Gero et al., 2008; Konrad et al., 2018). The "group" level is an association between one or several social units for a short time, ranging from hours to days (Whitehead et al., 1991; Christal et al., 1998; Whitehead, 2003). The highest level, "clans" are composed of multiple social units, which contain thousands of individuals spread across large areas and have in common a similar vocal repertoire (Rendell & Whitehead, 2003; Gero et al., 2016).

Aggregations depend on the habitat and circumstances; some possible drivers could be oceanographic differences, predation, effects of whaling, and culture. For example, in the Pacific Ocean, grouping is more common than in the North Atlantic Ocean, probably for protection against predation by killer whales, because in the Atlantic they are not a significant threat (Pitman et al., 2001; Whitehead et al., 2012).

A common practice among female groups is the communal care of the calves. Many Studies of social behaviour reported alloparental care: different females babysitting the same calf, and sometimes even suckling them (Best, 1979; Gordon, 1987; Gero et al., 2009; Gero et al., 2013). When calves are present, deep dives seem less synchronised, so at least one adult stays on the surface babysitting the calf (Whitehead, 1996), although it is not always the case and can be sighted alone. This behaviour might be a driver for the social evolution of sperm whales, to protect the calves and increase offspring survival (Whitehead, 1996; Gero et al., 2013).

Male sperm whales have a different social pattern. After dispersing from their natal groups, they form bachelor groups (Best, 1979; Richard, 1995). As males mature, they form increasingly smaller groups until they tend to be solitary at sexual maturity at around 18 years of age and move increasingly to higher latitudes (Best 1979; Richard, 1995; Schakner et al., 2014). The typical prey of sperm whales, squids, may be less abundant in high latitudes, so their feeding habitats change to species with higher energetic content. This change may be the main reason to have the most significant sexual dimorphism in the cetacean world, although there are other theories, such as contest competitions to access females or for a better adaptation to cold (Best, 1979; Ralls & Mesnick, 2009). Only for breeding, sperm whales return to tropical and temperate waters to encounter the mixed groups, integrated by females and immature individuals, which spend their lives in temperate and/or tropical waters (Best, 1979; Richard, 1995; Christal & Whitehead, 1997).

Sperm whale is a deep-diving predator (Papastavrou et al., 1989) that has a generalist teuthophagous diet, that is, it preys on cephalopod species (Whitehead et al., 2003). The foraging dives are usually below 500 meters depth, in the meso and benthopelagic area, where they prey on different species of squids, represented in 17 families (Kawakami, 1980; Martin & Clarke, 1986; Whitehead, 2003). Prey range in size, and activity, from the small chiroteuthids (less than 100 g) to the architeuthids, or giant squids (up to 400 Kg) (Whitehead, 2003). Larger squids like *Dosidicus gigas* provide a better meal from a nutritional point of view, but also present a bigger challenge to capture than smaller gelatinous species, which are the primary food for sperm whales most of the time (Clarke et al., 1993; Whitehead, 2003). In general, adult male sperm whales eat larger squid species and larger individuals from the same species than females (Clarke, 1980; Clarke et al., 1993; Best, 1999) and because of that difference, Clarke (1980) estimated males to eat 350 squid per day and females 750.

Fish are the second most abundant prey in the sperm whale diet, usually at very low rates compared to cephalopods, but can be rather important at the northern parts of Pacific and Atlantic Oceans as well as in New Zealand waters, and off Iceland, fish appear to be more important than cephalopods (Kawakami, 1980; Whitehead, 2003). Fishes occur in 13% or less of sperm whale stomachs in the Azores (Clarke, 1956), whereas in Iceland occur in 98% (Roe, 1969).

The diet composition is based on stomach content and faecal samples studies, counting, and identifying the lower beaks of the cephalopods (Martin & Clarke, 1986; Clarke et al., 1993; Smith & Whitehead, 2000). Recent studies, conducted with Carbon and Nitrogen isotopes have corroborated the results (Ruiz-Cooley et al., 2004; Marcoux et al., 2007).

To locate prey in the darkness of the deep ocean sperm whales need to echolocate. The sound is produced thanks to the air sacs inside the spermaceti, which create and concentrate the clicks for a powerful directional echolocation (Norris & Harvey, 1972; Cranford, 1999; Mohl et al., 2000), in fact, sperm whale sound is the highest biologically produced sound ever recorded, reaching 223 dB re 1 μPa (Mohl et al., 2000).

Apart from echolocation, sperm whale vocalizations are also a way to communicate, and depending on the pattern of clicks, will serve a purpose or another, or in some cases, both (Whitehead, 2003). Scientists agree in five click patterns: “usual clicks”, the most common and used during deep dives in search for prey, characterised to be a long train of regular spaced clicks (Norris & Harvey, 1972; Jaquet et al, 2001); “creaks” are much more closely spaced than usual clicks and are produced both at surface and at depth (Jaquet et al., 2001); “codas” are mainly produced by social females and consist in three to twenty clicks made during exchanges with other whales, and are the ones that define clan association level (Watkins & Schevill, 1977; Rendell & Whitehead, 2003); “slow clicks” are produced by males, and consist in repeated ringing clicks every 6-8 seconds, thought to be related with mating systems, to attract females (Weilgart & Whitehead, 1988); “gunshots” are the least know sounds because there are few recordings, they are loud, impulsive broadband sounds of long duration (ca. 400ms) that look similar to slow clicks, so might be a variant of them (Goold, 1999). Alternative hypothesis suggests that gunshots serve to stun prey (Norris & Mohl, 1983).

Sperm whales spend around 75% of the time foraging (Whitehead & Weilgart, 1991; Gordon & Steiner, 1992; Whitehead, 2003). When not foraging, they have a diverse behaviour that ranges from resting to energetic breaches (Whitehead, 2003). Some of the behaviours that can be observed on the surface are lobtail, spy hop, or side fluke. Individuals can also cluster together and socialize by different types of sound production, as mentioned, or by touching and rubbing each other under the surface (Whitehead, 2003).

Sperm whales are well adapted to their ecological role and their possible competitors for resources are not a threat, so the competition is basically within members of the same species, – always with the permission of human fisheries – with populations being regulated by the carrying capacity of the environment, the basis of a K-selected mammal (Whitehead, 2003; Whitehead, 2018). Slow growth, slow maturation, high survival and longevity and low birth characterize these animals.

Females reach sexual maturity at age nine and give birth usually at ten, after 14-16 months of gestation (Best et al., 1984). Once mature, females produce offspring once every four to six years, although the rate can vary, and experience a decrease in birth rates with age, only a few individuals giving birth after 40 (Rice, 1989; Best et al., 1984). Males have a prolonged puberty, that extends from ten to 20 years old, but do not seem to actively participate in breeding until late twenties (Best, 1979).

Mortality rates are difficult to assess due to the indirect and imprecise information, apart from whaling being an extra source of bias in most of the estimates (Whitehead, 2003). The best approach is to use killer whale mortality rates, which show an "U-shape" and males with higher mortality than females (Whitehead, 2003). Longevity is estimated using tooth layering, but as animals age the layers are difficult to discern. Thus, the oldest estimates are around 70 years, but could be substantially underestimated (Rice, 1989).

Sperm whale has always been a species of interest, first, when whalers targeted it until 1986, where whaling finished in the Azores, and in recent years for research and the increasing whale-watching industry, which started two years after the whaling ended (Linde & Eriksson, 2019).

Research's main focus has been on the social structure (Gordon, 1987; Best, 1979; Whitehead et al., 1991; Christal et al., 1998; Gero et al., 2008), behaviour (Papastavrou et al., 1989; Whitehead, 1996; Gero et al., 2009; Cantor & Whitehead, 2015), diet (Clarke, 1980; Kawakami, 1980; Clarke et al., 1993; Best, 1999; Marcoux et al., 2007) and acoustics (Weilgart & Whitehead, 1988; Goold, 1999; Møhl et al., 2000; Jaquet et al., 2001). Still, almost any study has been made about the relation of sperm whales with biological and environmental parameters, exploring if there is a distribution preference or any kind of behavioural patterns. The little literature available suggests that sperm whales concentrate in downwelling, and upwelling areas and a correlation was found between sperm whale abundance and primary productivity (Jaquet, 1996; Smit & Whitehead, 1993). Also, Fiori et al. (2014) found for the Mediterranean sub population a higher probability of encounter in submarine canyons and seamounts.

Most of the research in the Azores occurred in São Miguel, and other islands of the Archipelago are poorly studied. The latest research papers are related to sperm whale distribution and photo-identification, as it can be seen, for example, in Linde & Eriksson (2019), where they test the efficiency of using not only the flukes of the animals but also the dorsal marks to identify individuals. All photo-identification studies and the eagerness to assess sperm whale populations and their distribution have led to developing a photo-identification sperm whale catalogue for the Azores Islands, and another catalogue just for São Miguel.

REFERENCES

Ballance, L. T. (2018). Cetacean Ecology. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of Marine Mammals* (3 ed., 172–180).

Berta, A., Sumich, J. L., & Kovacs, K. M. (1999). Cetacean evolution and systematics. *Marine Mammals: Evolutionary Biology* (49-85). Academic Press, San Diego, CA.

Best, P. (1979). Social Organization in Sperm Whales, *Physeter macrocephalus*. In H. E. Winn & B. L. Olla (Eds.), *Behavior of Marine Animals: Current Perspectives in Research* (227–289). Springer, Boston, MA.

Best, P. B., Canham, P. A. S., & Macleod, N. (1984). Patterns of reproduction in sperm whales, *Physeter macrocephalus*. *Report of the International Whaling Commission*, *6*, 51-79.

Best, P. B. (1999). Food and feeding of sperm whales *Physeter macrocephalus* off the west coast of South Africa. *African Journal of Marine Science*, *21*.

Branch, T. A., & Williams, T. M. (2006). Legacy of industrial whaling. *Whales, whaling and ocean ecosystems*, 262-278.

Braulik, G. T., Kasuga, M., Wittich, A., Kiszka, J. J., MacCaulay, J., Gillespie, D., Gordon, J., Said, S. S. & Hammond, P. S. (2017). Cetacean rapid assessment: An approach to fill knowledge gaps and target conservation across large data deficient areas. *Aquatic Conservation: Marine and Freshwater Ecosystems, 28*(1), 216–230.

Borges P., Costa, A., Cunha, R., Gabriel, R., Gonçalves, V., Martins, A., Melo, I., Parente, M., Raposeiro, P., Rodrigues, P., Santos, R., Silva, L., Vieira, P., Vieira, V. (2010). A List of the Terrestrial and Marine Biota from the Azores. Cascais, Portugal: Princípia.

Bowen, W. D. (1997). Role of marine mammals in aquatic ecosystems. *Marine Ecology Progress Series*, *158*, 267-274.

Cantor, M., & Whitehead, H. (2015). How does social behavior differ among sperm whale clans? *Marine Mammal Science*, *31*(4), 1275–1290.

Christal, J., Whitehead, H., & Lettevall, E. (1998). Sperm whale social units: variation and change. *Canadian Journal of Zoology*, *76*(8), 1431-1440.

Christal, J., & Whitehead, H. (1997). Aggregations of mature male sperm whales on the Galapagos Islands breeding ground. *Marine Mammal Science*, *13*(1), 59-69.

Christensen, L. B. (2006). *Reconstructing historical abundances of exploited marine mammals at the global scale* (Doctoral dissertation). University of British Columbia.

Clarke, R. (1956). Sperm whales off the Azores. *Discovery Rep*, *28*, 239-298.

Clarke, M. R. (1980). Cephalopoda in the diet of sperm whales of the Southern Hemisphere and their bearing on sperm whale biology. *Discovery Reports*, *37*, 1–324.

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 B: Biological Sciences*, *339*(1287), 67–82.

Cranford, T. W. (1999). The sperm whale's nose: sexual selection on a grand scale? *Marine mammal science*, *15*(4), 1133-1157.

Fiori, C., Giancardo, L., Aïssi, 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*(S1), 41-49.

Fordyce, R. E. (2018). Cetacean evolution. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.). *Encyclopedia of marine mammals* (3 ed., 180-185). Academic Press.

Gero, S., Engelhaupt, D., & Whitehead, H. (2008). Heterogeneous social associations within a sperm whale, *Physeter macrocephalus*, unit reflect pairwise relatedness. *Behavioral Ecology and Sociobiology*, *63*(1), 143-151.

Gero, S., Engelhaupt, D., Rendell, L. & Whitehead, H. (2009). Who Cares? Between-group variation in alloparental caregiving in sperm whales, *Behavioral Ecology*, *20*(4), 838–843.

Gero, S., Gordon, J., & Whitehead, H. (2013). Calves as social hubs: dynamics of the social network within sperm whale units. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1763), 20131113.

Gero, S., Milligan, M., Rinaldi, C., Francis, P., Gordon, J., Carlson, C., Steffen, A., Tyack. P., Evans, P. & Whitehead, H. (2014). Behavior and social structure of the sperm whales of Dominica, West Indies. *Marine Mammal Science*, *30*(3), 905-922.

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

Gero, S., Bøttcher, A., Whitehead, H., & Madsen, P. T. (2016). Socially segregated, sympatric sperm whale clans in the Atlantic Ocean. *Royal Society open science*, *3*(6), 160061.

Goold, J. C. (1999). Behavioural and acoustic observations of sperm whales in Scapa Flow, Orkney Islands. *Journal of the Marine Biological Association of the United Kingdom*, *79*(3), 541-550.

Gordon, J. C. (1987). Sperm whale groups and social behaviour observed off Sri Lanka. *Reports of the International Whaling Commission*, *37*, 205-217.

Gordon, J., & Steiner, L. (1992). Ventilation and dive patterns in sperm whales, *Physeter macrocephalus*, in the Azores. *Report of the International Whaling Commission, 42*, 561-565.

Gordon, J., Moscrop, A., Carlson, C., Ingram, S., Leaper, R., Matthews, J., & Young, K. (1998). Distribution, movements and residency of sperm whales off the Commonwealth of Dominica, Eastern Caribbean: implications for the development and regulation of the local whale watching industry. *Reports of the International Whaling Commission*, *48*, 551-558.

Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, *23*(4), 202-210.

Jaquet, N. (1996). How spatial and temporal scales influence understanding of sperm whale distribution: a review. *Mammal Review*, *26*(1), 51-65.

Jaquet, N., Dawson, S., & Douglas, L. (2001). Vocal behavior of male sperm whales: Why do they click? *The Journal of the Acoustical Society of America*, *109*(5), 2254-2259.

Jewell, R., Thomas, L., Harris, C. M., Kaschner, K., Wiff, R., Hammond, P. S., & Quick, N. J. (2012). Global analysis of cetacean line-transect surveys: detecting trends in cetacean density. *Marine Ecology Progress Series, 453*, 227–240.

Kawakami, T. (1980). A review of sperm whale food. *The Scientific Reports of Whales Research Institute 32*, 199–218.

Kiszka, J. J., Heithaus, M. R., & Wirsing, A. J. (2015). Behavioural drivers of the ecological roles and importance of marine mammals. *Marine Ecology Progress Series, 523*, 267-281.

Konrad, C. M., Frasier, T. R., Rendell, L., Whitehead, H., & Gero, S. (2018). Kinship and association do not explain vocal repertoire variation among individual sperm whales or social units. *Animal Behaviour*, *145*, 131-140.

Lewison, R. L., Crowder, L. B., Read, A. J., & Freeman, S. A. (2004). Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology & Evolution*, *19*(11), 598-604.

Linde, M. L., & 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, 19*(1), 47-6.

Magalhães, S., Prieto, R., Silva, M. A., Gonçalves, J., Afonso-Dias, M., & Santos, R. S. (2002). Short-term reactions of sperm whales (*Physeter macrocephalus*) to whale-watching vessels in the Azores. *Aquatic Mammals, 28*(3), 267-274.

Marcoux, M., Whitehead, H., & Rendell, L. (2007). Sperm whale feeding variation by location, year, social group and clan: evidence from stable isotopes. *Marine Ecology Progress Series, 333*, 309–314.

Martin, A., & Clarke, M. (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.

Mesnick, S. L. (2001). Genetic relatedness in sperm whales: evidence and cultural implications. *Behavioral and Brain Sciences, 24*(2), 346-346.

Møhl, B., Wahlberg, M., Madsen, P. T., Miller, L. A., & Surlykke, A. (2000). Sperm whale clicks: Directionality and source level revisited. *The journal of the Acoustical Society of America*, *107*(1), 638-648.

Norris, K. S., & Harvey, G. W. (1972). A theory for the function of the spermaceti organ of the sperm whale. *Animal orientation and navigation*, 393-417.

Norris, K. S., & Mohl, B. (1983). Can odontocetes debilitate prey with sound? *The American Naturalist*, *122*(1), 85-104.

Notarbartolo di Sciara, G., Frantzis, A., Bearzi, G., & Reeves, R. (2012). *Physeter macrocephalus* (Mediterranean subpopulation). *The IUCN Red List of Threatened Species*, 2012-1.

Papastavrou, V., Smith, S. C., & Whitehead, H. (1989). Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galapagos Islands. *Canadian Journal of Zoology*, *67*(4), 839-846.

Pitman, R. L., Ballance, L. T., Mesnick, S. I., & Chivers, S. J. (2001). Killer whale predation on sperm whales: observations and implications. *Marine mammal science*, *17*(3), 494-507.

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

Ralls, K., & Mesnick, S. (2009). Sexual Dimorphism. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of Marine Mammals* (2 ed., 1005–1011). Academic Press.

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

Rice, D. W. (1989). Sperm whale *Physeter macrocephalus* Linnaeus, 1758. *Handbook of Marine Mammals, 4*, 177-233.

Richard, K. R. (1995). *A molecular genetic analysis of kinship in free-living groups of sperm whales* (Doctoral Dissertation). Dalhousie University, Halifax, Nova Scotia.

Richard, K. R., Dillon, M. C., Whitehead, H., & Wright, J. M. (1996). Patterns of kinship in groups of free-living sperm whales (*Physeter macrocephalus*) revealed by multiple molecular genetic analyses. *Proceedings of the National Academy of Sciences*, *93*(16), 8792-8795.

Roe, H. S. J. (1969). The food and feeding habits of the sperm whales (Physeter catodon L.) taken off the west coast of Iceland. ICES Journal of Marine Science, 33(1), 93-102.

Roman, J., & McCarthy, J. J. (2010). The Whale Pump: Marine Mammals Enhance Primary Productivity in a Coastal Basin. *PLoS ONE, 5*(10), *e13255.*

Roman, J., Estes, J.A., Morissette, L., Smith, C., Costa, D., McCarthy, J., Nation, J., Nicol, S., Pershing, A. and Smetacek, V. (2014), Whales as marine ecosystem engineers. *Frontiers in Ecology and the Environment*, *12*: 377-385.

Ruiz-Cooley, R. I., Gendron, D., Aguíñiga, S., Mesnick, S., & Carriquiry, J. D. (2004). Trophic relationships between sperm whales and jumbo squid using stable isotopes of C and N. *Marine Ecology Progress Series*, *277*, 275-283.

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.

Schakner, Z. A., Lunsford, C., Straley, J., Eguchi, T., & Mesnick, S. L. (2014). Using Models of Social Transmission to Examine the Spread of Longline Depredation Behavior among Sperm Whales in the Gulf of Alaska. PLoS ONE, 9(10), 1–5.

Silva, M. A., Prieto, R., Cascão, I., Seabra, M. I., Machete, M., Baumgartner, M. F., & Santos, R. S. (2013). Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. *Marine Biology Research, 10*(2), 123–137.

Simon, M., Stafford, K. M., Beedholm, K., Lee, C. M., & Madsen, P. T. (2010). Singing behavior of fin whales in the Davis Strait with implications for mating, migration and foraging. *The Journal of the Acoustical Society of America*, *128*(5), 3200-3210.

Smith, S. C., & Whitehead, H. (2000). The diet of Galápagos sperm whales *Physeter macrocephalus* as indicated by fecal samples analysis. *Marine Mammal Science, 16*(2), 315–325.

Taylor, B. L., Baird, R., Barlow, J., Dawson, S. M., Ford, J., Mead, J. G., & Pitman, R. L. (2019). *Physeter macrocephalus* (amended version of 2008 assessment). *The IUCN Red List of Threatened Species*, *2019.*

Visser, F., Hartman, K. L., Pierce, G. J., Valavanis, V. D., & Huisman, J. (2011). Timing of migratory baleen whales at the Azores in relation to the North Atlantic spring bloom. *Marine Ecology Progress Series, 440*, 267-279.

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., 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. S., & Whitehead, H. (1988). Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*). *Canadian Journal of Zoology*, *66*(9), 1931-1937.

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., & Weilgart, L. (1991). Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. *Behaviour*, 275-296.

Whitehead, H., & Kahn, B. (1992). Temporal and geographic variation in the social structure of female sperm whales. *Canadian Journal of Zoology*, *70*(11), 2145–2149.

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

Whitehead, H. (2002). Estimates of the current global population size and historical trajectory for sperm whales. *Marine Ecology Progress Series*, *242*, 295-304.

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

Whitehead, H., Antunes, R., Gero, S., Wong, S., Engelhaupt, D., Rendell, L. (2012). Multilevel Societies of Female Sperm Whales (*Physeter macrocephalus*) in the Atlantic and Pacific: Why Are They So Different? *International Journal Primatology*, *33*(5)**,** 1142–1164.

Whitehead, H. (2018). Sperm Whale: *Physeter macrocephalus*. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of Marine Mammals* (3 ed., 919–925). Academic press.

Understanding sperm whales (*Physeter macrocephalus*) in Pico Island, Azores

Authors: Gerard Subiron[a,*], Rui Peres dos Santos[b], Rita Castilho[b]

[a]Faculty of Sciences and Technology, University of Algarve, campus de Gambelas, 8005-139 Faro, Portugal

[b]CCMAR – Center for Marine Sciences (CCMAR), University of Algarve, Campus de Gambelas, 8005-139 Faro, Portugal

***Corresponding author:** Gerard Subiron Moreso

E-mail: **gerardsubi97@gmail.com**

Keywords: sperm whale, photo-identification, distribution, Azores, behaviours, Pico Island

ABSTRACT

Photo-identification has proven a reliable tool to study cetacean species such as the sperm whale (*Physeter macrocephalus*). Sperm whales have a worldwide distribution that differs between females and males. Females and immature social units are mostly found in tropical and subtropical waters such as the Azores, and males more frequently in higher latitudes. In this study, the use of whale watching as an opportunistic platform to acquire almost year-round data, allowed to assess the sperm whale occurrence, distribution, social structure, and behaviours displayed around Pico Island, Azores during a seven-year period (2012 to 2018). Individuals were photo-identified, and a database of 4851 fluke photographs were visually analysed by three independent researchers, which yielded a sperm whale catalogue for Pico (n = 516). From all catalogued whales, most were sighted only one time in the study period (78%). However, for some individuals it was found a pattern of seasonal residency, with times of individual permanence up to 72 days. Most sightings accounted for females and immature individuals, including calves, which appeared more abundant in summer. Sperm whales off the Azores presented a similar unit size displayed in other regions of the Atlantic Ocean. Male sperm whales, despite the small sample size, were more abundant in summer, and presented different foraging diving times than females. Spatial distribution analysis was performed by calculating the encounter rates for the study area using the sightings and effort. We observed homogeneous distribution, although additional research should be made in some areas. Environmental variables such as depth, distance to coast and sea surface temperature appeared to be a factor influencing the sperm whale occurrence in the area, and more research is needed to provide conclusive answers. Opportunistic platforms such as whale watching, despite some limitations, have proven helpful to obtain cost-efficient and reliable data for research purposes.

INTRODUCTION

Sperm whale (*Physeter macrocephalus*) worldwide population largely declined due to commercial whaling (Whitehead, 2002). However, in the Azores it was mostly traditional whaling, which ceased in 1986. Research interest began shortly after whaling finished, and since 1989 the whale watching industry started first in Pico Island, and after spread to almost all islands in the Archipelago.

The sperm whale is the most emblematic species in the Azores and the main target of whale watching. Thanks to this activity we obtained most of the data to develop the study. Sperm whale has a characteristic and extreme nature that makes it a unique species: the sexual dimorphism, deep and long dives, large body size, and wide distribution, among many other traits (Whitehead, 2003; Whitehead, 2018).

The distribution ranges from the equator to the edges of the pack ice, through all deep oceans of the world (Rice, 1989), although it is completely different between sexes. Females inhabit latitudes less than 40º, with few exceptions, and with water deeper than 1000 m (Rice, 1989). When young males separate from female groups, something between 4 and 21 years of age, migrate gradually to high latitudes (Whitehead, 2018). Larger males are found until the edge of the pack ice in both hemispheres, and contrary to females, are regularly sighted at less than 1000 m depth (Whitehead, 2018).

The social behaviour of sperm whales was first studied in Sri Lanka (Gordon, 1987) and shortly afterwards in other regions (e. g. Whitehead et al., 1991; Whitehead & Kahn, 1992; Christal et al., 1998; Gordon et al., 1998). These studies demonstrated a social structure based on a hierarchy of levels (Whitehead et al., 2012). First, the “unit”, consisting in small group of females and immature whales that have a partially matrilineal membership stable over several years (Whitehead et al., 1991; Christal et al., 1998; Whitehead et al., 2012; Gero et al., 2014), with the individuals often being related (Richard et al.,1996; Christal et al., 1998; Mesnick, 2001; Gero et al., 2008; Konrad et al., 2018). The “group” level is an association between one or several social units for a short time, ranging from hours to days (Whitehead et al., 1991; Christal et al., 1998; Whitehead, 2003). Finally, “clans" are composed of multiple social units, which contain thousands of individuals spread across large areas and have in common a similar vocal repertoire (Rendell & Whitehead, 2003; Gero et al., 2016).

Male sperm whales have a different social pattern. After dispersing from their natal groups, they form bachelor groups (Best, 1979; Richard, 1995). As males mature, they form increasingly smaller groups until they tend to be solitary at sexual maturity at around 18 years of age and move increasingly to higher latitudes (Best 1979; Richard, 1995; Schakner et al., 2014). Only for breeding, they return to tropical and temperate waters to encounter the mixed groups, integrated by females and immature individuals (Best, 1979; Richard, 1995; Christal & Whitehead, 1997).

Sperm whale is a deep-diving predator (Papastavrou et al., 1989) that has a generalist teuthophagous diet (Whitehead et al., 2003). The foraging dives are usually below 500 meters depth, in the meso- and benthopelagic area, where they prey on different species of squids, represented in 17 families (Kawakami, 1980; Martin & Clarke, 1986; Whitehead, 2003). Prey range in size, and activity, from the small chiroteuthids (less than 100 g) to the architeuthids, or giant squids (up to 400 Kg), although the smaller gelatinous species are the primary food most of the time (Clarke et al., 1993; Whitehead, 2003). Fish are the second most abundant prey in sperm whales, usually at very low rates compared to cephalopods, but can be rather important in some regions (Kawakami, 1980; Whitehead, 2003). Fishes occur in 13% or less of sperm whale stomachs in the Azores (Clarke, 1956), whereas in Iceland occur in 98% (Roe, 1969).

Research's main focus has been on the social structure (Gordon, 1987; Best, 1979; Whitehead et al., 1991; Christal et al., 1998; Gero et al., 2008), behaviour (Papastavrou et al., 1989; Whitehead, 1996; Gero et al., 2009; Cantor & Whitehead, 2015), diet (Clarke, 1980; Kawakami, 1980; Clarke et al., 1993; Best, 1999; Marcoux et al., 2007) and acoustics (Weilgart & Whitehead, 1988; Goold, 1999; Møhl et al., 2000; Jaquet et al., 2001). However, fewer studies have been made about the relation of sperm whales with biological and environmental parameters.

Most of the research in the Azores occurred in Sao Miguel. In this study, we analyzed the population of Pico Island and increased the knowledge of the species in another region of the Archipelago, based on photo-identification data from an opportunistic platform such as whale watching. The main objective of the study was to assess the sperm whale population of Pico, with a special focus on the occurrence, social structure, and behaviour, as well as environmental patterns that could define its distribution in the study area. We wanted to test the hypothesis that sperm whales in Pico have the same social organization and behavioural patterns displayed in other regions of the world. In addition, we believe that sperm whale distribution is linked to certain environmental parameters.

METHODS

Study Area

The Azores archipelago consists of nine volcanic islands, forming three groups (Western, Central and Eastern) spread along the Mid-Atlantic Ridge, between 37º to 40ºN and 25º to 32ºW. The focal study area was south of Pico Island, sometimes spreading until the south coast of São Jorge or Faial (Figure 1).

Data collection

Sperm whale boat-based encounter data used for this project were collected opportunistically from 2012 until 2018 during 1452 commercial whale watching trips from two whale watching companies (Espaço Talassa and Futurismo). The companies use local and experienced *lookouts* positioned in land surveys to spot the animals. Situated in watching towers or viewpoints at around 100 meters above sea level, they use potent binoculars (15*80mm or 20*80mm) to find different species and to communicate their position with boats by radio VHF. All operations comply with the Decreto-Lei Legislativo Regional 10/2003/A, de 22 de Março and DLR 13/2004/A.

Tracking of the trips was recorded (GPS Garmin Etrex20). After a cetacean detection, biologists on board registered the location and time of the sighting, group size and composition, behaviour, and other observations when possible (e.g., size, sex, and dive cycle). Additionally, pictures of the flukes of the sperm whales were taken for photo-identification using a camera canon 7D lens 100-400mm.

Data analysis

Statistical analyses on the spatial data were conducted in R version 1.2.5001 (R Core Team, 2021). We performed a Shapiro-Wilk test to check for the normality of each year of data ($p<0,05$) and then an F-test to compare the variances between all years for the monthly sightings. To test for significant differences in group sizes between female and male groups, we performed a Shapiro-Wilk test for both sexes, followed by a t-test to compare the mean group size. The same procedure was done for the group composition, and the resulting mean values for each class were summed to estimate the unit size.

The time between successive identifications of the same individual was used to calculate the dive cycles, consisting of a dive time and a surface time. Dive cycles of females above 1h 15min were excluded from the analysis, as they could belong to two dives cycles instead of one.

Predominant behaviour(s) were inferred from the observation of surface characteristics. We grouped behaviours into seven categories: (1) Foraging; (2) socializing, which includes socializing, breaching, breaching sideways, breaching forward, breaching backwards, and lob tailing; (3) travelling, which includes travelling slow (1-4 kn), average (4-6 kn), and fast (> 6 kn); (4) resting, which includes resting, and milling; (5) nursing; (6) others, which includes all the behaviours not mentioned in the list above, such as hiding (shallow dive), or spy-hopping and (7) non-identified (Whitehead, 2003).

To create the sperm whale catalogue of Pico Island from 4851 pictures, 926 were selected with the best quality. In these photos, it is possible to notice all the notches, scars, and sometimes pigmentation of the fluke at a 90º degree angle without sun glare or water covering the marks (Arnbom, 1987). All fluke pictures were matched by eye by three independent researchers. Dorsal photos eventually aided the identification when a fluke picture was also available for the individual.

Spatial distribution analysis was performed by dividing the area in a 4 x 4 Km grid to calculate the encounter rate in each square. Encounter rate accounted for sightings divided the effort and multiplied by 100. As “effort” we considered the sum of all tracks in the study period. Distance to the coast and depth from each sighting were calculated with QGIS, using as a reference high-resolution coastline data provided by the Instituto Hidrográfico Português (https://www.hidrografico.pt/), and the bathymetry extracted from EMODnet (https://emodnet.ec.europa.eu/en). Sea Surface Temperature (SST) daily average data for the study area were obtained from E.U. Copernicus Marine Service Information (https://marine.copernicus.eu/), and an SST value was associated with each sighting.

RESULTS

Whale watching trips yielded 837 sperm whale sightings in the 83.794 Km covered during the study period, of which 397 sightings provided identifiable individuals with photo-identification data. Most of the sightings were located South of Pico Island, where Lajes do Pico harbour is found, and a few closer to Faial and South of São Jorge Islands (Figure 1).

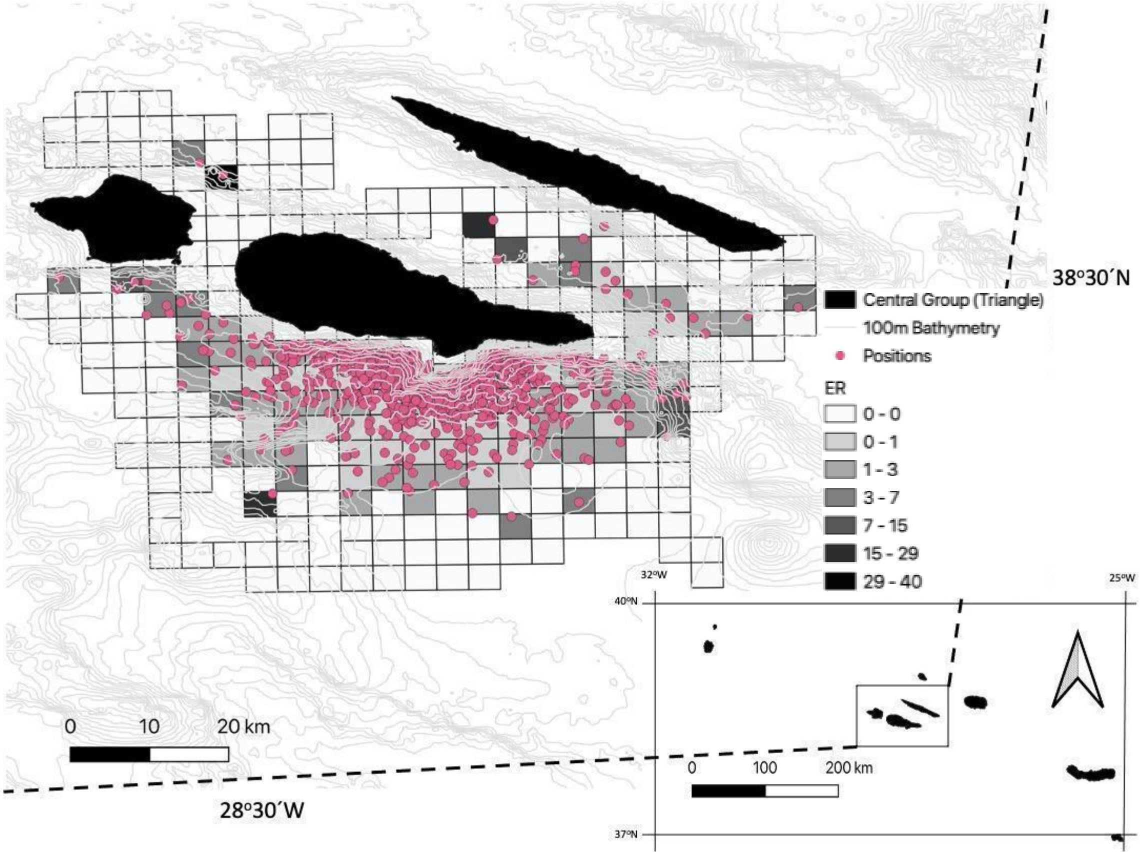

Figure 1. Map of the Azores archipelago (bottom right) and the central group of Islands: Pico, Faial, and São Jorge. Red dots represent every sperm whale sighting between 2012 and 2018. Squares represent the encounter rate. Bathymetry is represented by 100m isobath.

Most of the animals were sighted during summer months, between June and August (Figure 2A). Every year of data was tested for normality in a Shapiro-Wilk test and all of them were normally distributed (p-value <0,05). The monthly variance of each year was found to be significantly different between the years 2012-2016 (0,65, p <0,05), 2013-2016 (0,67, p <0,05), 2014-2016 (0,63, p <0,05), 2015-2018 (1,42, p <0,05), 2016-2018 (1,83, p <0,05) and 2017-2018 (1,56, p <0,05).

Groups of females were significantly larger, and on average, had three more individuals than male groups (paired-t-test=27,907, df=15, p<0.05) (Figure 2B). The group composition had an average of 4,351 adults, 0,203 juveniles, 0,619 calves, and 0,00358 newborns (Figure 2C). The approximate average unit size of 5.18 individuals.

Dive cycles differed notably between females (54 min 24 sec ± 9 min 15 sec) and males (77 min 36 sec ± 13 min 25 sec). However, males were accounted for on only two dives (Figure 2D).

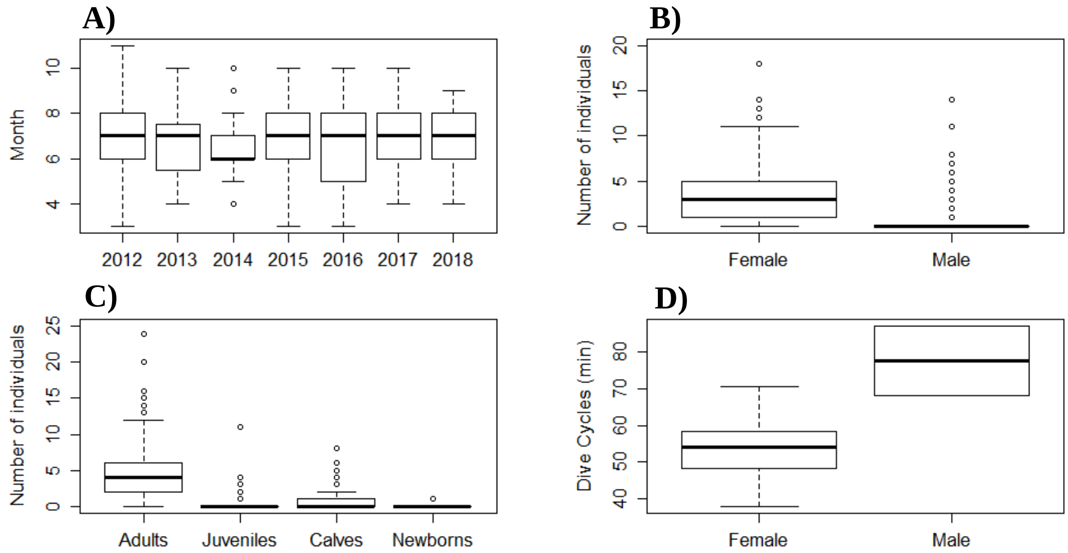

Figure 2. A) Monthly sightings for each year of the study period. **B)** Number of individuals per group of females and males. **C)** Group composition. Number of adults per group, number of juveniles, calves and newborns. **D)** Dive Cycles in minutes for females and males. Males represented only for two values.

Generally, sperm whales without calves were sighted more often (Figure 3). Average percentage sightings with calves were higher in the summer (22,3%, n = 186) compared to spring (7,8%, n = 65) and autumn (8,9%, n = 74). During 2012 and 2014, percentages of sightings with calves were higher (48,8% and 47,2%, respectively). Sightings with calves were highest during the summer of 2012 (39,4%, n = 63) (Figure 3).

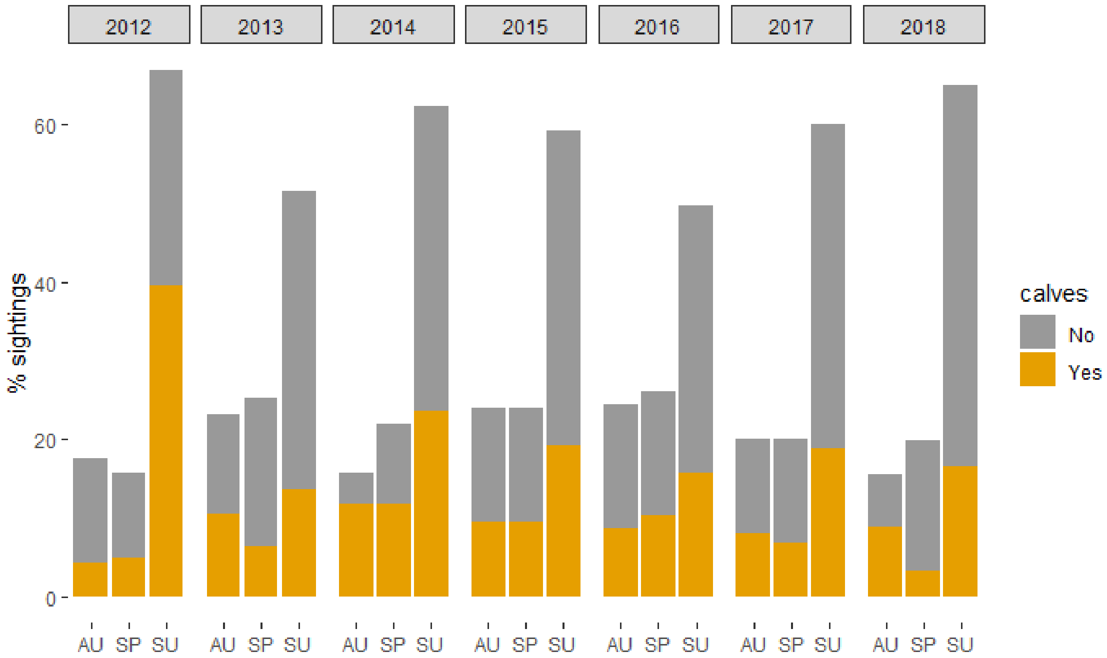

Figure 3. Seasonal percentages (%) of sightings with calves (orange) and without calves (grey). X axis represents the seasons autumn (AU), spring (SP) and summer (SU).

Foraging was the most common behaviour recorded (43,15%), followed by nursing (11,9%), travelling (11,0%), socializing (10%) and resting (4,3%). Higher foraging averages were found in spring (46,0%) and summer (44,5%) compared to autumn (38,9%). The lowest foraging rate was found in 2016 (29,6%). Nursing appears to have a high importance during autumn (14,5%) compared to spring (9,8%) and summer (11,4%). Socializing and traveling peak in autumn (12,2% and 13,3%, respectively). On the contrary, resting appears to be a residual behaviour in autumn (2,74%), compared to spring (4,62%) and summer (5,44%) (Figure 4).

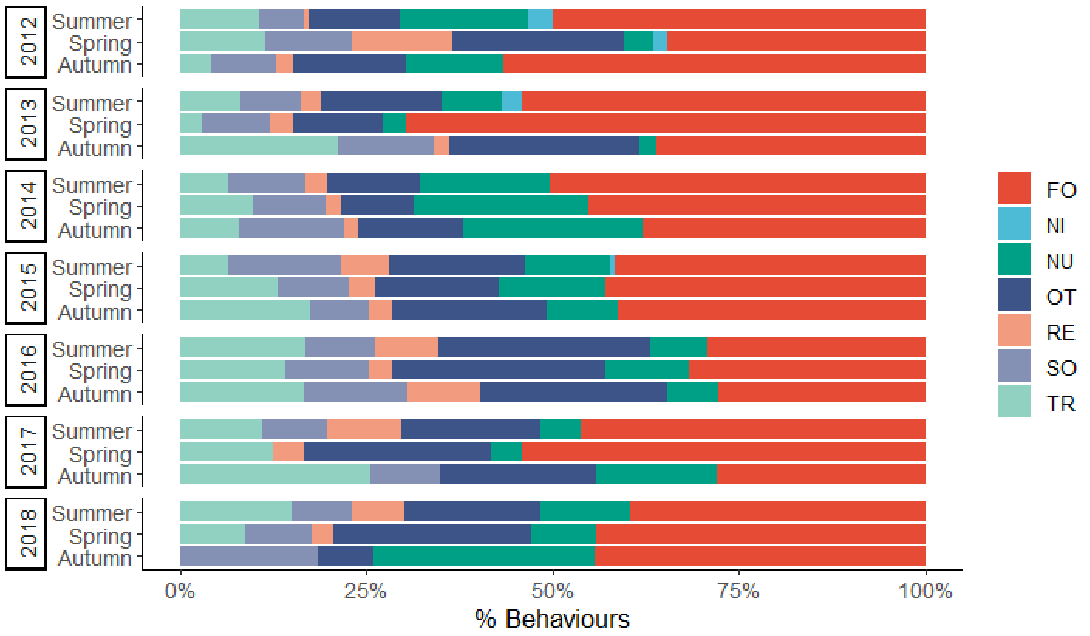

Figure 4. Seasonal percentages (%) of behaviours. Foraging (FO), socializing (SO), traveling (TR), resting (RE), nursing (NU), others (OT) and not identified (NI).

We identified 516 individuals from good quality fluke photographs. Most whales were photographed only one time (78,30%). However, a few specimens were frequently resighted throughout the study period. The most sighted individual was identified 20 times (Figure 5). The most commonly encountered individuals were repeatedly sighted during summer, and the maximum residency time registered belonged to Pm023 (Figure 5), which was recorded in the area for at least 72 days. Male sperm whales were sighted mostly during summer (60%), with a pronounced peak in July, while sightings in Spring decreased to 30% and 10% in Autumn.

Figure 5. Flukes of the five most sighted individuals in the catalogue. First row from left to right: Pm023 (20 sightings), Pm024 (16 sightings), Pm027 (13 sightings). Second row: Pm035 (14 sightings), Pm037 (14 sightings). Photographs courtesy of: R. Peres dos Santos.

Generally, encounter rates were inferior to 10%. The highest encounter rates were all obtained offshore from Lajes do Pico harbour, with the highest rates ranging between 26 to 51%. High encounter rate areas were scattered throughout the study location, and no distinct clusters were observed. The values were lower closer to shore, being inferior to 4% (Figure 1).

Most sightings occurred between two to ten Km from the coast (Figure 6A), and in areas of depths between 600 to 1700 m (Figure 6B). No sightings were recorded further than 20 Km from the coast or in depths higher than 1800 m or shallower than 300 m.

Temperatures ranged between 15 and 25ºC, with a warmer period that extended from July to the end of September (Figure 6C). More sperm whale recordings occurred during the warmer period, with 75% of the sightings occurring above 19ºC.

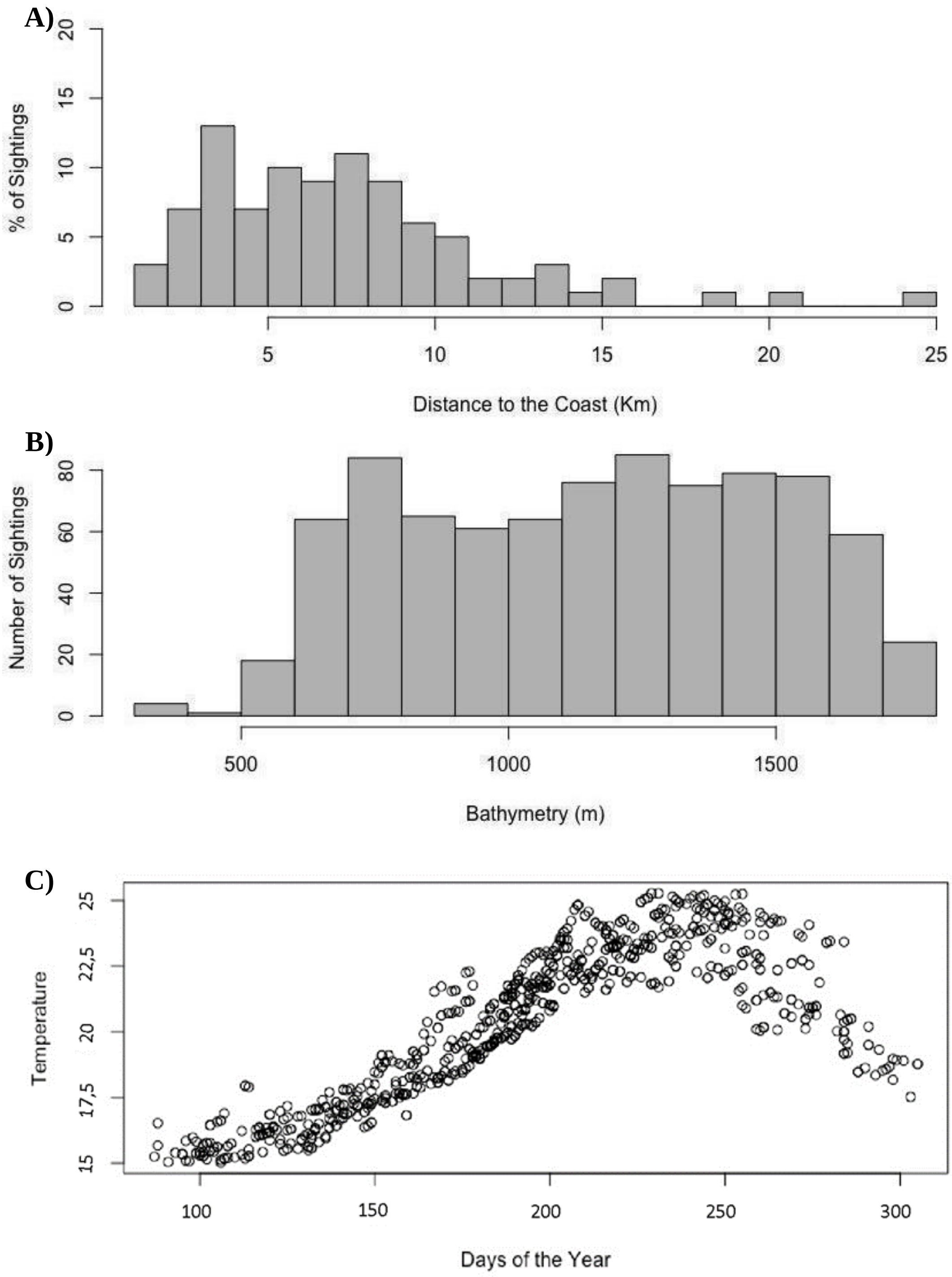

Figure 6. A) Distance to the coast in Km of each sperm whale sighting. X-axis shows distance to the coast in intervals of 1 Km. **B)** Sperm whale depth range. X-axis shows bathymetry in intervals of 100 m. **C)** Sea surface temperature (SST) of each sighting, temperature in ºC.

DISCUSSION

This study shows a pattern of annual, seasonal (except winter) and spatial variation in the presence of sperm whales in the region of Pico Island, Azores. However, limitations and biases of the data collection methodology, which might have influenced the results, should be considered. First, opportunistic platforms limit the randomness of the surveys, providing an unequal coverage of the area. Thus, the encounter rates estimated in the study may not be representative, and some artefacts could appear. Second, the 30 min limit to observe the animals could be insufficient to notice certain behaviours. Finally, the lack of trips in winter prevented year-round data acquisition.

The Pico sperm whale catalogue allows the identification of 516 individuals, which is higher than a study conducted in São Miguel during 2010-2017 with similar area coverage, in which they identified 393 individuals (Linde & Eriksson, 2019). These numbers suggest higher retention of sperm whales in Pico rather than São Miguel. In addition, our data does not cover winter months, unlike the São Miguel study, so we could expect an even higher difference if those months were covered. Existing estimates of sperm whale population size range between 300 and 800 individuals occurring in summer for the Central group of islands (Matthews et al., 2001). Results from this study fall into previously estimated population size ranges.

Sperm whales are considered a resident species in the Azorean archipelago. However, the data presented in this study show most animals appearing to be transient, as over 2/3 of the individuals were sighted only once (78%). These short stays are likely due to their seasonal migrations (Whitehead, 2003). Some of the resighted animals stayed in the study area for longer periods, especially during the summer months and showed seasonal residency. The same pattern was also observed in the Azores (Matthews et al., 2001) with periods of individual permanence of up to 73 days in summer, similar to the results observed herein with a maximum stay of 72 days.

Female sperm whales off Pico presented dive cycles of an average of 54 min (dive time and surface time). Assuming an average of 9 min surface time (Whitehead, 2018), the actual mean dive time would be equivalent to 45 min. Dive time estimates are lower than previous research in the Azores (55 min) (Gordon & Steiner 1992), but coincide with other sperm whale studies in Galapagos (Papastavrou et al., 1989), in Dominica (Gero et al., 2014), in Kaikoura (Jaquet et al., 2000), and in the Atlantic Ocean, Gulf of Mexico and Ligurian Sea (Watwood et al., 2006). The different results in the Azores can be attributed to the presence of males in the calculations (Gordon & Steiner 1992).

Male sperm whales showed substantially longer dive times than females, with an average of 77 min. Similar male dive times were observed in South Africa (Clarke, 1976), while other studies observed equivalent dive times for both males and females (Papastavrou et al., 1989; Whitehead et al., 1992; Jaquet et al., 2000). However, we had a high standard deviation in the results. More data acquisition should improve the results, especially regarding males, since we only had two records.

Two studies on sperm whale social structure in the Azores calculated the average unit size to be 12 individuals (Antunes, 2009) and 6,08 (Linde & Eriksson, 2019). These estimates were based on the analysis of key individuals and their constant companions. However, we used a different approach and obtained a value of 5,18 individuals per unit, closer to lower estimates from the Atlantic (Whitehead et al., 2012; Linde & Eriksson, 2019). In addition, and based on personal observations until 2019, we confirm that Pm023, the most sighted animal in the study, belongs to a group composed of five females, one juvenile and one calf (seven individuals) (R. Peres dos Santos, personal communication). As a point of comparison, the average unit size in the Eastern Pacific is around 13 individuals (Whitehead & Kahn, 1992). However, larger family groups in the Pacific are attributed to a higher density of killer whales (Whitehead et al., 2012), as sperm whales defend themselves from predators socially and communally (Pitman et al., 2001). Further research should be conducted in the Azores using standardized methods to comprehend the unit composition better and corroborate this study results.

The breeding season of sperm whales In the Azores spans from October to July (Clarke, 1956). The present study does not provide enough data to assess variables such as reproduction due to the scarcity in newborn and male sightings and the lack of mating observations. However, more males were sighted in summer (60% vs 30 and 10% in spring and autumn, respectively), with a peak in July, indicating a possible delay in the breeding season previously described by Clarke (1956). Assuming these results are accurate, more calves should be seen in autumn since the sperm whale gestation lasts between 14 to 16 months (Best et al., 1984).

The frequency of calves sightings varied with season and year, which may denote an irregularity in reproduction success of sperm whales, but this might be a typical pattern, taking low reproductive rates and long postnatal care periods into account. It appears that 2012 and 2014 were good years in terms of sperm whale population, as a higher number of calves were sighted. Calve sightings peaked in summer, which might imply a seasonality in the mating of sperm whales. In São Miguel Island, a peak in calves was also observed in July and August (Gonzalez Garcia, 2019), coinciding with our data. These results suggest the breeding season to be as Clarke (1956) estimated from October to July.

Foraging was the primary behaviour observed in the study (43,15%). Most authors found this behaviour to be prevalent (75 to 80%) (e. g. Whitehead & Weilgart, 1991; Gordon & Steiner, 1992; Whitehead, 2003). However, foraging behaviour only represented 12,6% of the spectrum in São Miguel (Gonzalez Garcia, 2019), although using a non-standardized method to register behaviour could potentially explain the difference. Lower foraging rates observed in our study are thought to be linked to a different approach to data collection and a result of the limited time available for observations, possibly missing specific behavioural patterns. A focused study in sperm whale behaviour in the Azores would help to improve our results.

We identified areas with higher encounter rates near Faial, South of São Jorge Pico, and offshore the coast in South of Pico, all far from the harbour of origin. This observation might be explained by the fact that whale watching companies only venture far from the harbour when the presence of large cetacean species such as sperm whales is confirmed, therefore creating a potential bias in the data. Additional research is needed to verify if these areas are, in fact, more essential for sperm whales or whether these areas are under-sampled and actual sperm whale presence is lower than estimated herein. With higher sampling effort, areas closer to shore have similarly lower encounter rates, which points towards a homogeneous distribution of sperm whales off Pico. Similar patterns of homogeneity were obtained for the rest of the Azorean archipelago, but with a higher abundance displayed in deep waters between the central and western islands, and north of the eastern islands (Silva et al., 2013), which were not covered by our study. Most sightings were concentrated between two to ten kilometres from the coast, which could imply the animals' preference towards coastal areas. Still, as previously mentioned, the opportunistic nature of the data collection methodology may influence results. Interestingly, in the Strait of Gibraltar, the distribution pattern differed significantly, and a cluster of high encounter rates was found in the deeper part of the channel (Stephanis et al., 2008). This difference could be attributed to the different bathymetric conditions of the areas.

Observed sperm whale depth ranged from 600 to 1700 m. Few sightings above and below that range appeared occasionally. In the South of Pico, bathymetry descends rapidly within the first 20 Km close to shore and generally does not exceed 2000 m depth (Tempera et al., 2012), resulting in a suitable habitat for sperm whales. Similar results on depth range were obtained in São Miguel with a peak in depths between 700 and 1000m, although the depth range was narrower and heterogeneous (Gonzalez Garcia, 2019). No sperm whales were sighted at areas shallower than 300 m depth, which could be explained through the prey distribution and foraging behaviour of the sperm whale (Clarke, 1980; Kawakami, 1980; Watwood et al., 2006, Whitehead, 2003). The most significant part of the sperm whale's diet is composed of meso- and bathypelagic cephalopods (Kawakami, 1980), and all prey families consumed by sperm whales in the Azores inhabit waters deeper than 500 m (Clarke et al., 1993).

Periods of increased sea surface temperature (SST) coincided with higher sperm whale sightings, which could indicate a general preference of the species for warmer temperatures and could constitute an explanation for the seasonal residency described above. It seems that sperm whales prefer waters above 19ºC or at least higher temperatures that influence other variables affecting the species, such as higher food availability (Gannier et al., 2007). Correlation of sperm whale occurrence and SST have been previously reported (Gannier et al., 2007; Pirotta et al., 2011).

Pico Island seems to be an essential area for sperm whales inside the Azores, based on our results. More research should reveal missing knowledge gaps in population size and structure, reproduction, seasonality, and distribution around Pico Island and the Azores. Opportunistic platforms such as whale watching activities, despite their limitations, provide almost year-round data that can help improve the understanding of the population very cost-effectively. One of the aims of continued research should be to increase the number of individuals recorded in the catalogue. During the last year of photo-identification data analysis, many new individuals were recorded (76), therefore, similar increases can be expected in the near future. The next step is to compare the catalogues of Pico and São Miguel Island, to better understand the movements of individuals in the Azorean waters. Also, more data is needed to confirm and clarify some of the results obtained in the present study, especially of male sperm whales, since the data were scarce. Interestingly, there is a resident male in the Azores, "Mr. Liable" (Pm296), which is the most sighted animal in São Miguel (Gardoki et al., 2018), and on some occasions has been seen in Pico, for example in 2016 and recently in 2021 (data not shown). Finally, we gave some insights on sperm whale distribution considering some environmental variables, but more research on specific aspects is needed to provide conclusive answers.

CONCLUSIONS

Sperm whales identified in Pico displayed a similar social structure than other Atlantic populations, with small units of females and immature individuals. Males appeared at lower rates in the area, but their presence, together with many calves sighted, places the Azorean waters, not only a feeding area but also an important breeding ground for sperm whales in the Eastern North Atlantic. In addition, we observed a pattern of seasonal residency for some individuals, which were resighted at the same time of the year throughout the study period. However, most animals appeared to be transients. Despite the small sample size in male feeding dives, we encountered differences in the foraging times between females and males.

Generally, we found a homogeneous distribution of sperm whales in Pico Island, and a solid depth range for the species. Finally, more than 3/4 of sperm whale sightings were recorded when temperatures were above 19ºC. Overall, this study helped to place the waters around Pico Island as an essential area for North Atlantic sperm whales´ population, especially to some “unit” groups of females.

ACKNOWLEDGEMENTS

I would like to thank Dr. Rita Castilho for the help and guidance provided, I learned a lot in terms of writing thanks to her corrections and constructive advice.

To Rui Peres, I am extremely grateful for giving me the opportunity to do this research project, to be able to go to the Azores and work for a whale watching company, and to learn so much about marine mammals. Thank you for sharing all the cetacean knowledge and experience with me. And of course, thanks for all the help provided and implication you had to carry out this study.

My special thanks are extended to the staff of Futurismo. First, to César and Roxane, for being amazing team members, and sharing their passion and knowledge with me. I have also learnt a lot with you two. Then, to João and Ricardo, for making the stay in the Azores more fun.

To my parents and Clara, I am also grateful for the support in the tough moments and to always cheer me up when I needed it. You have been a great support during this process.

Finally, to all the Faro people, we shared amazing moments and suffered to finish the thesis. Struggling together and helping each other united us and helped to carry on. And especial thanks to berni, for the help and support given through this master.

REFERENCES

Antunes, R. (2009). *Variation in sperm whale (Physeter macrocephalus) coda vocalizations and social structure in the North Atlantic Ocean* (Doctoral dissertation, University of St Andrews).

Arnbom, T. (1987). Individual identification of sperm whales. *Report of the International Whaling Commission*, *37*(20), 1-204.

Best, P. (1979). Social Organization in Sperm Whales, *Physeter macrocephalus*. In H. E. Winn & B. L. Olla (Eds.), *Behavior of Marine Animals: Current Perspectives in Research* (227–289). Springer, Boston, MA.

Best, P. B., Canham, P. A. S., & Macleod, N. (1984). Patterns of reproduction in sperm whales, *Physeter macrocephalus*. *Report of the International Whaling Commission*, *6*, 51-79.

Best, P. B. (1999). Food and feeding of sperm whales *Physeter macrocephalus* off the west coast of South Africa. *African Journal of Marine Science*, *21*.

Cantor, M., & Whitehead, H. (2015). How does social behavior differ among sperm whale clans? *Marine Mammal Science*, *31*(4), 1275–1290.

Christal, J., & Whitehead, H. (1997). Aggregations of mature male sperm whales on the Galapagos Islands breeding ground. *Marine Mammal Science*, *13*(1), 59-69.

Christal, J., Whitehead, H., & Lettevall, E. (1998). Sperm whale social units: variation and change. *Canadian Journal of Zoology*, *76*(8), 1431-1440.

Clarke, R. (1956). Sperm whales off the Azores. *Discovery Rep*, *28*, 239-298.

Clarke, M. R. (1976). Observation on sperm whale diving. *Journal of the Marine Biological Association of the United Kingdom*, *56*(3), 809-810.

Clarke, M. R. (1980). Cephalopoda in the diet of sperm whales of the Southern Hemisphere and their bearing on sperm whale biology. *Discovery Reports*, *37*, 1–324.

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 B: Biological Sciences*, *339*(1287), 67–82.

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, Marina & González García, Laura & Steiner, Lisa & van der Linde, Miranda & Azevedo, Jose & Fernandez, Marc. (2018). *Mr. Liable: A resident male sperm whale in the Azores?* Poster presented at the 32nd European Cetacean Society, Italy.

Gero, S., Engelhaupt, D., & Whitehead, H. (2008). Heterogeneous social associations within a sperm whale, *Physeter macrocephalus*, unit reflect pairwise relatedness. *Behavioral Ecology and Sociobiology, 63*(1), 143-151.

Gero, S., Engelhaupt, D., Rendell, L. & Whitehead, H. (2009). Who Cares? Between-group variation in alloparental caregiving in sperm whales, *Behavioral Ecology, 20*(4), 838–843.

Gero, S., Milligan, M., Rinaldi, C., Francis, P., Gordon, J., Carlson, C., Steffen, A., Tyack. P., Evans, P. & Whitehead, H. (2014). Behavior and social structure of the sperm whales of Dominica, West Indies. *Marine Mammal Science, 30*(3), 905-922.

Gero, S., Bøttcher, A., Whitehead, H., & Madsen, P. T. (2016). Socially segregated, sympatric sperm whale clans in the Atlantic Ocean. *Royal Society open science, 3*(6), 160061.

Gonzalez Garcia, L. (2019). *Cetacean distribution in São Miguel (Azores): influence of environmental variables at different spatial and temporal scales* (Doctoral dissertation, Física aplicada).

Goold, J. C. (1999). Behavioural and acoustic observations of sperm whales in Scapa Flow, Orkney Islands. *Journal of the Marine Biological Association of the United Kingdom, 79*(3), 541-550.

Gordon, J. C. (1987). Sperm whale groups and social behaviour observed off Sri Lanka. *Reports of the International Whaling Commission, 37*, 205-217.

Gordon, J., & Steiner, L. (1992). Ventilation and dive patterns in sperm whales, *Physeter macrocephalus*, in the Azores. *Report of the International Whaling Commission, 42*, 561-565.

Gordon, J., Moscrop, A., Carlson, C., Ingram, S., Leaper, R., Matthews, J., & Young, K. (1998). Distribution, movements and residency of sperm whales off the Commonwealth of Dominica, Eastern Caribbean: implications for the development and regulation of the local whale watching industry. *Reports of the International Whaling Commission, 48*, 551-558.

Jaquet, N., Dawson, S., & Slooten, E. (2000). Seasonal distribution and diving behaviour of male sperm whales off Kaikoura: foraging implications. *Canadian Journal of Zoology, 78*(3), 407-419.

Jaquet, N., Dawson, S., & Douglas, L. (2001). Vocal behavior of male sperm whales: Why do they click? *The Journal of the Acoustical Society of America, 109*(5), 2254-2259.

Kawakami, T. (1980). A review of sperm whale food. *The Scientific Reports of Whales Research Institute 32*, 199–218.

Konrad, C. M., Frasier, T. R., Rendell, L., Whitehead, H., & Gero, S. (2018). Kinship and association do not explain vocal repertoire variation among individual sperm whales or social units. *Animal Behaviour, 145*, 131-140.

Linde, M. L., & 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, 19*(1), 47-6.

Marcoux, M., Whitehead, H., & Rendell, L. (2007). Sperm whale feeding variation by location, year, social group and clan: evidence from stable isotopes. *Marine Ecology Progress Series, 333,* 309–314.

Martin, A., & Clarke, M. (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.

Mesnick, S. L. (2001). Genetic relatedness in sperm whales: evidence and cultural implications. *Behavioral and Brain Sciences, 24*(2), 346-346.

Møhl, B., Wahlberg, M., Madsen, P. T., Miller, L. A., & Surlykke, A. (2000). Sperm whale clicks: Directionality and source level revisited. *The journal of the Acoustical Society of America*, *107*(1), 638-648.

Papastavrou, V., Smith, S. C., & Whitehead, H. (1989). Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galapagos Islands. *Canadian Journal of Zoology*, *67*(4), 839-846.

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.

Pitman, R. L., Ballance, L. T., Mesnick, S. I., & Chivers, S. J. (2001). Killer whale predation on sperm whales: observations and implications. *Marine mammal science*, *17*(3), 494-507.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

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

Rice, D. W. (1989). Sperm whale *Physeter macrocephalus* Linnaeus, 1758. *Handbook of Marine Mammals, 4*, 177-233.

Richard, K. R. (1995). *A molecular genetic analysis of kinship in free-living groups of sperm whales* (Doctoral Dissertation). Dalhousie University, Halifax, Nova Scotia.

Richard, K. R., Dillon, M. C., Whitehead, H., & Wright, J. M. (1996). Patterns of kinship in groups of free-living sperm whales (*Physeter macrocephalus*) revealed by multiple molecular genetic analyses. *Proceedings of the National Academy of Sciences*, *93*(16), 8792-8795.

Roe, H. S. J. (1969). The food and feeding habits of the sperm whales (Physeter catodon L.) taken off the west coast of Iceland. ICES Journal of Marine Science, 33(1), 93-102.

Schakner, Z. A., Lunsford, C., Straley, J., Eguchi, T., & Mesnick, S. L. (2014). Using Models of Social Transmission to Examine the Spread of Longline Depredation Behavior among Sperm Whales in the Gulf of Alaska. *PLoS ONE*, *9*(10), 1–5.

Silva, M. A., Prieto, R., Cascão, I., Seabra, M. I., Machete, M., Baumgartner, M. F., & Santos, R. S. (2013). Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. *Marine Biology Research*, *10*(2), 123–137.

Stephanis, R., Cornulier, T., Verborgh, P., Sierra, J. S., Gimeno, N. P., & Guinet, C. (2008). Summer spatial distribution of cetaceans in the Strait of Gibraltar in relation to the oceanographic context. *Marine Ecology Progress Series*, *353*, 275-288.

Tempera, F., Giacomello, E., Mitchell, N. C., Campos, A. S., Henriques, A. B., Bashmachnikov, I., Marins, A., Mendonça, A., Morato, T., Colaço, A., Porteiro, F. M., Catarino, D., Gonçalves, J., Pinho, M. R., Isidro, E. J., Santos, R. S., & Menezes, G. (2012). Mapping Condor seamount seafloor environment and associated biological assemblages (Azores, NE Atlantic). In P. T. Harris, E. K. Baker (Eds.). *Seafloor Geomorphology as Benthic Habitat* (807-818). Elsevier.

Watwood, S. L., Miller, P. J., 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. S., & Whitehead, H. (1988). Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*). *Canadian Journal of Zoology*, *66*(9), 1931-1937.

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., & Weilgart, L. (1991). Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. *Behaviour*, 275-296.

Whitehead, H., & Kahn, B. (1992). Temporal and geographic variation in the social structure of female sperm whales. *Canadian Journal of Zoology*, *70*(11), 2145–2149.

Whitehead, H., Brennan, S., & Grover, D. (1992). Distribution and behaviour of male sperm whales on the Scotian Shelf, Canada. *Canadian Journal of Zoology*, *70*(5), 912-918.

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

Whitehead, H. (2002). Estimates of the current global population size and historical trajectory for sperm whales. *Marine Ecology Progress Series, 242*, 295-304.

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

Whitehead, H., Antunes, R., Gero, S., Wong, S., Engelhaupt, D., Rendell, L. (2012). Multilevel Societies of Female Sperm Whales (*Physeter macrocephalus*) in the Atlantic and Pacific: Why Are They So Different? *International Journal Primatology, 33*(5)**,** 1142–1164.

Whitehead, H. (2018). Sperm Whale: *Physeter macrocephalus*. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), Encyclopedia of Marine Mammals (3 ed., 919–925).